BULLETINS OF AMERICAN PALEONTOLOGY

VOL. 65, 1975

Biology and Paleobiology of Ostracoda

A Symposium

University of Delaware, 1972

205

1905-

Betty K. Maclean

1899-

Frank McKim Swartz

BIOLOGY AND PALEOBIOLOGY OF OSTRACODA

A SYMPOSIUM

UNIVERSITY OF DELAWARE 14-17 AUGUST, 1972

FREDERICK M. SWAIN, Editor
University of Delaware; University of Minnesota

LOUIS S. KORNICKER AND ROBERT F. LUNDIN
Associate Editors
National Museum of Natural History Arizona State University

Published by
Paleontological Research Institution
Ithaca, New York

1975

BULLETINS AMERICAN PALEONTOLOGY
VOLUME 65, NUMBER 282

Library of Congress Card Number: 73-90558

THE SYMPOSIUM VOLUME

IS DEDICATED TO

BETTY KELLETT NADEAU
AND
FRANK McKIM SWARTZ

PREFACE

Three previous meetings of Ostracoda workers were held in Naples, Italy, organized by H. S. Puri; in Hull, England, arranged by J. W. Neale; and in Pau, France, assembled by H. J. Oertli. It has been a pleasure to welcome the group of Ostracoda workers to this latest meeting at the University of Delaware.

The pattern of organization of the three earlier meetings was generally followed in the present one.

The field trip to the middle Miocene outcrops of the Calvert Cliffs, Maryland, was led by Mrs. Dabney Hart and Mr. C. W. Hart, Jr., who also provided the guidebook for the trip. The post-meeting field trip in the Holocene sediments of southern Delaware was led by Dr. J. C. Kraft, and that in the Paleozoic rocks of the Appalachian Mountains was led by Dr. A. L. Guber. Mr. D. L. Zalusky assisted with the Appalachian trip. A short field trip to the Upper Cretaceous outcrops along the Chesapeake and Delaware Canal, Delaware, was led by Dr. T. E. Pickett. Dr. and Mrs. Pickett also entertained the group at their home following the field trip.

Dr. Frank B. Dilley, Associate Provost for instruction at the University of Delaware gave a welcoming address at the opening of the symposium.

John C. Kraft, Chairman of the Geology Department at the University, secured the University Funds necessary to hold the Symposium. These funds were made available from a Unidel Grant for the University of Delaware.

Funds in support of the publication of this volume were provided by the Smithsonian Institution on behalf of Drs. R. H. Benson and L. S. Kornicker. Dr. H. V. Howe provided a personal contribution in support of publication.

Louis S. Kornicker and Robert F. Lundin have provided valuable assistance as Associate Editors. Claudia Converse also assisted in editorial matters. Annette Craig aided in preparation of final drafts of tables and other typing.

Mrs. Nancy Gerrity, secretary of the Geology Department, assisted greatly with administrative matters. The following University students aided in many aspects of the meeting: John Sherman, Alan Crossan, Robert Caulk, Xenia Goluvchenko, Roger Moose, Christine Dutton and James Pittman.

PREFACE

I am sincerely grateful to all of the individuals named above for their assistance and support.

It was a great pleasure to have in attendance at the Symposium two of the foremost American workers on Ostracoda: Mrs. Betty Kellett Nadeau and Dr. Frank McKim Swartz. This volume is dedicated to them in sincere appreciation of their contributions to the study of fossil Ostracoda.

Dr. Henry V. Howe, who attended our symposium and was co-author of two of the papers appearing in this volume, died September 27, 1973. We deeply regret the loss of our friend, colleague, and mentor.

Newark, Delaware
November, 1973

F. M. Swain

PARTICIPANTS

Baker, Mr. James H., Department of Biology, University of Houston, Houston, Texas 77004

Bate, Dr. Raymond H., Department of Palaeontology, British Museum (NH) London, SW 7, England. (Not attending; paper read by J. W. Neale.)

Benson, Dr. Richard H., Room 204 E, National Museum of Natural History Smithsonian Institution, 10th and Constitution Ave., N.W., Washington, D.C. 20560

Berdan, Dr. Jean M., U.S. Geological Survey, Washington, D.C. 20242

Bertels, Dr. Alwine, Ciudad Universitaria, Fac. Ciencias, Univ. Buenos Aires Pabellon II-1a piso, Dept. Geol. Ciencias, Buenos Aires, Argentina. (Not attending; paper read by R. C. Whatley.)

Bless, Dr. M. J. M. Geologisch Bureau v.h. Mijngebeid, Akerstr 86-88 Heerlen 5200, The Netherlands

Bold, W. A. van den, Dr., Department of Geology, Louisiana State University, Baton Rouge, Louisiana 70803. (Not attending; joint paper with H. V. Howe read by Dr. Howe).

Brondos, Mr. M. D., Department of Geology, University of Kansas, Lawrence, Kansas 66044.

Cadot, Mr. Meade, Department of Geology, University of Kansas, Lawrence, Kansas 66044. (Not attending; paper read by R. L. Kaesler as joint author.)

Carbonel, Dr. P., Laboratoire de Geologie et Ocean., University de Bordeaux, 33 Talence, France. (Not attending; paper read by J. E. Hazel.)

Carbonnel, Dr. G., Univ. Lyon-l-Claude Bernard, Dept., Sci. de la Terre, 15 et 43 boul. du 11 Novembre 1918, 69 Villeurbanne, France. (Not attending, but submitted paper.)

Christensen, Dr. Ole Brunn, Geological Survey of Denmark, Thoraves 31, 2400 Kobenhavn NV, Denmark

Damotte, Dr. Renée, Centre National de la Recherche Scientifique Laboratoire de Micropaléontologie, Université de Paris VI, Paris, France.

Danielopol, Dr. Dan L., Limnologische Inst., Vienna, Austria 1090. (Not attending, but submitted paper.)

PARTICIPANTS

Delorme, Dr. L. Denis, Inland Waters Branch, 3303-33rd Street NW, Calgary 44, Alberta, Canada

Dépêche, Dr. F., Laboratoire de Micropaleontologie, Université de Paris VI, Paris, France

East, Miss B. A., Dept. Chem. Eng-Tech., Imperial College, London SW7, England. (Not attending, paper read by J. W. Neale.)

Echols, Dr. Dorothy J., Department of Earth Sciences, Washington University, St. Louis, Missouri 63130

Gerry, Mr. E., 61170 Tel Aviv, Ramat Aviv, P O B 17081, Israel

Gio-Arguez, Sr. Raul, Instituto de Geologia, UNAM, Mexico 20 D.F., Mexico; and Sra. Gio-Argaez

Grigg, Miss Ursula M., Department of Geology, St. Marys University, Halifax, N.S., Canada

Groos-Uffenorde, Dr. Helga, D-3400 Göttingen, Geolog.-Paläont. Institut, Berliner Strasse 28, Germany

Guber, Dr. Albert L., Department of Geology, The Pennsylvania State University, University Park, Pennsylvania 16802

Hart, Mr. C. W., Jr., Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103

Hart, Mrs. Dabney, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103

Hartmann, Gerd. Prof., Dr., Zoologische Institut and Zoologisches Museum der Universitat, 2 Hamburg 13, v. Melle Park 10, Germany, and Frau G. Hartmann-Schröder.

Haskins, Dr. C. W., Robertson Research Laboratories, Tyn-y-Coed, Llanrhos, Llandudno, N. Wales, U.K.

Hazel, Dr. J. E., U.S. Geological Survey, E-501 U.S. National Museum, Washington, D.C. 20244

Howe, Prof. Robert C., Department of Geology and Geography, Indiana State University, Terre Haute, Indiana 47809. (Not attending; paper read by H. J. Howe.)

Howe, Prof. H. J., Department of Geology, Purdue University, Lafayette, Indiana 47907

Howe, Prof. H. V., Dept. Geological Sciences, Louisiana State Univ., Baton Rouge, Louisiana 70803 and Mrs. Howe

Ishizaki, Dr. K., Inst. Geol.-Paleont., Tohoku University, Sendai, Japan

PARTICIPANTS

Kaesler, Dr. Roger L., Department of Geology, University of Kansas, Lawrence, Kansas 66044

Keen, Dr. Michael Charles, Department of Geology, University of Glasgow, Glasgow W 2, United Kingdom

Keyser, Mr. D., Zool. Institute und Museum der Univ. Hamburg, 2 Hamburg von Melle Park 10, Germany

Kornicker, Dr. L. S., National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. NW, Washington, D.C. 20560

Kraft, Prof. John C., Department of Geology, University of Delaware, Newark, Delaware 19711

Liebau, Dr. Alexander, Geol.-Palaont. Inst., D-4, Tübingen, Germany

Löffler, Prof. H., Limnological Department, University of Vienna, Bergasse 18, Vienna, Austria 1090

Lundin, Dr. Robert F., Department of Geology, Arizona State University, Tempe, Arizona 85281

McKenzie, Dr. K. G., School of Applied Science, Riverina College of Adv. Ed., Wagga Wagga, NSW, Austrilan 2560. (Not attending, paper jointly with R. L. Kaesler, read by R. L. Kaesler.)

Maddocks, Dr. R. F., Geology Department, University Houston, Houston, Texas 77004

Moguilevsky, Dr. Alicia, Department Biol., Facultad Ciencias, Ciudad Universitaria, Pabellon 2, piso 4th, Cabital Federal BS, AS Argentina. (Not attending, paper jointly with R. C. Whatley, read by R. C. Whatley.)

Moyes, Prof. Jean, Institut de Geologie, Faculte des Sciences, 33 Talence, France. (Not attending; paper read by J. E. Hazel.)

Nadeau, Mrs. Betty Kellet, Westview Lane, Norwalk, Connecticut 06854

Neale, Dr. John W., Geology Department, Hull University, Hull, Yorkshire, England

Oertli, Dr. H. J., SNPA Centre de Recherches, 64 Pau, France, and Mme. Oertli

Petersen, Dr. L. E., Department of Geology, Arizona State University, Tempe, Arizona 85281

PARTICIPANTS

Peypouquet, Dr. J. P., Laboratoire de Geologie, Faculte des Sciences de Bordeaus, 351 Cour de la Liberation, 33 Talence, France. (Not attending; paper read by J. E. Hazel.)

Pollard, Dr. J. E., Department of Geology, University of Manchester, Manchester, England. (Not attending; paper read by M. J. M. Bless as joint author.)

Price, Mr. L. Greer, Department of Earth Sciences, Washington University, St. Louis, Missouri 63130

Puri, Dr. Harbans S., Bureau of Geology, P.O. Box 623, Tallahassee, Florida 32304

Rafle, Miss Mary Ann, Dept. Earth Sciences, Washington Univ., St. Louis, Missouri 63103. (Not attending; paper jointly with Dr. Echols and Mr. Price, read by L. Price.)

Reyment, Prof. R., Paleontologiska Institutionen, Uppsala Universitet, S-751, 22 Uppsala, Sweden

Sandberg, Dr. P. A., Department of Geology, University of Illinois, Urbana, Illinois 61801

Schulz, Mr. K., Zool. Institut und Museum der Univ. Hamburg, 2 Hamburg, von Melle Park 10, Germany

Siddiqui, Dr. Q. A., Department of Geology, St. Marys University, Halifax N.S., Canada

Sohn, Dr. I. G., U.S. Geological Survey, Washington, D.C. 20244

Swain, Prof. F. M., Department of Geology, University of Delaware, Newark, Delaware 19711; Department of Geology, University of Minnesota, Mpls., Minn. 55455

Swartz, Dr. F. M., 6665 North Donna Beatrix Circle, Tuscon, Arizona 85718

Uffenorde, Dr. Henning, D-3400 Gottingen, Geol.-Palaont. Institut, Berliner Str. 28, Germany

van Morkhoven, Dr. F. P. C. M., Shell Oil Co., Box 60775, New burg 13, Papendamm 3, Germany

Vesper, Dr. B., Zool. Institut u. Museum, Univ. Hamburg, 2 Hamburg, von Melle Park 10, Germany

Watling, Mr. Les, Field Station, University of Delaware, Lewes, Delaware 19958

Whatley, Dr. Robin C., Division Micropalaeontologia, Facul. Ciencios Nationales y Mineo, Nat. Univ. de la Plata, Paseo del Bosque, La Plata, Argentina; and Department of Geology University College of Wales, Aberystwyth, G. B.

CONTENTS

I. Morphological and physiological studies

II. Environmental aspects

III. Stratigraphic and ecologic studies of fossil Ostracoda

IV. Zoogeographic and ecologic studies of Holocene Ostracoda

V. Microscopic structures of the Ostracoda carapace

VI. Classification and nomenclature of Ostracoda

MORPHOLOGIC STABILITY IN OSTRACODA

Richard H. Benson
Smithsonian Institution

ABSTRACT

The carapace of the ostracode is an important functioning part of its anatomy. Specialized through time, the carapace encapsulates and protects the animal's more vulnerable organs from predators and from crushing by movement in the substrate, and it adds weight to improve the animal's benthic positional stability. Several different structural "solutions" to the problem of maintaining armor, wall strength, and ballast have been employed through modification of fundamental shell construction patterns. From an engineering viewpoint the study of "ornamentation" and carapace form suggests that better design is often substituted for shell-wall material as thicker walls are replaced by more complicated systems of ribbing, reticulation, and the evolution of a more efficient structural system. Structural "failure" can be detected in some early stages of wall construction. Alignment of mass takes place within the basic working elements and surfaces in the direction of stress. In animals living in deeper water where economy of shell material is important, nonworking mass is removed to lighten the shell structure. Following the distribution of various modern taxa from regions of high to low levels of mechanical and thermal energy shows morphologic change commensurate with the principles of good engineering design.

LA STABILITE MORPHOLOGIQUE DANS LES OSTRACODA

Richard H. Benson

RÉSUMÉ

Le carapace de l'ostracode est une importante partie fonctionnante de son anatomie. Spécialisé à travers les années, le carapace encapsule et défend les organes de l'animal les plus vulnérables, des prédateurs et de la possibilité de l'écrasement par du mouvement dans le substratum, lui ajoutant en même temps du poids, pour ainsi améliorer la stabilité Benthique positionnelle de l'animal. Plusieures "solutions" structurales variées au problème du maintien de l'armature, la force du mur, et du lest, ont été employées à travers la modifications des models fondamentaux pour la construction des conches. D'un point de vue technique, l'étude de "l'ornamentation" et la forme du carapace suggère qu'un meilleur dessein se substitue souvent au matériel du mur de la conche, lorsque les murs plus épaisses sont remplacés par de plus compliqués systèmes d'ossature et de réticulation, et l'évolution plus avancée d'un système structural plus éficace. Des "échecs" structuraux peuvent être constatés dans quelques étapes primitives de la construction du mur. Un allignement de la masse a lieu dans les éléments fonctionnants fonciers, ainsi que dans les surfaces, vers la direction de la pression. Chez des animaux qui habitent dans de l'eau plus profond, où l'économie dans le matériel de la conche est importante, toute masse non-fonctionnante est éliminée pour rendre la structure plus légère. Un examen de la distribution de plusieurs *taxa* modernes, qui vont d'un haut nivau d'énergie méchanique et thermale à un nivau bas d'énergie, montre du changement morphologique qui est d'accord avec les principes de la bonne technique d'ingénieur.

INTRODUCTION

Paper was expensive in ancient Egypt. It was used only for very important state and religious records. The common, everyday communication of instructions or tabulations of construction and commerce were written on smooth fragments of broken pottery. Later, these were referred to by Greek scholars as *ostracons*. Today these ostracons serve as important bits of evidence in reconstructing the functions and history of this ancient culture.

The tenure of the Ostracoda is about 10^5 times longer than the oldest Egyptian construction or the notations of the ancient engineers and tradesmen. And yet there are corollaries in the application of principles of the science of statics that prophesied the ability of the pyramids to withstand the test of time, and understanding of these same principles of structural reaction that permitted the continuance and repetition of some kinds of ostracode carapace form. In fact the ostracodes probably have employed more sophisticated design principles than did the ancient Egyptians.

Students of the history of ostracodes are not used to thinking of carapace morphology as functional working structure; certainly not in the engineering sense of forces reacting within a static frame. The present study continues to explore (Benson, 1970; Benson, in press) some of the philosophical concepts and mechanical principles that may explain how this morphology can succeed under differing environmental loads and pressures. The view that stability in form has special significance will be examined from several different directions: structurally, to some extent genetically, and as subsets of changing form relative to a comparative steady state reference system. Several approximations of morphologic shape as geometric form are realized and shown to be explainable in terms of stress models.

ACKNOWLEDGMENTS

Appreciation is expressed to Alan H. Cheetham, Joseph E. Hazel, and Ronald E. Schaeffer for their valuable comments regarding this study, and to Laurie J. Brennan, Marie J. Ladd, and Larry Isham for their help in preparing the report. The study was supported in part by a grant from the Smithsonian Research Foundation.

OSTRACODE BIVALVEDNESS, FORM AND STRUCTURE

The ancestors of the ostracodes were encased in a skeleton consisting of an articulated system of thin tubes capable of responding to external stress by reaction at joints and through flexure or bending in its tough wall structure. The ostracodes developed a heavier, rigid, uniformly stressed and static system of unyielding protective armor that could encapsulate the whole animal when necessary. This enveloping, bivalved shell remained an effective solution to survival for the Ostracoda through a multitude of structural experiments under many kinds of environmental conditions. In fact this solution may have been too effective as no other arthropod group is known to have evolved from the Ostracoda.

In the past, before it was convenient to examine details of carapace morphology, differences in overall shape were often described after analogous organ shapes borrowed from experience outside of the study of arthropods, using terms like mucronate, almond-shaped, or reniform. Surface texture was thought to be independent of shell structure and was simply characterized in general terms such as spinose, reticulate, even rough or smooth. It is difficult to use these terms to define functional adaptive reactions. They are often conceptually sterile, or even perhaps misleading. Many are certainly not adequate as neutral descriptors. In any event, attempts to synthesize general architectural responses to environmental change using these concepts were not successful. Elofson's (1941) admirable effort to relate carapace roughness or smoothness to increasing depth can now be shown to be erroneous (Text-fig. 1). Only with the development of the scanning electron microscope has it been possible to see enough carapace detail to begin to understand ornament.

The present use of mechanical explanation of carapace function makes assumptions about the need for structural success in carapace form. The term "form" is used here in the sense of a conceptual model of morphologic shape, reduced to its basic system of descriptive components (in the sense of kinematics), without reference to its structural properties of size, strength or materials (kinetics with force relationships implied). Structures respond to mechanical principles of transmission of force and are employed by carapace form primarily for the purpose of resisting environmental pressures that would bring about injurious changes in morphology. The usefulness of the distinction between the concepts of form and structure will become more evident as the discussion progresses.

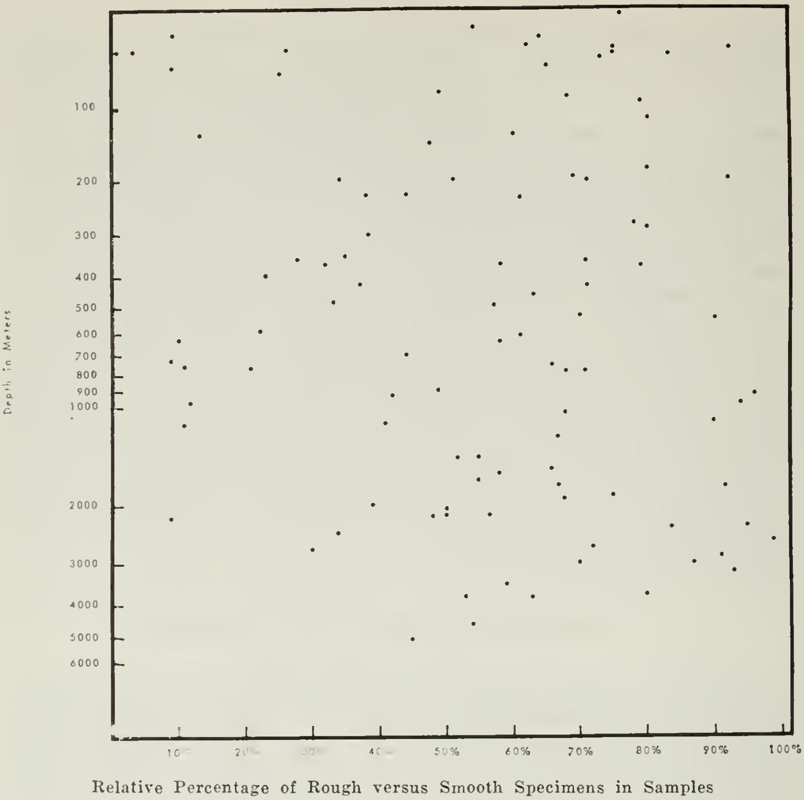
ESTIMATING STABILITY IN FORM

In studies of ostracode allometry, it is customary to use a measure of size (length and height, sometimes width) which tends to vary in a rectilinear series with molting, and can also be found to some degree among adults along an environmental gradient (Text-figs. 11, 12, 13). These measures are not very accurate estimates of shape, even though a bivariant plot of a growth series strongly suggests stability in overall form. One must remember that size and form are independent parameters.

The models of form implicit in bivariant plots of length-height ratios are rectangles. Inherent within the assumption of a mathematics based on a Cartesian system is a problem of fit that occurs between this system and one based on differential growth of surface areas. D'Arcy Thompson's (1961) deformations are based on changes in rectilinear distance even though the reference grid may become curvilinear (*i.e.*, the x or y transformations distance change would still be Cartesian).

Any description of change in form is one of change in the locations of established homologous points relative to a more conservatively changing or fixed reference system. D'Arcy Thompson used curvilinear grids (Dürer transformations) referred to an initial Cartesian grid for visual but not quantitative comparisons. Implicit within this technique, however, is the lack of change of relative distance measures. As the transformations of the grids occur the reference coordinates remain the same. What is actual instability of shape remains as stability in measured form.

It is obvious that the geometry of organic form is not based on a system



Text-figure 1. The distribution with increasing depth of rough and smooth ostracodes found in about 100 samples from various parts of the world chosen at random. The data refute the hypothesis formerly held by Elofson (1941) and Van Morkhoven (1962) that smooth species compared to rough species become proportionately more numerous with depth.

of right angles (sometimes called the *urban angle* system). The basic geometry of morphologic form and that of the mechanical model should be congruent. I am not confident that a disparity between these analytic systems and that of the essential geometry of the skeletal system may obscure more than is revealed. Therefore, I would like to explore another way of model construction based on effective cause, *i.e.,* functional as opposed to descriptive allometry.

The pattern of distribution of pore conuli, the pattern of the reticulum (Benson, 1970), a model of the interaction of the major structural ridges and surfaces of the carapace; all of these simplifications of structural systems represent different but related functional levels of reaction (stress response) included in the carapace. These systems do not all react through selection to

Text-figure 2. Two patterns of spine and pore conuli distribution in (a) deep-sea, very spinose species related to *"Cythere" acanthoderma* Brady, 1880, and in (b) a shallower, less spinose species related to *"Cythere" scutigera* Brady, 1868 (see Text-figure 12). The principal spines and their pores are homologous with those found in reticulate species which are otherwise different in general shape and sculpture.

environmental stress at the same rate, however. The distributional pattern of receptors of the tactile nervous system (possibly expressed in the setae extending from the pore conuli distribution) seems adequate for many ostracodes with very different shell sculpture. The dermal tissue pattern of shell-forming cells (shown in the reticular pattern) seems to be present in heavily murate ostracodes and ones with no ridges at all. These systems may be genetically more conservative, their form or intrinsic geometric pattern of distribution more stable than that of the mechanically more reactant skeletal system. Also with growth the requirement for skeletal mass is a function of volume change and tends to increase exponentially at a faster rate than that of the tactile surface, which is a function of change in area. If the tactile surface area remains constant between strong and weak forms the pore conular pattern might remain static while the structural configurations could vary radically.

Therefore, assuming adaptive response varies among functional systems according to their sensitivity to selective pressures, and that skeletal response is primarily mechanical reaction to preserve the forms of the other systems, a hierarchy of inertial relationships (expressing resistance or immunity to change) can be recognized. This hierarchy of changing patterns also expresses a series of sets of geometric form whose proportions vary at different rates and whose changes can be described relative one to the other.

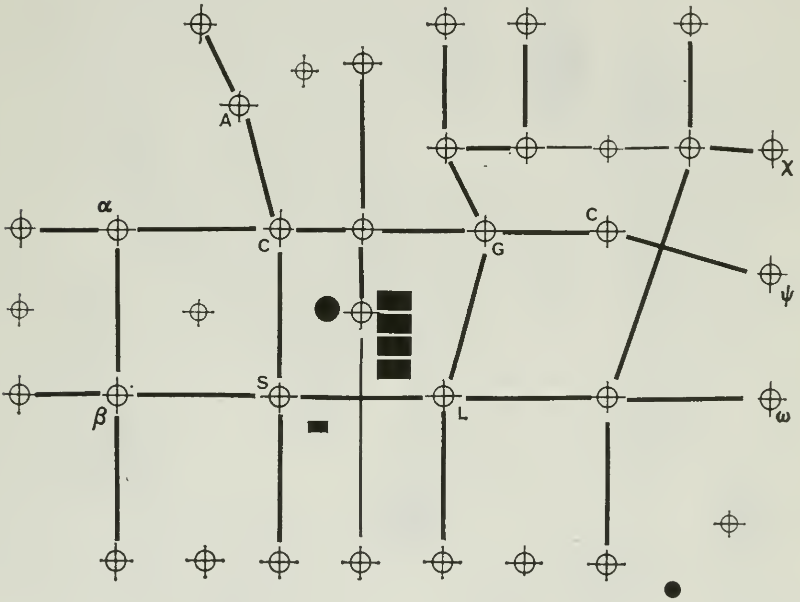
In celestial mechanics, which deals with relative motion within and among star and planetary systems, the reference system used for description is that of the constellar network of the positions of the so-called "fixed stars". This primary inertial system serves as the foundation of the reference coordinate system for the description of relative celestial motion. If such a primary inertial system can be found among homologous points in ostracode carapace morphology (Text-figures 2-3), a basic natural coordinate system could be established for description of relative deformation among related organic forms. If skeletal form is a natural diagram of forces, as D'Arcy Thompson (1961) has suggested, the departure from or tendency toward structural stability, expressed as substitution among structural members within a system of changing work capacity, may be the best way to describe relative change and functional adaptation (Text-fig. 4). The reordering of the system under different loads can be best visualized by reducing a succession of stages of substitution to the same reference base. When relative mechanical stress increases (independent of size), the number of skeletal elements is reduced departing from the basic, commonly held pattern of reticulation.

I began exploration of this principle earlier with the study of *Agrenocythere* and some related forms (Benson, 1972), in which the pore conuli appear to be the most consistently arranged of the carapace features examined. Constellar networks, connecting named and identified pore conuli, were constructed in this work and shown to vary among some 16 sexually and taxonomically distinct forms. This network seems to be the primary inertial system of reference for a very large group of ostracodes. In the present work the same basic system of reference is refined and extended to the Bradleyinae (Text-figs. 4-5). Elements within the patterns of fossae and reticulation change at more accelerated rates. It is possible to define relationships among forms whose reticular patterns may be dominated by the emphasis or the replacement of certain murae by following the fission or fusion among the fossae.

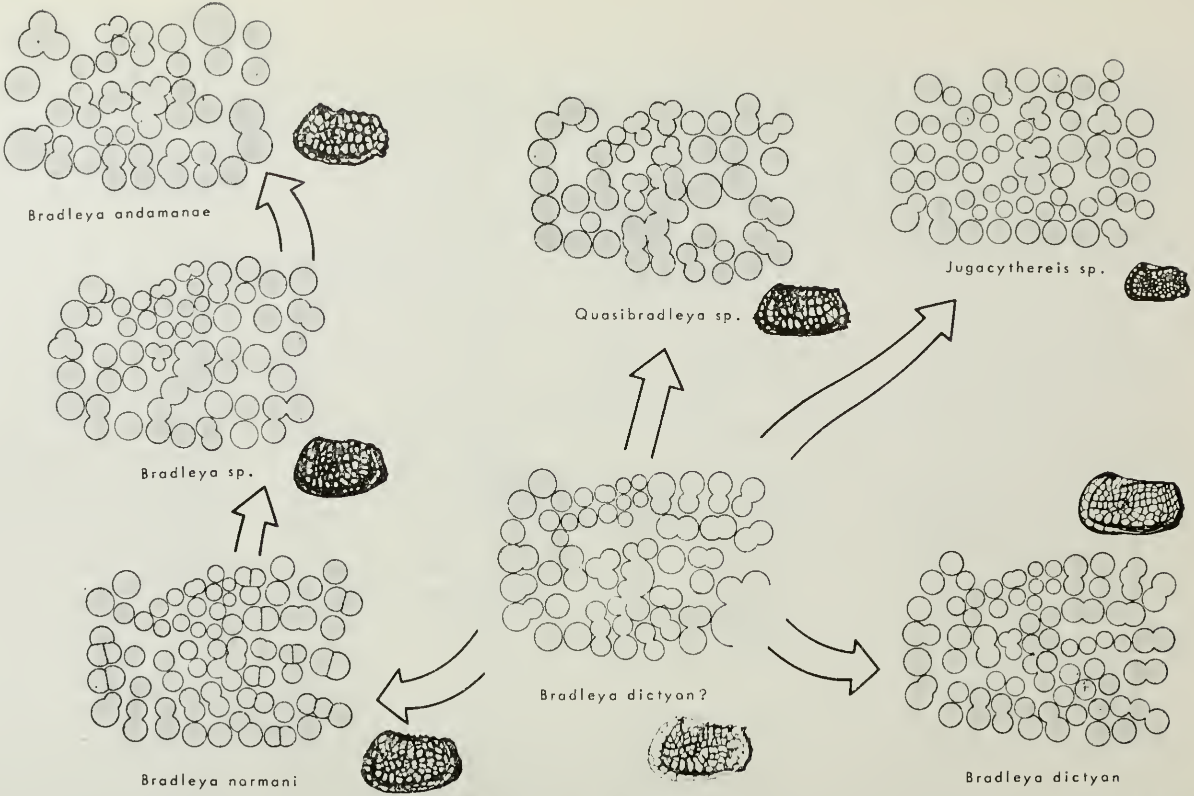
STRUCTURAL STABILITY

To an engineer the concept of structure refers to the organization of form responsive to physical properties for its continuance against those forces that would alter it. Structure also helps to define form in efficient and logically consistent physical terms. A structural system is an ordered assemblage of structural elements that physically react in concert depending on the properties of the materials of which they are constructed. The biologic concept of organ and that of structure are compatible. The same is true of certain relationships between mechanics and geometry or proportionate relationships set in mathematical space, consequently mechanics can often be reduced to mathematical terms. Mechanical determinism and morphological stability may therefore be related.

Stability, strength and economy, are the principal functional requirements of most skeletal structures. These properties of skeletal systems are often assumed by the morphologist. The animal exists and obviously was selected as structurally more successful. However, explaining how one form potentially reacts or reacted (in extinct species) requires a hypothesis of force. This Newtonian position is not an easy one for the biologist. There is an extensive literature on the limits of the mechanistic philosophy (Russell, 1916; Beckner, 1959; Bertalanffy, 1962) which will not be debated here; however, it does seem possible to stipulate that skeleton systems do exhibit stress reactions



Text-figure 3. A schematic diagram or constellar map of the relative distribution of the normal pore canals and pore conuli which constitute a primary inertial system for reference in studying relative change in other aspects of the ostracode carapace sculpture (see text and Benson, 1972).



Text-figure 4. Comparative topological diagrams of the changes in patterns of fossae within seven species of *Bradleya, Quasibradleya,* and *Jugosocythereis,* made using the pore map as a base, shown in Text-figure 3, and illustrating mural accommodation or adaptive response to the increased need for strength. The lower three forms are deep-sea, the upper three are shelf species from separate parts of the world. The lower central one is Eocene in age, the rest are Recent. Division and union of the fossae can be traced through all of these forms with the deeper ones, being always more complex and the shallow smaller ones with fewer fossae separated by more massive murae.

Text-figure 5. The great variation in form of the reticular pattern of *Bradleya* and closely related taxa including *Jugosocythereis*. The murae are reduced in number and become more massive to form stronger ridges in shallower water (depths indicated below figures). Detailed comparison of these patterns is difficult without some points of reference in common. Five of these forms are demonstrated to be related by use of the constellar pore map (Text-figure 3) and the topological reductions of the fossae patterns (Text-figure 4).

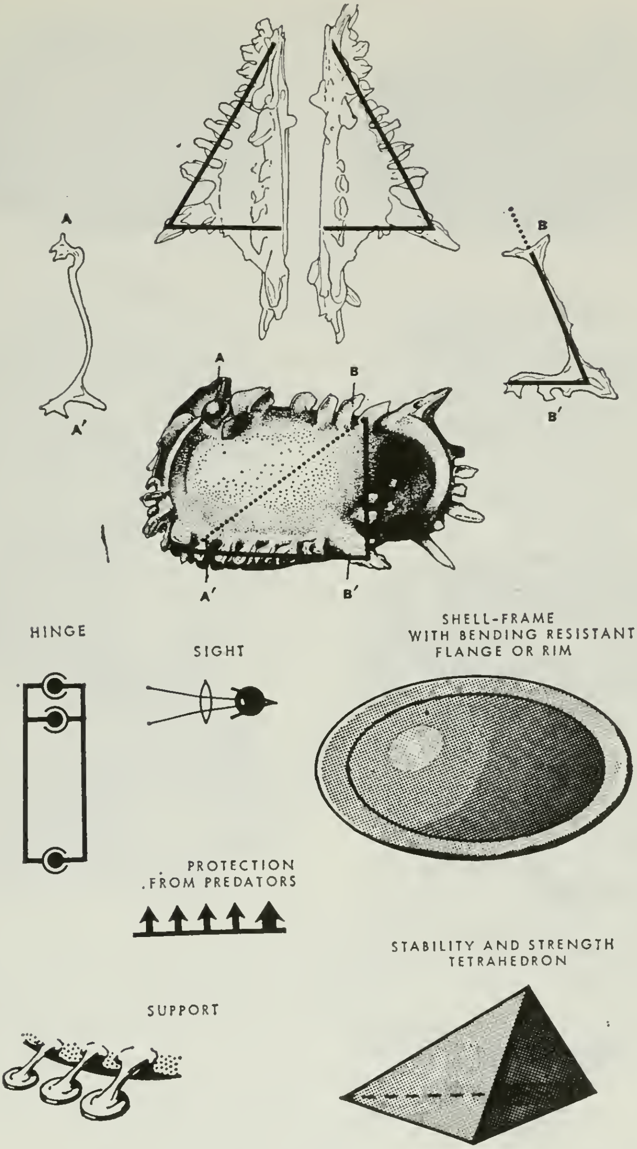
(Wolff's Law) and that the assumption of the existence of force is not unrealistic. Stability in this sense refers to the retention of shape under load; remaining in position (re: the sinking factor of Neale, 1964); the maintenance of static equilibrium (a balance among structural members). The stable skeletal system is expressed in its geometric completeness and stability of form through time.

Strength and economy are factors that may determine the choice of materials in the building of a structure. Wherein the choice of material is limited by its availability, or the energy required to transform it to structure is excessive some compromise in design is required. We can assume that stability in form is the ultimate test of ostracode success in survival in a changing selective system, and that this compromise is always effectively met. In fact some of the longest surviving ostracode taxa live in environments of great change (*i.e., Cyprideis,* fresh-water cyprids). Ostracodes seem to react conservatively in evolution to perturbations of environmental change. However, it is less certain that this can be stated about a more stable environmental situation or a gradually changing one.

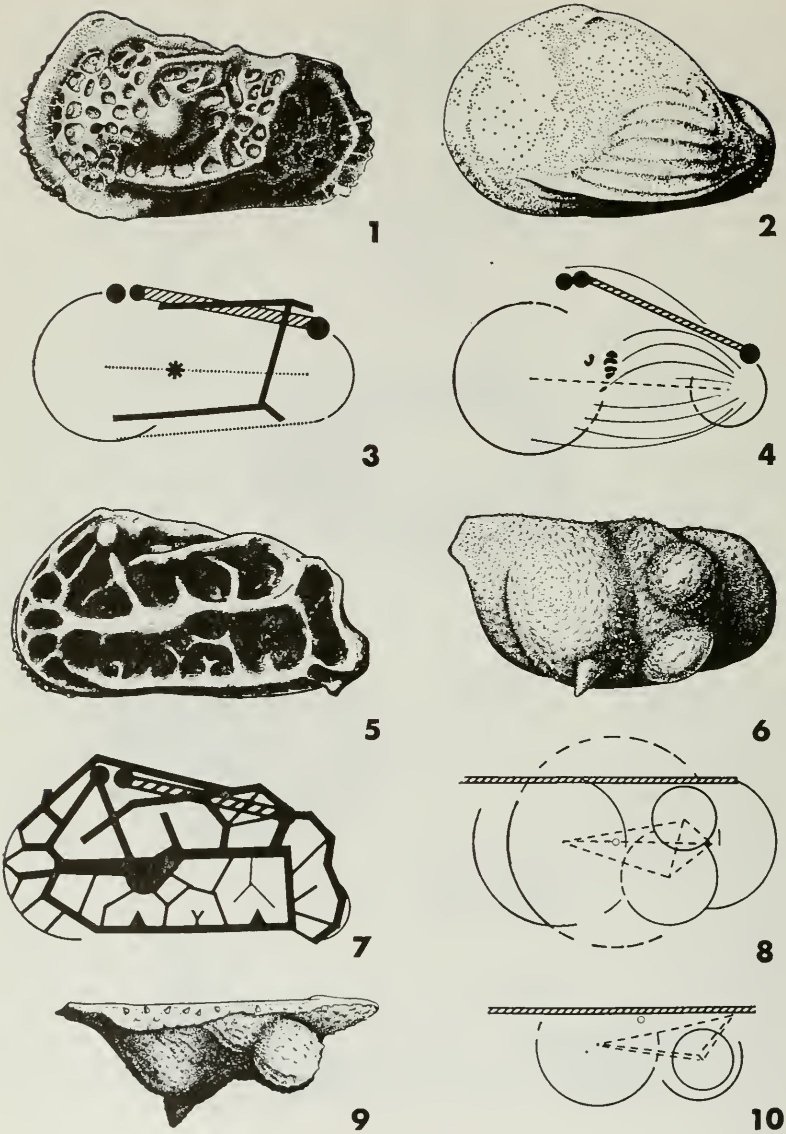
The concept of morphologic skeletal structures as reactant mechanical systems of form, selected because of their success in maintaining their conservative position in a more rapidly changing external world of disturbing influences, is an intriguing one. It is basically one of the description of motion (kinematics) among ranked inertial systems. It allows considerations of mechanical properties through geometrically defined form. Numerical values can now be applied to morphologic characters so long as they are functionally defined.

With the view that carapace structure is a system of mechanically reactive elements of form existing to preserve the species under environmental load, we have now departed from the use of neutral descriptors to define the configurations of sculpture (Text-fig. 6), so often used to discriminate taxa. The carapace of a particular taxon is no longer adorned with "ornamentation" as obviously we have become committed to test a functional hypothesis. This hypothesis stipulates that variation in carapace form provides for different degrees of strength, for whatever purpose, and that substitution of structural elements requires the maintenance of strength (Text-figs. 7-8). Phyletic convergence (Text-fig. 9) can be described, as with other animal groups, in terms of functional convergence.

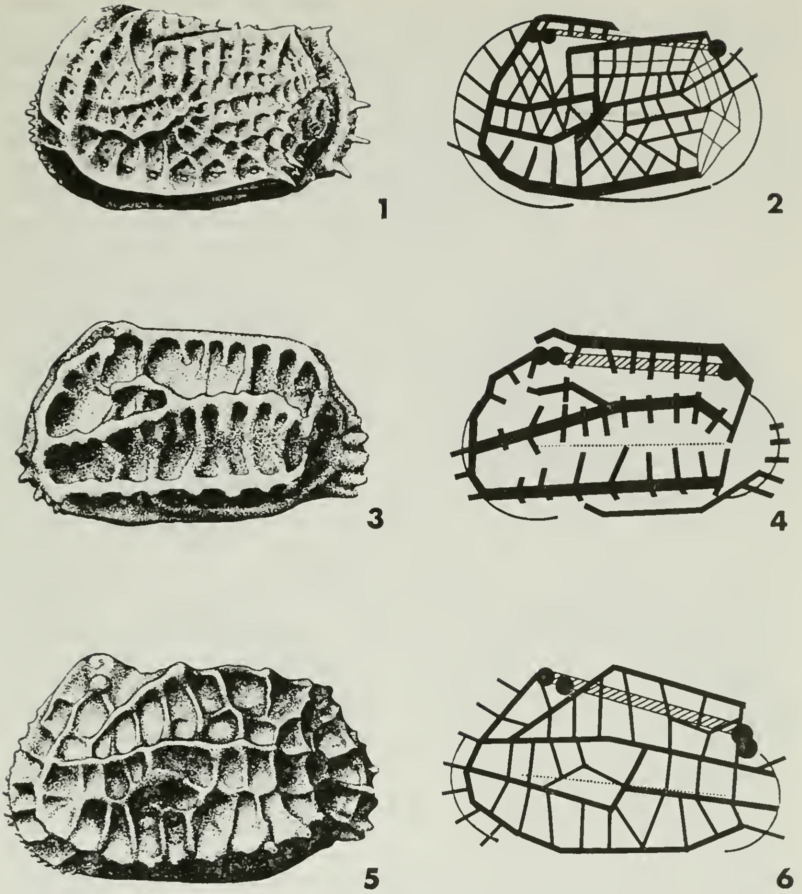
This is an important philosophical step. It requires more than just the usual empirical assumptions, although certainly nothing teleological in the older and much critized sense is implied here. These ostracode structures, stable phases in changes of form, are at least temporarily successful experiments in ordering geometric and therefore mechanical properties of form.



Text-figure 6. Elements of geometric form and functional structure of the carapace of *Pterygocythereis ceratoptera* (Brady, 1868).



Text-figure 7. Basic structural elements of three different architectural types of cytheracean species, box-frame (1, 3, 5, 7), corrugate (2, 4) and compound spherical (6, 8, 9, 10), with two stages of truss (ridge) development shown in the box-frame type. 1, 3 —*Hermanites?*; 2, 4 — *Quasibuntonia*; 5, 7 — *Ambostracon glauca* (Skogsberg, 1928); 6, 8, 9, 10 — *Bythoceratina*.



Text-figure 8. Three different stages of box-frame truss development toward eventual replacement of cross members by elevated compression members to displace the reaction moment farther from the form center (centrum) of the shell. 1, 2. *Bradleya dictyon* (Brady, 1880). 3, 4. New bradleyid from South Africa, Recent. 5, 6. *Bradleya andamanae* Benson, 1972.

CLASSES OF ARCHITECTURAL TYPES

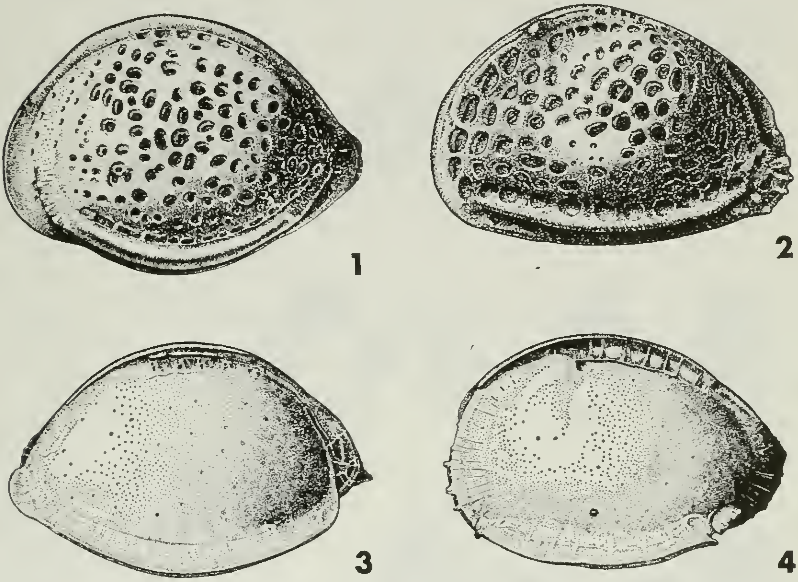
Architectural orders of human structures are classes of changing art styles and reflect the evolution of the understanding of mechanical principles, the development of materials and construction techniques. Henningsmoen (1965) suggested that Paleozoic ostracodes have shapes in common that may not result just from phyletic proximity. Elsewhere, I have compared carapace structures with aircraft engineering structures (Benson, in press). Aircraft fuselages react as thin elastic shells. The materials of which they are constructed have nearly equal properties of tension and compression. This is not likely to be the case with ostracodes whose skeletons are largely calcite, which has great compressive strength and little tensile strength. The degree to which chitin compensates for this lack of tensile strength is not yet known, but I suggest that it reacts like steel in reinforced concrete to make up for this deficiency. Therefore, it is not inappropriate to borrow some structural analogies from the field of concrete architecture as well. A classification of post-Paleozoic ostracode structural morphotypes is given here, somewhat modified over the one suggested earlier. It is based on common geometric or structural properties. All of these classifications infer that similar forms behave in the same way mechanically (Text-fig. 10).

Monocoque shell frames transmit all of their load in a thin-walled smooth calcified "skin" (term used in the engineering sense; "monocoque" is an aircraft engineering term). In the ostracodes they are basically a pair of domes without supplementary reinforcement except to prevent bending at the margin. *Cypridopsis* is this type. They are often swimmers or live in quiet water. External mechanical forces are weak and uniformly distributed. The thrust, or outwardly resolved force, is absorbed within the shell along the latitudinal parallels from the meridian or arch lines of force. The walls are thin but strong with most of the force originating with the closing muscles being dissipated at the margin. The thin shell can carry loads efficiently only if the stress is distributed uniformly. It is not able to withstand substantial impact.

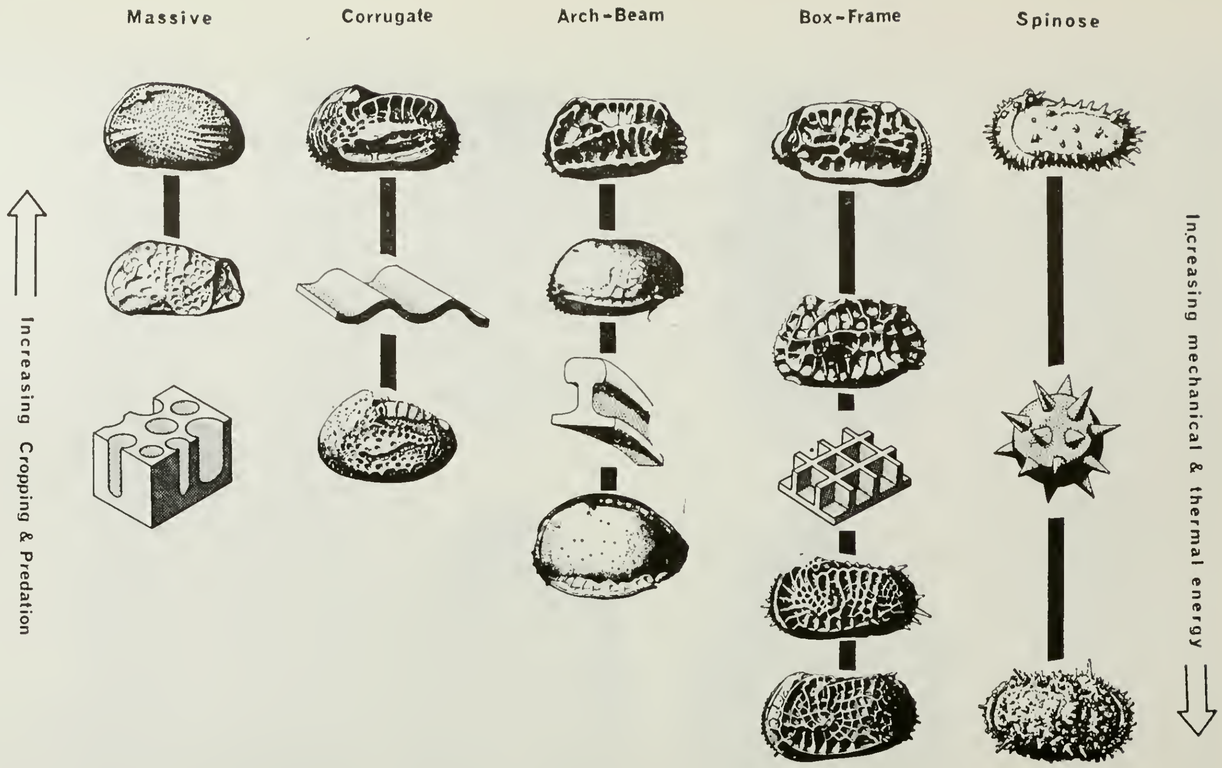
More mass is required to maintain strength and positional stability in the zone of the mechanically active water-sediment interface. *Massive* ostracodes may be derived from almost any phyletic lineage or other structural morphotype. All of the massive forms share the characteristic of strength through added shell wall thickness and partial obliteration of other structural properties inherited from their past. *Cythere lutea* (Müller, 1785) and *Hemicythere villosa* (Sars, 1865) are possible examples. This design is more capable of anticipating variable loads by utilizing material to resist shearing stress or buckling.

Arch-beam ostracodes translate much of their strength through a few curved ridges or velate structures that lie outboard from the principle and often smoother than remainder of the shell. This structural morphotype has positional stability and strength along the venter combined with some configuration of a beam or arch system to transmit force along the hinge or over the lateral surface. They can be very strong with thick shells or very delicate. *Aurila* and *Eocytheropteron* (Text-fig. 9) are two examples of the stronger type, although the same principle is approached in delicate genera like *Cytheropteron* and *Cativella.* This type also may become tetrahedronal as the arch components are straightened. Some become alate as the venter is extended farther.

The *box-frame* type is the strongly reticulate ostracode. Its cross-members may be individually emphasized to dominate the remainder of the system of mural struts. *Bradleya* is of this type. Shallow, smaller species are usually simpler with fewer mural struts than deep, larger species (Text-fig. 11). This can be a very strong yet economical structural system, which can increase its strength further by adding mass outboard. Some reticulate species actually become smooth in external appearance as the top flanges of the strut members broaden and join.



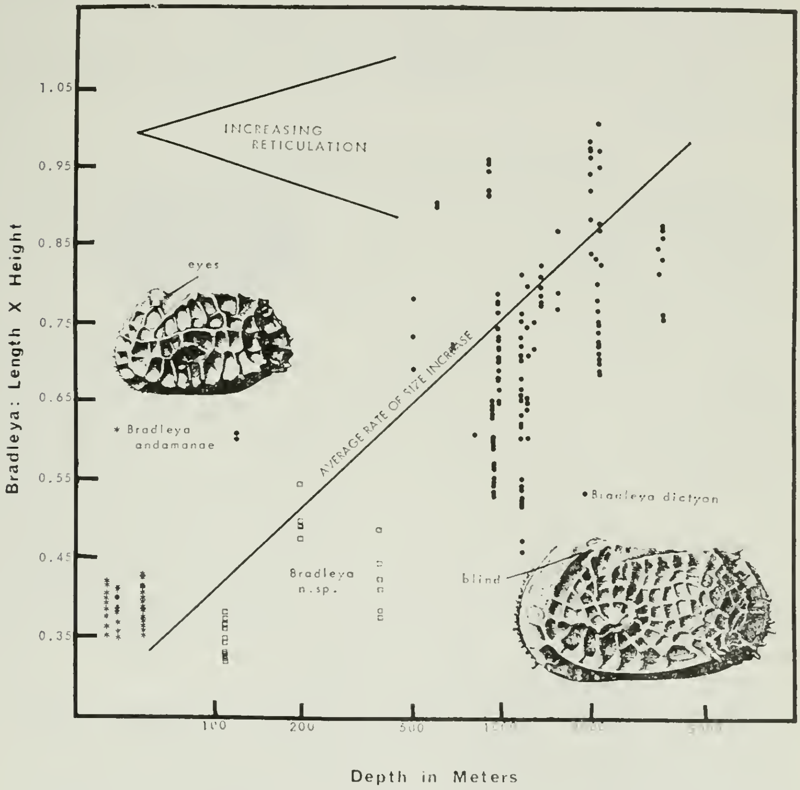
Text-figure 9. Convergence in form in four ostracodes with arch-beam structure. The upper two are relatively shallow water and massive, the lower two are deep-sea and much more delicate. The two on the left belong to the genus *Eocytheropteron* or a closely related genus and the two on the right are *Aurila* and *Pterygocythere?.* Note the coincidence of structural detail in support of the main structural members.



Distribution Of Structural Morphotypes

Text-figure 10. Hypothetical distribution of five of the different architectural styles or forms (structural morphotypes) in reaction of the selective forces responsible for their development. Note that the features used in their definition tend to intergrade between some of the styles and that all tend to become more massive in regions of higher mechanical energy.

Corrugate or plicate ostracodes increase their area-to-volume ratio more rapidly during growth than does a monocoque shell thereby increasing the stiffness of a relatively thin wall. Placing mass symmetrically away from the surface of geometric stability increases the reaction moment (moment of inertia). This gives mechanical advantage, resistance to longitudinal stress, by creating distance between that part of the wall under tension and that part under compression. This is similar to the beam, but with less local concentration of mass and representing a more primitive solution in terms of ostracode growth. This type of construction requires only that the area of the shell be slightly increased over its prior condition by an accelerated growth rate. Its evolution is fairly simple, however its reaction is less controllable. The possibility of bending can only be prevented by development of crossing structural members. *Veenia, Procythereis,* and many other late Mesozoic cytheracean ostracodes fit this category.



Text-figure 11. Increase in average size (in mm) with depth of species of *Bradleya.*

Spinosity is a special structural attribute. It has great functional importance but is not either statically determinate or geometrically stable. *Spinose* ostracodes usually become larger and more spinose with depth (Text-fig. 12). However, as *Echinocythereis* becomes larger, it does not necessarily acquire more spines (Text-figure 13). The function of spines is presumed to be defensive to ward off predators or to extend sensory setae. The relative length of the spines does not seem to correlate directly with changes in depth as does their number. The positions of the major spines are not random but appear to be genetically fixed (Text-fig. 2). Some shallow forms have very long spines. These species must live in quiet water, as is true of deep-sea species, to prevent breakage of the spines. An increase in spinosity with depth may be the result of an increase of potential predator selection over mechanical selection, but this is speculation.

Other classes might include compound tetrahedronal forms (Text-fig. 14) or compound spherical forms (Text-fig. 7). These simplest geometric shapes, often found in joined sets, tend to reinforce one another as parts of another architectural type or becoming dominant on their own.

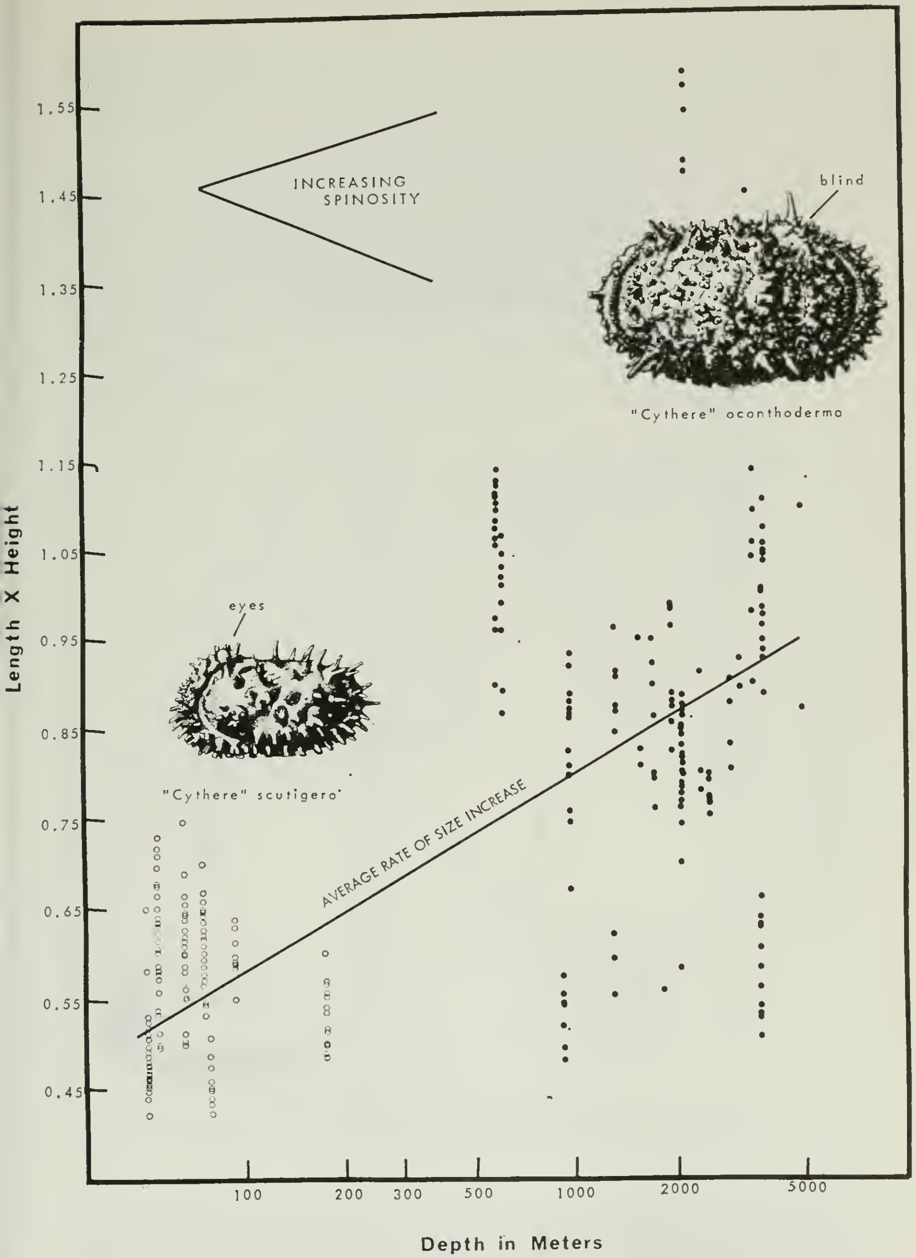
All of these structural morphotypes intergrade with one other. It is conceivable that a large ostracode taxon may find stable structural solutions in all of these types.

STRUCTURAL MECHANICS

The structural problem of the ostracode carapace is to be able to encapsulate the animal beyond its distal-most, softer regions, and yet remain divided into two parts for appendage extension and general access. A single valve must economically, yet with strength, span a broad space. Much of this space may remain unoccupied by any compressive, body-fluid support.

The most economical space-enclosing structure for spanning a considerable distance with the least mass is a dome, that is a three-dimensional structural derivative of the catenary arch (Text-figs. 15-16), having the capacity to react latitudinally as well as in the planes of the arch-shaped meridian sections. To enclose a maximum volume with the minimum surface, the sphere is most efficient. However, when it is divided, the margins of the sphere are weakened and subject to bending; and when it sits on a support, the stress of a sphere is not uniform. A hemisphere is not strong compared to a domal system with catenary arch sections. A catenary arch is strongest to resist force normal to its crown and uniformly distributed along its span. A horizontal force, oblique to the crown of an arch or against its side, would have to be transmitted unequally through the crown and down the other side producing high bending moments. A dome however, transmits the oblique forces through latitudinal resistance causing rapid dampening of the bending.

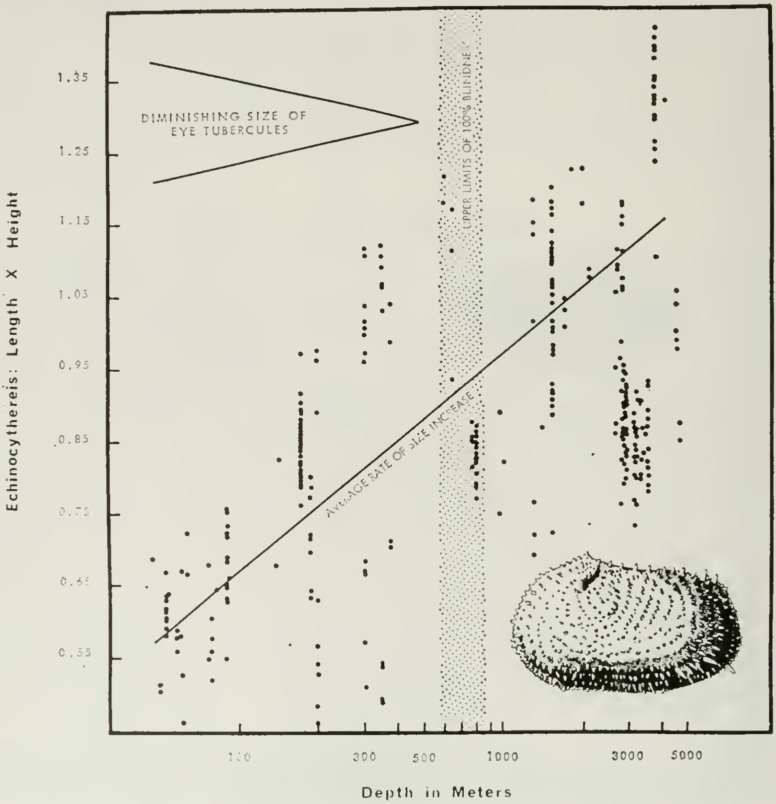
For benthic ostracode species the domes of the valves must be modified to form a strong union along the hinge, provide ventral stability, and support the free margins against bending and unresolved thrust. The elongate dome, modified vault structure, and shell-frame all are used to satisfy these requirements. These are the most common structures in benthic ostracodes. Their



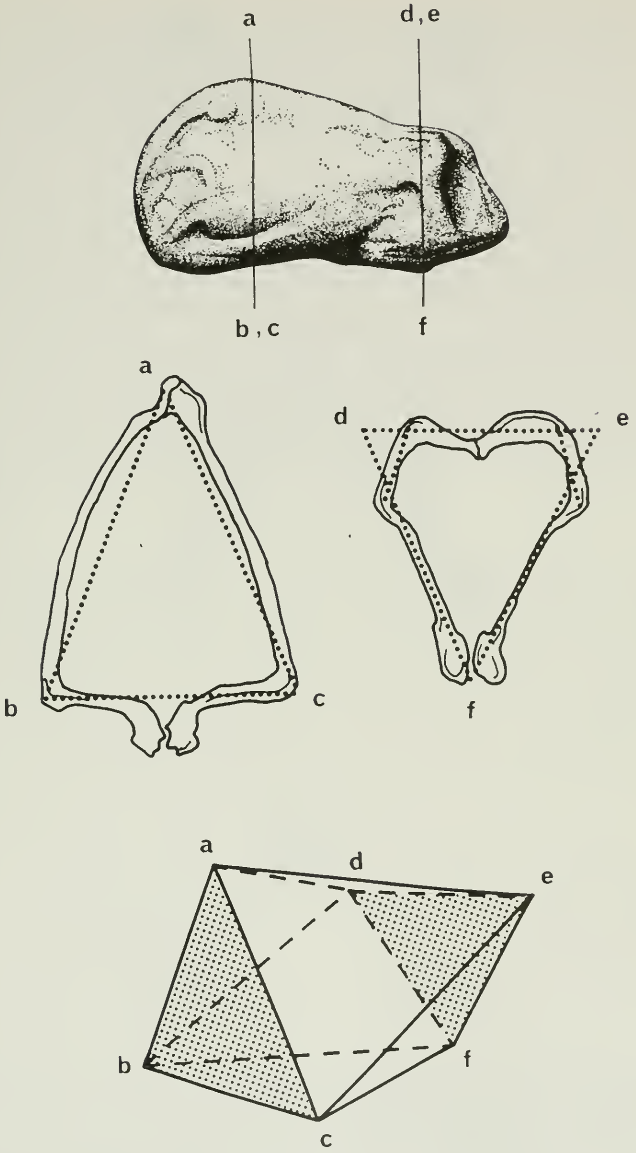
Text-figure 12. Increase in average size (in mm) and spinosity with depth of end members of a series of trachyleberid species including *"Cythere" scutigera* Brady, 1868, and *"Cythere" acanthoderma* Brady, 1880.

efficient cross-section approaches some portion of a catenary arch, depending on the orientation and the interference of other structures (Text-fig. 17). Understanding the structural properties of the catenary arch suffices, at least as an introduction to structures that obviously become more complicated as they are combined in actual carapaces.

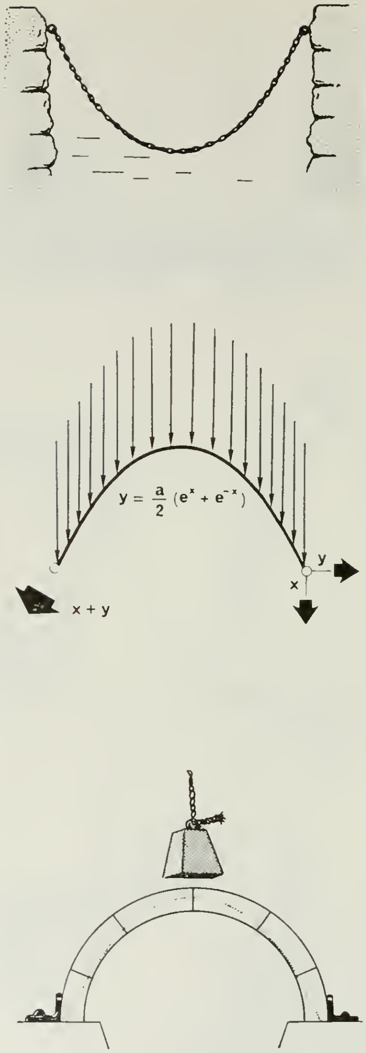
The major structural problem posed by the catenary arch, or the dome forming the valve of the ostracode, is the resolution of the thrust that causes bending near the free margin. This may be of considerable magnitude in forms of low rise relative to the span. Because it is not practical to join the margins with cross tension resisting members, a tension ring must be employed. It should be remembered that the calcite composing the shell has considerable compressive, but little tensile strength. So that either calcite mass or chitin,



Text-figure 13. Increase in average size (in mm) with depth of species of *Echinocythereis*. Other changes include thinner, less massive spines (also fewer), and the gradual attrification of the eyes (inferred) and reduction of eye tubercles with depth.



Text-fig. 14. The compound tetrahedroid shape contained within *Caudites*. A tetrahedron is the most direct solution to the problem of reaction of a space enclosure of compression inducing loads received along a line. This compound structure could conceivably be very strong to resist impact from several directions from objects much larger than the carapace itself, or it could also support its shape with a very thin wall.



Text-figure 15. The principle of the catenary. A chain or cable has great capacity to span long distances because it assumes the form of stress equilibrium plus placing a considerable reaction moment between the realized line of inward thrust at the points of attachment and the mass itself. A catenary arch is equal in compression to stress distribution to a cable under tension. The vertical load is distributed equally along the extent of mass. An unloaded arch with a uniform radius diverges in form from the catenary and is not in static equilibrium unless the wall thickness and strength is sufficient to provide sufficient reaction moment.

which has tensile but not compressive strength, must be added near the margin to resist a high bending moment. Close examination of the shell margin (Text-fig. 18) at the infold shows that the calcite laths (the parallel layers of calcite crystals — like bricks) of the shell wall continue across the so-called zone of fusion, mistakenly thought in past to unite the "inner" and "outer" lamella. Strength is continued through a change of direction and shape, plus the addition of mass, usually with only minor alterations in composition.

In very thin monocoque shells, the possibility of bending caused by the thrust of the catenary form is increased, and accessory stiffening structures or a considerable increase in mass may be required to maintain the shape and prevent buckling (Text-fig. 16). There are several solutions to prevent bending and to absorb or redirect the thrust, within the shell and infold, or on the outside of the shell (Text-figs. 19-20). These outside structures, which stiffen and strengthen the margins, may eliminate the primary strength purpose of the infold, and this function of the infold may become vestigial (fused).

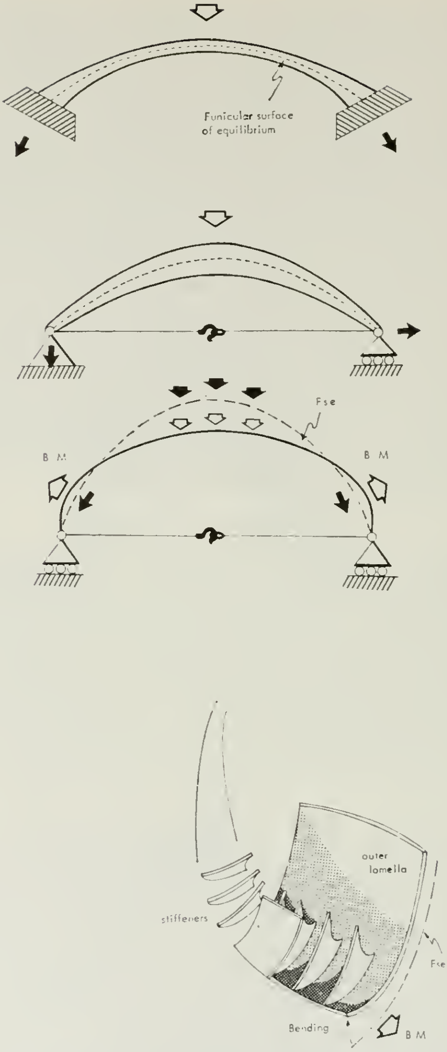
The principle of the catenary can be seen well exhibited in fresh-water monocoque shelled ostracodes (Text-fig. 21), where the infold is best developed and auxiliary external shell structures are fewest.

SOURCES OF STRESS

The forces that are capable of producing strain, deformation, and failure in the ostracode carapace are both internal and external to the shell (not to be confused with the forces in the shell wall itself). The internal forces originate principally from the support of the non-skeletal inner organs, the appendages, reproductive organs and their activity, and especially from the closing adductor muscles. The sources of external forces are less obvious. These involve those resulting from the position and movement of the animal at the interface between the water and the substrate and the movement of these media around the ostracode.

Examination of the attachment of the adductor muscles at the so-called "scars" shows that the tensor muscle fibers penetrate into the shell to be anchored to wedge-shaped calcite prisms. The prisms are similar to keystones in an arch. They are clustered and extend to the outside surface of the shell. Their outer surface is larger than the inner, resulting in an effective structure to prevent shear that could occur with the force being concentrated normal to the shell. Often there are local compensating structures on the outside of the shell such as the "bridge" in the bradleyids, the muscle-scar node in the trachyleberids, and the circular castral structure as in *Agrenocythere*.

The presence of external forces should be implicit in the apparent strength of the shells. The valves are often far stronger than is necessary to support their own weight or to react to the forces originating with the closing muscles. Controlled breakage of the valves under the microscope, in order to examine their inner structure, requires considerable force. In spite of the absence of observational data, it must be assumed that protection against crushing or impact force is the foremost reason for a massive, stronger shell. For those ostracodes living in the upper zone of actively moving or agitated substrate, the



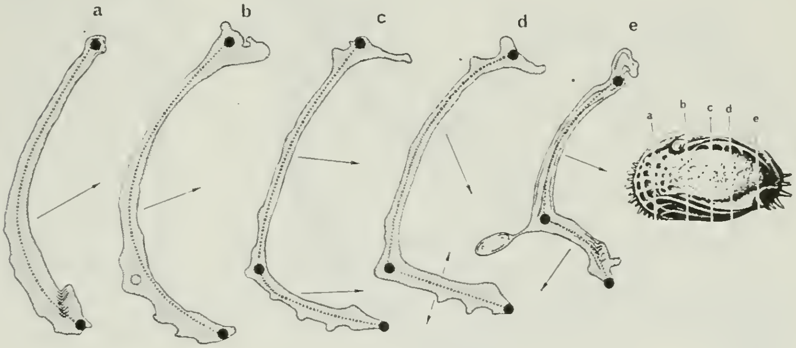
Text-figure 16. Solutions to problems of spanning great distances with the least possible mass under compression. Considerable lateral thrust is developed which may be expressed as bending or which must be absorbed either in the supports or in a reaction element under equal and opposite tension. In a dome the bending may be absorbed in the latitudinal "hoop" forces developed around its axis. A section through the marginal region of the thin shelled ostracode *Cypretta* shows how the curvature near the edge departs from the surface of equilibrium and stiffeners are required to translate the thrust from the outer lamella into the infold forming the reacting tension ring.

shell walls must be reinforced especially against impact from above. For those ostracodes that live on the surface of fine, stable, yet soft substrate, the venter is extended and the dorsal lateral walls may require less strength.

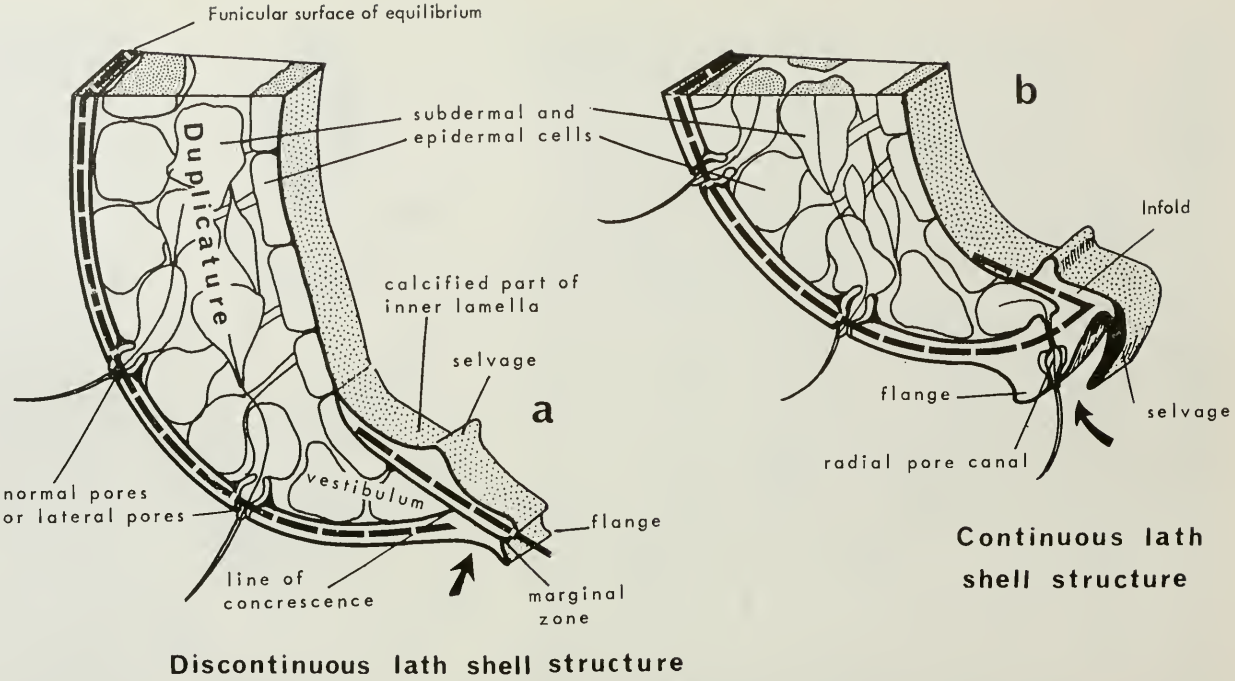
THE ROLE OF ECONOMY IN DESIGN

The carapace of the podocopid ostracode encapsulates the animal in protective armor at a considerable metabolic expense. Not once, but as many as nine times, the animal doubles its size secreting a rigid skeletal mass nearly equal to the volume of its own body fluids. With the possible exception of the barnacle, which is sessile, no other arthropod expends as much energy for the purpose of developing a protective cover or skeletal support. It must be assumed that no more mass is created than is necessary for the potential requirements of strength and positional stability.

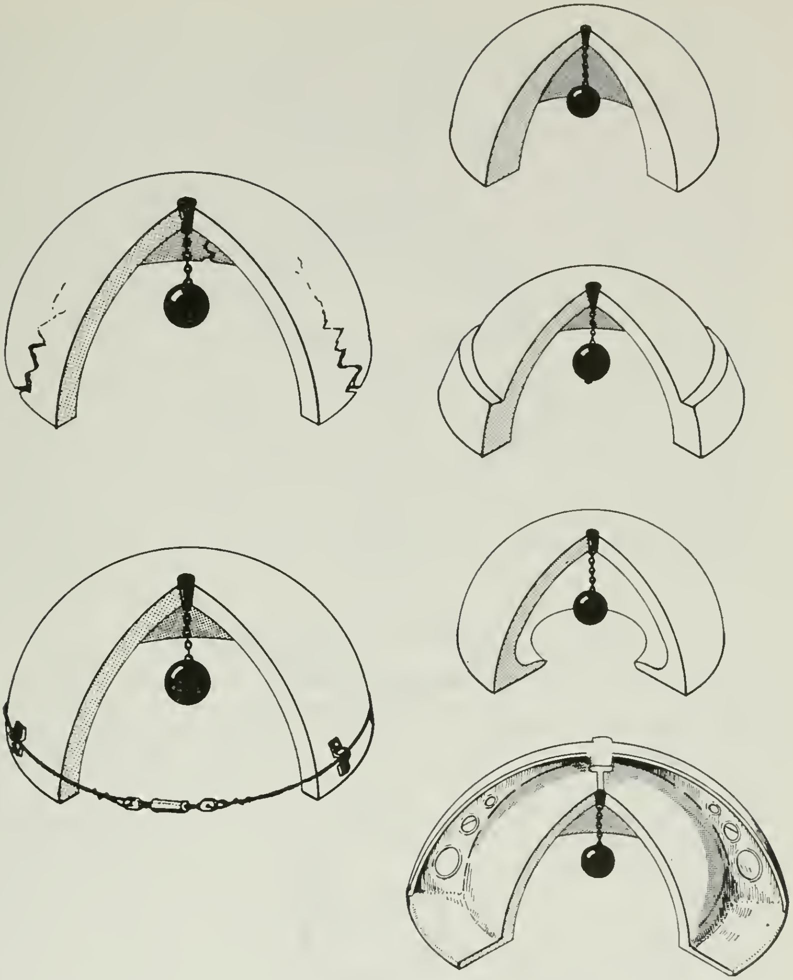
Other mobile invertebrates secrete or excrete rigid skeletal frames that are proportionally equal to or greater than the relative mass of the ostracode, but these are built gradually by accretion over the life span of the individual. Those that build by continued addition save mass, but suffer the problem of adding efficient structures to existent frames built to carry less load. The ostracode must generate a series of increasingly larger and consequently lighter working designs which are significantly modified each time it inflates the nonrigid membranous patterns to which supporting, compression resistant mass is then added. The difference between these two systems is not only long term economy, but also the vulnerability of the structure of the ostracode as a static frame at the time of ecdysis. The arrangement of structure of the ostracode carapace is probably more efficient and flexible in design than other bivalves, although more costly in constructional metabolic energy.



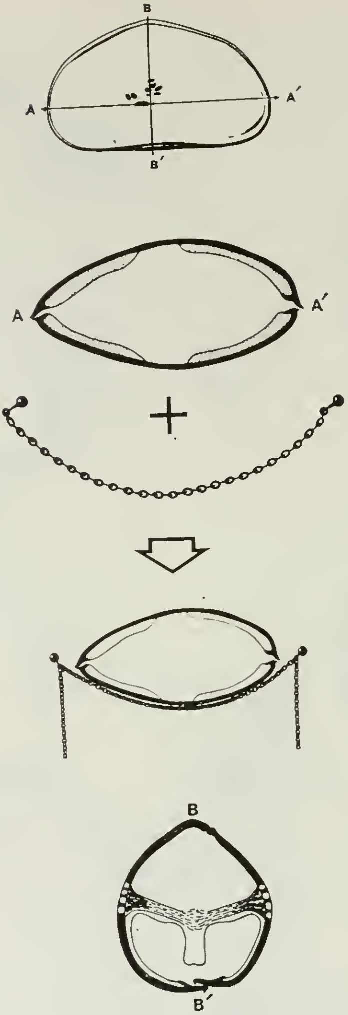
Text-figure 17. Serial sections through a relatively simple species of trachyleberid shallow-water ostracode from Madagascar showing the coincidence of the catenary form through the shell between major structural members. In the anterior, where the shell is nearly unsculptured, the catenary form and the whole span are identical. Passing to the posterior the ventrolateral ridge appears in a plane normal to those of the sections causing interference, division, and the reversal of the catenaries. The arrows show the vertical axis of the catenaries of which only a section is represented (drawn from actual chains in suspension).



Text-figure 18. Two interpretations of the margin of the ostracode shell. One (a) showing the bilamellar model with the fusion of the inner and outer lamella along a zone of concrescence (after Kesling, 1951), the other (b) showing the continuity of the outer lamella as an infold with no separation. The latter is obviously stronger and is confirmed by scanning electron photomicrographs of broken sections in this region.



Text-figures 19 and 20. Conditions of a dome showing the problem of thrust and several solutions similar to those found in ostracodes. These models are made on the assumption that the material used has much less tensile strength than compressive strength.



Text-figure 21. Longitudinal and saggital sections of *Potamocypris? steueri* Klie, 1935 (taken from Gauthier, 1939) showing a comparison between the catenary form of a spanning chain in tensional stress equilibrium (the equal and opposite of compressional span stress equilibrium) and the longitudinal shape of the carapace. The lower illustration of the chain and section together is an actual high contrast photograph of the experiment. The fit is better than 90 percent with the ends departing from the catenary form, presumably under the influence of local increased thickness to resist bending near the edge and the presence of the infold (duplicature *sensu lato*).

As a general working premise, it seems reasonable to assume that an ostracode, regardless of its size or structure, does not build a stronger or heavier carapace than is likely to be required during its lifetime, based on the adaptive experience and success of its predecessors. The variability of design becomes consequently restricted by genetic factors. Environmental change in its many complex and often unknown or unknowable progressive or oscillatory forms is much more rapid than average genetic change within a population. Therefore, both genetic and the consequent form of structural systems react conservatively within a series of subsets of more active surrounding systems of external influences. These systems are progressively more or less inertial toward the system of skeletal frames, which is the most effective reactant against the pressures of change.

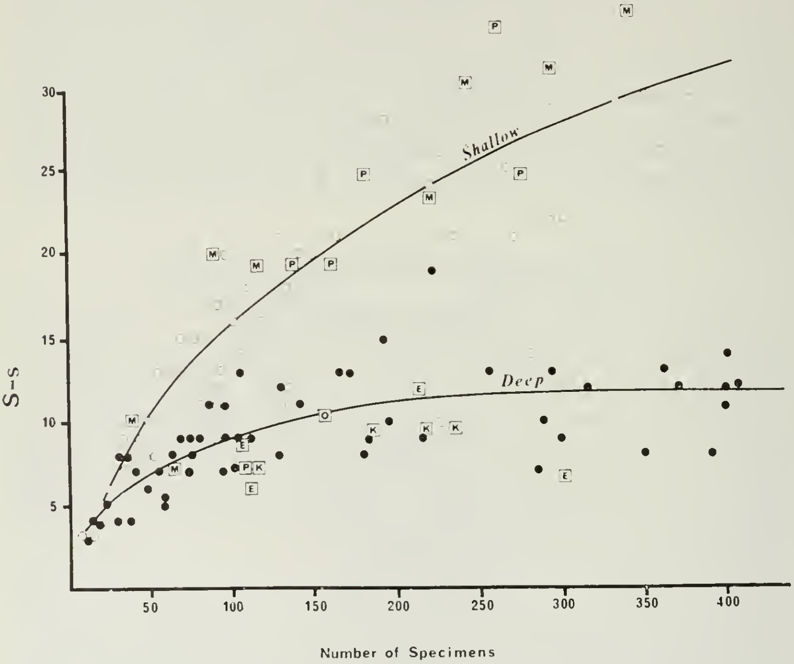
Not all of the structural systems are in equilibrium with the environmental systems that brought them into being. There is a lag perpetuated genetically. This is especially evident if the structure represents a very minor metabolic taxation for its construction. Of course structures generally exist somewhere between this potential and realized functional status. If a trade in functional roles of structures is gradually brought about, such as a gradual increase in general or local shell thickness that may eliminate the need for a ponticulate compression-resisting ridge, the replaced structure diminishes and disappears. I would judge that this is happening with the dorsal ridge of *Pterygocythereis jonesii* (Baird, 1850).

EVOLUTION OF STRUCTURAL TYPES

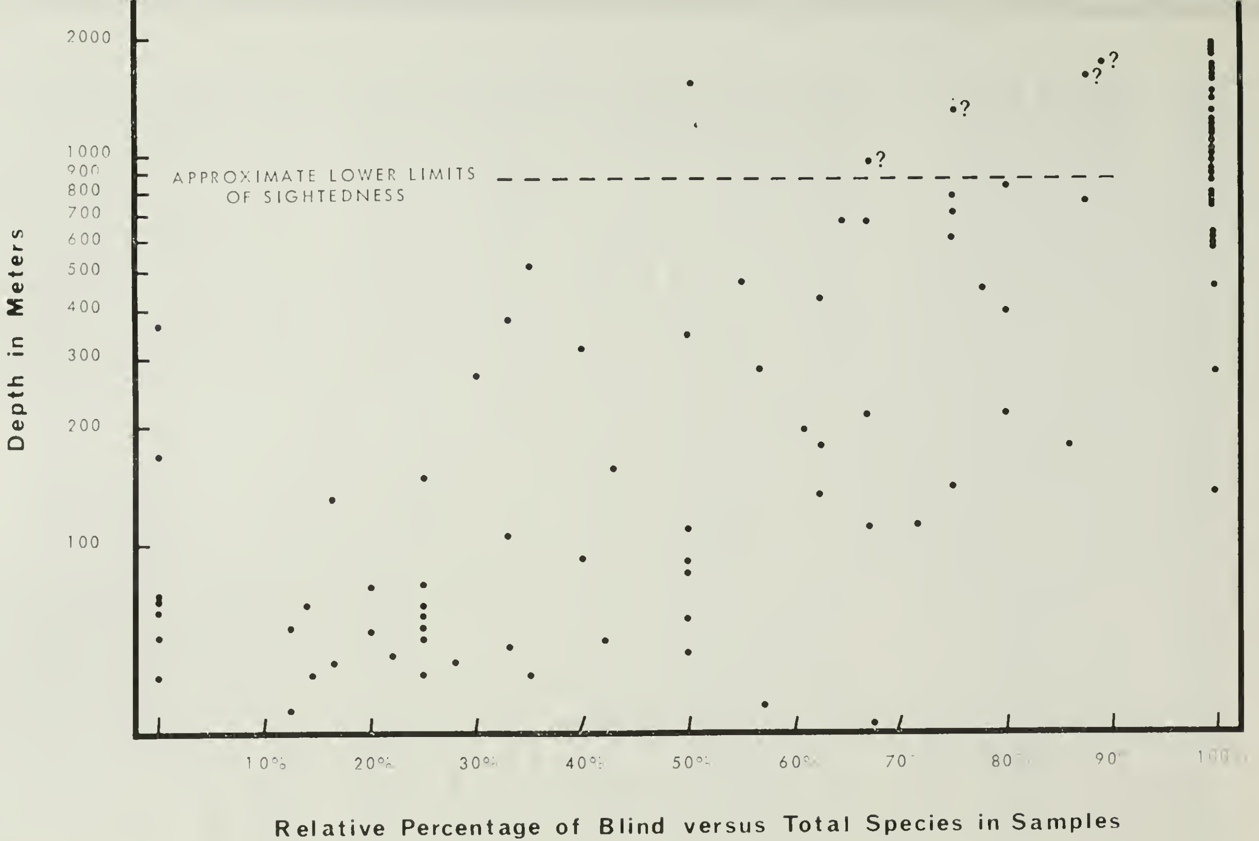
Thus as a result of a hierarchy of functional responses and the presence of potentially equal series of operating mechanical reactions, there may be a definable number of architectural solutions or structural systems available as options toward the evolution of a successful carapace design. Convergence of form from among ancestral stocks with differing recombinations of structural systems has been commonplace in the history of ostracodes. Arch-beam designs are present in velate beyrichaceans. There are corrugate quadrijugatorids, box-framed kirkbyaceans, and so on. The fact that there are several ways to achieve strength besides just an increase in mass has made the diversity of ostracode form, as we know it, possible.

How are these recombinations achieved? I suggest that changes in the depth in the habitats of benthic ostracode species subjecting them to changes in mechanical to predator selection pressures may be responsible. This is to say that when either of these pressures is great and predictable, the morphologic variability as well as the geometric complexity of the design decreases. The morphologic choices are locked in as structural responses. With relaxation of these pressures, the inherent morphologic patterns of the carapace, those that control the basic pore and reticular patterns and tend to be temporarily geometrically more complex, reassert themselves. These more complex, perhaps mixed, structures, while weaker to resist mechanical pressures, provide the "roughness", or pseudospinosity necessary to ward off predators. Where severe predation, such as occurs in deep-sea cropping, defensive structures such as spinosity, become extremely exaggerated. If almost no stress is present, or if it tends to be uniform, the smooth thin shell would result leaving only the traces of the basic carapace patterns. As the "complex" forms reinvade regions of high selection pressure they may not reappear in the same structural mode as before. Variation in *Bradleya* in geographically isolated shallow shelves tends to follow this differential structural selection.

Morphologic stability therefore tends to occur in two regions; that which represents a relatively simple but locked-in structural solution under continual mechanical, thermal or chemical (salinity change) selective pressure, and that which seems to occur in very stable physical conditions like the deep-sea where predator selection pressure and metabolic restrictions on shell con-



Text-figure 22. Relative species diversity among samples collected from the deep-sea (depths greater than 1000 meters; dots) and samples collected on the shelf (depths generally between 10 and 200 meters). Fossil samples of the same depths are also indicated (squares) with the ages shown (K, Cretaceous; E, Eocene; M. Miocene; P, Pliocene). The species diversity (S-s is total species minus species with only one specimen found in a sample) of deep-sea psychrospheric faunas seems to have remained about half of that of temperate shelf faunas over the last 20 million years or perhaps longer.



Text-figure 23. The distribution of relative blindness among potentially sighted species (ones known to have eye tubercles or closely related to species with eye tubercles) with increasing depth. Almost all species become blind in depths greater than 600 to 800 meters. More than half of the species living in depths greater than those typical of shelf conditions are apt to be blind.

struction are great. Brackish and littoral environments have low species diversity and long tenured taxa. This is also true of deep-sea faunas (Text-fig. 22). The middle and outer shelf seems to be the major breeding ground for new taxa.

A clue to the history of invasions of the deep-sea or from deeper waters to shallower waters may be found in the presence and absence of eyes among some related species. Presumably eyes once lost cannot be regenerated. Therefore a sighted shallow species has not phyletically descended from a deep form. Contrarily, the occurrence of a sighted form, which has many related deep-sea blind species, may indicate the place of origin of this species group.

A distributional study of blindness with depth is given in Text-figure 23 which may also have value for paleoecological interpretations.

CONCLUSION

I have purposely focused this discussion on concepts that are not generally considered by students of ostracodes. Simulation of form by mathematical modeling is not yet possible. As in other study areas, mechanical relationships are appreciated before they can be formalized. And yet the difference between our view of carapace form as descriptive and functional will be founded on principles similar to the ones discussed here. Some of these are: (1) that relative change in carapace morphology is better described through a coordinate reference system implicit in the animal, and that this reference system is inertial or the most stable; (2) that the lack of change in the evolution of carapace morphology represents successful reaction to external pressures; because (3) the purpose of carapace shape or structure is to uniformly transmit stress from the environment to be protectively absorbed into the strength of shell material without causing failure in any one of its structural elements. If there are stability phases in the evolution of ostracode carapace form, these may be interrupted, not by increases in environmental pressure, but by its relaxation.

The difference between an engineer and a morphologist is not as great as might be first imagined. It is the task of both to abstract the functional characteristics of structural systems with the aid of the best theory available.

REFERENCES

Beckner, M.

1959. *The biological way of thought.* Columbia Univ. Press (New York), pp. 1-200.

Benson, R. H.

1970. *Architectural solutions to structural stress in rigid micro-organisms, through SEM examination. Proc. Third Ann. Stereoscan Colloq.,* Kent Cambridge Sci. Inc., pp. 71-77.

1972. *The Bradleya problem, with description of two new psychrospheric ostracode genera, Agrenocythere and Poseidonamicus (Ostra., Crust.).* Smithsonian Contr. Paleobiology 12, pp. 1-150.

[In press]. *The role of ornamentation in the design and function of the ostracode carapace.* In Geoscience and Man, Louisiana State Univ. Press.

Bertalanffy, L. von
1962. *Modern theories of development; An introduction to theoretical biology.* Harper Torch Books, Harper & Brothers (New York), pp. 1-204. (Reprint and translation of the 1933 book by J. H. Woodger).
Elofson, O.
1941. *Zur Kenntnis der Marinen Ostracoden Swedens.* Zoologiska Bidrag fran Uppsala 19, pp. 215-534.
Gauthier, Henri
1939. *Sur la Structure de la Coquille chez quelques Cypridopsides a furca réduite et sur la validite du genre Cyprilla (Ostracodes).* Bull. Soc. Zool. France 64, pp. 204-228.
Henningsmoen, Gunnar
1965. *On certain features of Paleozoic ostracodes.* Geol. Foreningens i Stockholm Fordhandl. 86, pp. 329-334.
Kesling, R. V.
1951. *The morphology of ostracod molt stages.* Univ. Illinois Biological Mon. 21, pp. 1-317.
Morkhoven, F. P. C. M. van
1962. *Post-Paleozoic Ostracoda; their morphology, taxonomy and economic use.* Elsevier Publ. Co., 1, pp. 1-204.
Neale, J.
1964. *Some factors inflencing the distribution of Recent British Ostracoda, In Ostracods as ecological and paleoecological indicators.* Pubbl. Stazione Zoologica di Napoli 33, pp. 247-296.
Russell, E. S.
1916. *Form and function.* John Murray Publishers (London), pp. 1-383.
Thompson, D'Arcy W.
1961. *On growth and form.* Cambridge Univ. Press (original 1917 edition abridged and edited by J. T. Bonner), pp. 1-346.

Richard H. Benson,
National Museum of Natural History,
Smithsonian Institution,
Washington, D.C. 20560.
U.S.A.

DISCUSSION

Dr. A. Liebau: First of all, you have used only one of the two main pore systems. There are the cone pores and there are the mesh pores. The cone pores are not so valid for this compilation as are the mesh pores. There is at least one group in which the cone pores are useful, that is the *Acanthocytheris* group. But the mesh pores have only undergone reduction in the Trachyleberididae. You will not find a species with more than 140 mesh pores, and that only in the oldest ones. From that point onward only a reduction in mesh pores is to be observed. New mesh pores are not developed.

Dr. Benson: I agree with some of what you say. As far as my own observations are concerned the problem is that the mesh pores are not always so easy to find. To identify these in some of the smoother animals is very difficult. Of course there are changes in the pore conulae, there are new ones I'm sure, but it is easier to work with 20 pore conulae than it is 140 of the mesh pores.

Dr. A. Liebau: Well one remark should be confirmed if we compare two genera of Pokorny, but I should not mention Pokorny because he cannot be here. It is too bad that Dr. Pokorny cannot be here, as he would give a good lecture on this subject. It would be very interesting to see what he would say to this lecture.

Dr. Benson: As you know Professor Pokorny spent a year with me in 1967. Some of the ideas that I have shown here originated from that time. We discussed much of this at that time, in fact some of the diagrams that you saw were drawn then.

Dr. H. Uffenorde: Do the specimens, on which your correlation between size of carapace and depth is based, come from sediments with the same physical properties?

Dr. Benson: No attempt has been made to correlate changes in sediment properties with the increase in carapace size. It is my impression that in general the smaller sizes are associated with shelf clastic sediments and the larger sizes with pelagic sediments.

Dr. H. Uffenorde: Did you get any data concerning the degree of exposure to light from the microenvironments from which your ostracode species, showing a reduction of eye tubercles, come?

Dr. Benson: Only that available from the literature.

Dr. H. Puri: I think we should commend Dr. Benson for an excellent study. He has tried to relate ostracode structure to known engineering principles. I think most of the work he has done has been with the trachyleberids, and I would like for him to continue this and study the polycopids.

Dr. Benson: Thank you Harbans, I am very interested in *Polycope* because it seems to approach one of the simplest engineering solutions. However, I am not very well informed about its taxonomy.

Dr. H. Loffler: If I understood you correctly, you studied the mechanical stability of ostracode shells. I wonder whether you have taken into account that the animal in water has specific weight of between 1 and 1.5 so that if you compare this with the Roman arches the latter increase proportionately to give a thickness of 100 to 200 meters. There is such a bend in the shell anyway that I don't really believe it is necessary to explain its strength in terms of mechanical principles. You can notice the same thing with plant seeds and so forth. This structure is known only to follow evolutionary trends, with relation to selection and other things, without requiring an explanation in terms of mechanical principles.

Dr. Benson: You're implying the effect of gravity as the basic efficient cause and I did not intend to do that. I'm talking primarily about potential impact, and potential impact implies mechanical instability of the substrate and the crushing capability of predators. I do recognize the importance of mass as it increases the sinking factor however. As to the matter of relative thickness, I might also interject that your analogy of the Roman Arch, if you will study new engineering designs of pre-stressed concrete, you'll find that it is possible to span the English Channel with that much concrete, and still follow the basic principles of catenary suspension. The principles of distribution of stress apply no matter what scale it is, or in what medium. I would add that in thinner shells I think the adductor muscles are the principle source of the stress.

REMARQUES SUR LA DIVERSIFICATION MORPHOLOGIQUE DE TROIS NOUVELLES ESPECES D'*ELPIDIUM* (OSTRACODA) A CUBA

Dan L. Danielopol
Limnologisches Institut, Wien, Austria

RÉSUMÉ

Le genre *Elpidium* F. Müll. était connu jusqu'a présent, par une seule espèce, *E. bromeliarum* F. Müll., vivant dans les coupes des Broméliacés de l'Amerique du Sud et l'Amerique Centrale.

En étudiant plusieures populations d'*Elpidium*, des Bromeliacés de Cuba, l'auteur a decouvert trois nouvelles espèces: *Elpidium* n. sp. A, *Elpidium* n. sp. B et *Elpidium* n. sp. C.

Dans l'une des localitées cubaines, *Elpidium* n. sp. A et *Elpidium* n. sp. C. vivent ensemble. Très probablement, il y a un isolement sexuel entre ces deux espèces, comme on n'a pas trouvé de formes hybrides.

Les nouvelles espèces d'*Elpidium* diffèrent par les détails de l'organe copulateur mâle et des valves. On décrit brièvement l'organe copulateur mâle et les caractères sexuels secondaires des *Elpidium* de Cuba. On remarque que les plus importantes différences entre ces trois espèces sont données par les lobes génitaux de l'organe copulateur mâle qui trés probablement jouent un role sensoriel. A l'avis de l'auteur se sont ces appendices a fonction sensorielle que assurent dans une grande mesure, l'isolement sexuel.

L'étude comparative des valves des nouvelles espèces d'*Elpidium* de Cuba révéle des différences morphologiques significatives.

En s'etayant aussi sur d'autres exemples l'auteur attire l'atention que l'examination attentive de l'organe copulateur mâle des Ostracodes est absolument nécessaire, étant donné que cet organe assure l'intégrité de l'espèce par l'intermediaire du processus de l'isolement sexuel.

En général, les différences morpholgiques interspécifiques de l'organe copulateur mâle sont couplées aussi avec des différences morphologiques des valves. Cette derniére remarque peut avoir quelque intérêt pour le paléontologiste.

REMARKS ON THE MORPHOLOGICAL DIVERSIFICATION OF THREE NEW SPECIES OF *ELPIDIUM* (OSTRACODA) FROM CUBA

ABSTRACT

The genus *Elpidium* F. Müll., is known by a single species, *E. bromeliarum* F. Müll., living in the bromeliads cups from South America and Central America.

Studying several *Elpidium* populations from the bromeliads of Cuba Islands, the author discovered three new species: *Elpidium,* n. sp. A, *Elpidium,* n. sp. B, *Elpidium,* n. sp. C.

In one of the cuban localities, *Elpidium,* n. sp. A and *Elpidium,* n. sp. C live together. Most probably there is a sexual isolation between these two species, as no hybrids were found.

The new *Elpidium* species differ both by the male copulatory organ and the valve details.

The male copulatory organ and the secondary sexual characters of the Cuban *Elpidium* are briefly described. It is noticed that the most important differences between these three species are the details of the genital lobes of the male copulatory organ which probably display a sensorial role. In the author's opinion these limbs having a sensorial role insure, to a large extent, the sexual isolation.

The comparative study of the valves of the new *Elpidium* species from Cuba Islands, shows significant morphological differences.

Based on other examples, the author believes that it is absolutely necessary to make a careful examination of the ostracod male copulatory organ as their peculiarities insure the integrity of the species by the intermediary of the sexual isolation process.

Generally, the interspecific morphological differences of the male copulatory organ are connected with morphological differences of the valves. This last remark can be of some interest for the paleontologist.

INTRODUCTION

Il y a presque cent ans (1880), F. Müller décrivait au Brésil un ostracode remarquable, *Elpidium bromeliarum,* nouveau genre, nouvelle espèce, qu'il avait trouvé dans les coupes des broméliacés, plantes épiphytes des palmiers.

Récemment Pinto et Purper (1970) ont effectué la révision du genre *Elpidium,* arrivant à la conclusion qu'à l'intérieur de ce genre on peut reconnaître, pour le moment, une seule espèce, *E. bromeliarum,* F. Müller. D'après les auteurs brésiliens cités, le genre *Elpidium* est répandu au Brésil, au Costa Rica et à la Jamaïque.

Les recherches que Monsieur le Professeur Tr. Orghidan (Bucarest) et Monsieur N. Vina (La Havane) ont effectuées en 1970 à Cuba sur les coupes des broméliacés de la région Santiago-Baracoa, ont permis la mise en évidence d'une riche faune d'*Elpidium* représentée par trois nouvelles espèces que je nommerai *E.,* n. sp. A, *E.,* n. sp. B. et *E.,* n. sp. C.

Je rappellerai que les coupes de broméliacés sont des petites cuvettes formées par les feuilles de cette plante épiphyte qui se remplissent d'eau et de détritus et ou s'installe une riche faune. Ces microbiotopes aquatiques sont perchés à plusieurs mètres de hauteur sur les palmiers; en conséquence, la dispersion de la faune ne peut avoir lieu que passivement.

Parmi les trois espèces d'*Elpidium* cubains, *E.,* n. sp. A a une répartition vaste étant donné qu'elle a été trouvée sur la Gran Piedra et dans la vallée de Rio Indio (près de Santiago de Cuba), sur le Rio Sabanilla (près de Baracoa), dans la localité Yumuri (sur la route qui mène à Sabanilla). *E.,* n. sp. C a été récolté dans la vallée de Rio Indio, dans la même station que *E.*, n. sp. A; enfin, *E.,* n. sp. C a été trouvé près de Siboney à une douzaine de kilomètres de Rio Indio (Text-fig. 1). Le fait que les stations de deux des nouvelles espèces sont très proches l'une de l'autre et que deux des nouvelles espèces ont été trouvées dans la même station pose le problème de l'isolement sexuel comme facteur important pour le maintien de l'intégrité de l'espèce.

La question de l'isolement sexuel chez des espèces d'ostracodes proches du point de vue morphologique avait déjà attiré mon attention à l'occasion de l'étude des *Candona* du groupe *neglectoida* (Danielopol, 1969). Dans le cas

Text-fig| 1. Répartion géographique d'*Elpidium*, n. sp. A (●), *E.*, n. sp. B (◉) et *E.*, n. sp. C (★) à Cuba dans la région Oriente (1. Gran Piedra 2. Rio Indio 3. Yumuri 4. Baracoa 5. Siboney).

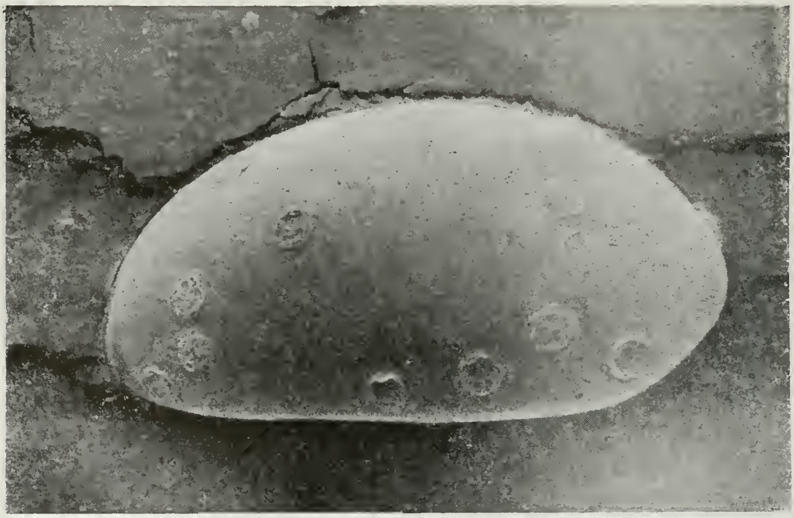
des *Elpidium* de Cuba, comme dans le cas des *Candona* citées, il m'a semblé utile de rechercher quelles sont les particularités morphologiques qui pourraient assurer un isolement sexuel; d'autre part il m'a paru intéressant de voir s'il existe une relation entre la diversification des appendices et la diversification des valves.

REMERCREMENTS

Monsieur le Professeur Tr. Orghidan et Monsieur N. Vina ont bien voulu me confier l'étude des ostracodes cubains; je les remercie vivement.

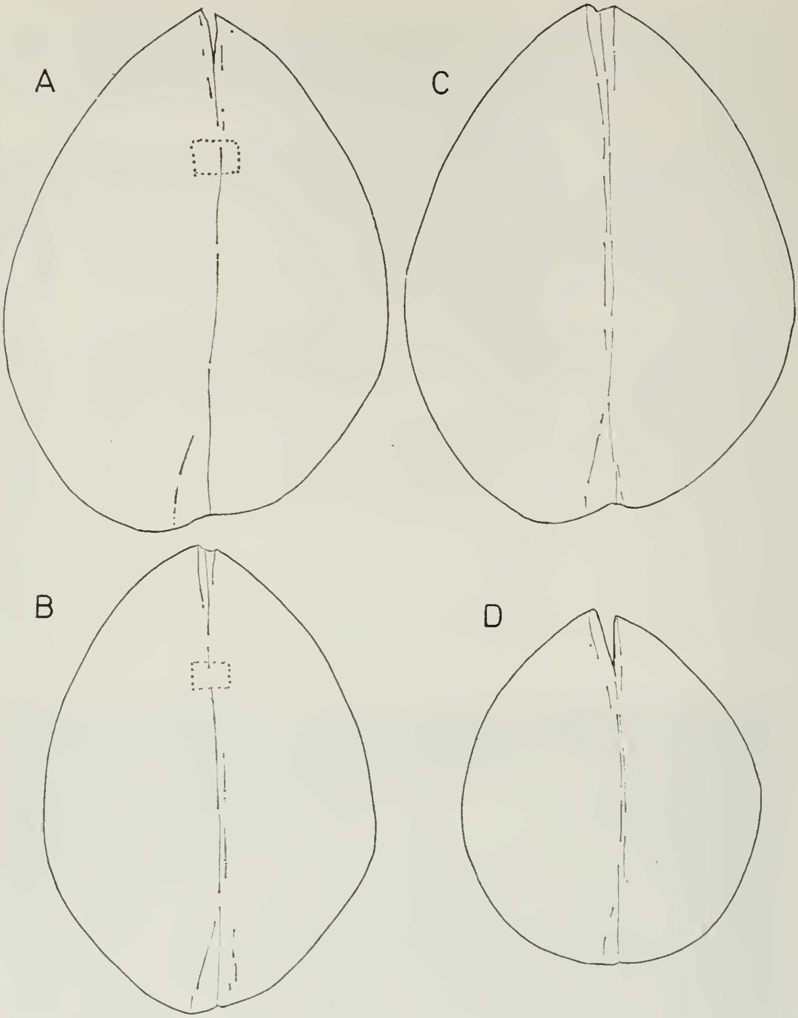
PARTICULARITÉS MORPHOLOGIQUES DES *ELPIDIUM* DE CUBA

Les trois nouvelles espèces d'*Elpidium* possèdent quelques traits morphologiques communs tout à fat remarquables, qui sont probablement des caractères génériques: la charnière est faiblement développée, l'antennule possède une bosse antérieure sur le premier article, l'antenne a un dimorphisme de griffes endopodiales distales ainsi qu'une chétotaxie très spéciale (voir pour plus de détails, la figure 3). Le palpe mandibulaire possède un poil distal bifide. L'organe copulateur mâle a un flagelle placé sur la face externe d'un lobe A, large, le crochet accessoire petit et fort entre le manchon placé à l'extérieur de la gaine pénienne. Le complexe copulateur placé sur la face ventrale est orienté en position normale avec le lobe A vers l'avant et le manchon et le crochet du côté médial (Figure 4). Le squelette interpénien possède une pièce *interzygum* tout à fait spéciale par rapport à ce qu'on connaît chez les autres groupes de Cythéracés.



Text-fig. 2. *Elpidium,* n. sp. A ♀, valve gauche (photo prise au SEM par Fr. Saffon, S.N.P.A., Pau). (Dimensions in text.)

Text-fig. 3. A-D, *Elpidium*, n. sp. A (exemplaires de Gran Piedra). A-C, détails de l'antenne. A, B, chétotaxie distale de l'endopodite. A, femelle. B, mâle. C, région proximale de l'exopodite. D, poil distal du palpe mandibulairé, mâle. E, F, *Elpidium*, n. sp. B, détails de l'antenne, mâle. E, chétótaxie distale du l'endopodite. F, région proximale de l'exopodite (Ga, Gm, Cp — griffes distales; e — poil vestigial; hy — formation hyaline ressemblant à un aesthétasc; Ps — poil simple; bex — base de l'exopodite).

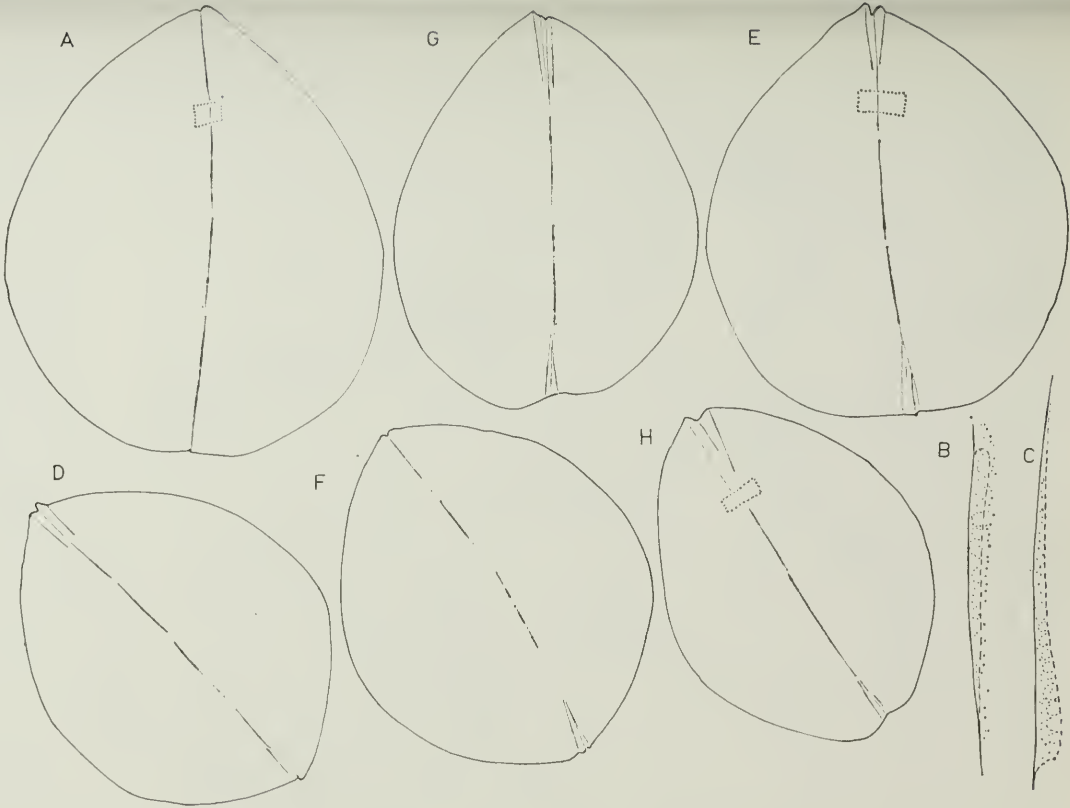


Text-fig. 4. Coquilles d'*Elpidium* en vue dorsale. A-C, *E*. n. sp. A (exemplaires de Grant Piedra). A, femelle sans oeufs. C, femelle ovigère. B, mâle. D, *E. bromeliarum* F. Müll., femelle (d'après Pinto et Purper, 1970). (Dimensions in text.)

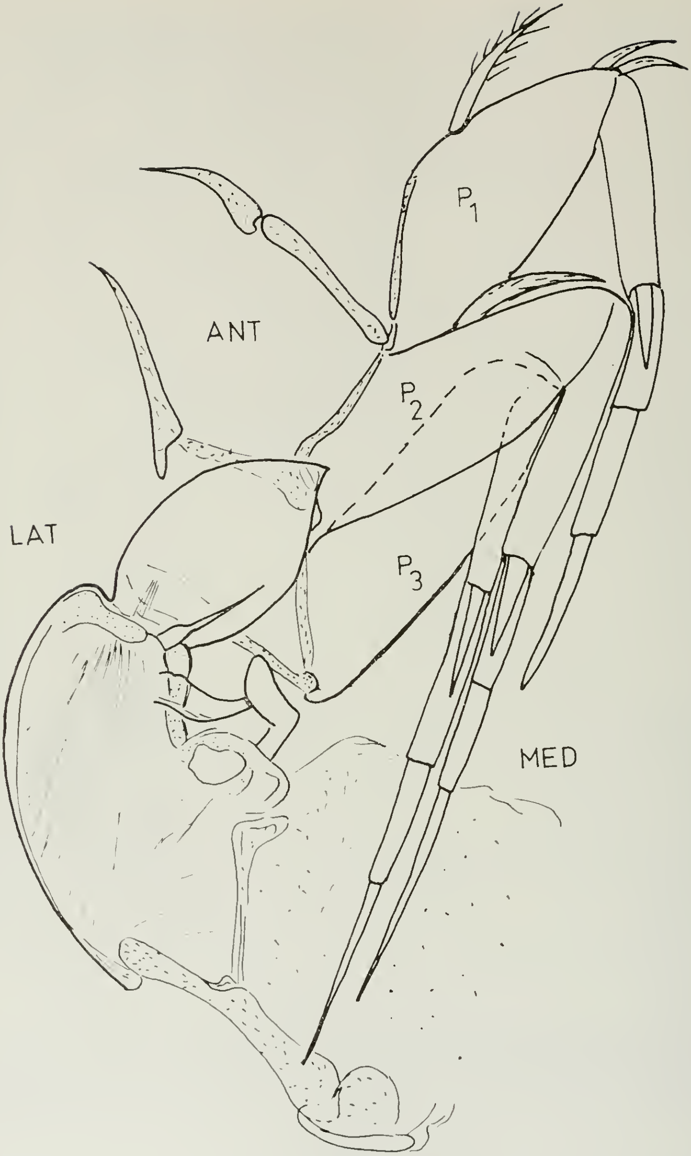
SYSTEMATIQUE

Elpidium, n. sp. A Text-figs. 2, 3 A-D, 4 A-C, 5 G, H, 7A, B

La femelle possède une coquille qui, en vue dorsale (Text-figs. 4, A, C et 5, G), est ovoïde allongée. Elle a la largeur maximale, un peu en arrière de la moitié de la longueur et représente 0.80 de la longueur de la valve gauche.



Text-fig. 5. Coquilles d'*Elpidium* en vue dorsale. A-D, *E.*, n. sp. C. A, **femelle.** B, C, fossettes antérieure et postérieure de la charnière de la valve droite femelle. D, mâle. E, F-E., n. sp. B. E, femelle. F, mâle. G, H, *E.*, n. sp. A (exemplaires de Rio Indio). G, femelle. H, mâle. (Dimensions in text.)



Text-fig. 6. *Elpidium,* n. sp. B, mâle. L'organe copulateur droit en position normale sur la partie postero-ventrale du corps (P1 — P3 — thoracopodes. LAT — côté latéral. MED — côté médial; ANT — antérieur).

L'extrémité antérieure de la coquille, pointue, tandis que celle postérieure est légèrement rétrécie. L'espace de la coquille utilisé comme cavité incubatrice est réduit. Par sa forme générale, la coquille femelle ressemble plutôt à un juvénile d'*Elpidium*. Seule la présence des oeufs dans le tiers postérieur de la coquille m'a donné la certitude qu'il s'agissait d'une femelle adulte. Les valves assymétriques; la valve gauche (Text-fig. 2) ayant une expansion postérieure qui n'existe pas chez la valve droite. Le repli de la valve gauche placé dans la région postéro-ventrale plus à l'intérieur. La valve droite recouverte par la valve gauche. La charnière possède des fossettes cardinales sur la valve gauche. Longueur valve gauche: 0.72 mm; valve droit: 0.69 mm; largeur de la coquille: 0.59 mm.

La coquille du mâle (Text-fig. 4, B et 5, H), plus petite que celle de la femelle, possède aussi des valves assymétriques. La valve gauche pourvue de l'expansion postérieure; elle est un peu moins évidente que celle de la femelle. Le tiers postérieur de la coquille en vue dorsale, aigu, ressemblant à celui antérieur.

La largeur maximale placée un peu en arrière de la moitié de la longueur; elle représente 0.73 de la longueur de la valve gauche. La charnière ayant des fossettes cardinales sur la valve gauche. Longueur: valve gauche: 0.66 mm; valve droite: 0.64 mm; largeur de la coquille: 0.49 mm (1).

L'organe copulateur mâle (Text-fig. 7, A, B), massif, posséde un lobe A lamellaire pointu; le bord latéral du lobe A presque droit, le bord médial oblique par rapport au bord latéral. Le bord médial forme une excroissance digitiforme un peu en arrière de la moitié de la longueur du lobe; la moitié proximale de ce bord est sclérifiée. La position du lobe A est modifiée par le muscle M3. Dans la position normale, en repos, le lobe A forme un angle avec le corps pénien, du côté de la face dorsale. Le flagelle, inséré dans l'angle médial formé par le corps pénien et le lobe A, siège normalement sur la face externe de ce dernier. Le flagelle est un poil glabre qui atteint la moitié de la longueur du lobe A.

Le crochet accessoire, court, est massif et très coudé. La portion proximale en forme de plaque sclérifiée est englobée dans le corps pénien s'articulant à des rainures sclérifiées r1, r2. La portion distale du crochet, légèrement creuse sur la face interne, possède une protubérence saillante du côté central. Le bord distal du crochet largement arrondi. Le crochet accessoire est déplacé grâce à l'action du muscle M2. Le tube éjaculateur entre dans le corps pénien par un orifice O placé près de la base de la rainure r1. La première portion membraneuse est à peine visible; après avoir fait un coude, il entre dans le manchon étant colé à la parois interne du côté distal. Le manchon est externe et mobile par rapport au corps pénien, étant déplacé par le muscle M1. Le manchon sclérifié est en forme d'entonnoir sygmoïde. L'orifice du manchon fortement oblique (voir la Text-figure 7 B).

Elpidium, n. sp. B Text-figs. 3 E, F, 5 E, F, 6, 8 A-C

La femelle possède une coquille qui en vue dorsale (Text-fig. 5, E) est ovoïde. La largeur maximale, placée à la moitié de la longueur, représente environ 0.87 de la longueur de la valve gauche. L'extrémité antérieure de la coquille pointue, tandis que celle postérieure est largement arrondie. Les valves presque symétriques: celle gauche recouvre la droite. Les fossettes de la charnière placée sur la valve gauche. Longueur valve gauche: 0.75 mm, valve droite: 0.74 mm; largeur de la coquille: 0.65 mm.

---

(1) Tenant compte de la figure de Tressler (1956), *Metacypris bromeliarum* citée à la Jamaïque pourrait être *Elpidium*, n. sp. A. La coquille femelle de la forme jamaïquaine en vue dorsale ressemble beaucoup à celle décrite ci-dessus.

Text-fig. 7. Organe copulateur, mâle. A, B, *E.*, n. sp. A (Gran Piedra). A, vue générale de la partie droite, face dorsale (ou interne); B, détail, de la face ventrale (ou externe). C-D, *E. bromeliarum* F. Müll. le lobe A. C, d'après F. Müller, 1881. D, d'après Pinto et Purper, 1790 (LA — le lobe A; M1 — M3 — muscles érecteurs intrapéniens. CA, crochet accessoire; r, r2 —rainures sclérifiées supportant les insertions musculaires; ma — manchon; O — orifice proximal du tube éjaculateur; tep — tube éjaculateur, région proximale; ted — tube éjaculateur, région distale; Fl — flagelle; Pr — protubérance; Izy — interzygum; Zy — zygum; st — sterynx; tro — tropis; Fu — lobe furcal)).

La coquille du mâle (Text-fig. 5, 6), plus petite que celle de la femelle, possède aussi des valves presque symétriques. Le tiers postérieur de la coquille, en vue dorsale, pointu. La largeur maximale placée vers la moitié de la longueur; elle représente 0.83 de la valve gauche. Longueur valve gauche: 0.67 mm, valve droite: 0.66 mm, largeur de la coquille: 0.56 mm.

L'organe copulateur mâle (Text-fig. 8, A, B, C) possède un lobe A lamellaire pointu distalement.

Le bord latéral de ce lobe est légèrement courbé tandis que le bord médial est presque droit. Le flagelle ressemble à celui des espèces d'Elpidium déjà décrites. Le crochet accessoire possède une portion proximale sclérifée moins large que celle de *E.*, n. sp. A. La partie distale du crochet accessoire est creuse, dépourvue de protubérance centrale. La parois de la cavité de ce crochet du côté distal possède quelques striations. Quatre points (des faibles protubérances ?) sont visibles près du bord de cette cavité. Le manchon, mobile, coudé, a l'orifice distal presque circulaire.

Elpidium, n. sp. C Text-figs. 5 A-D, 8 D

La femelle possède une coquille qui en vue dorsale (Text-fig. 5, A) est ovoïde. La largeur maximale à l'arrière de la moitié de la longueur représente environ 0.75 de la longueur. L'extrémité antérieure de la coquille pointue, tandis que celle postérieure est arrondie (elle est moins large que celle de *E.*, n. sp. B). Les valves presque symétriques: la valve droite recourvre la valve gauche. Les fossettes de la charnière sont placées sur la valve droite. (Text-fig. 5, B, C). Longueur valve gauche: 0.80 mm, valve droit: 0.81 mm; largeur de la coquille: 0.68 mm.

La coquille du mâle (Text-fig. 5, D) bien plus petite que celle de la femelle. Le dimorphisme de la taille très marqué par rapport à celui des deux autres espèces déjà décrites ci-dessus.

Les valves sont presque symétriques. Le tiers postérieur pointu. La largeur maximale placée vers la moitié de la longueur représente 0.8 de la longueur. Les fossettes cardinales placées sur la valve droite. Cette dernière recouvre la valve gauche. Longueur valve droite: 0.68 mm, valve gauche: 0.67 mm; largeur de la coquille: 0.54 mm.

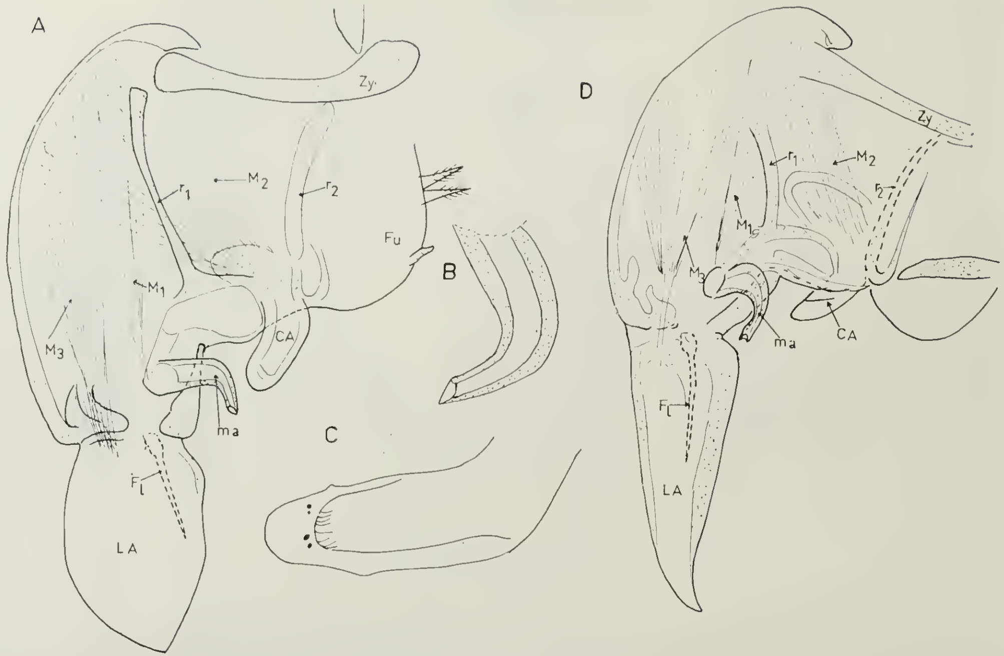
L'organe copulateur (Text-fig. 8, D) possède un lobe A long élancé, fortement angulaire. Le bord latéral de ce lobe droit; le bord médial, légèrement oblique, plus sclérifié que le bord opposé, a une dépression du côtê distal. Le flagelle tout à fait semblable à ceux déjà décrits. Le crochet accessoire du côté distal ayant une dépression sur la face interne, l'extrémité distale du crochet aigue. Le manchon ayant un orifice presque circulaire.

SUR LES STRUCTURES MORPHOLOGIQUES QUI POURRAIENT ASSURER UN ISOLEMENT SEXUEL CHEZ *ELPIDIUM*

Les trois nouvelles espèces d'*Elpidium* de Cuba ainsi que *E. bromeliarum* F. Müller (2) diffèrent essentiellement par les détails de l'organe copulateur mâle et en moindre mesure par les détails des valves.

---

(2) Je rappellerai que *Elpidium bromeliarum* redécrit récemment par Pinto et Purper (1970) d'après des exemplaires de Itajai (Brésil) possède les caractéristiques suivantes: coquille forte taille; 0.96 mm, longueur de la femelle et 0.84 mm le mâle. Le tiers postérieur de la coquille (Text-fig. 4, D) largement arrondi. Les fossettes cardinales placées sur la valve gauche. Le lobe A (Text-fig. 7, D) d'après Pinto et Purper (1970) est largement arrondi et présente du côté médial, près de l'extrémité distale, une expansion conique descendante. D'après F. Müller (1881), le lobe A (Text-fig. 7, C) est plus pointu et l'expansion conique est placée plus haut sur le bord médial.



Text-fig. 8. Organe copulateur mâle. A-C, *E.*, n. sp. B; A, vue générale de la partie droit. B, manchon, détail. CA — crochet accessoire détail. D, *E.*, n. sp. C, vue générale de la partie droite.

En revenant à l'organe copulateur mâle, on remarquera que les pièces qui revêtent les formes les plus diverses sont le lobe A et le crochet accessoire. Par contre, le flagelle est semblable chez toutes les quatres espèces d'*Elpidium.*

En regardant l'organe copulateur en position de repos (Text-fig. 6), sur l'animal, on aperçoit qu'il est placé d'une manière postero-ventrale et un peu latérale par rapport à l'axe longitudinal du corps, avec le lobe A orienté vers l'avant, ce qui fait que durant l'érection, il n'a pas besoin de faire une rotation de 180° comme celà se produit pour les Entocytheridae (Hart et Hart, 1969). Pendant l'accouplement, le manchon se fixe probablement dans la capsule génitale femelle. La forme du manchon est semblable chez *E. bromeliarum, E.,* n. sp. B et *E.,* n. sp. C. Elle diffère considérablement chez *E.,* n. sp. A. Le crochet accessoire placé dans le voisinage du manchon pourrait avoir, non seulement un rôle fixateur, mais aussi un rôle sensoriel comme chez les Entocytheridae. Celà expliquerait les formes diverses de l'extrémité distale sur la face interne de cette pièce.

Le lobe A, lamellaire, a une position très avancée par rapport au manchon; il doit venir en contact avec la face médiale de la carapace de la femelle, jouant ainsi un rôle tactile. Il pourrait assurer l'isolement sexuel interspécifique. Le flagelle qui est placé sur la face ventrale (ou face externe) de l'organe copulateur ne peut pas venir en contact direct avec le corps de la femelle. Or, fait intéressant, cette pièce est semblable chez tout les *Elpidium* connus. Par contre, chez les Entocytheridae (voir, par exemple, les Sphaeromicolini), le flagelle qui vient souvent en contact avec le femelle revêt des formes variées.

La diversification des valves des trois nouvelles espèces décrites ici est bien plus discrète que celle de l'organe copulateur. Par rapport aux caractères morphologiques différentiels des appendices qui se retrouvent seulement chez le mâle, les caractères différentiels propres à la carapace sont présents chez les deux sexes. Les tailles différentes des carapaces des trois espèces d'*Elpidium* de Cuba pourraient jouer un rôle dans l'isolement sexuel.

Il est à remarquer que la région distale antennaire du mâle, présentant un fort dimorphisme de la griffe G1 (voir Text-fig. 3) et jouant très probablement un rôle important dans l'accouplement est semblable chez les trois nouvelles espèces.

Le principe de la diversification des *Elpidium* de Cuba se retrouve aussi dans le cas des *Candona* du groupe *neglectoïda.* J'ai souvent trouvé en Roumanie, dans les sources limnocrènes, des couples d'espèces de *Candona* appartenant à la lignée *neglectoïda* vivant parfaitement isolées du point de vue sexuel. Elles sont toujours reconnaissables d'après des détails de l'organe copulateur et d'après les particularités des valves (surtout des tailles différentes).

En étudiant *Candona aff. neglecta* Sars et *Candona fasciolata* Petk., j'ai remarqué (Danielopol, 1969) que ce sont les pièces de l'organe copulateur mâle qui diffèrent le plus chez ces deux espèces, c'est-à-dire la pièce M et le crochet de la bourse copulatrice. Les valves mâles et femelles diffèrent surtout par la taille; elles sont beaucoup plus grandes chez *C. fasciolata* que chez *C. aff. neglecta.* J'ai observé que la pièce M, par sa forme et par sa position, joue un rôle sensoriel important. Or, c'est justement cette pièce qui revêt les formes les plus diverses parmi les Candoninae. Par contre, les caractères sexuels secondaires mâles, de même que les poils antennaires et les palpes prèhensiles du P1 sont semblables.

CONCLUSIONS

Dans le cas des *Elpidium* de Cuba, comme dans le cas des *Candona* du groupe *neglectoïda,* parmi tout les caractères, morphologiques, les pièces de l'organe copulateur mâle ayant un rôle sensoriel se diversifient le plus; elles pourraient assurer l'isolement sexuel interspécifique.

Les *Elpidium* examinés possèdent des caractères différentiels interspécifiques de la carapace qui sont présents tout aussi bien chez les mâles que chez les femelles.

Les tailles différentes des carapaces pourraient influencer l'isolement sexuel interspécifique.

On doit souligner, pour finir, que la diversification de l'organe copulateur mâle va de paire avec la diversification de la carapace chez les *Elpidium* présentés ci-dessus.

BIBLIOGRAPHIE

Danielopol, D. L.

1969. *Recherches sur la morphologie de l'organe copulateur mâle chez quelques ostracodes du genre Candona Baird (Fam. Cyprididae Baird).* In J. W. Neale ed.: *The Taxonomy, Morphology and Ecology of Recent Ostracoda,* pp. 138-153, Oliver & Boyd, Edinburgh.

Hart, C. V., and Hart, D.

1969. *The functional morphology of entocytherid copulatory appendages with a discussion of possible homologues in other ostracods.* In J. W. Neale ed.: *The Taxonomy, Morphology and Ecology of Recent Ostracoda,* pp. 154-167.

Müller, F.

1880. *Wasserthiere in Baumwipfeln Elpidium bromelarium.* Kosmos, 6, pp. 386-388.

1881. *Descripçao do Elpidium bromelarium crustaceo da familia dos Cytherideos.* Archivos do Museo Nacional, Rio de Janeiro, 4, pp. 27-34 (Apud. Pinto et Purper, 1970).

Pinto, I. D., and Purper, I.

1970. *A neotype for Elpidium bromelarium Müller, 1880, (type species for the genus) and a revision of the genus Elpidium (Ostracoda).* Esc. Geol. P. Alegre, Publ. Esp., 19, pp. 1-25.

Tressler, W.

1956. *Ostracoda from bromeliads in Jamaica and Florida.* Jour. Washington Acad. Sc., 46, 10, pp. 333-336.

Dan L. Danielopol
Limnologisches Institut
Berggasse 18
1090 Wien
Austria

SPECIES DETERMINATION OF MOLTS FROM THE SHUBUTA CLAY OF MISSISSIPPI

ROBERT C. HOWE AND HERBERT J. HOWE
Indiana State University; Purdue University

ABSTRACT

The Shubuta Clay (upper Eocene or lower Oligocene) of southeastern Mississippi yields a diverse and exceptionally well-preserved fauna of ostracodes and nannofossils. Recovery of more than 14,000 ostracodes provided abundant material for study of juveniles as well as adults. Of the 39 taxa recognized, seven yielded no immature specimens. Recognition of juveniles was accomplished in several ways, namely: 1) by morphologic comparisons (for example, surface ornamentation, valve outlines, and marginal denticulations); 2) by correlating occurrences and abundances of juveniles with the occurrences and abundances of adults; and 3) by statistical analysis of growth series using the parameters of length and height.

The juveniles of *Acanthocythereis howei* Huff, 1970 differ markedly from the adult form, but correlation is suggested by their similar occurrences and abundances. Statistical analyses of allometric growth series and studies of occurrence and abundance indicate that *"Archicythereis" yazooensis* Howe, 1936 is the juvenile of *Trachyleberis? montgomeryensis* (Howe and Chambers, 1935). Six juvenile forms can be assigned generically but not specifically. These include members belonging to the genera *Buntonia, Haplocytheridea,* and two species of the genus *Cytherella.* Bartlett's (1949) best fit method is well suited for bivariate analysis of A-1, A-2, and A-3 growth stages.

ZUSAMMENFASSUNG

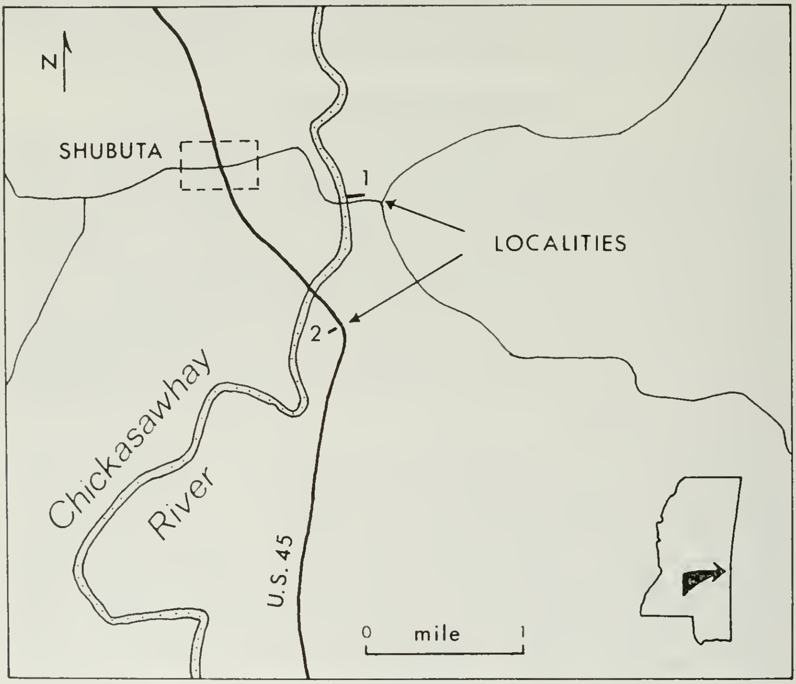
Der Shubuta Lehm (oberes Eozän oder unteres Oligozän) des südöstlichen Mississippi ergibt eine mannigfaltige und aussergewöhnlich gut erhaltene Fauna von Muschelkrebsen (Ordnung Ostracoda) und zwergartigen Fossilien. Die Auffindung von mehr als 14,000 Muschelkrebsen liefert eine Fülle von Material, das für das Studium von Jungtieren sowohl als auch erwachsenen Tieren geeignet ist. Bei sieben von den 39 taxonomischen Gruppen, die erkannt wurden, fehlte die Abstreifungserscheinung. Die Erkennung von Jungtieren wurde auf verschiedene Weisen durchgeführt, nämlich: 1) durch morphologische Vergleiche (zum Beispiel Oberflächenverzierung, Klappenumrisse und Zähnelung des Randes); 2) durch die Aufeinanderbeziehung des Vorkommens und der Fülle von Jungtieren einerseits mit dem Vorkommen und der Fülle von erwachsenen andererseits; und 3) durch statistische Analyse der Wachstumsreihenfolge, bei der die Parameter von Länge und Höhe benutzt wurden.

Die Jungtiere von *Acanthocythereis howei* Huff, 1970 unterscheiden sich ausgesprochen von der erwachsenen Form, aber eine Aufeinanderbeziehung wird nahegelegt durch Vorkommen und Fülle. Das statistische Studium von allometrischen Wachstumsreihenfolgen und Studien von Vorkommen und Fülle lassen darauf schliessen, dass *"Archicythereis" yazooensis* das Jungtier von *Trachyleberis ? montgomeryensis* (Howe und Chambers) ist. Sechs Jungtierformen können generisch aber nicht spezifisch bestimmt werden. Diese Formen schliessen Zugehörige zu den Gattungen *Buntonia, Haplocytheridea* und zwei Arten der Gattung *Cytherella* ein. Die am besten passende Methode von Bartlett (1949) eignet sich gut für die bivariate Analyse von A-1, A-2 und A-3 Wachstumsstadien.

INTRODUCTION

More than 14,000 ostracodes were recovered from samples of the Shubuta Clay taken at and near the type locality along the west half of the boundary between sections 3 and 10, T. 10 N., R. 7 W., across the Chickasawhay River from the town of Shubuta in southeastern Mississippi (Text-figure 1). The samples were collected at approximately five foot intervals and labelled with their equivalent elevation at the type locality (Text-figure 2). Samples 175, 180, 186, 192, 200, 205, 210, 215, 220, and 230 were collected from Locality 1 whereas samples 237, 240, 250, 255, and 260 were taken at Locality 2. Sample analyses included species identification (both adult and juvenile), tabulation of occurrence-abundance data, and biometrical studies. All illustrated specimens are deposited in the Henry V. Howe collection (HVH) at Louisiana State University.

Thirty-nine species were recognized in this exceptionally well-preserved fauna of ostracodes (Howe and Howe, 1973). During this taxonomic study we encountered varying degrees of difficulty in assigning juvenile forms to their adult counterparts. Seven species lacked juvenile representation. Of the 32 juvenile forms recognized, 21 were relatively easy to assign specifically. The purpose of this paper is to present ways in which the remaining 11 species were identified.

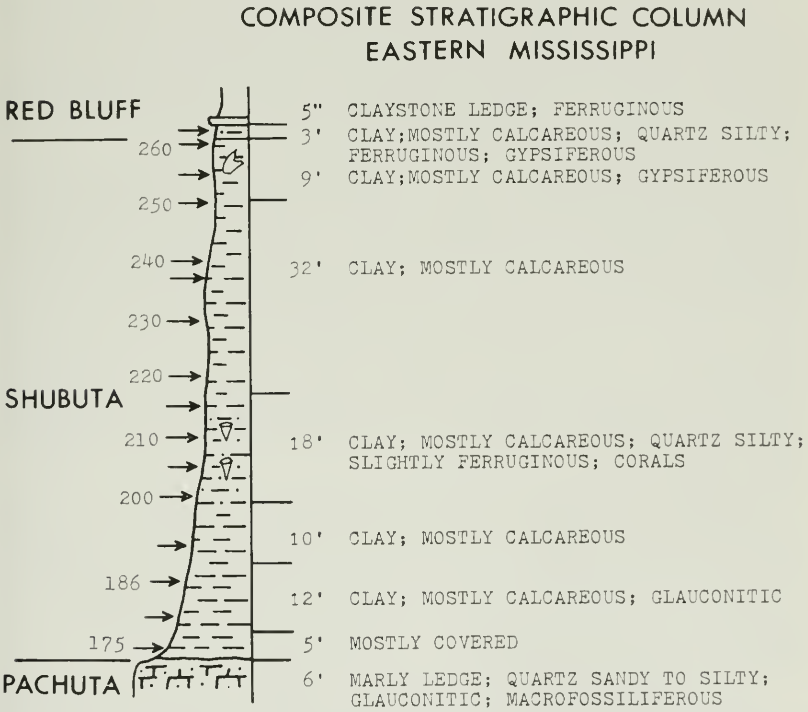


Text-figure 1. Map showing locations of sections of the Shubuta Clay collected for this paper. Locality 1 is the type locality of the Shubuta Clay.

PREVIOUS WORK

Kesling (1951, 1952, 1953) presented many of the problems associated with species recognition of instars. Several ontogenetic studies have been made (for example, Spjeldnaes, 1951; Martinsson, 1957, 1962; Hartmann, 1961; Sandberg, 1964; Sohn and Anderson, 1964). These and other papers have discussed the ontogeny of valve outline, surface ornamentation, hingement, muscle scars, marginal features, and normal pore canals; however, most papers utilizing data on immature instars have been biometrical in nature.

Fowler (1909) used the work of Brooks (1886) in determining growth factors for living ostracodes and stated that each stage increased by a fixed percentage of its length approximately constant for its species and sex. This statement he named "Brook's Law." In spite of Fowler's growth factors ranging from 1.26 to 1.78, Przibram (1931) used a growth factor of 1.26 for all arthropods assuming that mass is doubled at each molt, 1.26 being the cube root of



Text-figure 2. Composite measured section of the Shubuta Clay determined from localities near Shubuta, Mississippi. Arrows point to sampled horizons, the lowermost arrow corresponding to an elevation of 175 feet.

2.0. Kesling (1953) devised a circular slide rule based on the assumed 1.26 growth factor. Later work showed that the growth factor of a particular species is not necessarily constant and that ostracodes have a wide range of growth rates (Anderson, 1964; Sohn and Anderson, 1964). Anderson formulated a growth law which assumed that the length-height ratio could be altered by a constant value operating uniformly with each stage of molting. This was not indicated by data from Sandberg (1964) which supported the suggestion by Reyment (1960) that the growth relationship between length and height in ostracodes is allometric during the early instars but may tend toward isometry in later ones. This is further complicated by the fact that in the final two growth stages, allometric growth may again ensue during the attainment of greater length by male ostracodes (Reyment, 1960). Several multivariate analyses of ostracode data have also been presented including those of Reyment (1963, 1969).

EASE OF RECOGNITION

Twenty-one of the 32 types of immature forms found in the Shubuta Clay samples are easy to match with their adult counterparts. *Digmocythere russelli* (Howe and Lea, 1936) exemplifies this group (Pl. 1, figs. 1, 2). Many of these forms have easily distinguished morphological features, such as well-developed alae, that are present in the juveniles as well as the mature forms. Most are easy to sort on the basis of the valve outline alone.

Due to morphological similarity within three sets of molts, seven kinds of juveniles in the Shubuta Clay are more difficult to assign specifically. This category of recognition is illustrated by the similarity among the immature forms of *Acanthocythereis multispicata* Howe and Howe, 1973, *Acanthocythereis spinomuralis* Howe and Howe, 1973, and *Henryhowella florienensis* (Howe and Chambers, 1935) (Pl. 1, figs. 3-8). Without the aid of a scanning electron microscope, these juveniles are almost indistinguishable. Immature forms of *Haplocytheridea ehlersi* (Howe and Stephenson, 1935) and *Haplocytheridea montgomeryensis* (Howe and Chambers, 1935) are also very much alike. Juveniles belonging to two species of the genus *Cytherella* are difficult to match with the mature forms due to the lack of morphological distinctness among them.

Even more difficulty is encountered when trying to separate the juveniles belonging to the genus *Buntonia*. Juveniles of *Buntonia levinsoni* Huff, 1970, and *Buntonia shubutaensis* Howe, 1935, lack the markedly different ornamentation characteristic of the adult forms (Pl. 1, figs. 11-13). Size differences do not appear to be detectable even though *B. levinsoni* is slightly more elongate as an adult; consequently, juveniles of these species remain grouped on our slides.

The remaining two juvenile forms (Pl. 1, figs. 10, 14) are very difficult to assign specifically because they differ morphologically from the remaining nine adult forms. They are placed in *Trachyleberis? montgomeryensis* (Howe and Chambers, 1935) (Pl. 1, fig. 9) and *Acanthocythereis howei* Huff, 1970 (Pl. 1, fig. 15), respectively, on the basis of observations and results of techniques discussed in the following section.

SPECIES DETERMINATION TECHNIQUES

A number of morphological features permit identification of 21 juvenile representatives in the Shubuta Clay. Foremost of these is the valve outline. Obvious examples are *Digmocythere russelli* (Howe and Lea, 1936), *Paracypris media* Howe and Howe, 1973, and *Bythocypris? gibsonensis* Howe and Chambers, 1935. In contrast, species belonging to the Trachyleberidinae do not have diagnostic valve outlines. For example, all species belonging to the genera *Acanthocythereis, Actinocythereis, Trachyleberis?*, and *Henryhowella* have the same general outline (Pl. 1, figs. 3-10, 14-16).

Surface ornamentation is another discriminatory feature. *Digmocythere russelli* has a distinctive valve outline; however, a strong ventral ala is its most diagnostic feature (Pl. 1, figs. 1, 2). *Alatacythere ivani* Howe, 1951, and *Pterygocythere murrayi* Hill, 1954, have similar surface features that are present in the immature forms. There are molts that have a similar surface ornamentation to those of the adult forms, for example, *Ouachitaia caldwellensis* (Howe and Chambers, 1935) and *Echinocythereis jacksonensis* (Howe and Pyeatt, 1935).

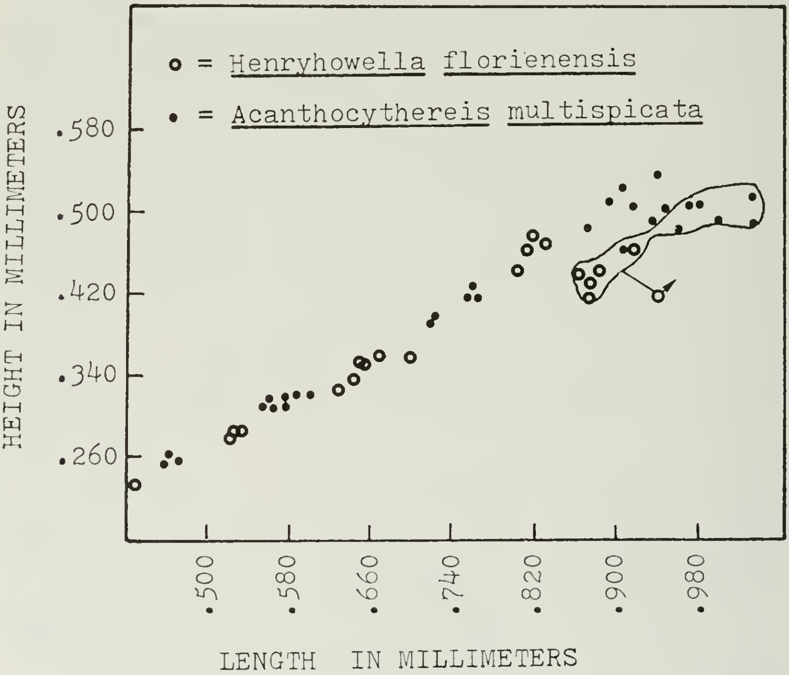
Other morphological features are less easy to use. Muscle scar patterns tend to be consistent from early larval stages through the adult; however, the patterns within the Trachyleberidinae are so similar from species to species that this is a difficult criterion to use. Moreover, muscle scar patterns are commonly more difficult to observe than the features mentioned above. Study of pore canals requires high magnification and the number of normal and radial pore canals tends to increase throughout ontogeny. A distinctive hinge structure sometimes occurs in early stages but hinge elements may be virtually identical in several kinds of immature forms such as in juveniles belonging to the Trachyleberideinae. Marginal denticulation is a fairly constant character in juveniles whose adult forms have this feature; too often, however, compaction has destroyed these distinguishing features.

Eleven juvenile forms in the Shubuta Clay lack obvious discriminatory features. Two species of the genus *Acanthocythereis* and one species of *Henryhowella* have juveniles which are nearly identical. Immature specimens of *Acanthocythereis spinomuralis* can be recognised under high power because they have characteristic subcircular fossae with tiny spines projecting inward from the muri. Molts of *A. multispicata* and *H. florienensis* are separable by plotting a scattergram of length versus height (Text-fig. 3). The largest juveniles are nearly as large as *H. florienensis;* consequently, they must be the last immature stage of *A. multispicata.*

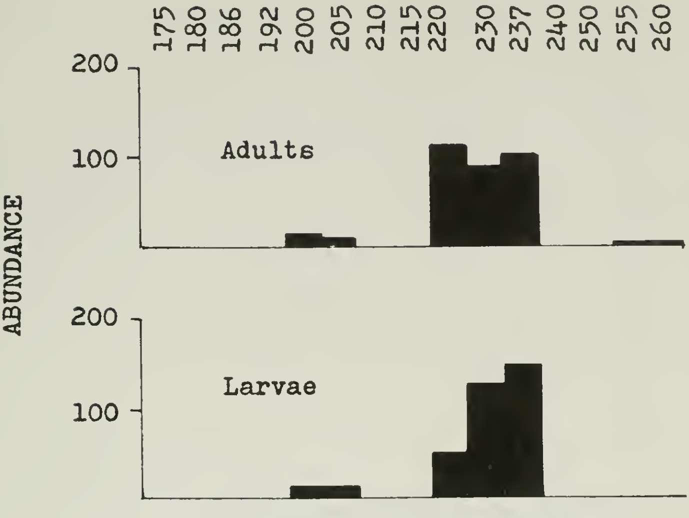
Six of the remaining eight kinds of juveniles can be assigned generically but not specifically. These include forms which belong to the genera *Buntonia* and *Haplocytheridea* and two species of the genus *Cytherella.* They have valve outlines characteristic of their genus, but lack specific characters.

The last two juvenile types appear to match with *Acanthocythereis howei* and *Trachyleberis? montgomeryensis,* respectively, on the basis of occurrence and abundance data (Text-fig. 4). In particular, immature forms assigned to

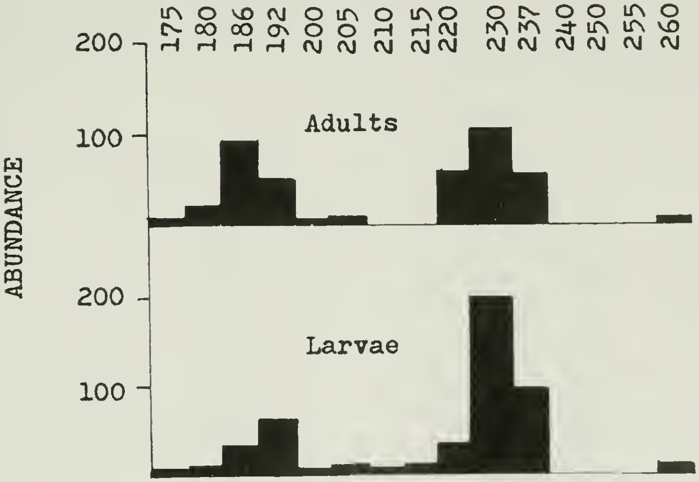
A. howei and the adults show an occurrence and abundance pattern that is unusual for species occurring in the Shubuta Clay. They are one of only two species that occur chiefly within the upper half of the type Shubuta section. For these reasons we group the two forms together in spite of their considerable morphological differences (Pl. 1, figs. 14, 15). A scattergram of length versus height further indicates that these juveniles are the precursors of the indicated adults (Text-fig. 5). Even greater morphological differences are noted between *Trachyleberis? montgomeryensis* and its assigned juveniles (Pl. 1, figs. 9, 10). Occurrence and abundance data for the immature individuals and adults is somewhat less conclusive than those for *A. howei;* consequently, the lengths and heights of these forms were measured and plotted on a scattergram. Due to breakage of spines, parameters were determined as shown in Text-figure 6. Because of allometric growth the measurements were logarithmically transformed. Designation of instars followed the system used by Christensen (1963).



Text-figure 3. Scattergram for length and height of *Henryhowella florienensis* and *Acanthocythereis multispicata*. Adult males delineated. All specimens collected at elevation 205 feet.

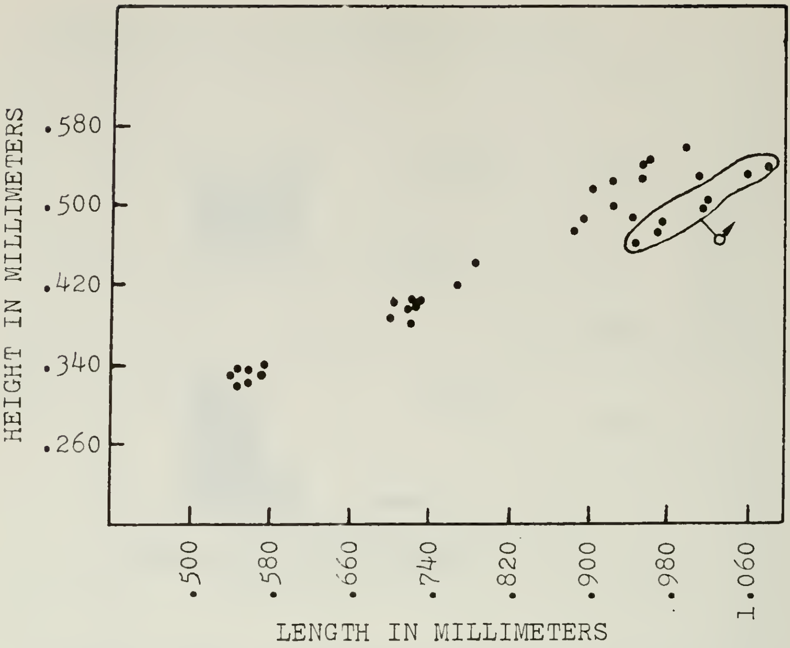


<u>Acanthocythereis howei</u>

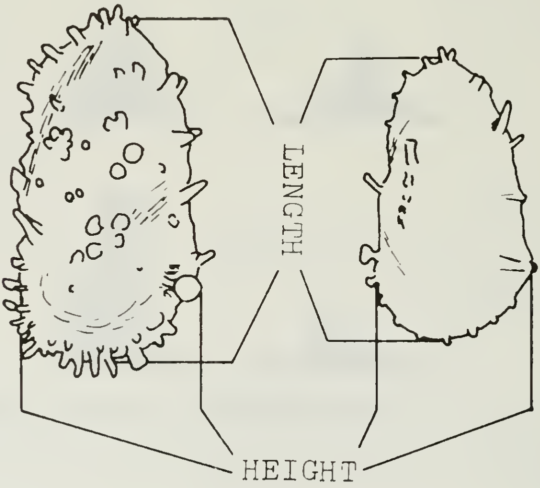


<u>Trachyleberis</u>? <u>montgomeryensis</u>

Text-figure 4. Occurrence and abundance diagram for adults of *Acanthocythereis howei* and *Trachyleberis? montgomeryensis* and the juveniles assigned to them.



Text-figure 5. Scattergram for length and height of *Acanthocythereis howei* and the juveniles grouped with them. Adult males delineated. All specimens collected from elevations 200 to 205 feet.



Text-figure 6. Diagram to illustrate how parameters of length and height were determined for statistical analysis.

In order to attempt to match the juveniles in question with the adults of *T? montgomeryensis,* Bartlett's (1949) "best fit" line was found using data for the A-1, A-2, and A-3 growth stages. A-4 molts were also present in the samples but their extremely fragile nature negated their use; besides, Bartlett's method required grouping data into three sets preferably of equal numbers of observations in ascending order of magnitude. At first, thirty specimens each of the A-1, A-2, and A-3 stages were randomly selected for statistical treatment; however, it soon became apparent that males could be distinguished within the A-1 population. The males are considerably more elongate than the females at this stage; therefore, for the A-1 data, presumed males were arbitrarily excluded.

If two log-transformed variables are related by a linear function, then the relationship between them may be expressed by a "best fit" line with the formula

$$Y = \alpha + \beta X$$

where α is the Y-intercept estimated by the expression

$$A = \overline{Y} - \beta \overline{X};$$

and β is the slope of the line estimated by

$$\beta = \frac{\overline{Y}_3 - \overline{Y}_1}{\overline{X}_3 - \overline{X}_1}$$

($\overline{X}$, $\overline{Y}$ equal means of the whole sample population; X_3, Y_3 equal means of the A-1 population; X_1, Y_1 equal means of the A-3 population.)

Statistical results are listed in Table 1. Text-figure 7 illustrates that the mean adult female of *T? montgomeryensis* clearly fits the prediction made possible by the "best fit" line whereas the mean adult female of *Actinocythereis purii* (Pl. 1, fig. 16), also considered to be possibly the adult form for this set of juveniles, is well off the line. As expected, the adult males of *T? montgomeryensis* plot well off the line. In conclusion, due to the availability of the A-1, A-2, and A-3 molt stages and due to the results of the "best fit" line method, we believe that the forms called *"Archicythereis" yazooensis* in the literature are in reality the immature representatives of *T? montgomeryensis.*

DIFFICULTIES ENCOUNTERED

Although the Shubuta Clay yielded a remarkable ostracode fauna in which most species displayed at least five growth stages, it does not seem possible to solve all the problems which arose in regard to identification of juveniles. A significant problem is to explain why seven species apparently show no immature forms. Reyment (1960, pp. 14-17) suggested that where a sediment contains only adults, perhaps they lived a different mode of life than the larvae. He further has stated that the adults may have been selectively transported; however, it seems unlikely that there was much transport prior to deposition in the case of the very fine-grained Shubuta Clay because more than 99 percent of the material is finer than one-sixteenth of a millimeter.

Another problem which causes concern is how to accurately measure the smallest larval stages. The adults, the A-1, the A-2, and usually the A-3 stages can be measured easily but the A-4 individuals are so small that accuracy of measurement is impaired. At higher magnification, errors are magnified.

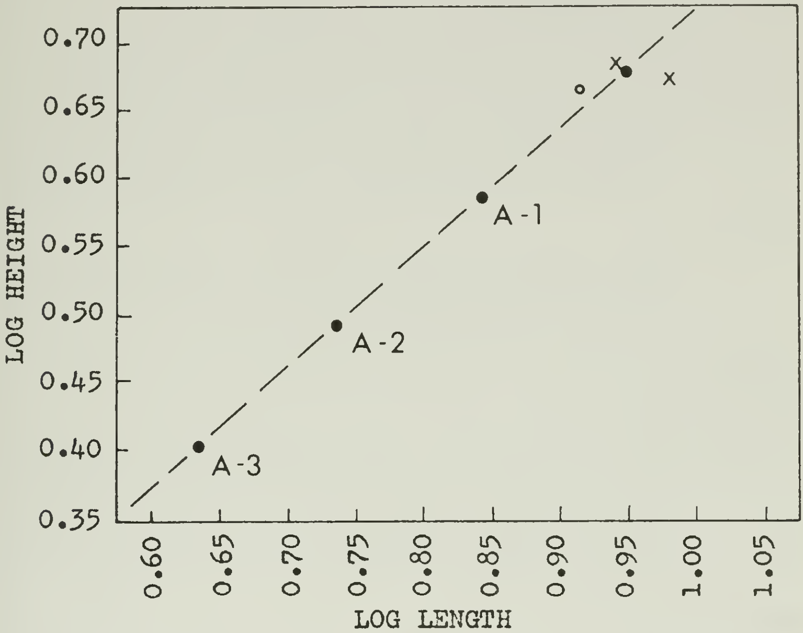
Table 1. Statistical results for *Trachyleberis*? *montgomeryensis*, molts assigned to that species, and *Actinocythereis purii*.

All specimens collected at elevation 192 feet.

Symbols follow those of Simpson, Roe, and Lewontin, 1960.

	X	S	O.R.
		MALES (N=22)	
Log Length	0.9822	0.0151	0.9474-1.0067
Log Height	0.6697	0.0158	0.6277-0.6962
		FEMALES (N=22)	
Log Length	0.9543	0.0132	0.9138-0.9705
Log Height	0.6872	0.0172	0.6539-0.7187
		A-1 (N=30)	
Log Length	0.8437	0.0115	0.8119-0.8606
Log Height	0.5850	0.0140	0.5543-0.6093
		A-2 (N=30)	
Log Length	0.7357	0.0128	0.7038-0.7621
Log Height	0.4938	0.0098	0.4851-0.5182
		A-3 (N=30)	
Log Length	0.6315	0.0147	0.6022-0.6539
Log Height	0.4018	0.0167	0.3795-0.4213
		Actinocythereis purii-FEMALES (N=16)	
Log Length	0.9185	0.0082	0.9079-0.9320
Log Height	0.6642	0.0188	0.6321-0.6865
		Data for Grouped A-1, A-2, and A-3 specimens	
	N=90	$S_x^2=17089$	
	K=30	$S_{xy}=12869$	
	B=0.863	$S_y^2=19144$	
	A=−0.1425	95% cl for=0.863±0.022	

The most difficult problem is how to separate juveniles which appear to be morphologically identical when there are obviously two species of adults present in the sample. Size analysis and higher magnification are possible solutions; otherwise, we are left with an unsolved problem as in the case of the juveniles of the genus *Buntonia*.



Text-figure 7. Plot of the means listed in Table 1 and the position of the mean of the final growth stage predicted by the "Best Fit" line — dashed. (● = means of molts assigned to *Trachyleberis? montgomeryensis* and mean predicted by statistical analysis; X = means of adult males and females of *T? montgomeryensis;* and, o = mean for females of *Actinocythereis purii*) Measurements are in mm.

REFERENCES

Anderson, F. W.
1964. *The law of ostracod growth.* Paleontology, vol. 7, pp. 85-104.

Bartlett, M. S.
1949. *Fitting a straight line when both variables are subject to error.* Biometrics, vol. 5, pp. 207-212.

Brooks, W. K.
1886. *Report on the Stomatopoda collected by H. M. S. Challenger during the years 1873-6.* Challenger Report, Zoology, vol. 16, pl. 2.

Christensen, O. B.
1963. *Ostracods from the Purbeck-Wealden beds in Bornholm.* Danmarks Geologiske Undersgelse, ser. 2, pp. 1-58.

Fowler, G. H.
1909. *The Ostracoda. Biscayan Plankton, Pt. 12.* Trans. Linn. Soc. Lond. (Zool.), vol. 10, pp. 219-336.

Hartmann, G.
1961. *Beitrag zur ontogenie des ostracoden-schlosses (mit beschreibung von 2 neuen arten).* Zeitschrift fur wissenschaftliche Zoologie, vol. 65, pp. 428-452.

Howe, R. C., and Howe, H. J.
1973. *Ostracodes from the Shubuta Clay (Tertiary) of Mississippi.* Jour. Paleont. vol. 47, No. 4, pp. 629-656, pls. 1-5.

Kesling R. V.
1951. *The morphology of ostracode molt stages.* Illinois Biol. Monograph, vol. 21, pp. 1-126.
1952. *Doubling in size of ostracode carapaces in each molt stage.* Jour. Paleont., vol. 26, pp. 772-780.
1953. *A slide rule for the determination of instars in ostracode species.* Contr. Mus. Geol. Univ. Mich., vol. 11, pp. 97-109.

Martinsson, A.
1957. *Ontogeny and development of dimorphism in some Silurian ostracodes: a study on the Mulde marl fauna of Gotland.* Bull. Geol. Instn. Univ. Uppsala, vol. 37, pp. 1-40.
1962. *Ostracodes of the family Beyrichiidae from the Silurian of Gotland.* Geol. Instn. Univ. Uppsala, Bull. 41, pp. 1-369.

Przibram, H.
1931. *Connecting laws of animal morphology.* University of London Press, 62 pp.

Reyment, R. A.
1960. *Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 1. Senonian and Maestrichtian Ostracoda.* Stockholm Contr. Geol., vol. 7, pp. 1-238.
1963. *Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 2. Danian, Paleocene, and Eocene Ostracoda.* Stockholm Contr. Geol., vol. 10, pp. 1-286.
1969. *A multivariate paleontological growth problem.* Biometrics, vol. 25, pp. 1-8.

Sandberg, P. A.
1964. *The ostracode genus Cyprideis in the Americas.* Stockholm Contr. Geol., vol. 12, 178 pp.

Simpson, G. G., Roe, A., and Lewontin, R. C.
1960. *Quantitative Zoology.* Harcourt, Brace, and World, Inc., New York.

Sohn, I. G., and Anderson, F. W.
1964. *The ontogeny of Theriosynoecum fittoni* (Mantell). Palaeontology, vol. 7, pp. 72-84.

Spjeldnaes, N.
1951. *Ontogeny of Beyrichia jonesi Boll.* Jour. Paleont., vol. 25, pp. 745-755.

Robert C. Howe
Department of Geography and Geology
Indiana State University
Terre Haute, Indiana 47809
U.S.A.

Herbert J. Howe,
Department of Geosciences
Purdue University
Lafayette, Indiana 47907
U.S.A.

DISCUSSION

Dr. A. Liebau: You have studied well ornamented forms. I have observed that the ornament changes in the ontogenies of such species follow certain rules. As an example, variation in the mesh configuration of instars is often followed by place constance in the reticulation of adults, while a contrary development seems to be impossible. I hope that I can touch upon these ornament relationships in my paper.

Dr. H. Uffenorde: Did you observe any sign of bioturbation in the Shubuta Clay sequence? At least in neritic environments of low energy level, bioturbation seems to be of some importance in destroying much of the more fragile shell material. Evidently bioturbation causes pre-diagenetic changes in faunal composition. This seems to be true also with regard to the relation between the abundance of adults and juveniles.

Dr. I. G. Sohn: The first slide showed the abundance of adults and juveniles. There should be more juveniles than adults if it is an actual population sample.

Dr. H. J. Howe: The discrepancy is probably due to selective preservation. The A-3, A-4, and A-5 molts in particular are very fragile and can be easily broken during clay compaction. Selective sorting may be a partial factor; however the wide variations in size observed in the Shubuta specimens do not indicate that sorting removed the smaller specimens to any significant degree. In the case of *Acanthocythereis howei* and *Trachyleberis? montgomeryensis,* occurrence and abundance data and scatter diagrams of growth demonstrate the correctness of the molt assignments that we have made. Several hundred specimens, representing both species, were gleaned from the samples making them among the most abundant elements in the Shubuta Clay.

Dr. J. Hazel: The species *montgomeryensis* is not a *Trachyleberis,* in my opinion.

Dr. H. J. Howe: There is a question regarding the generic assignment of *Trachyleberis? montgomeryensis.* The evidence presented here shows that the form identified as *"Archicythereis" yazooensis* in the literature is actually the molt of *Trachyleberis? montgomeryensis.* The generic assignment of the species is provisional pending revision of the genus *Trachyleberis* and other trachyleberid genera.

EXPLANATION OF PLATE 1

(All illustrations approximately ×50)

Figure

1, 2. **Digmocythere russelli** (Howe and Lea)
1. Right valve, HVH 9333, from elevation 180 feet.
2. Juvenile right valve, HVH 9759, from elevation 175 feet.

3, 4. **Acanthocythereis multispicata** Howe and Howe
3. Female right valve, HVH 9376, from elevation 237 feet.
4. Juvenile right valve, HVH 9379, from elevation 220 feet.

5, 6. **Acanthocythereis spinomuralis** Howe and Howe
5. Juvenile right valve, HVH 9760, from elevation 180 feet.
6. Female right valve, HVH 9380, from elevation 180 feet.

7, 8. **Henryhowella florienensis** (Howe and Chambers)
7. Female right valve, HVH 9399, from elevation 237 feet.
8. Juvenile right valve, HVH 9761, from elevation 192 feet.

9, 10. **Trachyleberis? montgomeryensis** (Howe and Chambers)
9. Female right valve, HVH 9360, from elevation 175 feet.
10. Juvenile right valve, HVH 9363, from elevation 230 feet.

11. **Buntonia levinsoni** Huff
Female left valve, HVH 9389, from elevation 186 feet.

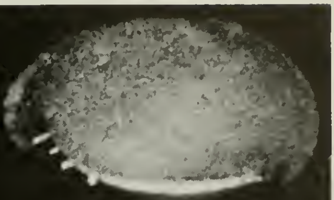
12. **Buntonia** sp.
Juvenile left valve, HVH 9762, from elevation 192 feet.

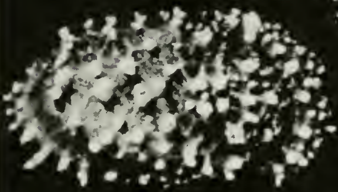
13. **B. shubutaensis** Howe
Female left valve, HVH 9391, from elevation 230 feet.

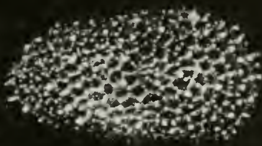
14, 15. **Acanthocythereis howei** Huff
14. Juvenile right valve, HVH 9367, from elevation 220 feet.
15. Female right valve, HVH 9369, from elevation 220 feet.

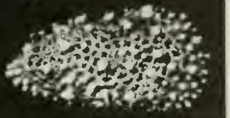
16. **Actinocythereis purii** Huff
Female right valve, HVH 9386, from elevation 186 feet.

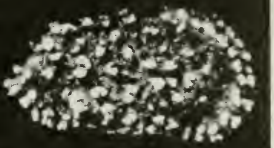

1


2


3


4


5

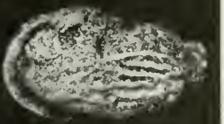

6


7

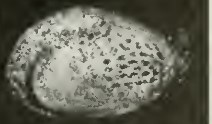

8


9

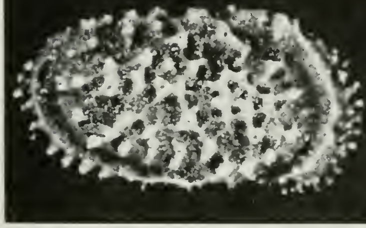

10

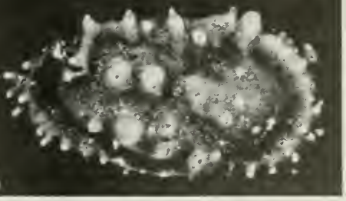

11


12


13


14


15


16

THE LEFT-RIGHT VARIATION OF THE OSTRACODE ORNAMENT

A. Liebau
Geolog. Paläontolog. Inst., Tübingen

ABSTRACT

In the introduction a general classification of ostracode ornaments is outlined, together with an hypothesis on calcification control of smaller ornament details.

In examples from the genera *Loxoconcha, Aurila, Beyrichia,* and *Oertliella* the ornament variation between left and right valve of the same carapace is studied. It seems to be a general rule that this "inter-valve variation" reflects the inter-individual one. Pits, meshes, and spines, which vary in their number from left to right side of a carapace, also vary when corresponding valves of different individuals are compared. Furthermore, intraspecific constancy of position of ornamental details is recognizable by the comparison of the two valves of a carapace. In respect to the numerical variation of sculpture details, left and right valves are like two separate "specimens" (*i.e.* examples for a species)and can be used for "twin researches in fossil ostracodes".

ZUSAMMENFASSUNG

In der Einleitung wird eine allgemeine Klassifizierung von Ostrakoden-Ornamenten umrissen. Angefügt ist eine Hypothese über Kalzifikationseinflüsse auf die Ausbildung kleinerer Feinskulptur-Elemente.

An Beispielen aus den Gattungen *Loxoconcha, Aurila, Beyrichia* und *Oert*tliella wird die Beziehung im Ornament zwischen linker und rechter Klappe untersucht. Anscheinend entspricht es einer allgemeingültigen Regel, dass die Ornament-Variabilität von Klappe zu Klappe diejenige zwischen konspezifischen Individuen widerspiegelt. Grübchen, Maschen und Stacheln, die beim Vergleich der beiden Seiten eines Gehäuses numerische Unterschiede zeigen, variieren ebenfalls, wenn einander entsprechende Klappen verschiedener Individuen verglichen werden. Auch Elementkonstanz im Ornament ist auf diese Weise erkennbar. Hinsichtlich der numerischen Variabilität von Skulptur-Details sind linke und rechte Klappe zwei vollwertige "Exemplare" (d.h. Beispiele für eine Art) und können quasi zu einer "Zwillingsforschung an fossilen Ostrakoden" benutzt werden.

INTRODUCTION

This paper is part of a more general study of ostracode ornament evolution. Some fundamentals were given in Liebau (1969, 1971). Two results concerning this subject, which have not yet been published, are presented as preliminary notes in the following introduction. They illustrate the importance of ornament variation analyses.

The scanning electron photographs are courtesy of the Cambridge Co., Dortmund.

The presentation of this paper at the Delaware conference has been supported by the Deutsche Forschungsgemeinschaft.

The finer sculptural elements on ostracode valves, i.e.: pits, meshes, spines, tubercles vary in number and configuration but also may be constant. In many ostracode studies these ornamental details are treated in a very general way. But there are reasons at least for distinguishing constant elements from varying ones:

1) Constant spines, meshes can be used as markings with defined positions (e.g. when ontogenetical allometries are observed).

2) Constant ornament details which are individually fixed in the genetic plan (*i.e.* can be mutated individually), are each, actually or potentially, taxonomical features.

3) Varying meshes occurring besides constant ones seem to reflect certain calcification stages of the shell. Such observations may reveal progressive stages of carapace construction or show calcification control by ecological influences (temperature, salinity). They help to distinguish ecologically-caused ornament changes from true phylogenetical developments.

In respect to their genetic plan the following main ornament classes are distinguished:

ornament class	position of single element and element number	individual evolution of single element	relation to pore systems
macro-ornament	constant	possible	usually present
meso-ornament	constant	impossible or not observed	usually present
proto-ornament	varying	impossible	usually present
micro-ornament	varying	impossible	spines: possible pits: absent

As mentioned before, the occurrence of numerically varying ornamental elements can often be correlated with certain calcification stages. An hypothesis on calcification-controlled ornamental changes includes fundamental observations by Herrig (1965, 1966). These ornamental developments have been observed in the Trachyleberididae *s.l.* (including Hemicytherinae), and they are also present in most, if not all, of the other Cytheracea.

The calcification hypothesis needs more proof and documentation of examples than is possible at this time. Nevertheless the complex of observations and interpretations is outlined here, as it helps in understanding the problems of sculpture analyses:

1) Macroreticulation (a system of meshes with constant positions) is replaced by microreticulation (varying meshes, smaller than neighboring macromeshes), in cases where a certain calcareous shell layer is reduced. In the final phase of this process a fine pitting or even a smooth surface is observed in place of the macroreticulation. But also in smooth specimens all genetic information about the macroreticulation may still be present, although not expressed in the phenotype.

2) Microconation (spinelets varying in number) does not occur together with microreticulation. It is, therefore, supposed that these two ornamental

components belong to opposite calcification stages of "Herrig's shell layer". There are likewise transitions from microconate macroreticulation to smooth surfaces. This type of smoothing down of the ornament corresponds to the interpretation of the "celation" by Sylvester-Bradley & Benson (1971). A useful rule is that meshes with microconate meshwalls have constant positions.

3) In the growth towards the adult stage the shell layer is gradually thickened. Therefore, microreticulate larvae may progress to macroreticulate adults, whereas the reverse combination has not been observed. Microconate adult ornamentation is obviously not preceded by a microreticulate one in the last instar.

In phylogenetic series ornamental changes in both directions are possible, corresponding to thickening as well as to thinning-out of that shell layer. This means that macroreticulation can be reduced and rejuvenated in a lineage without changes in the mesh configuration.

In shorter periods similar ornamental alterations may be caused by ecological influences in the writer's opinion. Decreasing temperature and salinity may induce weak calcification of the shell and in this way bring about the replacement of macro- by microreticulation.

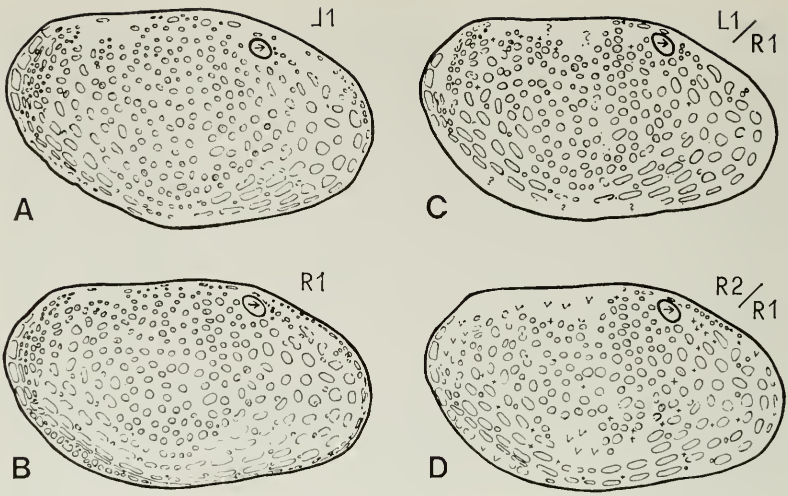
"Microreticulation" and "macroreticulation" were defined in Liebau (1971). "Microconation" replaces "Mikrotuberkulation" of the same publication. All these terms should be regarded as provisional until a comprehensive terminological paper is published and discussed. This terminology is in preparation.

The data and comments presented herein show some of the problems, in the study of ostracode ornamentation. These problems must be solved, because Cytheracean ornamentation is of major importance taxonomically. An important discussion of the application of homologized ornamental features is that of Benson (1972). Left-right variation studies will be, I hope, a practical tool to indicate the use of ostracode ornamentation where only a few specimens are available.

THE LEFT-RIGHT VARIATION

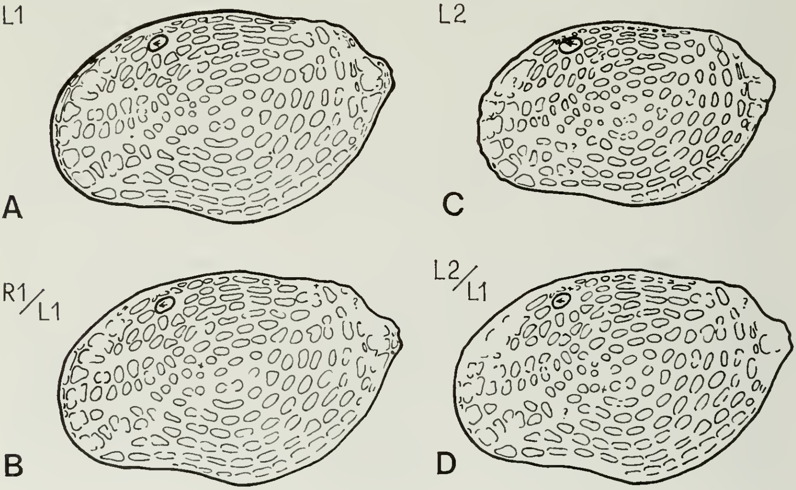
While studying the ornamental variation of ostracode species I have regularly observed that intraspecific variable ornamental details also show differences from the left to the right valve of the same carapace. Intraspecific element constance is also reflected by these inter-valve relations.

Of course certain exceptions must be noted. On one hand the sculpture patterns of the two valves of an ostracode are normally symmetrical. On the other hand, in some cases conspicuous differences are observed, *e.g.* in connection with a specialized carapace construction or with the sexual dimorphism. Such examples are excluded from the following considerations. Only the ornamental fields which are represented by equivalent patterns on both sides of the carapace, are considered here. Intraspecific ornamental variations due to changing (paleo-) ecology, are not reflected in inter-valve differences (as the two valves of a carapace are from the same biotope).



Text-fig. 1. *Loxoconcha* sp. 1, Recent, Adriatic Sea. A and B. Left and right valve of the same carapace (left valve: drawing inverted). C. "Inter-valve" comparison of L1 and R1. D. "Inter-individual" comparison of two right valves. Scale: Length of the R1 0.77 mm.

Signatures:
\+ + ornament details missing in one of the compared valves
v v general differences in number and arrangement of ornament details
(Further explanations in the text).



Text-fig. 2. *Loxoconcha* sp. 2, Recent, Mauritius. Scale: Length of the L1 0.67 mm.

A few examples may illustrate the principle idea of the left-right ornament comparisons:

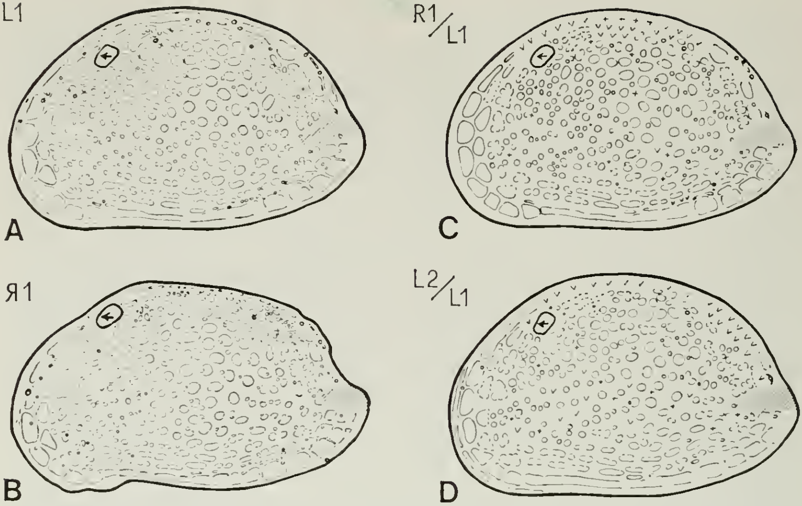
1) *Loxoconcha* sp. 1 Recent, beach sample, Adriatic Sea near Pessaro, Italy. The drawings A and B in Text-fig. 1 show the mesh patterns of left valve (L1) and right valve (R1) of the same carapace. Some sieve pores observed in scanning electron microscope photographs, were used as the basis for the drawings. In Text-fig. 1C all meshes and pores, which are common to both valves, are plotted within the outline of the right valve. Zones of varying meshes (differing from valve to valve in number and arrangement) are marked by groups of "V". Single meshes missing in one of the patterns are noted with a cross. In the same way (in Text-fig. 1D) the right valve (R2) of a second carapace is compared with the first right valve (R1). Now the inter-valve variation (R1/L1) and the inter-individual one (R1/R2) can be compared. In both cases the result is about the same.

2) *Loxoconcha* sp. 2 (*Loxocorniculum* sensu Benson & Coleman, 1963) Recent, beach sample, Mauritius (Indian Ocean).
In Text-fig. 2B the valves L1 and R1 (belonging to the same carapace) are compared as in Text-fig. 1C of the first example. Both valves have about the same mesh pattern. Then a rather differing L2, small, with thick mesh walls, has been chosen for the comparison with the L1. The results of the analyses L1/R1 compared to L1/L2 show, accordingly, that the mesh pattern is constant.

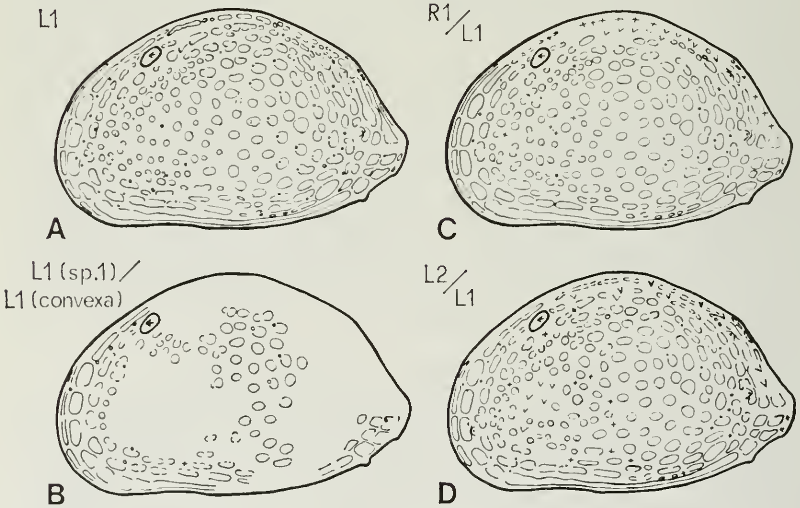
3) *Aurila* sp. 1 Recent, beach sample from the lagoon of São Martinho do Porto, Portuguese coast.
L1 compared with R1 (Text-figs. 3A, 3B, analysis: 3C) demonstrates that the pores and some of the meshes are constant, while others, especially small elements within the outlines of larger ones, vary. The uppermost pit row in the L1 has no equivalent in the R1. The comparison of the L1 with the L2 of another carapace yields about the same information on the ornamental variability as before (L1/R1). Only one exception is obvious: because of the carapace asymmetry, which is one of the characteristics of this genus, left and right valves do not correspond in the upper peripheral pit row. This problem does not occur, when left valves (or right ones) are compared. Nevertheless, many other meshes are common both to the two valves of a carapace and to the left valves of different individuals. These meshes are assumed to be constant.

4) *Aurila convexa* (Baird, 1850) Recent, same sample as in 3.
L1 and R1 of the same carapace and L1 and L2 of different carapaces are compared, all as in the example before. Text-figure 4 shows the L1 mesh pattern and the comparisons L1/R1 and L1/L2. Finally, the ornamental relations between *Aurila convexa* (L1) and *Aurila* sp. 1 (L2 of the example before) are demonstrated in Text-fig. 4B. The result shows a number of meshes to have supra-specific occurrence, and probably a phylogenetic relationship.

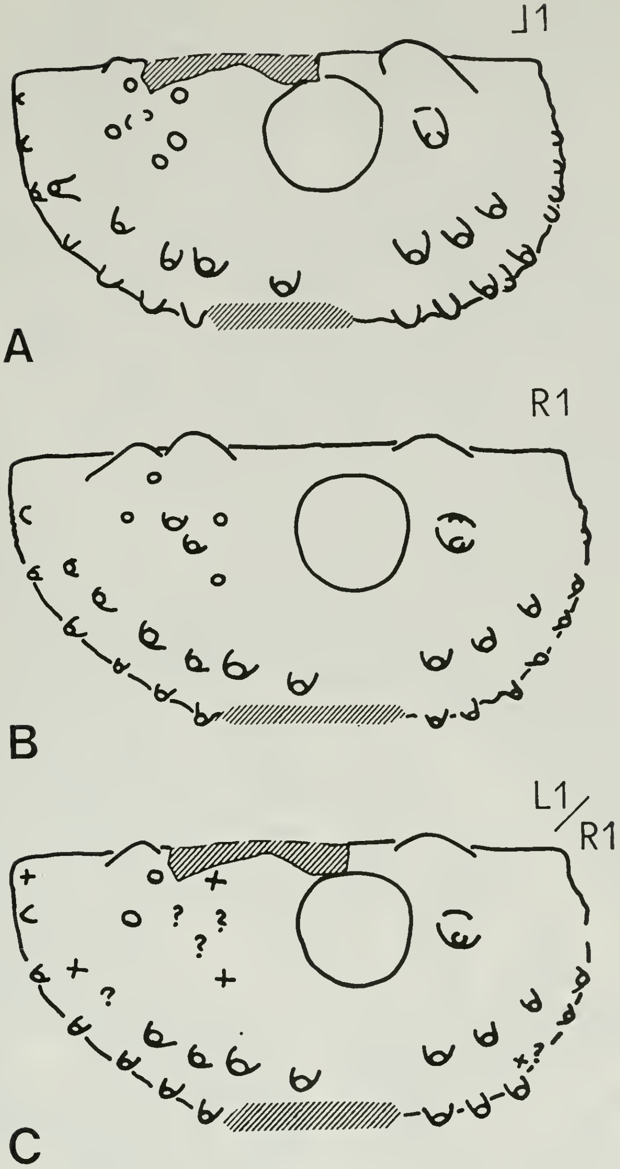
5) *Beyrichia peponulifera* Martinsson, 1962, Mulde marl, Mulde, Silurian of Gothland.



Text-fig. 3. *Aurila* sp. 1, Recent, Portuguese coast. — Scale: Length of the L1 0.76 mm.



Text-fig. 4. *Aurila convexa,* Recent, Portuguese coast. Scale: Length of the L1 0.76 mm.



Text-fig. 5. *Beyrichia peponulifera,* Silurian, Gothland. — Scale: Length of the R1 1.55 mm.

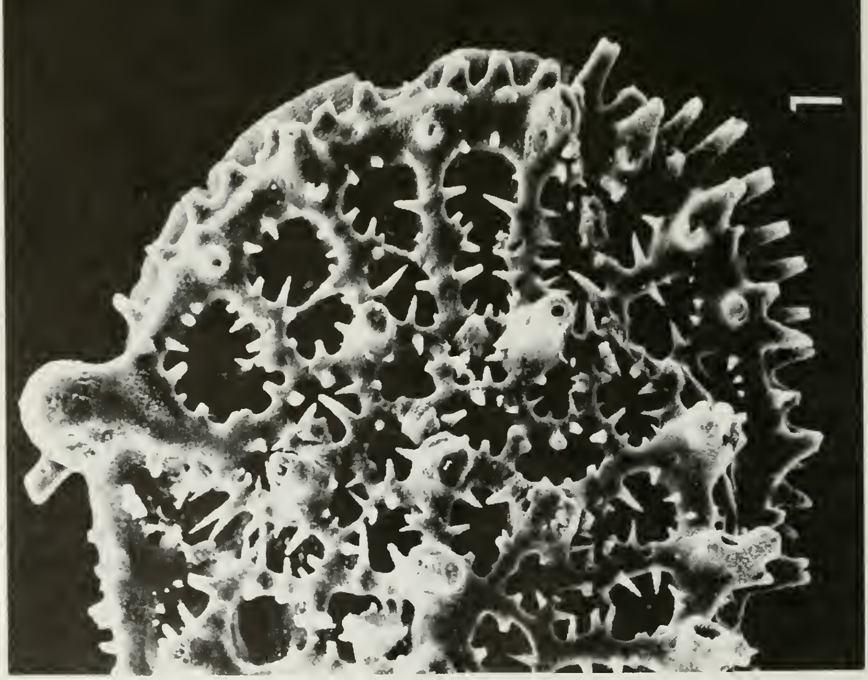


Plate 1. — Fig. 1. *Oertliella* sp. 1, Eocene, southern France. Anterior portion of the right valve. Scale as in figure 2.

Fig. 2. Same carapace as in figure 1, anterior portion of the left valve. Scale: Height 0.44 mm (incl. spines).

Only a pattern of spines and tubercles is present. Both the results of the inter-valve and the inter-individual comparisons show that certain spines of the velar row have constant positions. Additional information taken from Martinsson (1962) confirms that these spines are constant; at least some of them are also found in other species: one, named the "calcarine spine" (Martinsson), has suprageneric distribution.

6) *Oertliella* sp. Lower Cuisian (L. Eocene), Tuilerie de Gan near Pau (southern France).

The anterior part of left and right valve of the same carapace are figured on Plate 1. This very rich ornament consists of phylogenetically old, constant components, and varying younger ones. The meshes and the larger lateral spines show the same configuration on both valves and, indeed, they are constant (and of at least Lower Cretaceous age). But even in the confusing spine concentrations at the anterior margins left and right valve correspond in nearly all details. The explanation: these spines and spinelets have genetically fixed places. Each of them has an homologous feature corresponding with Cretaceous species and genera of *Cythereis* s. str.

Another class of spinelets surrounds the mesh openings. They vary in number; sometimes three or four of them are found on one valve, while the other valve has only two at the same place. Accordingly there is a corresponding inter-individual numerical variation. (Another conspecific specimen from the same sample is figured in Liebau, 1971, p. 57).

These examples indicate that there is a relationship between inter-individual and inter-valve variation of ostracode ornament. Of course this argument is not sufficient for an exact statement, but nevertheless many other species have been studied in this way and no observation has been made to the contrary.

In ostracode studies (left-right comparisons may have taxonomic interest when only a few carapaces are available. In those cases the two valves of a carapace can be used (except as noted before) in respect to the ornamental variation like two conspecific specimens. Moreover these "specimens" offer some advantages which are unusual among fossils: they are with certainity of the same stratigraphic age, of the same sex, of same ontogenetic stage, have lived in the same biotope and belong to the same population. They can be studied like twins from the same environment!

REFERENCES

Benson, R. H.

1972. The *Bradleya problem, with descriptions of two new psychrospheric ostracode genera, Agrenocythere and Poseidonamicus (Ostracoda: Crustacea).* Smithsonian Contrib. Paleont., *12,* pp. 1-138, 67 figs., 4 tbls., 14 pls.; Washington, D.C.

Herrig, E.

1965. *Cythereis reticulata varia ssp. n., eine neue Ostracoden-Unterart aus der Rügener Schreibkreide (Unter-Maastricht).* Ber. geol. Ges., DDR, 10 (4), pp. 403-419, 5 figs., pls. I-IV, Berlin.

1966. *Ostracoden aus der Weißen Schreibkreide (Unter-Maastricht) der Insel Rügen.* Paläont. Abh. A, II (4), pp. 693-1024, 144 figs., pls. I-XLV, Berlin.

Liebau, A.
1969. *Homologisierende Korrelationen von Trachyleberididen-Ornamenten (Ostracoda, Cytheracea).* Neues Jarb. Geol. Paläont., Mh., 1969 (7), pp. 390-402, 4 figs., Stuttgart.
1971. *Homologe Skulpturmuster von Trachyleberididen und verwandten Ostrakoden.* Dissertation at the Technical University Berlin, pp. 1-118, 32 figs., Berlin.

Sylvester-Bradley, P. C., and Benson, R. H.
1971. *Terminology for surface features in ornate ostracodes.* Lethaia, 4, pp. 249-286, 48 figs., Oslo.

Alexander Liebau
Geolog. Paläontolog. Inst.
Sigwartstr. 10
D-74 Tübingen
Germany

DISCUSSION

Dr. I. G. Sohn: You have proved that practically everything on the ostracode carapace is genetically controlled. But I wonder about those ostracodes that are not symmetrical. What happens when they have right and left valves that are distinctly different.

Dr. Liebau: Of course I cannot work with carapaces which have *e.g.* a nodose right valve and a smooth left one. But these cases are few and easy to recognize. In many species the ornamentation at the periphery of the valves shows significant differences. The *Aurila* examples have been chosen in order to demonstrate this problem.

THLIPSURA JONES AND HOLL: A REDESCRIPTION OF THE TYPE SPECIES

Robert F. Lundin and Lee E. Petersen
Arizona State University

ABSTRACT

The type species of *Thlipsura* Jones and Holl, 1869 is redescribed and reillustrated. In addition, one new species of *Thlipsura* from the Silurian of England is illustrated. The hinge and contact margin structures of *Thlipsura* are defined and illustrated. These are concluded to be critical in the definition of the genus. Comparison of *T. corpulenta* with numerous North American and European species now and formerly placed in *Thlipsura* is made, and a consequent revision of the species composition of the genus is presented. *Thlipsura* is found to be restricted to the Silurian of Europe and North America.

RÉSUMÉ

L'espèce de type de *Thlipsura,* Jones et Holl, 1869 est décrit et illustré encore une fois. En plus, une des nouvelles espèces de *Thlipsura* du Silurian d'Angleterre est illustrée. Les structures de la charnière et du bord de contact de le *Thlipsura* sont definis et illustrés. Celles-ci deviennent critiques dans la definition du genre. Une comparison est faite entre le *T. corpulenta* avec plusieurs espèces d'Amerique du Nord et d'Europe placées auparavant et encore maintenant dans *Thlipsura* et il y a une présentation d'une révision résultante de la composition due genre des espèces. On trouve que *Thlipsura* est limité au Silurian d'Europe et d'Amerique du Nord.

INTRODUCTION

The genus *Thlipsura* was erected by Jones and Holl in 1869 on the basis of material from the Woolhope beds (Wenlockian) of England. *T. corpulenta* Jones and Holl, 1869, has been generally recognized as the type species (Ulrich and Bassler, 1923; Swartz, 1932; Bassler and Kellett, 1934), as well it should be according to the International Code of Zoological Nomenclature. This species therefore took on special significance when Ulrich (1894) established the family Thlipsuridae, including in it *Thlipsura, Phreatura* and *Octonaria.* The original illustrations of *T. corpulenta* are remarkably accurate. Unfortunately, subsequent authors (Ulrich and Bassler, 1923; Swartz, 1932; Bassler and Kellett, 1934; Kesling, 1961; Krandijevsky, 1968) have revised or perpetuated revised versions of Jones and Holl's (1869) drawings without adequate knowledge of the true appearance of the type specimen. This has led to a grossly misleading diagnosis of the genus (Krandijevsky, 1968) and confused revisions of the family Thlipsuridae (Swartz, 1932 and Krandijevsky, 1968).

In view of these problems we have undertaken this study in order to:

(1) redescribe and reillustrate the type species of *Thlipsura.*

(2) establish the range of variation within *T. corpulenta.*

(3) determine the validity of the various species and varieties of *Thlipsura* erected by Jones and Holl (1869) and Jones (1887).

(4) establish the species composition of *Thlipsura* especially with respect to North American forms. These are the main objectives of this report. We in no way intend this to be a revision of the Thlipsuridae, a project which is in our future plans. Nevertheless, it will be necessary to comment

on and make special observations about other thlipsurid genera. These are meant to be preliminary in nature. Hopefully, this report will serve to clarify the very basis of the family Thlipsuridae and act as a starting point for a complete revision of this group.

ACKNOWLEDGMENTS

We wish to express special gratitude to Professor Anders Martinsson (Uppsala University) for supplying large collections of *Thlipsura* and Mr. David Siveter (University of Leicester) who guided Lundin in the field where additional collections were procured. Dr. R. H. Bate (British Museum of Natural History), Dr. R. H. Benson (United States National Museum of Natural History), M. J. Copeland (Geological Survey of Canada), A. L. Guber (Pennsylvania State University), and A. F. Abushik (All-Union Scientific Research Geological Institute, Leningrad) have been most helpful in supplying type specimens which have been critical to this study. To all of these people we express our deepest appreciation. Finally special thanks are given to the University Grants Committee of Arizona State University for providing financial support without which this report could not have been completed.

PREVIOUS INVESTIGATIONS

Jones and Holl (1869) initially placed three newly established species, *T. corpulenta, T. tuberosa,* and *T. v-scripta,* in the genus *Thlipsura.* Jones (1887) established *T. angulata* and *T. plicata* plus two varieties *T. plicata* var. *unipunctata* and *T. plicata* var. *bipunctata.* Except for four species added to the genus by Krause (1891) and Kummerow (1924) the major contributions to *Thlipsura* since the work of Jones (1887) have been made by North American workers. Recently Abushik (1971) placed Russian forms described by Krandijevsky (1963) in *Thlipsura.* Table 1 is a list of all species known to us which have been described, illustrated and classified under *Thlipsura.* Several species which are legitimate members of *Thlipsura* but were originally placed in other genera have been added to the list. The table summarizes the nomenclatural history of these species from literature in which important taxonomic changes have been made.

The taxonomic history of North American species placed in *Thlipsura* has been complex. An inconspicuous but significant contribution was made by Ulrich and Bassler (1923) when they reillustrated, by drawing, *T. corpulenta.* The illustration is erroneous to the extent that two posterior (considered anterior by Ulrich and Bassler) furrows and one anterior pit are shown. The type figure of Jones and Holl (1869) shows one posterior furrow and no anterior pit. Unfortunately, the erroneous illustration of Ulrich and Bassler (1923) was perpetuated by Swartz (1932), and Bassler and Kellett (1934). The error was accentuated in illustrations by Kesling (1961) and Krandijevsky (1968). This error in illustrating *T. corpulenta* has had an important effect on the placement of North American species in *Thlipsura.* It prompted Swartz (1932) to conclude that *T. corpulenta* and *T. furca* Roth, 1929, are closely related.

The latter species has two posterior furrows (reentrants) and has been adequately illustrated by various authors (Roth, 1929; Swartz, 1932; Lundin, 1968; and Kesling, 1961 who mistakenly labeled it *T. confluens*). Swartz (1932), in a revision of the Thlipsuridae, believed the posterior (anterior, according to Swartz) depressed area to be diagnostic, and accordingly placed five species and one variety in *Thlipsura* as indicated in Table 1. At the same time Swartz removed *T. angulata, T. tuberosa, T. plicata,* and its two varieties to a new genus, *Thlipsurella.* He divided the latter into five sections, one of which is entitled "Section of *Thlipsurella plicata*". Division of *Thlipsurella* into five sections has prompted various authors (Swartz, 1932; Bassler and Kellett, 1934; Copeland, 1962; Lundin 1965 and 1968; and others) to place species in *Thlipsurella* which are only remotely related to *T. ellipsoclefta* Swartz, 1932, the type species. *Thlipsurella* has become something of a catch-all for a wide variety of forms, a situation which is complicated by the fact that the type species is represented only by molds and casts.

Kesling's (1961) illustration of *T. corpulenta* served only to confirm the error of supposed similarity between it and *T. furca.* It is the least representative of the various illustrations of *T. corpulenta,* a situation which is most unfortunate because of the impact the American Treatise has had as a reference on ostracodes.

Krandijevsky (1968) attempted a revision of the Thlipsuridae. He, like others, apparently did not study specimens of *Thlipsura corpulenta,* and his diagnosis of the genus, as well as his illustration of the species, demonstrate that he too was under the illusion that *T. corpulenta* has two posterior furrows. Accordingly, he placed *T. furca, T. furcoides, T. subfurca* and *T. corpulenta* in *Thlipsura* and added conditionally *T. triloba* (see Table 1). Also, Krandijevsky (1963) erected *Thlipsohealdia* in which he placed two species *T. jonesi* and *T. binodosa.* Abushik (1971) recognized the similarity of these species and placed them in synonymy. She further recognized their similarity to *T. corpulenta* and transferred *Thlipsohealdia jonesi* Krandijevsky, 1963 to *Thlipsura,* thus invalidating *Thlipsohealdia.* We concur with Abushik (1971) on the basis of studying specimens of *Thlipsura jonesi* supplied by her.

The most important contribution of Krandijevsky (1968) relative to North American species placed in *Thlipsura* is his new genus *Neothlipsura.* Unfortunately, he designated *T. confluens* Swartz, 1932, as the type species, a species which is represented only by external molds. We have studied the types and conclude on the basis of outline and general construction of the valves that *Neothlipsura confluens* (Swartz, 1932) is congeneric with several North American species formerly placed in *Thlipsura.* Krandijevsky (1968) has placed an inordinate emphasis on details of ornamentation. The shape of *N. confluens* suggests valve relationships and hinge arrangement identical to *T. furcoides* which, without question, is congeneric with *T. furca* and *T. primitiva.* Accordingly, we believe the following species belong in *Neothlipsura.*

N. robusta (Ulrich and Bassler, 1913)
N. furca (Roth, 1929)
N. primitiva (Roth, 1929)

N. conflucns (Swartz, 1932)
N. robusta var. *tricornis* (Swartz, 1932)
N. furcoides (Bassler, 1941)
N. thyridioides (Swartz and Swain, 1941)
N. subfurca (Polenova, 1958)
N. whitcavsi (Copeland, 1962)

We should point out that *N. subfurca* (Polenova, 1958) is known to us only through the illustrations of Polenova (1958) and Polenova and Zanina (1960). Accordingly, this is a questionable assignment. Lundin (1968) indicated that *T. robusta* (Ulrich and Bassler, 1913) is not congeneric with *Eucraterellina randolphi* Wilson, 1935. If this is true, we see no reason at present for not placing the former species and *T. robusta* var. *tricornis* Swartz, 1932 in *Neothlipsura*. It is possible, however, that *Neothlipsura* will require emendation in the future, in which case these forms may be excluded from it.

Adamczak (1967) emphasized the significance of the hinge and contact margin structures in defining the genus *Silenis* Neckaja, 1958 which Adamczak placed in the Thlipsuridae. According to Adamczak's (1967) illustrations, however, it appears that the hinge in *S. bassleri* is somewhat more complex than that of *Thlipsura corpulenta* and other *Thlipsura* species. Furthermore, Adamczak's photographs of *S. bassleri* suggest a more extensive contact groove than is shown in his drawings. *T. corpulenta* has neither the anterior and posterior hinge sockets nor the tongue-shaped projections of the right valve, as on *S. bassleri* (Adamczak, 1967, fig. 1). On the other hand, *S. bassleri* apparently has a poorly developed contact groove along the posterior margin, posterior part of the ventral margin, and anterior margin of the left valve (see Adamczak, 1967, fig. 8A) much like that of *T. corpulenta*. Nevertheless, Adamczak's contribution is an important one because it shows the basic construction of the Thlipsuracean hinge and contact margin structures.

SPECIES REJECTED FROM *THLIPSURA*

Table 1 lists those species which are herein rejected from *Thlipsura*. The hinge, contact margin, and general morphology of *Thlipsura* are described below. The following discussion is a justification for removal of the various species from *Thlipsura*.

Adamczak (1967) has shown *Thlipsurella? discreta* to have a well-developed complete contact groove in the left valve. The same is true for *T? v-scripta*. Furthermore, the surface morphology of these species easily distinguishes them from *Thlipsura*.

We have not studied specimens of the species erected by Krause (1891) and Kummerow (1924). Published illustrations of these, however, indicate that they do not belong to *Thlipsura* on the basis of outline and surface morphology.

T. multipunctata (Pl. 4, figs. 4-7) clearly belongs to *Thlipsurella*. It is closely related to *T. ellipsoclefta*, Swartz, 1932, the type species.

We have not presently studied *Neothlipsura robusta* (Ulrich and Bassler, 1913) or *N. robusta* var. *tricornis* (Swartz, 1932). Lundin (1968), however,

Table 1. Nomenclatural history of species placed in *Thlipsura*.

SPECIES	Swartz, 1932	Bassler and Kellett, 1934	Lundin, 1965	Lundin, 1968	Krandijevsky 1968	Abushik, 1971	This report
Craterellina robusta Ulrich & Bassler, 1913	Thlipsura	Thlipsura			Craterellina		Neothlipsura
Thlipsura angulata Jones, 1887	Thlipsurella	Thlipsurella			Euthlipsurella		Thlipsura
Thlipsura confluens Swartz, 1932	Thlipsura	Thlipsura			Neothlipsura		Neothlipsura
Thlipsura corpulenta Jones & Holl, 1869	Thlipsura	Thlipsura			Thlipsura	Thlipsura	Thlipsura
Thlipsura curvistriata Roth, 1929	Thlipsurella	Thlipsurella	Thlipsurella?		Euthlipsurella		Rejected
Thlipsura fossata Roth, 1929	Thlipsurella	Thlipsurella		Thlipsurella?	Euthlipsurella		Rejected
Thlipsura furca Roth, 1929	Thlipsura	Thlipsura		Thlipsura	Thlipsura		Neothlipsura
Thlipsura furcoides Bassler, 1941					Thlipsura		Neothlipsura
Thlipsura n. sp.							Thlipsura
Thlipsura multipunctata Ulrich & Bassler, 1913	Thlipsurella	Thlipsurella			Thlipsurella		Thlipsurella
Thlipsura muricurva Roth, 1929	Thlipsurella	Thlipsurella		Thlipsurella?	Euthlipsurella		Rejected
Thlipsura parallela Roth, 1929	Thlipsurella	Thlipsurella	Thlipsuroides		Rothellina		Thlipsuroides
Thlipsura personata Krause, 1891	Thlipsurella?	Thlipsurella?			Krausellina		Rejected
Thlipsura plicata Jones, 1887	Thlipsurella	Thlipsurella			Euthlipsurella		Thlipsura
Thlipsura plicata bipunctata Jones, 1887	Thlipsurella	Thlipsurella			Euthlipsurella		Thlipsura
Thlipsura plicata unipunctata Jones, 1887	Thlipsurella	Thlipsurella			Euthlipsurella		Thlipsura
Thlipsura primitiva Roth, 1929	Thlipsura	Thlipsura	Healdia		Thlipsohealdia		Neothlipsura
Thlipsura robusta tricornis Swartz, 1932	Thlipsura	Thlipsura			Craterellina		Neothlipsura
Thlipsura simplex Krause, 1891	Thlipsurella?	Octonaria			Krausellina		Rejected
Thlipsura striatopunctata Roth, 1929	Thlipsurella	Thlipsurella	Thlipsuroides		Rothellina		Thlipsuroides
Thlipsura subfurca Polenova, 1958					Thlipsura		Neothlipsura?
Thlipsura tetragona Krause, 1891	Thlipsurella?	Thlipsurella			Krausellina		Rejected
Thlipsura thyridioides Swartz & Swain, 1941					Neothlipsura		Neothlipsura
Thlipsura triloba Kummerow, 1924	Rejected	Thlipsura			Thlipsura?		Rejected
Thlipsura tuberosa Jones & Holl, 1869	Thlipsurella	Thlipsurella			Euthlipsurella		Thlipsura
Thlipsura v-scripta Jones & Holl, 1869	Thlipsurella	Thlipsurella			Thlipsurella		Thlipsurella?
Thlipsura v-scripta discreta Jones, 1887	Thlipsurella	Thlipsurella			Thlipsurella		Thlipsurella?
Thlipsura whiteavesi Copeland, 1962							Neothlipsura
Thlipsohealdia binodosa Krandijevsky, 1963					Thlipsohealdia	Thlipsura	Thlipsura
Thlipsohealdia jonesi Krandijevsky, 1963					Thlipsohealdia	Thlipsura	Thlipsura
Thlipsurella? sp. A Lundin & Newton, 1970							Thlipsura?
Thlipsurella? sp. B Lundin & Newton, 1970							Thlipsura

studied the types of the former species and they certainly do not belong to *Thlipsura*. Furthermore, we doubt that *N. robusta* is congeneric with *Eucraterellina randolphi* Wilson, 1935 (see Lundin, 1968). *N. robusta* var. *tricornis* (Swartz, 1932) is very similar to *N. robusta* hence the same generic designation. The posterior nodes on forms like *N. robusta* and *N. robusta* var. *tricornis* probably formed through fusion of the complex posterior furrows of *N. confluens*.

N. furca (Roth, 1929), Pl. 3, figs. 4-7, *N. furcoides* (Bassler, 1941), Pl. 4, figs. 10-13, and *N. primitiva* (Roth, 1929), Pl. 4, figs. 1-3, have an uninterrupted contact groove in the left valve although it is poorly developed along the mid-venter of the latter species. These species are placed in *Neothlipsura* on the basis of their similar outline and morphology to *N. confluens* (Swartz, 1932) the type species of the genus. The latter similarity justifies placement of *N. thyridioides* (Swartz and Swain, 1941), Pl. 4, fig. 8, and *N. whiteavsi* (Copeland, 1962), Pl. 4, fig. 9, in the same genus. Illustrations of *T. subfurca* Polenova, 1958, show that it does not belong to *Thlipsura* but probably *Neothlipsura*.

The hinge structure of *T. fossata* (Pl. 2, figs. 3, 4) is basically like that of *T. corpulenta,* but the orientation of the hinge and the carapace morphology are distinctly different. Accordingly, *T. fossata, T. muricurva,* and *T. curvistriata* are removed from *Thlipsura*. Krandijevsky (1968), placed these species in a new genus, *Euthlipsurella*. That genus is, however, invalid because it is based on *T. plicata* Jones, 1887, which is a synonym of *T. corpulenta* Jones and Holl, 1869. Accordingly, the species discussed above most probably belong in a new genus along with several other species.

The hingement of *Thlipsuroides* Morris and Hill, 1952, has not been adequately studied. A few specimens of *T. thlipsuroides* Morris and Hill, 1952 in our collections from the Newsom (Waldron) Shale (Silurian) and the Brownsport Formation (Silurian) have a hinge and hinge orientation which is like that of *Thlipsura,* as far as can be determined from the material available for study. *Thlipsuroides* can be distinguished from *Thlipsura* on other grounds, however. *Thlipsuroides* species have two distinct horizontal pitted furrows which are terminated by a posterior ridge. Accordingly, the morphology of the posterior portion of the shell is distinctly different from that of *Thlipsura*. Therefore, *T. parallela* Roth, 1929 and *T. striatopunctata* Roth, 1929 are placed in *Thlipsuroides*.

SYSTEMATIC SECTION

Family **THLIPSURIDAE**

Genus **THLIPSURA** Jones and Holl, 1869

1869. *Thlipsura* (part), Jones and Holl, Ann. Mag. Nat. Hist., ser. 4, vol. 3, No. 15, pp. 213-14, pl. 15, figs. 1-2.

1887. *Thlipsura* Jones and Holl, (part) Jones, Ann. Mag. Nat. Hist., ser. 5, vol. 19, No. 114, pp. 400-403, pl. 12, figs. 9-13.

1923. *Thlipsura* Jones and Holl, (part) Ulrich and Bassler, Maryland Geol. Sur., Silurian volume, p. 317, fig. 23, No. 6.
1932. *Thlipsura* Jones and Holl, (part) Swartz, Jour. Paleont., vol. 6, pp. 38-39, pl. 10, fig. 1.
1932. *Thlipsurella* (part) Swartz, *idem,* pp. 44-45.
1934. *Thlipsura* Jones and Holl, (part) Bassler and Kellett, Geol. Soc. Amer., Spec. Paper, No. 1, pp. 36, 483-487, fig. 16, No. 6.
1934. *Thlipsurella* Swartz, (part) Bassler and Kellett, *idem,* pp. 485-487.
1961. *Thlipsura* Jones and Holl, (part) Kesling, Treatise on Invertebrate Paleontology, part Q, *Arthropoda 3,* Geol. Soc. Amer., pp. 378, fig. 304, No. 2d.
1963. *Thlipsohealdia* Krandijevsky, Akad. Nauk Ukr. SSR, Inst. Geol. Nauk, pp. 85-88, pl. 8, figs. 15, 16.
1968. *Thlipsura* (part) Krandijevsky, Akad. Nauk. Ukr. SSR, Inst. Geol. Nauk, p. 67, pl. 11, fig. 1.
1968. *Thlipsohealdia* (part) Krandijevsky, *idem,* pp. 67-68.
1968. *Euthlipsurella* (part) Krandijevsky, *idem,* pp. 71-72.
1970. *Thlipsurella*? Swartz, Lundin and Newton, Geol. Sur. Alabama, Bull. No. 95, pp. 44-45, pl. 6, fig. 4, pl. 7, fig. 2.
1971. *Thlipsura* Jones and Holl, Abushik, Academy of Science, USSR, *"Nauka",* Moscow, pp. 114-116, pl. 41, figs. 1-8, pl. 42, figs. 1-2.

Type species. — *Thlipsura corpulenta* Jones and Holl, Silurian, England.

Diagnosis. — Shell subreniform in lateral view with poorly-to well-developed straight, curved or sinuate furrow extending anteriorly between two horizontal lobes from near the posterior border. Left valve larger than right and overlapping it along free border. Surface smooth. Hinge straight, inclined consisting of groove in right valve and list in left valve. Groove anterior and posterior to hinge list merges with poorly developed contact groove which disappears ventrally. Stop-ridges poorly developed or absent.

Species composition. — The following species are here placed in *Thlipsura.*

Thlipsura corpulenta Jones and Holl, 1869
Thlipsohealdia jonesi Krandijevsky, 1963 = *T. binodosa* Krandijevsky, 1963
?*Thlipsurella*? sp. A Lundin and Newton, 1970
Thlipsurella? sp. B Lundin and Newton, 1970
Thlipsura, n. sp.

Remarks. — We consider the hinge structure and orientation (inclined to longitudinal axis of the valve, Adamczak, 1966, p. 13) and the contact margin structure to be critical in the definition of the genus. The contact groove disappears along the midventral border and is best developed along the posterior border but is nowhere deep. The surface morphology of the posterior portion of the valves in all species consists of a depressed area (furrow) with a horizontal lobe above and below.

Thlipsurella? sp. A Lundin and Newton (1970) is questionably placed in

Thlipsura because material available for study is inadequate to clearly define the contact margin structures. One left valve in our collection, however, has a hinge like that of *T. corpulenta.*

Occurrence. — Silurian of Europe and North America.

Thlipsura corpulenta Jones and Holl Pl. 1, figs. 1-19; Pl. 2, figs. 1, 2; Pl. 3, figs. 8-14; Text-fig. 1

1869. *Thlipsura corpulenta* Jones and Holl, Ann. Mag. Nat. Hist., ser. 4, vol. 3, No. 15, p. 214, pl. 15, fig. 1.

1869. *Thlipsura tuberosa* Jones and Holl, *idem.,* p. 214, pl. 15, fig. 2.

1887. *Thlipsura angulata* Jones, Ann. Mag. Nat. Hist., ser. 5, vol. 19, No. 114, p. 402, pl. 12, fig. 9.

1887. *Thlipsura plicata* Jones, *idem.,* p. 402, pl. 12, fig. 10.

1887. *Thlipsura plicata* var. *unipunctata* Jones, *idem.,* p. 403, pl. 12, figs. 11-12.

1887. *Thlipsura plicata* var. *bipunctata* Jones, *idem.,* p. 403, pl. 12, fig. 13.

1923. *Thlipsura corpulenta* Jones and Holl, Ulrich and Bassler, Maryland Geol. Sur., Silurian volume, p. 317, fig. 23, No. 6.

1932. *Thlipsura corpulenta* Jones and Holl, Swartz, Jour. Paleont., vol. 6, p. 38, pl. 10, fig. 1.

1934. *Thlipsura corpulenta* Jones and Holl, Bassler and Kellett, Geol. Soc. Amer., Special Paper, No. 1, p. 36, 483, fig 16, No. 6.

1961. *Thlipsura corpulenta* Jones and Holl, Kesling, Treatise on Invertebrate Paleontology, part Q, Arthropoda 3, Geol. Soc. Amer., p. 378, fig. 304, No. 2d.

1968. *Thlipsura corpulenta* Jones and Holl, Krandijevsky, Akad. Nauk. Ukr. SSR, Inst. Geol. Nauk, p. 67, pl. 11, fig. 1.

1971. *Thlipsura corpulenta* Jones and Holl, Abushik, Academy of Science, USSR, "Nauka", Moscow, p. 115, pl. 42, figs. 1-2.

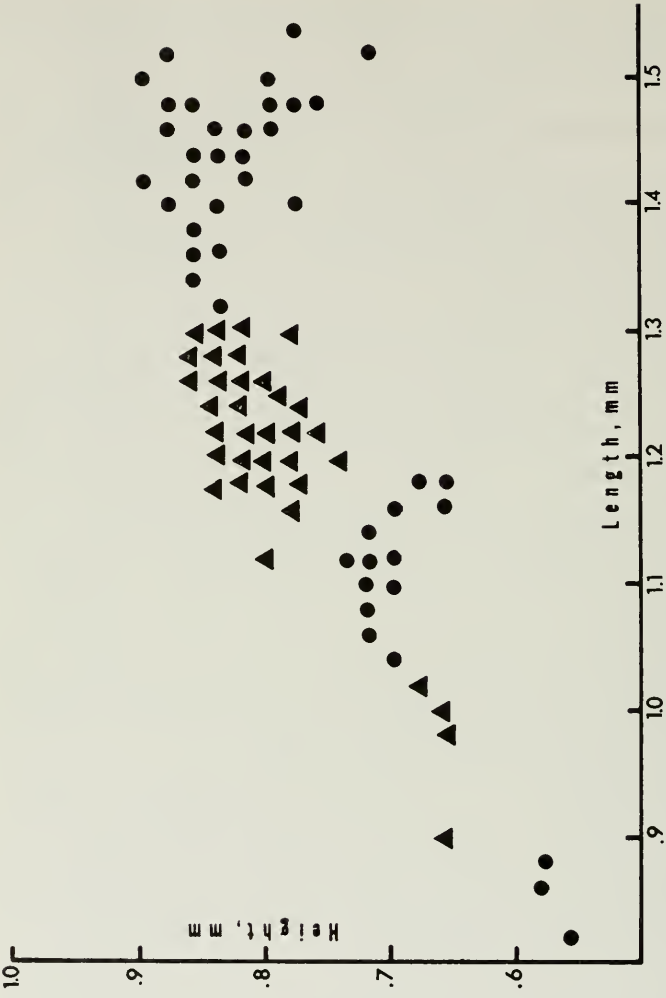
Lectotype. — B.M.N.H. I 2059, pl. 1, figs. 16-19.

Type locality and stratum. — Woolhope beds (Wenlockian) near Malvern, Worcestershire, England.

Diagnosis. — Species of *Thlipsura* with straight to curved (concave dorsally) posterior furrow between two (dorsal and ventral) horizontal lobes which are moderately well to well developed. Pit at midheight anterior to midlength may be present. Position of adductor muscle marked by circular depression on interior surface. Hinge and contact margin as for genus. Surface smooth.

Description. — The carapace is subreniform in lateral view, subelliptical in dorsal and ventral views and subquadrate in end view. The dorsal border of the left valve is evenly convex to slightly angulate, that of the right valve more distinctly angulate. The anterior and posterior borders of the left valve and the anterior border of the right valve are sharply rounded whereas the posterior border of the right valve is sharply rounded to angulate.

The ventral border of the left valve is slightly convex to straight, that of the right valve is slightly sinuate. The greatest height is at or slightly behind midlength, the greatest length is just below midheight, and the greatest width is medial. The valves are unequal, the left overlapping the right along the entire



Text-fig. 1. Size dispersion diagram of left valves of *Thlipsura corpulenta* Jones and Holl (triangles) from the Wenlock Limestone of the Malverns (sample No. MS-529) and *Thlipsura*, n. sp. (dots) from the Buildwas beds along the River Severn at Buildwas (sample No. MS-537).

free border. The surface of the valves is smooth. The posterior portion of the valves is depressed. From a position of midheight at the posterior end of the valve the depression extends anterodorsally forming a furrow between two horizontal lobes. The latter merge anteriorly with the general surface of the valves. The furrow is variable in length, depth, and shape. On some specimens a weak dorsoventrally elongate depression is present at midheight anterior to midlength. Generally it is poorly developed and it is absent from most specimens.

The hinge consists of an inclined, straight, simple groove in the right valve and a straight list on the left valve. A groove (socket) occurs at either end of the list which merges with a poorly developed contact groove. Posteriorly the contact groove extends from the posterior end of the hinge to the posterior portion of the ventral margin. The contact groove is poorly developed or absent along the anteroventral margin but is present from about midheight of the anterior margin to the anterior end of the hinge. On one specimen (Pl. 3, fig. 11) the grooves at either end of the hinge nearly merge to split the hinge list. A circular depression which represents the position of the adductor muscle attachment is present on the interior surface of the valve (Pl. 3, fig. 13). It is anterior to midlength at midheight. Muscle scars are unknown.

Variation. — Size variation in *T. corpulenta* for a population from the Malverns, England, is shown in Text-figure 1. Other recognizable variation concerns the development, shape, and length of the posterior furrow and associated horizontal lobes, and the development of the anterior depression. Jones and Holl recognized variation in these features in 1869. The posterior furrow may be weak or strong but in all cases it is clearly recognizable. It may be essentially straight or it may be curved (concave dorsally). It may be short or long. On some specimens it does not reach midlength (Pl. 1, fig. 3), on others it extends slightly beyond midlength (Pl. 1, fig. 2). The furrow is inclined in an anterodorsal-posteroventral direction on all specimens. The angle of inclination to a line tangent to the ventral border, however, varies from four degrees to thirty degrees in a population from Lincoln Hill, England. This variation in depth, shape, length, and orientation of the furrow has a corresponding influence on the same characteristics of the adjacent horizontal lobes.

The anterior depression is generally absent but it is poorly developed on a small proportion of specimens of the populations studied. We have seen it distinctly developed on only one specimen (Pl. 1, fig. 15).

Ontogeny. — Immature specimens are rare in our collections and probably represent only instars II and III (the adults being designated instar I). Those juveniles available for study shown no significant morphological differences from the adults except for their smaller size and corresponding reduction in development of the posterior furrow. It is likely that the furrow and horizontal lobes would be absent from the earlier instars of this species, but we have no specimens to demonstrate this.

Remarks. — *T. tuberosa* is based on an internal mold of *T. corpulenta.*

The node on the former form is nothing more than a reflection of the interior circular depression described above (Pl. 2, figs. 1, 2). *T. angulata, T. plicata,* and *T. plicata* var. *unipunctata* are based on minor variants of *T. corpulenta* (see discussion of variation above). Variants of these kinds are present in numerous populations from the Wenlockian of England. *T. plicata* var. *bipunctata* is based on a damaged specimen. It is not "bipunctate" as photographs of the type specimen, B.M.N.H. In 52413, show (Pl. 1, figs. 8, 9). Accordingly, all of these species and varieties are here placed in synonymy with *T. corpulenta.* This has obvious effects on previous taxonomic revisions of the Thlipsuridae. For example, Swartz's (1932) "Section of *Thlipsurella plicata*" and Krandijevsky's (1968) genus *Euthlipsurella* are meaningless, because both are based on *T. plicata.*

Specimens designated as the type specimens for *T. corpulenta, T. angulata, T. plicata* and *T. plicata* var. *bipunctata* in the collections of the British Museum of Natural History are illustrated on Plate 1.

Materials studied. — In addition to the type specimens, thousands of specimens from numerous Wenlockian localities of England have been studied. Preservation varies from poor to excellent but generally is good.

Thlipsura, n. sp. Pl. 2, figs. 5-14; Text-fig. 1

Holotype. — ASU X-15, Pl. 2, figs. 7, 8.

Locality and stratum. — Buildwas beds (Wenlockian) along River Severn near Buildwas, England (National Grid Reference No. SJ 6435/0450).

Diagnosis. — Species of *Thlipsura* on which the posterior furrow is well developed, straight to sinuate (never concave dorsally) and generally short. Ventral horizontal lobe longer than dorsal horizontal lobe. Dorsal horizontal lobe forms posterodorsal border.

Remarks. — This species has been recognized only from the Buildwas beds (Wenlockian) of England, and has not been found associated with *T. corpulenta.*

Material studied. — Hundreds of specimens (all carapaces) have been studied. Preservation varies from good to excellent.

REPOSITORIES

All specimens illustrated in this report are deposited in the collections of the British Museum of Natural History (B.M.N.H.), United States National Museum of Natural History (U.S.N.M.), Geological Survey of Canada (G.S.C.), Pennsylvania State University (P.S.U.), or Arizona State University (A.S.U.).

REFERENCES CITED

Abushik, A. F.

1971. *Paleozoic ostracodes of the European part of the Russian Platform.* Academy of Science, USSR, "Nauka", Moscow, pp. 1-248, 58 pls. (in Russian).

Adamczak, F.

1966. *On kloedenellids and cytherellids (Ostracoda, Platycopa) from the Silurian of Gotland.* Stockholm Contr. Geology, vol. 15, pp. 7-21, 5 pls., 7 text-figs.

1967. *Morphology of two Silurian metacope ostracodes from Gotland.* Geologiska Föreningens i Stockholm Förhandlingar, vol. 88, pp. 462-475, 12 text-figs.

Bassler, R. S.

1941. *Ostracoda from the Devonian (Onondaga) chert of western Tennessee.* Washington Acad. Science, Jour., vol. 31, pp. 21-27, 37 figs.

Bassler, R. S., and Kellett, B.

1934. *Bibliographic index of Paleozoic Ostracoda.* Geol. Soc. America, Spec. Paper 1, 500 pp., 24 text-figs.

Copeland, M. J.

1962. *Canadian fossil Ostracoda, Conchostraca, and Phyllocarida.* Canada Geol. Sur., Bull. 91, 57 pp., 12 pls., 2 text-figs.

Jones, T. R.

1887. *Notes on the Paleozoic bivalved Entomostraca. No. XXIV. On some Silurian genera and species* (continued). Ann. Mag. Nat. Hist., ser. 5, vol. 19, pp. 400-416, pls. 12, 13.

Jones, T. R., and Holl, H. B.

1869. *Notes on the Paleozoic Entomostraca.* No. IX. *Some Silurian species.* Ann. Mag. Nat. Hist., ser. 4, vol. 3, pp. 211-229, pls. 14, 15, text-figs. 1-7.

Kesling, R. V.

1961. *Family Thlipsuridae.* Pp. Q377-Q380, text-figs. 304-307, *in* Benson, R. H., and others. *Arthropoda 3. Part Q,* Treatise on Invertebrate Paleontology (R. C. Moore, Editor), Univ. Kansas Press and Geol. Soc. America.

Krandijevsky, V. S.

1963. *Fauna ostrakod silurijskich vidkladiv Podillia.* Akad. Nauk. Ukr. SSR, Inst. Geol. Nauk, pp. 1-149 (in Russian).

1968. *Revision of the Family Thlipsuridae Ulrich (Ostracoda).* Pp. 63-79, pl. 11, *in* Krandijevsky, V. S., Ishchenko, T. A., Kiryanov, *V. V. Paleontology and straigraphy of the lower Paleozoic of Volyn-Podolia,* Acad. Nauk Ukr. SSR, Inst. Geol. Nauk (in Russian).

Krause, A.

1891. *Beitrag zur Kenntnis der ostrakoden-Fauna in Silurischen Diluvialgeschieben.* Deutsch. Geol. Ges. Zeitschr., vol. 43, No. 2, pp. 488-529.

Kummerow, E.

1924. *Beitrage zur Kenntnis der Ostracoden und Phyllocariden aus nordischen Diluvialgeschieben.* Preuss. Geol. Landesanst., Jahrb., vol. 44, pp. 405-448.

Lundin, R. F.

1965. *Ostracodes of the Henryhouse Formation (Silurian) in Oklahoma.* Oklahoma Geol. Sur., Bull. 108, 104 pp., 18 pls., 45 text-figs.

1968. *Ostracodes of the Haragan Formation (Devonian) of Oklahoma.* Oklahoma Geol. Sur., Bull. 116, 121 pp., 22 pls., 51 text-figs.

Lundin, R. F., and Newton, G. D.

1970. *Ostracoda and the Silurian stratigraphy of Northwestern Alabama.* Alabama Geol. Sur., Bull. 95, 51 pp., 7 pls., 6 text-figs.

Morris, R. W., and Hill, B. L., Jr.

1952. *New Ostracoda from the middle Silurian Newsom Shale of Tennessee.* Bull. Amer. Paleont., vol. 34, pp. 131-148, pls. 9, 10.

Neckaja, A. I.

1958. *Novye vidy i rody ostrakod ordovika i Silura Severo-Zapada Russkoi platformy, in Voprosy sistematiki i opisanie novykh vidov,* *rodov i podsemeistv Foraminifer i ostrakod, sbornik IX of Microfauna SSSR. Vses. Neft. Nauchno-Issled Geol.-Razved.* Inst. (VNIGRI), Trudy, new ser., No. 115, pp. 349-373, 3 pls. (in Russian).

Polenova, E. N.

1958. *New genera and species of Ostracoda,* p. 261, pl. 3, figs. 6a, b, *in* Abushik, A.F., and others. Microfauna SSR, vol. 9, All-Union Sci.-Res. Geol.-Prosp. Petrol. Inst. (VNIGRI), new series, No. 115, pp. 232-287, pls. 1-6 (in Russian).

Polenova, E. N., and Zaninia, I. E.

1960. *Superfamily Thlipsuridacea.* Pp. 334-336, text-figs. 847-854, *in* Zanina, I. E., Polenova, E. N., and others. Volume VIII, *Arthropoda, Trilobitomorpha and Crustacea.* Foundations of Paleontology USSR. Handbook for paleontologists and geologist USSR, Moscow (in Russian).

Roth, R. I.

1929. *Some ostracodes from the Haragan Marl, Devonian, of Oklahoma.* Jour. Paleont., vol. 3, pp. 327-372, 4 pls.

Swartz, F. M.

1932. *Revision of the ostracode family Thlipsuridae, with descriptions of new species from the lower Devonian of Pennsylvania.* Jour. Paleont., vol. 6, pp. 36-58, pls. 10, 11.

Swartz, F. M., and Swain, F. M.

1941. *Ostracodes of the Middle Devonian Onondaga beds of central Pennsylvania.* Geol. Soc. America, Bull., vol. 52, pp. 381-457, pls. 1-8, 2 text-figs.

Ulrich, E. O.

1894. *The lower Silurian Ostracoda of Minnesota.* Pp. 629-693, pls. 43-46, text-figs. 46-52, *in* Ulrich, E. O. and others. *The geology of Minnesota.* Minnesota Geol. Nat. Hist. Sur., Rept., vol. 3, pt. 2.

Ulrich, E. O., and Bassler, R. S.

1913. *Ostracoda,* Pp. 513-542, pls. 95-98, *in* Swartz, C. K., and others. *Systematic paleontology of the lower Devonian deposits of Maryland.* Maryland Geol. Sur., Lower Devonian volume.

1923. *Paleozoic Ostracoda: Their morphology, classification and occurrence.* Pp. 271-391, text-figs. 11-26, *in* Swartz, C. K., and others. Maryland Geol. Sur., Silurian volume.

Wilson, C. W., Jr.

1935. *The ostracode fauna of the Birdsong Shale, Helderberg, of western Tennessee.* Jour. Paleont., vol. 9, pp. 627-646, pls. 77-78.

Robert F. Lundin
and Lee E. Petersen
Department of Geology
Arizona State U.
Tempe, Arizona 85281

DISCUSSION

Dr. F. M. Swartz: I was very pleased to have this paper read. It provides another example of the value of reillustration of type examples of a classical species.

ADDENDUM

During preparation of this paper we were not aware of the work of Gailite (1967)*. In this paper she has placed *Thlipsura simplex* Krause, 1891 and *T. personata* Krause, 1891 in a new genus *Scaldianella* Gailite, 1967. She established another new genus, *Hebellum* Gailite, 1967, in which she placed *T. tetragona* Krause, 1891. Table 1 shows that Krandijevsky (1968) placed all of these species in *Krausellina* Krandijevsky, 1968.

Gailite (1967) described two new species *T. lubrica* Gailite, 1967 and *T. panda* Gailite, 1967. We are familiar with these species only through Gailite's (1967) illustrations but agree that both are species of *Thlipsura*.

***Gailite, L. K.**

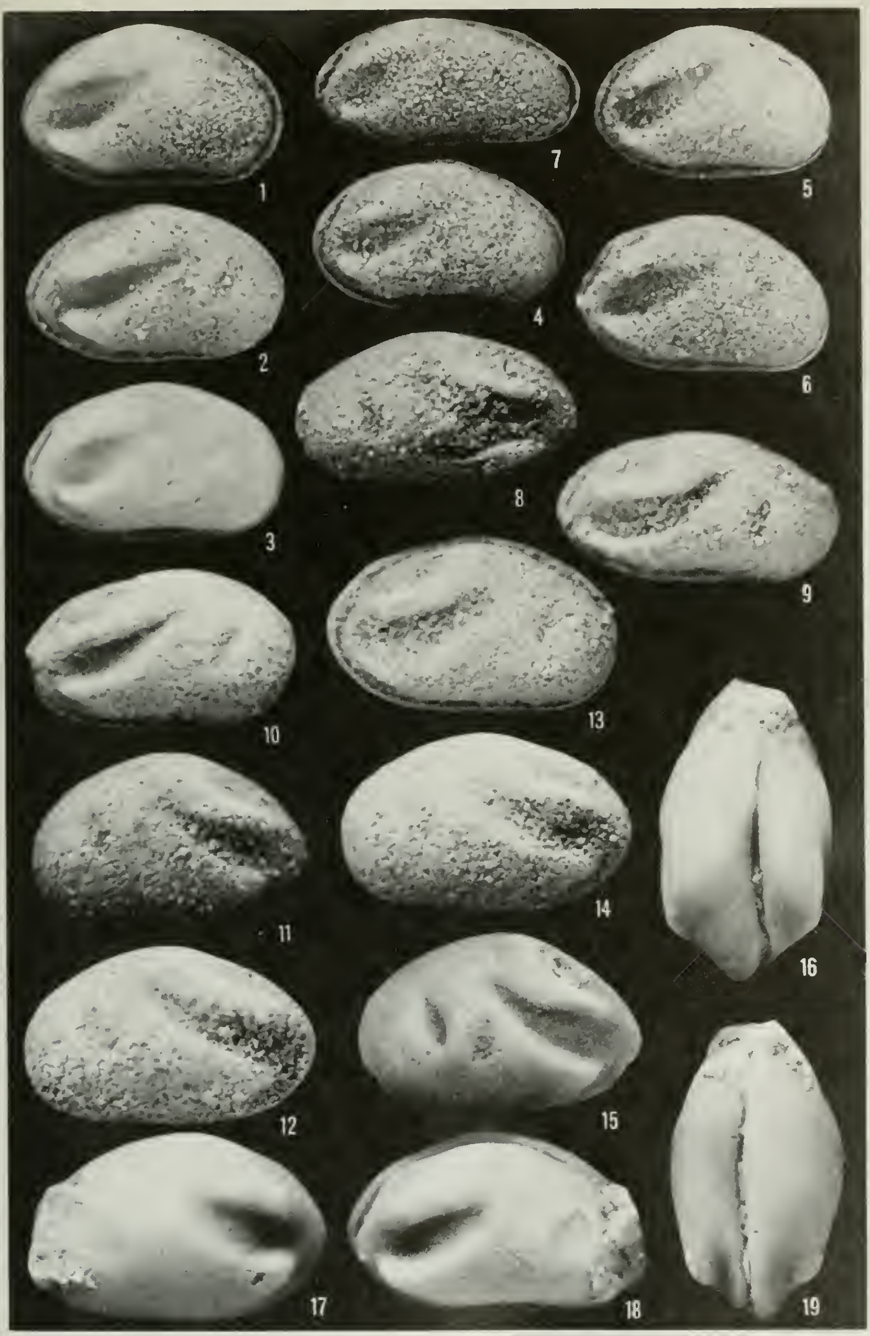
1967. *Opisanie ostrakod.* Pp. 89-168, pls. 1-13, *in* Gailite, L. K., Pybnikova, M. B., and Ulste, P.Zh. *Stratigrafiya, fauna i usloviya obrazovaniya silurijskikh porod srednej Pribaltiki.* Isdatel'stuv "Zinatne", Riga, (in Russian).

EXPLANATION OF PLATE 1

(All figures × 30)

Figure		Page
1-19.	**Thlipsura corpulenta** Jones and Holl	93

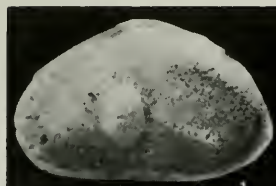
1-3, 5-6. Right lateral views of adult carapaces showing variations in surface morphology. Wenlock Limestone, Lincoln Hill, England. A.S.U. X-24, X-25, X-22, X-21, X-23. 4, 7. Right lateral views of two adult carapaces. Wenlock Limestone, Much Wenlock, England. A.S.U. X-26, X-27. 8-9. Left lateral and right lateral views of type specimen of *Thlipsura plicata* var. *bipunctata* Jones. Shales over Wenlock Limestone, England. BMNH In 52413. 10-12. Right lateral view of carapace, lateral view of left valve, and left lateral view of carapace of type specimens of *Thlipsura angulata* Jones. Shales over Wenlock Limestone, England. BMNH I 1923. 13-14. Right lateral and left lateral views of carapace of type specimen of *Thlipsura plicata* Jones. Shales over Wenlock Limestone, England. BMNH IN 52410. 15. Lateral view of left valve showing well-developed anterior depression. Woolhope beds, near Malvern, England. BMNH I 2077. 16-19. Lectotype. Dorsal, left lateral, right lateral, and ventral views of type specimen. Woolhope beds, near Malvern, England. BMNH I 2059.

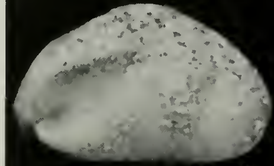

1
7
5
4
2
6
8
3
9
13
10
16
14
11
15
12
19
17
18

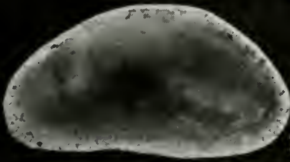
EXPLANATION OF PLATE 2

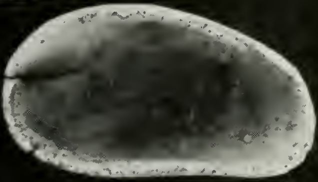
(All figures × 30 unless designated)

Figure		Page
1-2.	**Thlipsura corpulenta** Jones and Holl Left lateral and right lateral views of adult carapace identified as *Thlipsura tuberosa* Jones and Holl. Outer shell of left valve has been removed exposing internal mold. Node is reflection of the interior depression. England. BMNH I 1925.	93
3-4.	**"Thlipsurella" fossata** (Roth) Interior views of adult right valve and adult left valve showing hinge and orientation of hinge. × 24. Haragan Formation (Devonian), Oklahoma. ASU X-18, X-17.	91
5-14.	**Thlipsura,** n. sp. 5. Right lateral view of instar III carapace. 6. Left lateral view of instar II carapace. 7-8. Right lateral and left lateral views of adult carapace. 9. Left lateral view of adult carapace. 10-12. Left lateral, right lateral, and dorsal views of adult carapace. 13-14. Ventral and right lateral views of adult carapace. Buildwas beds, along River Severn, Buildwas, Shropshire, England. ASU X-20, X-19, X-15, X-16, X-13, X-14.	95

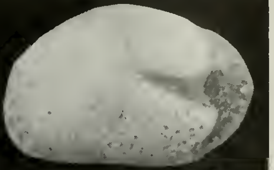

1

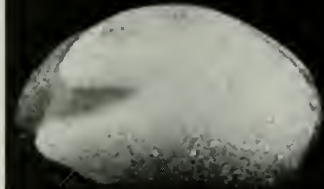

2

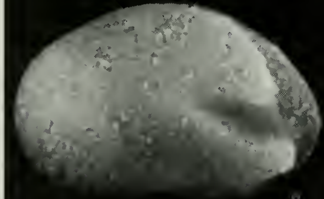

3

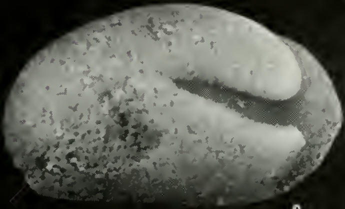

4

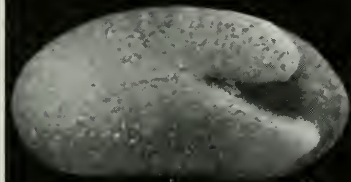

5

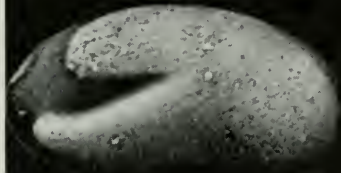

6

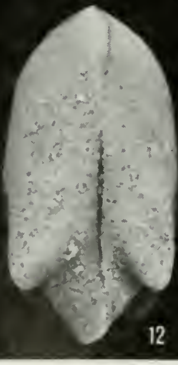

7

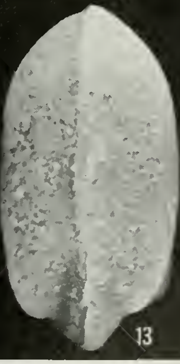

8


9


10


11


12


13


14

Explanation of Plate 3

(All figures × 40)

Figure	Page

1-3. **Thlipsura** sp. B (Lundin and Newton) 92

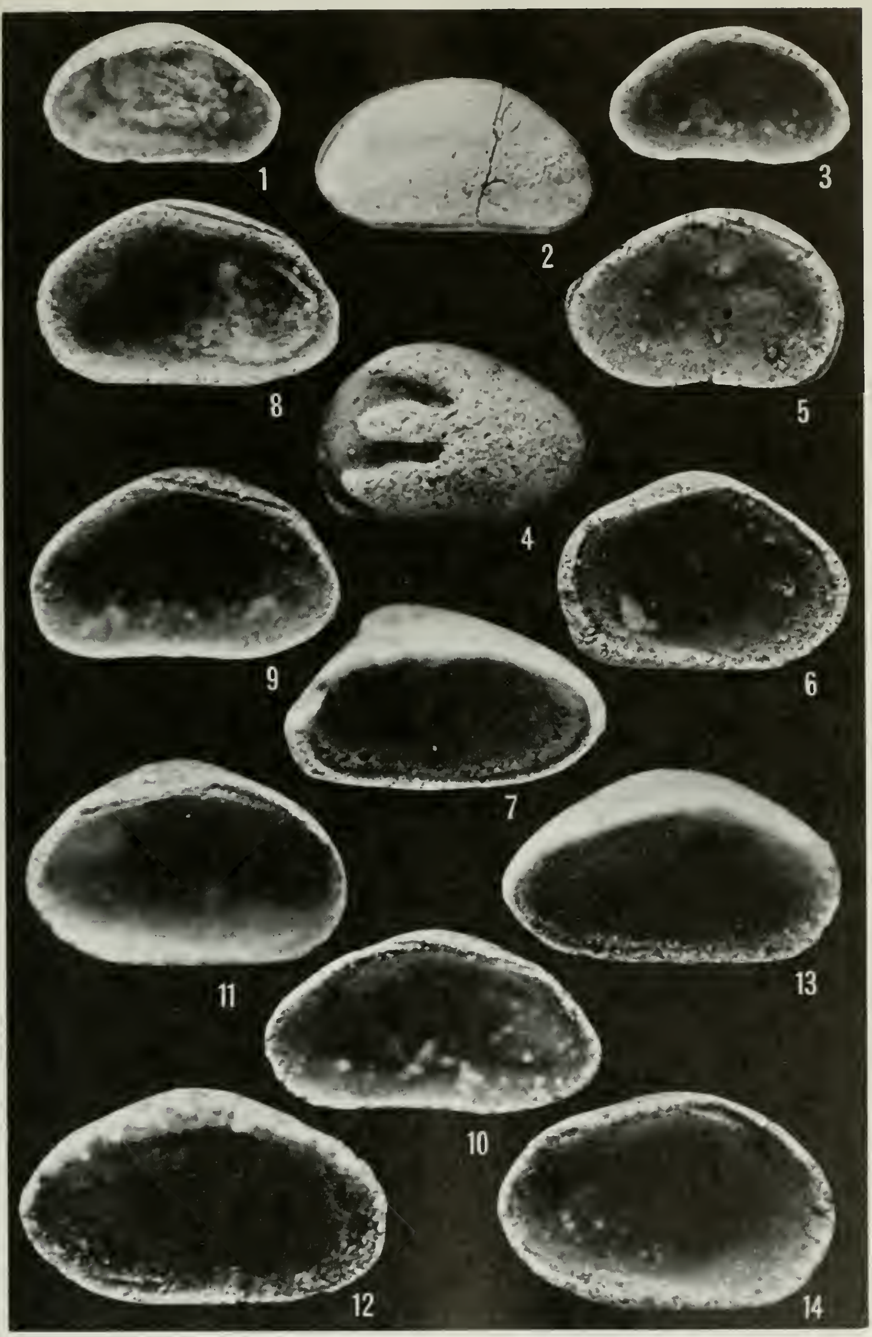
1. Oblique interior view of adult left valve. Posterior portion of hinge list is broken. 2. Right lateral view of of adult carapace. 3. Interior view of adult right valve. Brownsport Formation (Silurian), Tennessee. ASU X-12, X-10, X-11.

4-7. **Neothlipsura furca** (Roth) 91

4-5. Right lateral and interior views of adult right valve. Note hinge groove and contact list. 6. Interior view of adult left valve showing hinge list and contact groove. 7. Oblique interior view of adult left valve showing contact groove along venter. Birdsong Formation (Devonian), Tennessee. ASU X-9, X-8, X-7.

8-14. **Thlipsura corpulenta** Jones and Holl 93

8-10. Matrix obscures posterior portion of figure 8. Interior views of adult right valves showing hinge groove. 11. Oblique interior view of adult left valve showing merging of grooves at posterior and anterior ends of hinge nearly splitting the hinge list. 12. Oblique interior view of adult left valve showing poorly developed posterior stop ridge. 13-14. Oblique interior and interior views of adult left valve. Oblique view shows interior depression marking position of adductor muscle. Interior view shows hinge list. Note weak contact groove. Wenlock Limestone, Lincoln Hill, England. A.S.U. X-6, X-5, X-3, X-2, X-4, X-1.


1
2
3
8
5
4
9
6
7
11
13
10
12
14

Explanation of Plate 4

(All figures × 40 unless designated)

Figure Page

1-3. **Neothlipsura primitiva** (Roth) 91

Interior view of adult left valve showing hinge list and contact groove and right lateral and oblique interior view of adult right valve. Note hinge groove on right valve. × 48. Henryhouse Formation (Silurian), Oklahoma. ASU X-29, X-28.

4-7. **Thlipsurella multipunctata** (Ulrich and Bassler) 90

Holotype. Right lateral, left lateral, ventral and dorsal views of adult carapace. Lower Oriskany, West Virginia. USNM 53381.

8. **Neothlipsura thyridioides** (Swartz and Swain) 91

Holotype. Right lateral view of external mold of adult right valve. Onondaga beds, West Virginia. PSU 108-2.

9. **Neothlipsura whiteavesi** (Copeland) 91

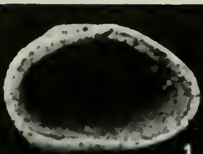
Holotype. Right lateral view of adult carapace. Dalhousie beds, New Brunswick. GSC 14519.

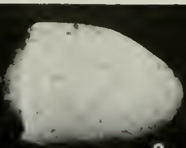
10-13. **Neothlipsura furcoides** (Bassler) 91

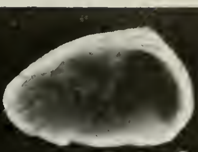
10, 11, 13. Interior, oblique interior, and left lateral views of adult left valve. Note hinge list and uninterrupted contact groove. Hinge list is chipped. 12. Interior view of adult right valve showing hinge groove and contact list. × 32. Camden Formation, Tennessee. USNM 101035.

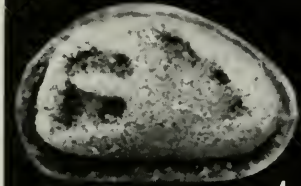
14-15. **Neothlipsura confluens** (Swartz) 91

Photographical replica of external molds of adult left and right valves. Photographs are prints of positive slides made from negatives of the molds. × 32. Shriver Chert, Pennsylvania. USNM 86495.


1


2

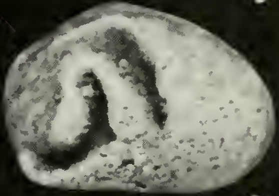

3


4

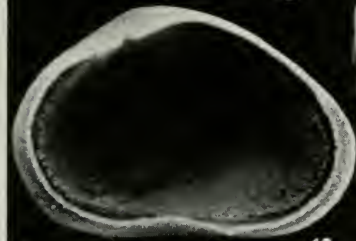

6

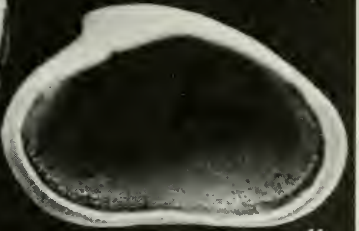

8

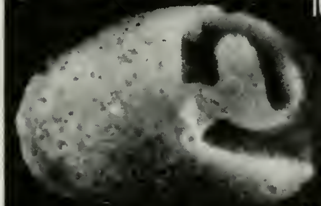

5

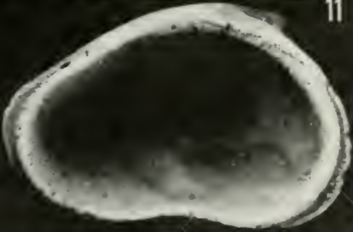

9


7


10


11


14


12


15


13

QUANTITATIVE ANALYSIS OF DIMORPHISM IN *CARBONITA HUMILIS* (JONES AND KIRKBY)

Martin J. M. Bless
Geological Bureau
Heerlen, Netherlands
and
John E. Pollard
University of Manchester, England

ABSTRACT

Carbonita humilis (Jones and Kirkby) is a non-marine ostracode, occurring throughout the Westphalian of Western Europe, the Pennsylvanian of the United States, and the Upper Carboniferous of the Maritime Provinces of Canada.

In 1966 Pollard postulated sexual dimorphism for this species, distinguishing males and females by differences in H/L-ratios, lateral and dorsal outlines.

A quantitative study of two populations of *C. humilis* (one from the Upper Westphalian A of The Netherlands, and one from the Lower Westphalian C of Great Britain) shows that adult specimens may be differentiated according to sex by using dorsal outline, H/L-ratios and W/L ratios in some cases. However, variability of each sex may be greater than the average difference between them. These facts, when considered in the light of published work on Recent ostracodes, pose the question as to whether reproduction in *C. humilis* was syngamic, parthenogenetic, or variable depending on environment.

ZUSAMMENFASSUNG

Carbonita humilis (Jones und Kirkby) ist ein Süsswasserostracode, der im Westfal Westeuropas, im Pennsylvanian der Vereinigte Staaten, und im Oberkarbon Kanadas vorkommt.

Im 1966 wurde von Pollard Sexualdimorphismus in dieser Art nachgewiesen. Er fand männliche und weibliche Individuen mit unterschiedlichen H/L-Ratio und Dorsalumriss.

Ein quantitatives Studium von zwei Populationen von *C. humilis* — eine aus dem Oberwestfal A der Niederlanden, die andere aus dem Unterwestfal C Grossbritanniens — hat gezeigt, dass adulte Männchen und Weibchen sich voneinander unterscheiden können durch ihre Dorsal- und Seitenumriss, und durch ihre H/L- und W/L-Ratios. Die Variabilität innerhalb einer Dimorph kann aber grösser sein als der mittlere Unterschied zwischen den zwei Dimorphen. Diese Tatsachen rufen die Frage auf — vor allem wenn man die Arbeiten über rezente Ostracoden besieht — ob die Fortpflanzung in *C. humilis* syngam, parthenogenetisch oder variabel (abhängig der Fazies) war.

INTRODUCTION

Carbonita humilis (Jones and Kirkby, 1879) is one of the most common and widespread non-marine ostracodes from the Upper Carboniferous. This species has been recognized in Westphalian sediments of Great Britain, France, Belgium, The Netherlands, Germany, and Spain but is also known from Pennsylvanian strata of the United States and the Upper Carboniferous of the Maritime Provinces of Canada. It is a medium-sized, subovate ostracode of variable size and outline. Because of this often not recognized variation, several "species" have been erected in the course of the past 90 years, which were distinguished by slightly different shape and dimensions. The discovery of two ostracode bands with abundant and relatively well-preserved specimens from the Westphalian of Great Britain and The Netherlands has enabled the authors to study the variation within this species (Bless and Pollard, 1972). It has been shown that the variation of the lateral outline can best be expressed by using three parameters: H/L-ratio, degree of arching of the dorsum and relative position of maximum height. Also the dorsal outline is variable. This is shown by examination of the W/L-ratio and relative position of maximum width.

Pollard (1966) postulated sexual dimorphism in this species. He distinguished males and females by means of H/L-ratio and dorsal and lateral outline. Dimorphism was also postulated for *Carbonita inflata* by Anderson (1970), but we are still not sure if this latter species should be included as an extreme variant in *C. humilis*. According to Pollard and Anderson, sexual dimorphism in *Carbonita* is of domiciliar type, one dimorph being distinguished from the other by a more swollen posterior part of the carapace. Indeed, many specimens in any studied assemblage of *C. humilis* show this in dorsal view convincingly. On the other hand, qualitative studies do not show always a direct relationship between the different dorsal shape and the H/L-ratio or lateral shape. The present report contains a quantitative analysis of the possible relationship between these characters by means of pictographs, graphs, and statistical analysis of measurements.

Only univarate statistics have been applied because our study was confined to adult specimens. The following abbreviations are used for statistical parameters in this report: N (Number of specimens measured), $\overline{L}$ (mean length), $\overline{H}$ (mean height), $\overline{W}$ (mean width) $\overline{V}$ (mean volume, approximated as the product of ½x$\overline{L}$x$\overline{H}$x$\overline{W}$), $\overline{H}/\overline{L}$ (mean height/length ratio), $\overline{W}/\overline{L}$ (mean width/length ratio), OR (observed range for the length), S (standard deviation of length), S (standard deviation of height), v (variation coefficient of length), s (standard error of mean length), t (Student-t value). For the computation of parameters the reader is referred to Imbrie (1956) and Marsal (1967).

SYSTEMATIC DESCRIPTION

Carbonita humilis (Jones and Kirkby, 1879)

Pl. 1, figs. 1a-f; Pl. 2, figs. 3-9

1879. *Carbonia fabulina* var. *humilis* Jones and Kirkby, Ann. Mag. Nat. Hist., ser. 5, vol. 4, p. 31, pl. 2, fig. 14.

1879. *Carbonia fabulina* var. *inflata* Jones and Kirkby, *idem.,* p. 31, pl. 2, figs. 15-19.

1884. *Carbonia fabulina* Jones and Kirkby, Geol. Mag., ser. 3, vol. 1, p. 358, pl. 12, figs. 9a-d.

1889. *Carbonia fabulina* var. *altilis* Jones and Kirkby, Geol. Mag., ser. 3, vol. 6, p. 270, text-fig. 114.

1930. *Cytherella foveolata* Wright, Proc. Manchester Lit. Phil. Soc., Mem., vol. 74, p. 49, pl. 1, figs. 2-2b.

1955. *Whipplella cenisa* Kremp and Grebe, Geol. Jb., vol. 71, pp. 152-155, pl. 16, figs. 3, 4.

1955. *Whipplella rhenana* Kremp and Grebe, idem., pp. 155-157, pl. 16, figs. 5, 6.

1957. *Carbonita altilis* Copeland, Geol. Surv. Canada, Mem., 286, p. 25, pl. 1, figs. 1-3, 15-18.
1957. *Carbonita inflata* Copeland, *idem.*, p. 26, pl. 1, figs. 12-14, pl. 2, figs. 18, 19.
1966. *Carbonita humilis* Pollard, Palaeontology, vol. 9, pp. 683-685, text-fig. 6.
1967. *Whipplella cenisa* Bless, Freiberger Forschungschefte, C213, p. 162.
1967. *Whipplella rhenana* Bless, *idem.*, p. 162, pl. 1, figs. 10, 10a, pl. 2, figs. 10, 13.
1970. *Carbonita humilis* Anderson, Geol. Sur. Great Britain, Bull. 32, pp. 87-90, pl. 15, figs. 32-37, pl. 19, fig. 95.
1970. *Carbonita inflata* Vangerow, Palaeontographica, Abt. A, vol. 134, pp. 47, 48, pl. 13, figs. 14-20.
1972. *Carbonita humilis* Bless and Pollard, Meded. Rijks Geol. Dienst., N.S. 24, pp. 17-21, enclosures 2, 3, pl. 3, figs. 6-9, pl. 4, figs. 1-10, pl. 5, figs. 1-6, preprint available.

Diagnosis. — Medium-sized, subovate *Carbonita* with rounded ends, gently arched to flattened dorsum, venter straight to convex, cardinal angles may be distinct, prominent dorsal groove between the valves, surface punctate. Distinct muscle-scar and vertical furrows on both sides of the muscle-scar, the posterior one being more prominent.

Remarks. — As stated by Bless and Pollard in press, there exists considerable confusion in the literature about the distinction of species within the genus *Carbonita*, and even the genus is often poorly defined. This has resulted in an avalanche of names at the generic level and specific level.

We believe, that *C. humilis* is distinguished from typical *C. fabulina* by the more subtriangular lateral outline of the latter. However, extreme variants of these species may be confused. We suppose *C. humilis* to be a direct descendant from *C. fabulina*. *C. inflata* is less easily distinguished from variants of *C. humilis*. Unfortunately, this is a rare form, and statistical methods for the separation of *C. inflata* as a species in its own right cannot be used up to now. Anderson (1970) apparently confused *C. altilis* with *"Gutschickia" bretonensis* Copeland. Typical *C. altilis* as described and figured by Jones and Kirkby (1889) and by Copeland (1957), is very similar to typical *C. humilis*. Therefore, *C. altilis* is here included in *C. humilis*. American non-marine ostracodes from the Pennsylvanian, referred to as *e.g. Cypridopsis fabulina* (Scott and Summerson, 1943), *Whipplella carbonaria* (Scott, 1944), *Carbonita magma*, *C. inflata*, *Gutschickia ovata* (all described by Cooper, 1946) are most probably conspecific with *C. humilis*. We refer to them as "*C. humilis* group".

VARIATION AND DIMORPHISM

General. — Already in 1879 Jones and Kirkby (pl. 2, figs. 11-14) showed the variation in shape of *C. humilis*, figuring specimens with different positions of maximum height. Kremp and Grebe (1955) distinguished between *Whipplella cenisa* and *W. rhenana* (both considered here to be conspecific with *C. humilis*) because of differences in the relative position of maximum width and different H/L-ratios. Pollard (1966) was the first to postulate that these differences noted by Kremp and Grebe should be related to dimorphism. He stated that the supposed males were elongate-ovate in lateral outline, H/L ratio about .60, and had maximum height and width median, whilst the supposed females were subovate in lateral view, H/L ratio about .70, and had greatest height and width posterior of the middle. Unfortunately, his qualitative description was not supported by quantitative data.

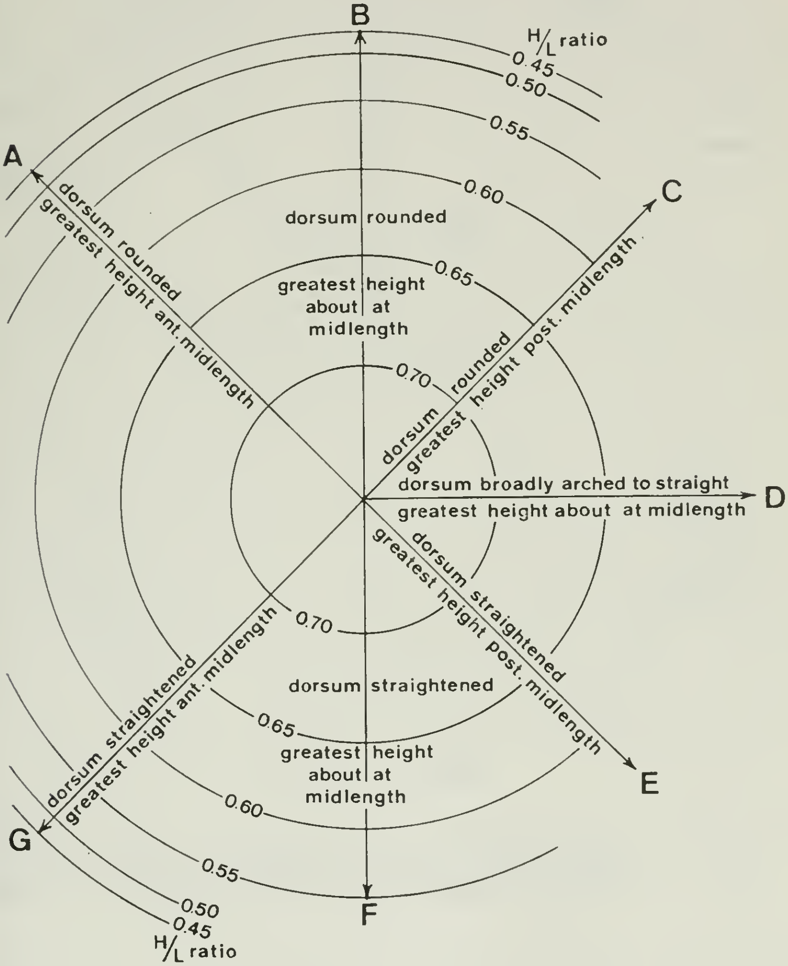
Examination of specimens from several horizons and locations of the Westphalian in NW Europe showed that the characters used by Pollard (1966) for the distinction of dimorphs may vary independently. In other words, dimorphs cannot be distinguished unless only one constant parameter is used. This observation renewed discussion about the value of such a parameter for the distinction of dimorphs. Moreover, a recent study on a living parthenogenetic fresh-water ostracode by Szczechura (1971) showed that the parameters used by Pollard for the distinction of dimorphs may vary because of seasonal influences. She noted variability in relative position of maximum width and height, absolute size of adults and shape. She pointed out that the differences noted might well have been explained as dimorphism, if it were not known from her observations that only female specimens were present. Thus, the parameters in Pollard's paper are not necessarily related to dimorphism.

K. G. McKenzie (personal communication) states that size-ranges in recent dimorphic freshwater ostracodes which he studied, do not or only slightly overlap, if the specimens are collected alive. But when dealing with fossils size overlaps are common because several generations may be preserved in the same layer of sediment. He suggests, therefore, that "for fossils, shape characteristics must be used, and, usually, these are easy to determine for individual species with a little experience". The unreliability of size as specific for dimorphic character in fossil ostracodes has also been pointed out by several other ostracode workers.

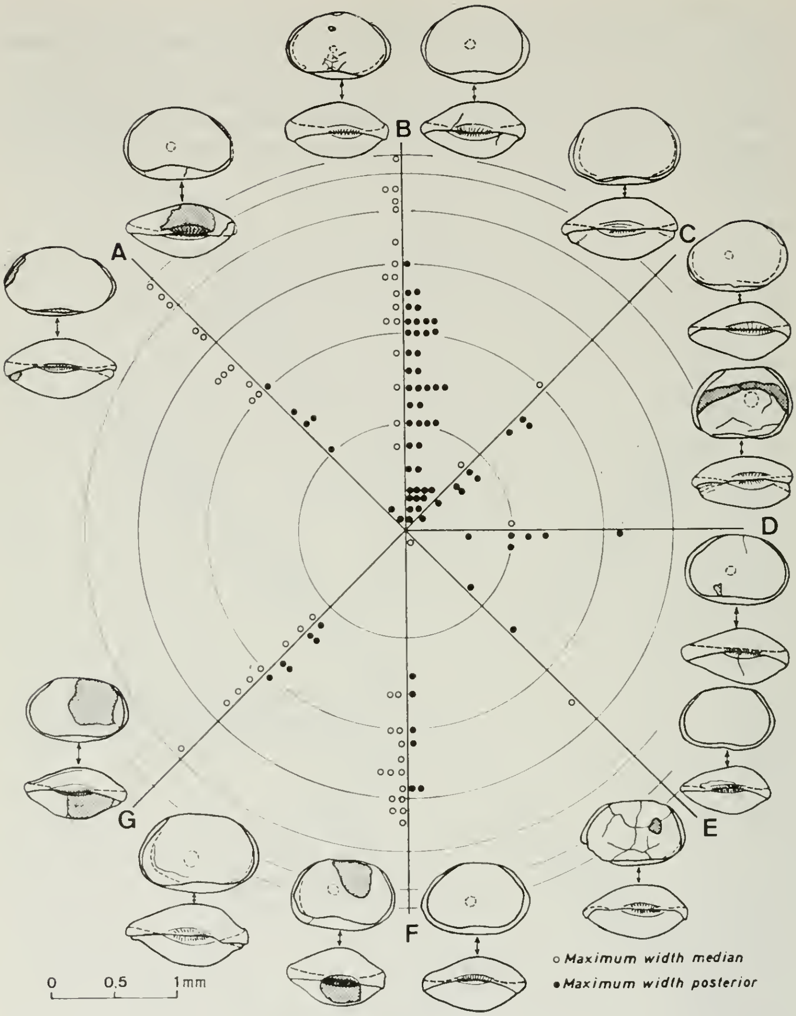
Summarizing the above experiences and opinions we find that the recognition of sexual dimorphism in fossil podocopids is a problem, because differences in shape, size and form-ratios may occur in parthenogenetic as well as in syngamic species. Especially the distinction of dimorphs by only one character seems questionable. Therefore, we have tried to determine the possible relationship between characters useful for this purpose.

First of all, we selected two relatively well-preserved assemblages of *C. humilis,* one from the G. B. 25 Band (Upper Westphalian A) of the Netherlands, and the other from the *foveolata* Band (Lower Westphalian C) of England. For a detailed description of these assemblages the reader is referred to Bless and Pollard (1972). One hundred and thirty-five specimens from the G. B. 25 Band, and 71 from the *foveolata* Band were then measured, and camera lucida drawings (scale 50:1) of left lateral and dorsal views made. The measurements included length, height and width. Also the relative position of maximum width and height, and the relative arching of the dorsum were determined. All these characters are variable and described below for the G. B. 25 Band. In specimens from the *fovelata* Band the arching of the dorsum and the relative position of maximum height appeared to be constant. Therefore, no further study was made of these two characters for the *foveolata* Band material.

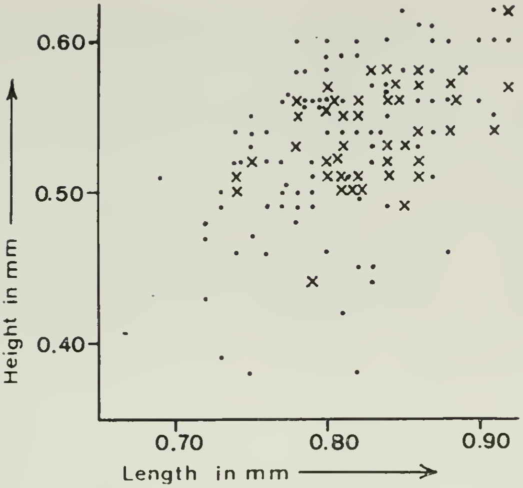
G. B. 25 Band. — The relationships between relative position of maximum height, relative position of maximum width, relative arching of the dorsum (as a function of variation of the lateral shape) and H/L-ratio for specimens from G. B. 25 Band is shown in a pictograph (Text-fig. 1b). The pictograph is explained in fig. 1a. One can immediately conclude that the relative position of maximum height is not related to dimorphism but is best considered to be related to the individual.



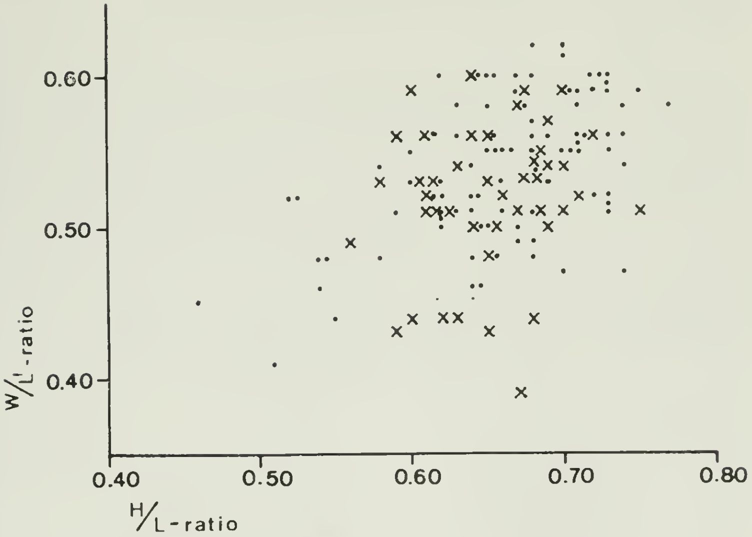
Text-fig. 1a. Variation diagram for *Carbonita humilis* from G. B. 25 Band; explanation of Text-fig. 1b.



Text-fig. 1b. Variation diagram of *Carbonita humilis* from G. B. 25 Band (Upper Westphalian A), The Netherlands, showing relationship between relative position of maximum width, relative position of maximum height, relative arching of dorsum and H/L-ratio.



Text-fig. 2a. Height vs. length diagram for *Carbonita humilis* from G. B. 25 Band.
. specimens with rounded dorsum
x specimens straightened dorsum



Text-fig. 2b. Diagram of ratios W/L' vs. H/L for *Carbonita humilis* from G. B. 25 Band.
. specimens with rounded dorsum
x specimens with straightened dorsum

Table 1. Statistical data for *Carbonita humilis* G. B. 25 Band, Upper Westphalian A, The Netherlands
measurements in mm

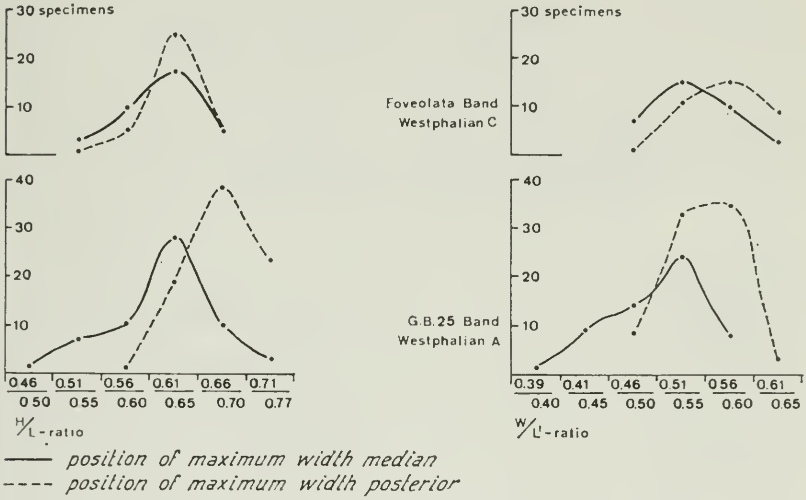
	dorsum straightened	dorsum rounded	t*
N	44	91	
$\bar{L}$	0.83	0.81	1.98
$\bar{H}$	0.54	0.53	2.61
$\bar{W}$	0.43	0.43	——
$\bar{V}$	0.095963	0.092299	
$\bar{H}/\bar{L}$	0.65	0.66	-0.99
$\bar{W}/\bar{L}$	0.52	0.54	-2.34
OR_L	0.74-0.92	0.69-0.92	
S_L	0.04	0.05	
S_H	0.03	0.05	
v	4.34	6.17	
s	0.0060	0.0052	

*Student-t (d.f. = 133) = 1.98 (95 percent confidence level)
Student-t (d.f. = 133) = 2.61 (99 percent confidence level)

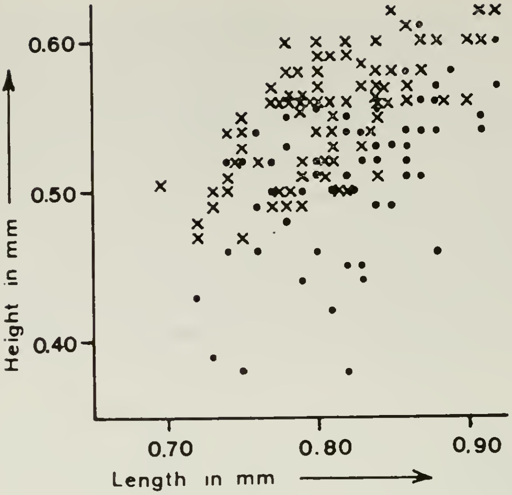
The relative arching of the dorsum may appear a more promising character when surveying the pictograph. Variability of H/L-ratio is less for specimens with a more or less straightened dorsum than for those with a more rounded dorsum. (Compare variation Series SW and S with Series NW and N). In the latter group the percentage of specimens with maximum width posterior is much higher (66% against 36% in the first group). However, plotting of specimens with straightened dorsum against specimens with rounded dorsum in a height vs. length diagram or W/L vs. H/L-diagram (Text-figs. 2a, 2b) does not reveal a marked separation between these points. Univariate analysis of the measurements for these two groups (Table I) reveals that there is no significant difference between the H/L-ratios, nor between the heights. There is a more significant difference (significant at the 5 per cent level) between the length and W/L-ratios for these groups. Only the difference between the heights is significant at the 1 per cent level. Because the relative arching of the dorsum remains constant (dorsum broadly arched) in the other assemblage from the *foveolata* Band, we feel that this character can hardly be used for the distinction of dimorphs.

The relative position of maximum width has been determined in terms of maximum width median and maximum width posterior. In the very few cases, where the maximum width was anterior this has been put in our computations as being median. The pictograph shows that specimens with maximum width median have a different H/L-ratio range than those with maximum width posterior. This is easily shown in a frequency polygon (Text-fig. 3, lower part), but also in a height vs. length and W/L-vs. H/L-ratio diagrams (figs. 4a and b). Univariate analysis of the measurements (Table II) indicates that the differences between the height, width, H/L- and W/L-ratios for these two groups are significant at the 1 per cent level. Only the difference for the length is not significant. The relative position of maximum width appears to be, therefore, a reliable character for the distinction of dimorphs in the G. B. 25 Band assemblage.

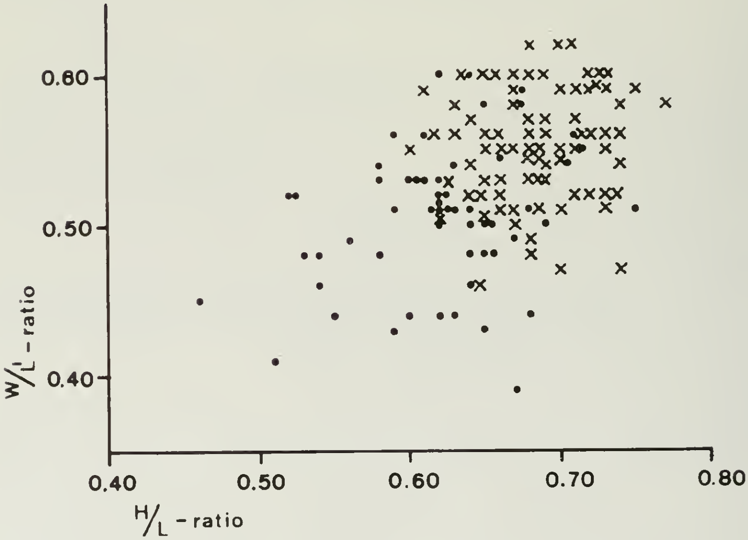
No pictograph has been made for the *foveolata Band* assemblage, because only two characters (relative position of maximum width and H/L-ratio) have been studied. As already explained above, the other characters are not believed to have any value for the distinction of dimorphs.



Text-fig. 3 Frequency polygon, showing relationship between position of maximum width and H/L and W/L'-ratios for *Carbonita humilis*.
——— maximum width median
.... maximum width posterior



Text-fig. 4a. Height vs. length diagram for *Carbonita humilis* from G. B. 25 Band.
. specimens with maximum width median
x specimens with maximum width posterior



Text-fig. 4b. Diagram of ratios W/L' vs. H/L for *Carbonita humilis* from G. B. 25 Band.
. specimens with maximum width median
x specimens with maximum width posterior

Table 2. Statistical data for *Carbonita humilis* G. B. 25 Band, Upper Westphalian A, The Netherlands
measurements in mm

	greatest width median	greatest width posterior	t*
N	56	79	
$\bar{L}$	0.82	0.81	1.14
$\bar{H}$	0.50	0.55	-7.15
$\bar{W}$	0.42	0.45	-8.89
$\bar{V}$	0.086100	0.100238	
$\bar{H}/\bar{L}$	0.62	0.68	-7.46
$\bar{W}/\bar{L}$	0.51	0.55	-8.09
OR_L	0.72-0.92	0.69-0.92	
S_L	0.05	0.05	
S_H	0.04	0.04	
v	6.07	6.17	
s	0.0067	0.0056	

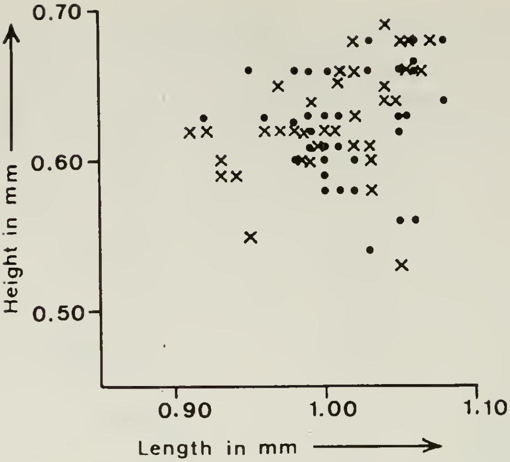
*Student-t (d.f. = 133) = 1.98 (95 percent confidence level)
Student-t (d.f. = 133) = 2.61 (99 percent confidence level)

Plotting of the H/L-ratios against relative position of maximum width in a frequency polygon (Text-fig. 3, upper part) does not show any significant separation, nor does the plotting of the W/L-ratio against the relative position of maximum width. Height vs. length and W/L-vs. H/L-ratio diagrams again do not show any separation for specimens with maximum width median and posterior (Text-figs. 5a, b). Univariate analysis of measurements (Table III) confirms this at least in part. No significant difference has been found for the H/L-ratios, and the differences between the heights, widths and W/L-ratios are only significant at the 5 per cent level. The only difference, significant at the 1 per cent level, is that between the length of these forms. It should be noted, that in the case of the G. B. 25 Band assemblage the only difference not significant was that between the lengths.

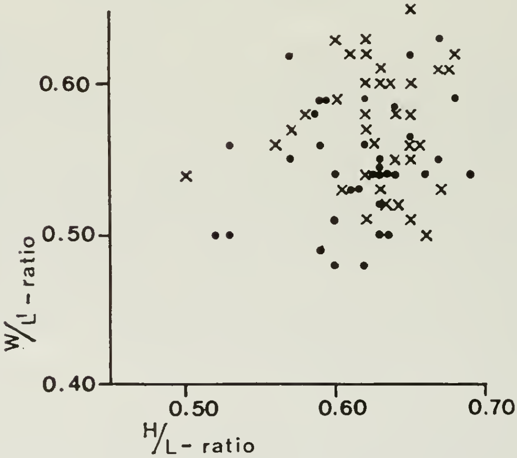
The mean volume ($\frac{1}{2}\ \bar{L}x\bar{H}x\bar{W}$) of the *foveolata* Band specimens is about twice the value of the specimens from G. B. 25 Band (Tables II, III). As ostracodes approximately double in size between instars this fact suggests that there was one more instar of this species present in the *foveolata* Band than at the lower horizon. The question arises, therefore, whether this extra instar is a function of time (stratigraphically speaking) or of environment?

DISCUSSION AND CONCLUSIONS

In the previous section we have seen that the relative position of maximum width may be related to size and size ratios in some assemblages (*e.g.*



Text-fig. 5a. Height vs. length diagram for *Carbonita humilis* from *foveolata* Band.
. specimens with maximum width median
x specimens with maximum width posterior



Text-fig. 5b. Diagram of ratios W/L' vs. H/L for *Carbonita humilis* from *foveolata* Band.
. specimens with maximum width median
x specimens with maximum width posterior

Table 3. Statistical data for *Carbonita humilis* from *foveolata* Band (Lower Westphalian C), England.
measurements in mm

	greatest width median	greatest width posterior	t*
N	35	36	
$\bar{L}$	1.02	1.00	5.26
$\bar{H}$	0.62	0.63	-2.63
$\bar{W}$	0.55	0.57	-2.25
$\bar{V}$	0.173910	0.179550	
$\bar{H}/\bar{L}$	0.62	0.63	-1.11
$\bar{W}/\bar{L}$	0.55	0.57	-2.13
OR_L	0.92-1.08	0.91-1.07	
S_L	0.04	0.04	
S_H	0.04	0.04	
v	3.92	4.00	
s	0.0068	0.0067	

*Student-t (d.f. = 69) = 2.00 (95 percent confidence level)
Student-t (d.f. = 69) = 2.65 (99 percent confidence level)

Westphalian A, Limburg and Durham, England). It is important to discuss whether this character may be related to sexual dimorphism or just to environmental influences.

The work on living fresh-water ostracodes referred to previously (Szczechura, 1791 and McKenzie, personal communication) implies that it can be very difficult to distinguish between domicilial dimorphism and parthenogenetic shape variability in some fossil cyprid ostracodes. Other workers (*e.g.* Morkhoven 1962; Keen, 1972) believe that certain ostracodes apparently may be either syngamic or parthenogenetic depending on environment. Pokorny (1965, p. 477) postulated that the parthenogenetic mode of reproduction may have been advantageous in a stable environment; presumably the reverse would also be true. Both Bate and Swain (discussion of Evenson, in Neale 1969, pp. 493-494) record the appearance of sexual dimorphism in pre-adult instars, or at least at different sizes, in both living and fossil ostracode species. The palaeoecology of these assemblages (Bless and Pollard 1972) suggested that while the faunal associations and fluctuating environment of the G. B. 25 Band are very close to those of the contemporaneous Hopkins Band (Pollard 1966, 1969) the *foveolata* Band was deposited in a more restricted stable environment and so lacks the faunal and lithological successions of the other two Bands.

These above considerations suggest that at the present state of our knowledge there must be at least three possible explanations of the apparent dimorphism we see in *C. humilis* depending on the mode of reproduction of the species and its ecology.

1) *C. humilis* syngamic. Westphalian A faunas show marked sexual dimorphism and wide variability in an earlier instar than the less variable and poorly dimorphic Westphalian C assemblage.

2) *C. humilis* parthenogenetic. In this condition we could explain the Westphalian A faunas as showing wide variability similar to Recent *Cyprinotus incongruens* (Szczechura 1971) and growth arrested at an earlier instar than the less variable *foveolata* Band fauna. Such a difference in variability could be related to the more unstable environment of Westphalian A faunas already indicated by palaeoecology.

3) *C. humilis* either syngamic or parthenogenetic depending on environment. This third possibility combines features of the other two. The G. B. 25 Band assemblage was a syngamic population living in an unstable possibly unfavourable environment producing wide variability and early sexual maturity or dwarfing, while the *foveolata* Band assemblage was a parthenogenetic population which grew to large size in a stable and favourable environment. It is interesting to record that assemblages of *C. "altilis"* (similar to *C. humilis*) of Westphalian B age from Joggins, Nova Scotia, are similar in size and variability to the *foveolata* Band population. They have similar faunal associates, preserved in shell beds which lack faunal or lithological phases, suggesting stable environmental conditions (see Bless and Pollard, 1972, p. 9).

Which of these three or other possibilities is the most likely one we prefer to leave open until further information is available on assemblages of *C. humilis* from other stratigraphic levels.

REFERENCES

Anderson, F. W.
1970. *Carboniferous ostracoda — the genus Carbonita Strand.* Geol. Sur. Great Britain, Bull. 32, pp. 69-121.

Bless, M. J. M., and Pollard, J. E.
1972. *Paleoecology and ostracode faunas of Westphalian ostracode bands from Limburg, The Netherlands and Lancashire, Great Britain.* Meded. Rijks Geol. Dienst, N.S. 24, pp. 1-34, preprint available.

Cooper, C. L.
1946. *Pennsylvanian ostracodes of Illinois.* Illinois Geol. Sur., Bull. 70, pp. 1-177.

Copeland, M. J.
1957. *The arthropod faunas of the Upper Carboniferous rocks of the Maritime Provinces.* Geol. Sur. Canada, Mem. 286, pp. 1-110.

Evenson, C. D.
1969. *Designation of lectotypes of fresh-water species described by Dobbin, 1941 (Ostracoda, Crustacea)* (*in* Neale, 1969, pp. 491-494).

Imbrie, J.
1956. *Biometrical methods in the study of invertebrate fossils.* Am. Mus. Nat. Hist., Bull. vol. 108, pp. 211-252.

Jones, T. R., and Kirkby, J. W.
1879. *Some Carboniferous species belonging to the genus Carbonia Jones.* Ann. Mag. Nat. Hist., ser. 5, vol. 4, pp. 28-40.
1889. *On some Ostracoda from the Mabou Coalfield, Inverness Co., Cape Breton (Nova Scotia).* Geol. Mag., ser. 3, vol. 6, pp. 269-271.

Keen, M. C.
1972. *Sannoisian and some other Upper Palaeogene Ostracoda from north-west Europe.* Palaeontology, vol. 15, pp. 267-325.
Kremp, G., and Grebe, H.
1955. *Beschreibung und stratigraphischer Wert einiger Ostracodenformen aus dem Ruhrkarbon.* Geol. Jb., vol. 71, pp. 145-169.
Marsal, D.
1967. *Statistische Methoden für Erdwissenschaftler.* Schweizer — bart'sche Verlagsbuchhandlung, Stuttgart, pp. 1-152.
Morkhoven, F. P. C. M. Van
1962. *Post-Palaeozoic Ostracoda. Their morphology, taxonomy and economic use.* Elsevier, Amsterdam, vol. 1, 204 pp.
Neale, J. W.
1969. Editor. *Taxonomy, morphology and ecology of Recent Ostracoda.* Olivier and Boyd, Edinburgh, 553 pp.
Pokorny, V.
1965. *Some palaeoecological problems in marine ostracode faunas demonstrated on the Upper Cretaceous ostracodes of Bohemia, Czechoslovakia.* Pubbl. Staz. zool. Napoli, vol. 33 (supl.), pp. 462-479.
Pollard, J. E.
1966. *A non-marine ostracode fauna from the Coal Measures of Durham and Northumberland.* Palaeontology, vol. 9, pp. 667-697.
———
1969. *Three ostracod mussel bands in Coal Measures (Westphalian) of Northumberland and Durham.* Proc. Yorks., Geol. Soc., vol. 37, pp. 239-276.
Scott, H. W.
1944. *Permian and Pennsylvanian freshwater ostracodes.* Jour. Paleont., vol. 18, p. 141-147.
Scott, H. W., and Summerson, C. H.
1943. *Non-marine ostracoda from the Lower Pennsylvania in the southern Appalachians and their bearing on inter-continental correlation.* Am. Jour. Sci., vol. 241, pp. 653-671.
Szczechura, J.
1971. *Seasonal changes in a reared fresh-water species, Cyprinotus (Heterocypris) incongruens (Ostracoda), and their importance in the interpretation of variability in fossil ostracodes.* Bull. Centre Rech. Pau, SNPA, 5 suppl., pp. 191-205.

Martin J. M. Bless,
Geological Bureau,
Akerstraat 86-88,
Heerlen, Netherlands.

John E. Pollard,
Department of Geology,
University of Manchester,
Manchester, England.

DISCUSSION

Dr. R. L. Kaesler: I think finding different sets of characters to be important in different faunas is a very important idea to recognize. It weighs against the outmoded idea that some characters are important at specific taxonomic levels.

Dr. Whatley: I was very interested in the possible dimorphism you have discussed and wonder whether you might consider this as being seasonal in origin. Dr. Wall and I have observed a number of marine and freshwater species which exhibit in the adult stage noticeable changes in size and or shape depending upon at which time of the year the adults reach maturity. For example if within the same species certain individuals winter as adults, others as instars and yet others as eggs, when spring temperatures become sufficiently elevated for development to begin again, the three, what are essentially distinct, races of the population, will each go through its appropriate life cycle without being caught up or catching up with each other. We believe this to be responsible for observable seasonal differences in shape and size in *Cythere lutea* perhaps *Heterocythereis albomaculata* and in certain freshwater cyprids which are as yet not identified.

PLATE I

All photographs of Plates I and II have been made in cooperation with the Working Group on Scanning Electron Microscopy of the University of Amsterdam.

Figure

1. **Carbonita humilis.** Specimen 5, MJMB-collections; G.B. 25 Band, Upper Westphalian A, Emma Colliery, The Netherlands.
    1a: dorsal view (scale = 200 microns).
    1b: oblique antero-dorsal view of left valve (scale = 100 microns).
    1c: left side of shell (scale = 200 microns).
    1d: detail of fig. 1c, showing smooth area reflecting position of muscle scar (scale = 100 microns).
    1e: detail of punctation posterior of muscle-scar area; note "striate" arrangement of punctae (scale = 20 microns).
    1f: detail of punctae in center of fig. 1e (scale = 10 microns).
2. **"Cythere cluthae."** Marine Pleistocene; North Sea Borehole (71H2, B11, 1 meter below substratum. Detail of punctation. Note remarkable resemblance to punctation of *Carbonita humilis*. Photograph by kind permission of A. Du Saar (Haarlem). (Scale = 200 microns).

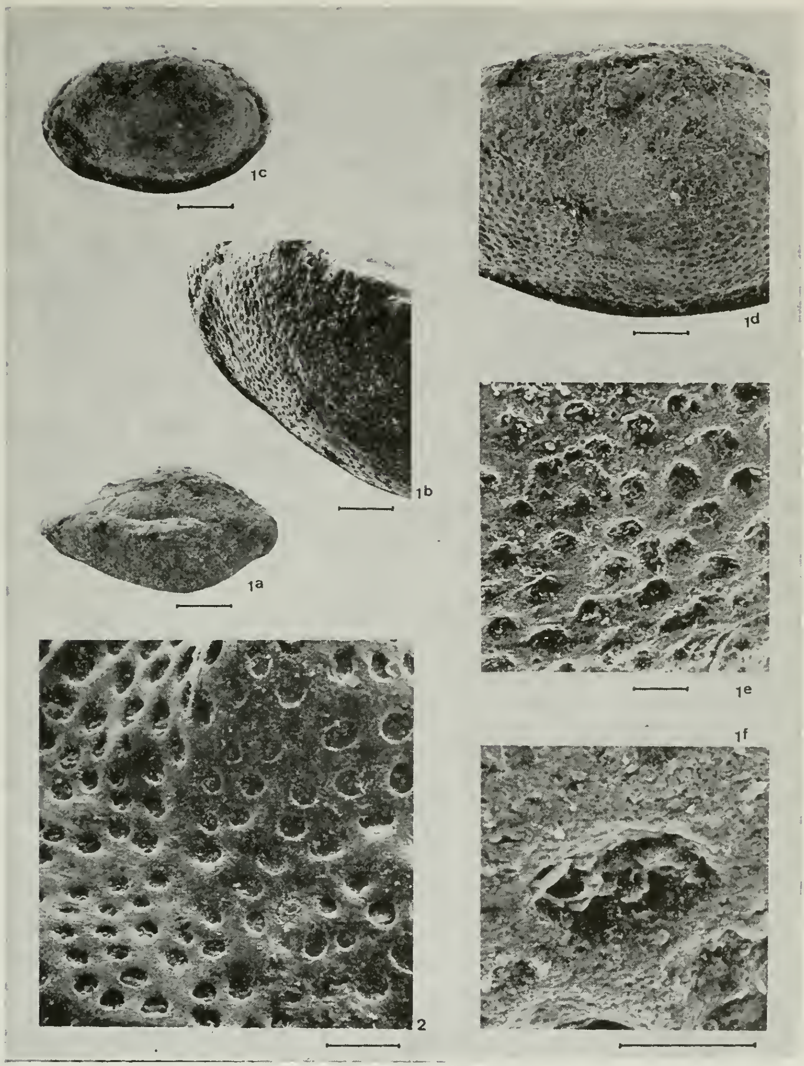

1c
1d
1b
1a
1e
1f
2

PLATE II

Figure

3. **Carbonita humilis.** Specimen 1, MJMB-collections; *foveolata*-Band, Lower Westphalian C, Farnworth, Lancashire, England.
   3a: left side of shell (scale = 200 microns).
   3b: detail of punctation; note honey-comblike structure of punctae with very small muri between them, the whole approaching a reticulate ornamentation (scale = 20 microns).

4. **Carbonita humilis.** Specimen B2, MJMB-collections; *foveolata*-Band, Lower Westphalian C, Farnworth, Lancashire, England.
   Left side of elongate shell partly coated with glue or matrix; note overlap along ends and venter (scale = 250 microns).

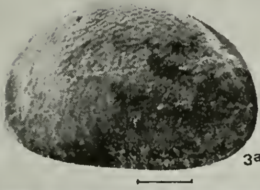
5. **Carbonita humilis.** Specimen 2, MJMB-collections; *foveolata*-Band, Lower Westphalian C, Farnworth, Lancashire, England.
   Left side of shell (scale = 200 microns).

6. **Carbonita humilis.** Specimen 3, MJMB-collections; *foveolata*-Band, Lower Westphalian C, Farnworth, Lancashire, England.
   Dorsal view, no overlap around ends (scale = 200 microns).

7. **Carbonita humilis.** Specimen t31, MJMB-collections; G.B. 25 Band, Upper Westphalian A, Emma Colliery, The Netherlands.
   Left side of shell (scale = 200 microns).

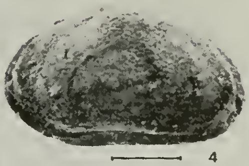
8. **Carbonita humilis.** Specimen 6, MJMB-collections; G.B. 25 Band, Upper Westphalian A, Emma Colliery, The Netherlands.
   Left side of shell (scale = 200 microns).

9. **Carbonita humilis.** Specimen 4, MJMB-collections; G.B. 25 Band, Upper Westphalian A, Emma Colliery, The Netherlands.
   9a: left side of partly abraded shell showing internal mold with muscle-scar and vertical furrow posterior of this (scale = 200 microns).
   9b: detail of muscle-scar (scale = 50 microns).

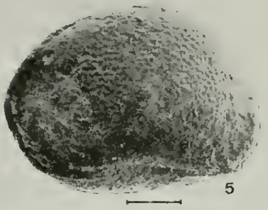


3a

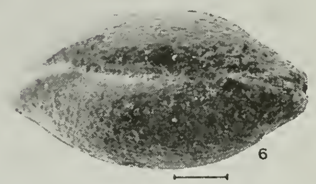
3b



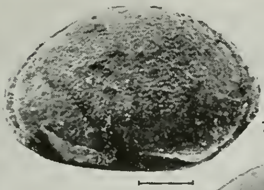
4



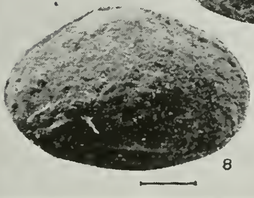
5



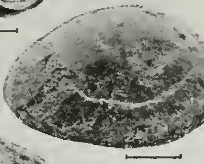
6



7



8



9a

9b

SPREAD OF OSTRACODES TO EXOTIC ENVIRONS ON TRANSPLANTED OYSTERS

Louis S. Kornicker
Smithsonian Institution

ABSTRACT

Sarsiella zostericola Cushman, 1906, is a highly ornamented, easily recognized myodocopid ostracode which has been previously reported along the northeast, West Coast and Gulf Coast of the United States. In 1967 and 1968, the species was collected along the coast of Essex, England. Because the ostracodes of England are well known, it is suggested that *S. zostericola* is a recent arrival. One species of polychaete worm and two gastropods in the same area, also considered by others to be recent arrivals, are believed to have introduced with oysters transplanted from the northeast coast of the United States. It is tentatively concluded that *S. zostericola* was introduced to England in like manner. It is also suggested that a population of the species living in San Francisco Bay, California, may have been introduced with oysters transplanted from the East Coast. There is a strong possibility that other species of ostracodes have been spread widely by oysters. Recognition of these species is necessary for correct ecological and zoogeographical interpretations.

LA DISSEMINATION DES OSTROCODES A DES ENDROITS EXOTIQUES SUR DES UITRES TRANSPLANTÉS

RÉSUMÉ

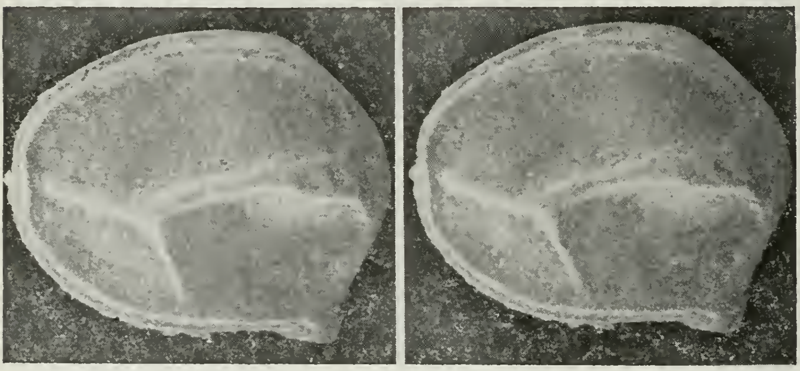
Sarsiella zostericola Cushman, 1906, est un ostracode myodocopide, hautement ornamenté et facile à reconnaître, qui a été rapporté antérieurement au long des côtes nordest, ouest, et celle du golfe des Etats-Unis. En 1967 et 1968, l'espèce fut receuillie au long de la côte d'Essex en Engleterre. Puisque les ostracodes de l'Engleterre sont bien connus, il est suggéré que *S. zostericola* n'y est arrivé que recemment. Une espèce de polychaete et deux gastropodes dans la même région, aussi considérés par d'autres comme des nouveaux venus, sont sensés avoir été introduits à travers des uitres transplantés des Etats-Unis. On arrive à la conclusion tentative que *S. zostericola* fut introduite en Engleterre dans une facon pareille. Il est aussi suggéré qu'unepopulation de l'espèce habitant dans la Baie de San Francisco en Californie, aurait pu s'introduire à travers des uitres transplantés de la côte de l'est. Il existe une forte possibilité de ce que d'autresespèce d'ostracodes ont été amplement disséminées par des uitres. La reconnaissance de ces espèces est nécessaire pour des interprétations écologiques et zoogéographique scorrectes.

INTRODUCTION

The ornate, easily recognized myodocopid ostracode, *Sarsiella zostericola* Cushman, 1906, (Text-fig. 1) was described originally from shallow waters of Vineyard Sound, Massachusetts. Blake (1933) extended the known range of the species north to the Mount Desert Island region on the coast of Maine. I am able to extend the range south to the mouth of Chesapeake Bay, based on a specimen received from Dr. Joseph Hazel, collected aboard the R/V *Gosnold* in 1964 (Station 2051, 5 August 1964, 37°00.0'N, 75°15.0'W, 36 m, USNM 135400). Mr. Les Watling has informed me (in litt., 1972) that the species is also present in the coastal bays of Delaware (Cape Henlopen at the mouth of Delaware Bay; through Rehoboth Bay, and in the more saline regions of Indian River Bay). Its known range along the northeast Atlantic coast then, is from Chesapeake Bay to Maine. The species was not among the several myodocopids found by Darby (1965) in the vicinity of Sapelo Island, Georgia. The distribution of *S. zostericola* is shown in Text-figure 2.

Kornicker and Wise (1962) identified the species in collections from coastal lagoons of Texas. The occurrence of disjunct populations of *S. zostericola* along the eastern Atlantic coast and the southwestern Gulf Coast suggests that the species in the past lived also along the southeastern Atlantic and the northern and eastern Gulf coasts, possibly during colder climates of the Pleistocene.

Jones (1958a, 1958b) reported *S. zostericola* (= *S. tricostata* Jones, 1958) from San Francisco Bay, California. I compared in detail specimens of the species from Massachusetts, Texas, and California, and could find no differences (Kornicker, 1967). I propose here that the population in San Francisco Bay was transported along with oysters which were transplanted from the East Coast during the years 1870 to 1910.



Text-figure 1. Lateral view of left valve of *Sarsiella zostericola* (USNM 139287) from station 139, River Blackwater, Essex, England, length 1.39 mm (stereographic pair).

ACKNOWLEDGMENTS

I thank Dr. Eric Robinson for sending specimens of *S. zostericola* from England, Dr. Joseph Hazel for a specimen of *S. zostericola* from the mouth of the Chesapeake Bay, and Mr. Les Watling for information concerning distribution of the species along the Delaware coast. I thank also the following individuals for information concerning oysters: Dr. Austin B. Williams, Dr. James E. Hanks, Dr. A. F. Chestnut, and Mr. J. Richards Nelson. Dr. M. Pettibone, in addition to criticizing the manuscript, supplied valuable information concerning the introduction of polychaetes to English waters. I thank also Dr. T. E. Bowman, Dr. I. G. Sohn, and Dr. J. E. Hazel for criticizing the manuscript. The SEM photograph of the ostracode valve was made by Mr. Walter Brown.

Text-figure 2. Map showing distribution of *S. zostericola.*

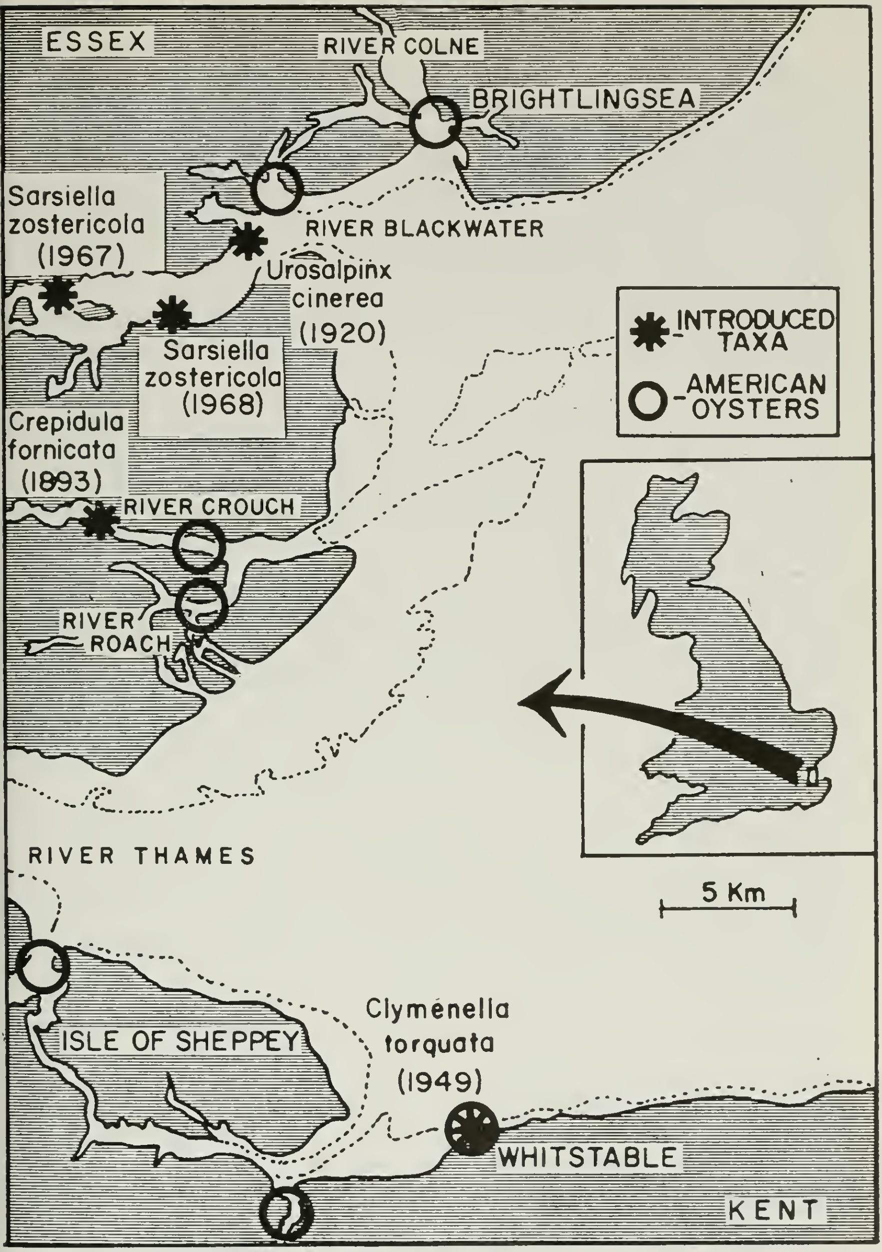
TRANSPORTATION BY OYSTERS

The oyster *Crassostrea virginica* (Gmelin) endemic to the Atlantic and Gulf Coast of the United States, was first transplanted from the East Coast to San Francisco Bay in 1869 or 1870, but it was not until 1875 that seed-oysters were imported in large quantities. About 9000 barrels of seed-oysters were transplanted each year from the East Coast until 1910 when the project was discontinued (Smith, 1896; Barrett, 1963). The source of the East Coast seed-oysters was in the vicinity of Chesapeake Bay, Connecticut, and New York. The oyster drill, *Urosalpinx cinerea* (Say) and the American slipper-shell, *Crepidula fornicata* Linné, both endemic to the Atlantic Coast, were introduced to the West Coast with the transplanted oysters (Walne, 1956; Elton, 1958; Galtsoff, 1964). Therefore, it is not unreasonable to suppose that *S. zostericola* was introduced the same way. Unfortunately, the absence of collections of ostracodes from San Francisco Bay prior to 1870 makes it impossible to give historical support to the hypothesis.

The living ostracodes of England have received considerable study and are better known than in most other areas (Neale, 1965). Although species of the genus *Sarsiella* have been reported from the well-studied coasts of the British Isles, *S. zostericola* was not among them. Thus, it is reasonably safe to assume that numerous specimens of *S. zostericola* collected in 1967-1968 along the shore of Blackwater estuary in Essex, are part of a population that only recently arrived in England. The ostracodes (USNM 139287) were sent to me by the collector, Dr. Eric Robinson. The history of some additional organisms, including two species of gastropods and a polychaete worm, makes it possible to postulate with some confidence that the ostracodes were introduced with oysters that had been shipped from the eastern coast of the U.S.A. and reset in estuaries along the coast of Essex (Text-fig. 3).

The oyster, *C. virginica,* does not establish breeding populations in the waters of England, but from about the late 1870's to 1940, young oysters and seed-oysters were transported from the East Coast of the U.S.A. (Chesapeake Bay, Conn., N.Y.) to England, where they were relaid in suitable coastal estuaries until ready for harvesting (Cole, 1956b; Philpots, 1891b). One such locality was in the River Colne, near Brightlingsea, Essex. Some of the oysters from that area were transferred to other localities in Essex, including River Blackwater, River Crouch, and River Rouch. An estuary near Whitstable, Kent, was another locality where American oysters were transplanted either directly from America or from the River Colne. These localities were important economically because of their proximity to the London Market. The ostracodes of the Thames estuary were studied by Brady and Robertson (1870).

The American slipper-shell, *Crepidula fornicata,* was transported on eastern oysters to England, probably in the 1880's (Loosanoff, 1955), but it was collected first in the River Crouch in 1893 (Crouch, 1895; Robson, 1929; McMillan, 1939; Cole, 1952, 1956a) and then in the River Colne near Brightlingsea



Text-figure 3. Map of southeast coast of England (Essex and Kent) showing areas where oysters, *Crassostrea virginica,* from the United States have been reset and the localities and dates of the initial appearance of other species introduced with the oysters.

in 1898 (Crouch, 1898; Mistakidis, 1951). The slipper-shell spread rapidly after 1920 along the south coast of England (Cole, 1956b) and subsequently extended its range into the coastal waters of western Europe (Loosanoff, 1955).

The American oyster drill, *Urosalpinx cinerea,* was first collected in Europe in 1920 in the oyster beds of the River Blackwater (Orton, 1930) (Text-fig. 3). By 1942 it was abundant in the River Blackwater and other creeks and rivers along the Essex coast, as well as at the mouth of the estuary near Whitstable in Kent. All these areas were used for culturing American oysters, and it has been assumed by all investigators that the drill was carried to these areas on transplanted oysters (Orton, 1927, 1930; Orton and Winckworth, 1928; Robson, 1929; Orton and Lewis, 1931; Cole, 1942, 1956a; Hancock, 1954; Newell, 1954).

More recently a polychaete worm, *Clymenella torquata* (Leidy), was discovered in the intertidal area of Whitstable by Newell (1949a, 1949b) (Text-fig. 3). He believed that the worms might have been introduced in 1936 when American oysters were introduced at Whitstable. The known range of *C. torquata* along the North American coast is from the Gulf of St. Lawrence to Florida, and on the Louisiana Coast of the Gulf of Mexico (M. Pettibone, written comm. 1972).

The proposition that *S. zostericola* was transported with oysters to Essex, England, is supported by both historical and circumstantial evidence. If ostracodes can be transported from the East Coast of the U.S.A. to England in this manner, it should also be possible for them to be transported from the east to west coasts of the U.S.A. Thus, the evidence from England lends support to the hypothesis that the population in San Francisco Bay was also derived from the East Coast. The known localities at which the species lives indicate that its climatic range is warm temperate to Boreal (Hedgpeth 1957).

It may be safe to assume that other ostracode species also have been transported elsewhere with oysters. According to Elton (1958, p. 100), the business of oyster culture must be the greatest of all agencies for spreading marine animals to new quarters of the world. Few areas seem to have been missed being at least tested for their potential for culturing foreign oysters. A major current operation, starting in 1902, is the transport of seed-oysters of *Crassostrea gigas* (Thunberg) from Japan to the west coast of the U.S.A. and Canada. As a result of this, an oyster drill, *Tritonalia japonica* Dunker, a Japanese clam, *Paphia philippinarum* (Adams and Reeve), and a parasitic copepod, *Mytilicola orientalis* Mori, have been introduced to the west coast of the U.S.A. and Canada (Elsey, 1934; Wilson, 1938; Odlaug, 1946; Kincaid, 1953; Galtsoff, 1964). Smaller numbers of seed-oysters have been transported from Japan to Hawaii (Edmundson and Wilson, 1940), Australia (Thomson, 1952), China and far-east islands (Cahn, 1950). The European oyster, *Ostrea edulis* Linné, was transplanted from Holland to Connecticut and Maine in 1949; young oysters from the resulting New England beds were later transplanted to the coast of Washington (Loosanoff, 1955). Considerable transplantation of oysters has taken place since early times among the countries of Europe, *e.g.,* from Portugal and France to Britain, from England and France to Italy, from Scotland and Ireland to England (Philpots, 1891a, 1891b). Along the northeast coast of the U.S.A., seed-oysters from the Chesapeake Bay area have been used to supply nurseries in Connecticut, New York, and Rhode Island; seed-oysters from the Connecticut nursery later formed the basis for oyster beds in Massachusettes (Philpots, 1891b).

In answer to a letter requesting information concerning current practices in the transplanting of oysters, I received from Mr. J. Richards Nelson, President, Long Island Oyster Farms, Inc., New Haven, Connecticut, a letter (Feb. 1972) containing the following excerpt, ". . . oysters have been transplanted from Gardiners Bay, Long Island [New York] to Tomales Bay, California, for at least the past forty years to my knowledge, and probably longer. Prior to 1940 they were sent by freight car, and it required thirteen days between the time they were taken from Gardiner Bay beds to the time of planting in California. Since that time the transportation has been by refrigerated trailer trucks and the trip is accomplished in five days. The J. & J. W. Elsworth Co. of Greenport, New York, furnished most of these oysters until 1968, when Long Island Oyster Farms bought the Elsworth Co. assets. It is my understanding that there have been some oysters transplanted from Delaware Bay and Chesapeake Bay to Tomales Bay, but I understand that the northern oysters from Gardiners Bay are preferred. The Gardiner Bay oysters all come from Connecticut in the vicinity of New Haven or Bridgeport and are generally transplanted at the age of two years, remaining on the Gardiner Bay beds from one to two years, the stock going to California being at least three years old and generally four. Gardiners Bay does not produce any natural set and all stock there is transplanted from Connecticut."

In an interesting paper entitled, "The shell of *Ostrea edulis* as a habitat", Korringa (1954, p. 113) reported the following podocopid ostracodes occurring on oysters shells in beds of the Netherlands: *Loxoconcha impressa* (Baird), *Leptocythere castanea* Sars, *Heterocythereis albomaculata* (Baird), *Hirschmannia viridis* (O. F. Müller), *Cytherura nigrescens* (Baird), *Cytherois fischeri* Sars, *Hemicythere villosa* (Sars). Swain (1955) and King and Kornicker (1970) listed podocopid ostracodes associated with oyster "reefs" in bays along the coast of Texas.

CONCLUSIONS

In summary, I have presented evidence supporting the hypothesis that *S. zostericola* was introduced to San Francisco Bay, California, and to the River Blackwater, England, with oysters from the east coast of the United States. Thus, there is a strong possibility that ostracodes have been introduced with transplanted oysters in, or near, areas where oysters are being, or have been, cultured. Therefore, this factor should be taken into account in investigations dealing with estuarine and coastal ostracodes.

LITERATURE CITED

Barrett, E. M.

1963. *The California oyster industry.* Resources Agency California, Department Fish and Game, Fish Bull., 123, 103 pages.

Blake, Charles

1933. *Ostracoda. In* Biological Survey of the Mount Desert Region conducted by William Procter, V, pp. 229-241, figs. 39, 40.

Brady, G. S., and Robertson, D.

1870. *The Ostracoda and Foraminifera of tidal rivers.* Ann. Mag. Nat. Hist., Ser. 4, 6, pp. 1-33, plates 1-10.

Cahn, A. R.

1950. *Oyster Culture in Japan.* United States Depart. Interior, Fish and Wildlife Ser., Fishery Leaflet, 383, 80 pages.

Cole, H. A.

1942. *The American whelk tingle Urosalpinx cinerea (Say), on British oyster beds.* Jour. Marine Biol. Assoc. United Kingdom, XXV (3), pp. 477-508.

1952. *The American slipper limpet (Crepidula fornicata L.) on Cornish oyster beds.* Fisheries Invest., London, Ser. 2, 17 (7), pp. 1-13.

1956a. *Benthos and the shellfish of commerce.* In *Sea Fisheries: Their Investigation in the United Kingdom* (Ed. M. Graham) London, pp. 139-206.

1956b. *Oyster cultivation in Britain.* A Manual of Current Practice, London, 43 pages.

Crouch, W.

1895. *On the Occurrence of Crepidula fornicata in Essex.* Proc. Malacol. Soc., London, 1, p. 19.

1898. *Further notes on the occurrence of Crepidula fornicata L., in Essex Waters.* Essex Natu., 10, p. 353.

Cushman, J. A.

1906. *Marine Ostracoda of Vineyard Sound and adjacent waters.* Boston Soc. Nat. Hist., Proc., 32 (10), pp. 359-385, pls. 27-38.

Darby, D. G.

1965. *Ecology and taxonomy of Ostracoda in the vicinity of Sapelo Island, Georgia.* Report No. 2 *in* Four Reports of Ostracod Investigations (offset report is issued by the University of Michigan), iii-vi + 1-76, text-figures 1-89.

Edmundson, C. H., and Wilson, I. H.

1940. *The shellfish resources of Hawaii.* Sixth Pacific Science Congress of the Pacific Science Association, Proc. III, pp. 241-243.

Elsey, C. R.

1934. *The Japanese oyster in Canadian Pacific waters.* Fifth Pacific Science Congress, Canada, 1933, Proc., pp. 4121-4127.

Elton, C. S.

1958. *The ecology of invasion by animals and plants.* Methuen & Co. Ltd., London; John Wiley & Sons Inc., New York, 181 pp.

Galtsoff, P. S.

1964. *The American oyster Crassostrea virginica Gmelin.* United States Depart. Interior, Fish and Wildlife Service, Fishery Bull., 64, 480 pages.

Hancock, D. A.

1954. *The destruction of oyster spat by Urosalpinx cinerea (Say) on the Essex oyster beds.* Journal du Conseil, Conseil Permanent pour L'Exploration de la Mer, XX (2), pp. 186-196.

Hedgpeth, J. W.
1957. *Marine biogeography.* Pages 359-382, *In* Treatise on Marine Ecology and Paleoecology, vol. 1, Ecology. The Geol. Soc. America, Mem. 67, 1296 pages.

Jones, M. E.
1958a. *Sarsiella tricostata, a new ostracod from San Francisco Bay (Myodocopa: Cypridinidae).* Jour. Washington Acad. Sci., 48 (2), pp. 48-52, figures 1, 2.
1958b. *Further notes on Sarsiella tricostata.* Jour. Washington Acad. Sci., 48 (7), p. 238, figs. 1-3.

Kincaid, T.
1953. *The acclimatization of the Pacific oyster (Ostrea laperousii = Ostrea gigas Thunberg) upon the West Coast of North America.* Seventh Pacific Science Congress of the Pacific Sci. Assoc. Zoology, Proc. IV, pp. 508-512.

King, C. E., and Kornicker, L. S.
1970. *Ostracoda in Texas bays and lagoons. An Ecologic Study.* Smithsonian Contrib. Zoology, 24, 92 pages, figs. 1-15, pls. 1-21.

Kornicker, L. S.
1967. *A study of three species of Sarsiella (Ostracoda: Myodocopa).* United States Nat. Mus., Proc., 122 (3594), 46 pp., figs. 1-19, pls. 1-4.

Kornicker, L. S., and Wise, C. D.
1962. *Sarsiella (Ostracoda) in Texas bays and lagoons.* Crustaceana, 4 (1), pp. 57-74, fig. 1-10.

Korringa, P.
1954. *The shell of Ostrea edulis as a habitat.* Archives Néerlandaises de Zoologie, X, pp. 32-152, figs. 1-13.

Loosanoff, V. L.
1955. *The European oyster in American waters.* Science, 121 (3135), pp. 110-121.

McMillan, N. F.
1939. *Early records of Crepidula in English waters.* Malacol. Soc. London, Proc. XXIII, p. 236.

Mistakidis, M. N.
1951. *Quantitative studies of the bottom fauna of essex oyster grounds.* Ministry Agriculture Fisheries, Fisheries Invest., London, ser. II, XVII (6), 47 pages.

Neale, J. W.
1965. *Some factors influencing the distribution of Recent British Ostracoda.* Pubblicazioni Della Stazione Zoologica Di Napoli, 33 suppl., pp. 247-307, figs. 1-11, plate 1.

Newell, G. E.
1949a. *The occurrence of a species of Clymenella Verrill (Polychaeta, fam. Maldanidae) on the North Coast of Kent.* Nature, CLXIII (5), pp. 111-115.
1949b. *Clymenella torquata (Leidy), a polychaete new to Britain.* The Ann. Mag. Nat. Hist., ser. 12, II (VI), pp. 147-155.
1954. *The marine fauna of Whitstable.* Ann. Mag. Nat. Hist., ser. 12, 7 (77), pp. 321-250.

Odlaug, T. O.
1946. *The effect of the copepod, Mytilicola orientalis upon the Olympia oyster, Ostrea lurida.* American Micro. Soc., Trans., LXV (4), pp. 311-317.

Orton, J. H.
1927. *The habits and economic importance of the rough welk tingle (Murex erinaceus).* Nature, 122 (3027), pp. 653-655.
1930. *On the oyster-drills in the Essex estuaries.* Essex Naturalist, XXII (VI), pp. 298-306.
Orton, J. H., and Lewis, H. M.
1931. *On the effect of the severe winter of 1928-1929 on the oyster drills of the Blackwater Estuary.* Jour. Marine Biol. Assoc. United Kingdom XVII, pp. 301-313.
Orton, J. H., and Winckworth, R.
1928. *The occurrence of the American oyster pest Urosalpinx cinerea (Say) on English oyster beds.* Nature, CXXII, p. 241.
Philpots, J. R.
1891a. *Oysters, and all about them.* John Richardson and Co., London, I, 642 pages.
1891b. *Oysters, and all about them.* John Richardson and Co., London, II, pp. 643-1370.
Robson, G. C.
1929. *On the Dispersal of the American Slipper Limpet in English Waters.* Malacol. Soc. London, Proc. XVIII, p. 273.
Smith, H. M.
1896. *A review of the history and results of the attempts to acclimatize fish and other water animals in the Pacific States.* United States Fish Commission, Bull. 1895, 15, pp. 379-472.
Swain, F. M.
1955. *Ostracoda of San Antonio Bay, Texas.* Jour. Paleont., 29 (4), pp. 561-646, figs. 1-39, pls. 61-64.
Thomson, J. M.
1952. *The acclimatization and growth of the Pacific Oyster (Gryphaea gigas) in Australia.* Australian Jour. Marine Freshwater Research, 3 (1), pp. 64-73.
Walne, P. R.
1956. *The biology and distribution of the Slipper Limpet Crepidula fornicata* in Essex rivers with notes on the distribution of the *larger epi-benthic invertebrates.* Fisheries Investigations, London, ser. 2, 20 (6), pp. 1-50.
Wilson, C. B.
1938. *A new copepod from Japanese oysters transplanted to the Pacific Coast of the United States.* Washington Acad. Sci. Jour., 28 (6), pp. 284-288.

Louis S. Kornicker
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560

DISCUSSION

Dr. R. C. Whatley: How are the ostracodes transported?

Dr. Kornicker: In between the oysters and in any sediment that might go along with the oysters.

Dr. P. A. Sandberg: How do the Japanese prepare the oysters for shipment?

Dr. Kornicker: Because of questions following my paper concerning details of shipping oyster spat from Japan, I think it best to replace my incomplete answers with the following quote from Barrett (1963, p. 50).

"Raising and packing seed oysters for export requires special care to enable the seed to survive the trans-Pacific voyage, and to ensure that it will be free of harmful organisms. Oyster spat is caught on empty shells of oysters and other mollusks, which are strung on wires and suspended from rafts or racks in areas where spat-setting is known to occur (Figure 8). The strings of shells are put into the water in July when the young oysters are ready to set, keeping them above the bottom, which is habitat of harmful oyster drills. The spat that set on the shells are left until about September, at which time the strings are removed from the floats and racks and piled horizontally on low racks in the intertidal zone where the spat are exposed to the air for several hours each day during ebb tides (Figure 9). This exposure causes the young oysters, which at this stage are less than 1/2-inch in diameter, to develop thick, strong shells that do not allow water to escape, thus enabling them to survive during the periods of exposure to the air. Spat not exposed to these conditions develop larger meats and thinner shells which are not water-tight and whose edges chip easily. The spat to be exported are left on the "hardening" racks until about January or February when packing for shipment begins.

"The spat containing shells are removed from the wire strings, washed, sorted, inspected and packed in wooden cases. Much of this work is done in the open air by women at many small sites in the growing areas (Figures 10, 11, 12). Women who do the sorting remove drills and drill egg cases, count the number of live spat per shell to make sure there are the minimum number required, and sort broken and unbroken shells."

Dr. H. Löffler: If this is true, passive dispersion by birds may not be excluded. I don't know how many species have been checked for the possibility of internal transportation by birds.

Dr. Kornicker: Well, we can speculate on quite a few ways ostracodes could be transported but I think in this case, being *Sarsiella zostericola* is found in an oyster area and with three other species that have been interpreted as having been carried in with oysters, species that could not have been transported by birds, transportation by oysters seems more likely.

Mr. L. Watling: Oysters transported from the West coast to the East coast are generally hosed down but sometimes mud remains in the crevices. Another point I would like to make is that a species I found in California and described as *Spinileberis hyalinus* would appear, from specimens that Dr. Ishizaki sent me, were the same as *S. quadriaculeata* from Japan. I believe it was transported since I found it near oyster beds in a small bay in California. These oysters (*Crassostrea gigas*) had come from Japan.

Dr. Kornicker: That's very interesting.

CANONICAL CORRELATION ANALYSIS OF HEMICYTHERINID AND TRACHYLEBERINID OSTRACODES IN THE NIGER DELTA

R. A. Reyment
Paleontologiska Institutionen, Uppsala Universitet

ABSTRACT

The multivariate statistical method of canonical correlation was applied to observations made on the interstitial environment of ostracodes occurring in the Niger Delta. The regression structure provided by this method was made up of the predictor set (pH, Eh, depth of sample (D), and total contents of phosphorous and sulfur), and the response set (total content of organic substance (OC), total content of calcium carbonate (CA), and total number of hemicytherinids and trachyleberinids (OSTR)). Only one of three canonical correlations proved significant; it is based almost entirely on a predictor set representing mainly S and a response set consisting of positive covariation in OC and OSTR. This canonical correlation indicates that much of the organic substance (divorced from shell) is correlated with S (probably derived from decomposing organic matter). The second, non-significant, canonical correlation indicates that the distribution of the shells (including ostracode shells) is determined by a predictor set dominated by D in negative covariation with P. The graphical analysis of the transformed data scores shows the ostracode-rich samples form a well defined cluster.

RÉSUMÉ

La méthode de la statistique multivariée, nommée "la corrélation canonique" était appliquée à des données du milieu interstitiel de quelques groupes d'ostracodes du delta nigérien. Cette méthode donne une structure de régression avec un ensemble de prédiction (ici pH, Eh, profondeur de l'échantillon, D, et les dosages de P et S) et un ensemble de résponse (ici les totalités de matière organique, OC, $CaCO_3$, CA, et le nombre d'ostracodes des groupes des hemicytherines et trachyleberines (OSTR). Une seule des racines de la corrélation canonique est significative; elle est basée, presque entièrement, sur un ensemble prédicteur composé uniquement de S, et un ensemble de réponse contenant les variables OC et OSTR dans une covariation positive. Cette relation montre qu'une grande partie de la matière organique (dépourvue de fragments des parties dures) est correlée avec S provenant probablement de la décomposition de la matière organique). La deuxième racine indique que la répartition des coquilles (y compris les carapaces des ostracodes) est déterminée par un ensemble prédicteur dont les variables dominantes, D et P, se trouvent en corrélation négative.

INTRODUCTION

M. E. Omatsola (1970) recently described the ostracodes of the Niger Delta in some detail. The samples from which his specimens were extracted were collected in a survey of the interstitial ecology of that delta (Reyment, 1969). These samples have been analyzed for a wide range of variables (pH, Eh, organic content of the sediment (OC), total calcium carbonate (CA), and various chemical constituents, including total phosphorus and total sulfur), and it was considered of interest to see whether the abundances of the ostracodes in the samples could be related to any of them. This report presents the results of a generalized regression approach to the problem. Interest is also attached to the isolation of redundant variables.

The calculations were made on the CDC 3600 machine of the Computing Centre of the University of Uppsala and financed by Computing Grant 104104 of that university.

THE VARIABLES

The variables on which this study was based are: pH and Eh of the interstitial water of the sediment, the total organic content of the sediment, the total content of calcium carbonate (mainly derived from shells from all sources), distance of the sampling site from the shore, counts of ostracode frequencies of each sample, total phosphorus in the sediment, and sulfur from all sources. Although it had already been established in another investigation (Reyment, 1972) that pH and Eh contribute little to an analysis of the interstitial deltaic environment, they were included here for completeness (pH can hardly be expected to vary much owing to the buffering effect of seawater).

BIVARIATE CORRELATIONS

It is instructive to consider the significant bivariate correlations before proceeding to the main analysis. These correlations are listed in Table 1. Most of these seem to make sense. Organic substance is a logical correlate of the soft parts of living ostracodes and the high value of 0.76 for its correlation with sulfur (also ostracodes) can reasonably be related to decomposing organic matter and associated S, and H_2S. The relatively high value for calcium carbonate and ostracodes, is also expected. The positive correlation between D and P is a well known characteristic of the sediments of shallow seas (cf. Degens, 1968).

Table 1. Significant bivariate correlations

Variables	r_{ij}	Variables	r_{ij}
pH - Eh	0.54	CA - OSTR	0.49
OC - OSTR	0.43	D - P	0.73
OC - S	0.76	D - S	0.49

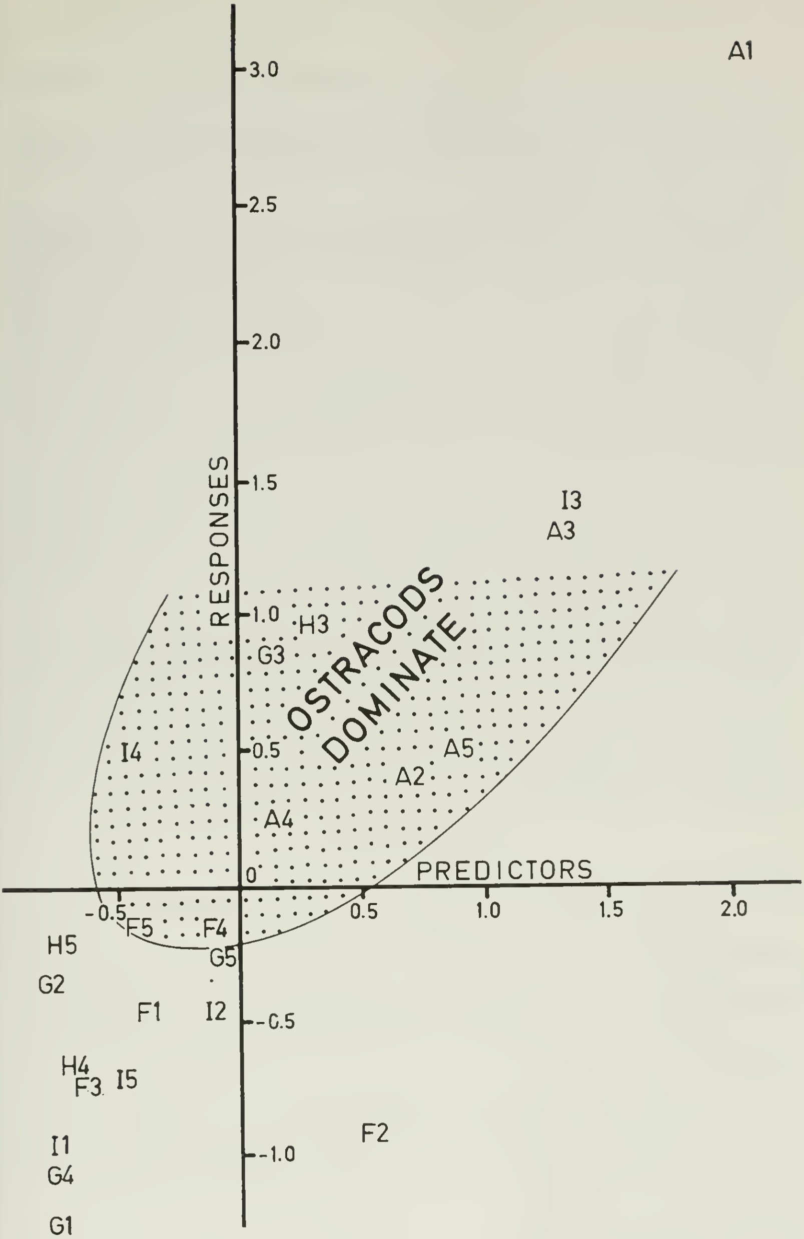
THE CANONICAL CORRELATION ANALYSIS

Inasmuch as the biological interpretation of canonical correlation studies has recently been discussed at length by Blackith and Reyment (1971) and Reyment (1972), I propose to pass directly to the interpretation of the present results and refer the reader who has not yet made contact with morphometric methods of analysis to the above sources.

There is only one significant canonical correlation, namely, $R_{c1} = 0.85$, which is associated with a chisquare value of 29.2 for 15 degrees of freedom. The second canonical correlation is 0.47, which for 8 degrees of freedom, is associated with a chisquare of only 5.7. Most of the information, therefore, resides in the first correlation.

The set of predictor variables for the first canonical correlation has the composition:

$$(0.4D, -0.3P, 1.2S);$$



Text-fig. 1. Graph of the transformed variates of the first canonical correlation. The axes denote the predictor and response variables. The letter-number combinations denote sampling sites (cf. Reyment, 1969).

here, pH and Eh are entirely without significance. The set of response variables corresponding is:

(0.6OC, -0.3CA, 0.6OSTR).

The important correlations between the original variables and the canonical variates are, for the predictors:

-0.2D: 0.2P: 1.0S.

This result indicates that the content of total S predicts the occurrence of organic matter in the sediment, including the soft parts of ostracodes, when these are not associated with shell. The poor performance of CA in this relationship is certainly a consequence of the masking effect of the shell substance of molluscan origin. The response correlations are: 1.0OC: 0.7OSTR. This pair of canonical variates may be taken to represent the relationship developing between decomposing organic substance and concentration of H_2S. A graph of the predictor and response canonical variates is shown in Text-fig. 1. All of the samples in the upper, dotted part of the graph are rich in ostracodes in relation to mollusks. The samples in the lower, left-hand part of the graph tend to be poor in ostracodes, or to lack them, but they are usually rich in molluscan shells and shell detritus. The graphical analysis brings out a second characteristic in the association between the two sets of variables, and is one of the major results of the analysis.

The second, non-significant canonical correlation is of interest, despite the fact that it does not represent more than a small part of the interrelationships in the material. The set of predictor variables is dominated by the covariational vector (0.8D, -0.6P). The response vector is (0.9CA, 0.4OSTR). This relationship suggests that where distance from the delta shore is negatively correlated with P, shell accumulations tend to occur, including the shells of ostracodes. It is necessary to bear in mind that this tendency is only represented in a fraction of the material.

REFERENCES

Blackith, R. E., and Reyment, R. A.
1971. *Multivariate Morphometrics.* Academic Press, London, New York, IX, 412 pp.
Degens, E. T.
1968. *Geochemie der Sedimente.* F. Enke Verl., Stuttgart, VIII, 282 pp.
Omatsola, M. E.
1970. *Studies on Recent Ostracoda (Crustacea, Arthropoda) from the Niger Delta, Nigeria.* Ph.D. Thesis, University of Uppsala.
Reyment, R. A.
1969. *The interstitial ecology of the Niger Delta.* Bull. geol. Instn. Univ. Upsala, NS 1, pp. 121-159.
1972. *Models for the study of zinc and lead in a deltaic environment.* Section 9b. 8th Internat. Sed. Congr. (Heidelberg, 1971). Plenum, New York.

R. A. Reyment,
Paleontologiska Institutionen,
Uppsala Universitet,
S-751 22 Uppsala,
Sweden.

DISCUSSION

Dr. J. W. Neale: Did you measure current velocity and was there any correlation with sulfur content and hence with your ostracode environments?

Dr. Reyment: That is, of course, a difficult question. The samples were taken in a delta of quite some size, the front of which is 300 miles, and while some work has been done by Longhurst (1964) on the currents in the delta, we have no exact measurements, nor the equipment to do such observations.

Dr. Neale: Were pH, Eh, S measured at the time or was there an appreciable time gap between the measurement of these and the date of the samples?

Dr. Reyment: The samples were taken by means of a Züllig sampler; they were analyzed on board ship immediately after having been taken up. I wrote this up in 1969 in the paper on the ecology of Niger Delta. The Züllig sampler enables one to sample directly by sticking a coarse hypodermic needle straight into the sediment.

Dr. J. E. Hazel: Did you do any other analyses other than ecological variations in order to see if you were getting similar results?

Dr. Reyment: I used principle components and a canonical variational study. I have a paper in the Sedimentological Congress Proceedings (Reyment, 1972) on this same technique, applying it to the same material, but in relation to the occurrence of zinc and lead in the sediments. If you do the analysis the other way around, you get only the roots and vectors extraction. You wouldn't recognize that this structure existed in the material just by inspection.

DYNAMICS IN RECENT MARINE BENTHONIC OSTRACODE ASSEMBLAGES IN THE LIMSKI KANAL (NORTHERN ADRIATIC SEA)

Henning Uffenorde
Geol.-Paläont. Institut, Göttingen, Germany

ABSTRACT

The population dynamics of twelve mediterranean ostracode species have been studied on the basis of 140 quantitative sediment samples from the euhaline clayey silt bottom of the Limski Channel (yugosl. Limski kanal). Samples were taken at monthly intervals between September 1967 and October 1968. The species belong to autochthonous benthonic assemblages inhabiting a biotope with a low energy level. Although all are perennial forms, the population dynamics show remarkable temporal differences, ranging from aperiodic or (?) long-periodic to seasonal periodic and short-periodic with all transitions. As most perennial species with distinct seasonal life-cycles hatch in fall and winter, it is assumed that food supply is one of the major controlling factors and that water temperatures are always above the thermopathic level. Species with long-periodic life-cycles have not been observed.

KURZFASSUNG

Zwölf mediterrane Ostracoden-Arten wurden hinsichtlich ihrer Populationsdynamik untersucht. Grundlage dafür bildeten 140 quantitative Sedimentproben von den euhalinen, tonigen Silt-Böden des Limski kanal. Die Probenahme erfolgte monatlich von September 1967 bis Oktober 1968. Die Arten gehören autochthonen benthonischen Assoziationen an, deren Biotop hinsichtlich der Wasserbewegung gering exponiert ist. Obwohl es sich um Dauerformen handelt, zeigt ihre Populationsdynamik erhebliche zeitliche Differenzierungen, die von aperiodischer oder (?) langperiodischer bis zu saisonal-periodischer und kurzperiodischer Dynamik reichen. Da die meisten Dauerformen mit deutlich saisonalem Lebenszyklus im Herbst und im Winter schüpfen, wird angenommen, daβ das Nahrungsangebot einer der bestimmendon Ökofaktoren ist und daβ die Wassertemperaturen stets über den Thermopathie-Niveaus der Arten liegen. Arten mit langpriodischem Lebenszyklus wurden nicht beobachtet.

INTRODUCTION

Studies on the dynamics of ostracodes living on the sublittoral sea floor are rare. In view of the comparative domination and importance euhaline sublittoral ostracodes have, we must acknowledge a pronounced deficiency of research in this field.

Some reasons for this deficiency are:

1. The normally very limited population density[1], especially in off-shore regions.
2. High variations in species abundance which become more obvious with increased exposure to water movement.
3. The drifting of dead as well as live ostracodes, especially in the more exposed coastal regions.

---

[1] The term 'population' is used here in common with Schwerdtfeger (1968, p. 18) for "the totality of individuals of one species in a defined area" (in free translation).

4. The rareness of observation areas that are euhaline and easy to reach during all seasons.
5. The complexity of the mutual influence of the ecological factors.
6. The complexity of the ostracode distribution patterns.
7. The difficulties involved in the breeding of euhaline ostracodes.
8. The lack of quantitative sampling techniques.
9. The tedium and logistic problems of seasonal studies.

Starting points to overcome these difficulties lie:

I. In the choice of an area of investigation,
   1. with a relatively high population density,
   2. with little variation in population abundance,
   3. with a minimum of allochthonous individuals,
   4. which reflects the conditions of the sea on a minor scale in near-shore areas,
   5. in which life underlies conditions that are close to a surveyable model.

II. In collecting data on environmental factors, which might have an influence on spatial and seasonal abundance, coinciding with the ostracode sampling.

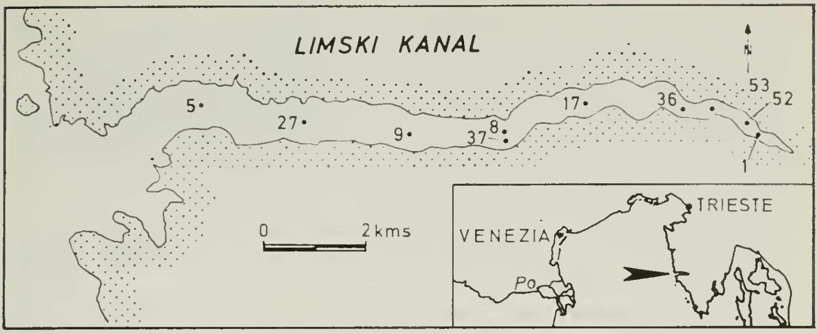
III. In developing a proper sampling technique.

These starting points in mind, a student group from the Institute of Geology and Paleontology, University of Göttingen, carried out a sedimentological and microfaunal research program, including oceanographic studies, in the Limski kanal. This program was initiated, organized, and directed by Dr. D. Meischner, who is to be gratefully acknowledged for his help along with my colleagues Drs. C. H. v. Daniels, D. Fütterer, J. Paul, and J. Schneider. The original research project was supported by the "Deutsche Forschungsgemeinschaft" with grants Me 267/2,3,4,7,9, without which the study would not have been possible. I wish here to express my gratitude.

The geographic position of the Limski kanal (Text-fig. 1) and its general thalassographic setting were repeatedly described by Vatova (1931), Vatova and Milo di Villagracia (1948, 1950), Hinze and Meischner (1968), v. Daniels (1970a, 1970b), Paul (1970a, 1970b), Uffenorde (1970, 1972), and others.

For the results concerning the sedimentological investigations I refer to Paul (1970a, b), for those concerning the hydrographical investigations from 1967 to 1969 to v. Daniels (1970b) and Uffenorde (1972).

The purpose of this paper is to give data on the seasonal variations in population dynamics of 12 mostly euhaline, sublittoral ostracode species, data which allow one in some cases to estimate the duration of development and the sex ratio, and further to show in a few examples the range of modification in the life-cycles of marine Ostracoda. This information might be useful for the understanding and interpretation of mediterranean ostracode faunas, whether they belong to biocenoses or autochthonous taphocenoses.



Text-figure 1. Map showing area of investigation and position of sampling stations.

A first account of the variation in the total ostracode abundance as well as on the population dynamics of 14 species was given by me on the basis of a study of 98 samples (Uffenorde, 1972). Forty-two (42) additional samples were examined in order to verify the earlier results and to get more data concerning the population dynamics of some other species. The seasonal variations of two of these species are briefly discussed here.

For references on this subject see Theisen (1966, pp. 254 ff.) and Uffenorde (1972, p. 37). It is also to be noted that the special terminology used here is in common useage with that of Schwerdtfeger (1968).

MATERIAL AND METHODS

One hundred and forty (140) sediment samples from 10 sampling stations were studied. The stations are shown on Text-figure 1. They are all situated in the median and inner part of the ria. The depth ranges from 6 ms at station 1 to 34 ms at station 5. The sediment is a clay-silt with a median grain size between 6 and 16 microns, mainly being agglutinated to fecal pellets (Paul, 1970a, p. 24).

The samples were taken with an improved Krumm-grab (v. Daniels, Meischner and Uffenorde, 1970) at monthly intervals from September 17th, 1967 to October 12th, 1968. Each sample contained 27.3 cm^2 of the sediment surface and usually 2 to 3 cms of the uppermost layer.

The laboratory treatment consisted of staining with rose bengal according to Walton (1952) modified by Lutze (1964), wet sieving on a screen with a mesh-size of 63 μs, and dry picking.

The criterion for being counted as a living ostracode, was the presence of the complete soft body. The rose bengal staining proved to be a helpful method to discover living individuals, particularly the larvae.

As the populations, even of the relatively common species, do not exceed 2 specimens per 10 cm^2, a study of the seasonal distribution of their instars is only possible with the assumption that the area studied is fairly homogenous with regard to the environmental factors. This being the case in the Limski kanal, we may summarize the counts from the sampling stations.

Because among the 44 living species I found some have similar larval stages, only a few of the relatively common and easily distinguishable species give information on population dynamics.

As to be expected in an environment of a low energy level, instars within the same developmental stage vary only slightly in their dimensions. Therefore the developmental stage of the instars studied were identified by measuring length and height of the carapaces.

Because of the methods used, no complete life-cycle was found. Usually the eggs, the nauplius larva, and the A-7 stage were washed away during the sieving; the latter stage may be present but only in small number.

For further details concerning the methods used see Uffenorde (1972, pp. 16 ff.).

POPULATION DYNAMICS

According to Theisen (1966, p. 254) most marine ostracodes seem to be perennial forms. As this statement is based on data concerning euryecological, especially mixohaline Ostracoda studied by him and other authors, we should expect a high majority of perennial forms in a mainly stenecological, euhaline environment. This indeed proved to be true for the species studied in the Limski kanal.

The term 'perennial' is used here in the sense of Alm (1916), Theisen (1966), and others. According to their definition, perennial forms occur during the whole year as adults and larval stages or in larval stages.

Between the perennial forms, however, a differentiation in the seasonal distribution can be observed.

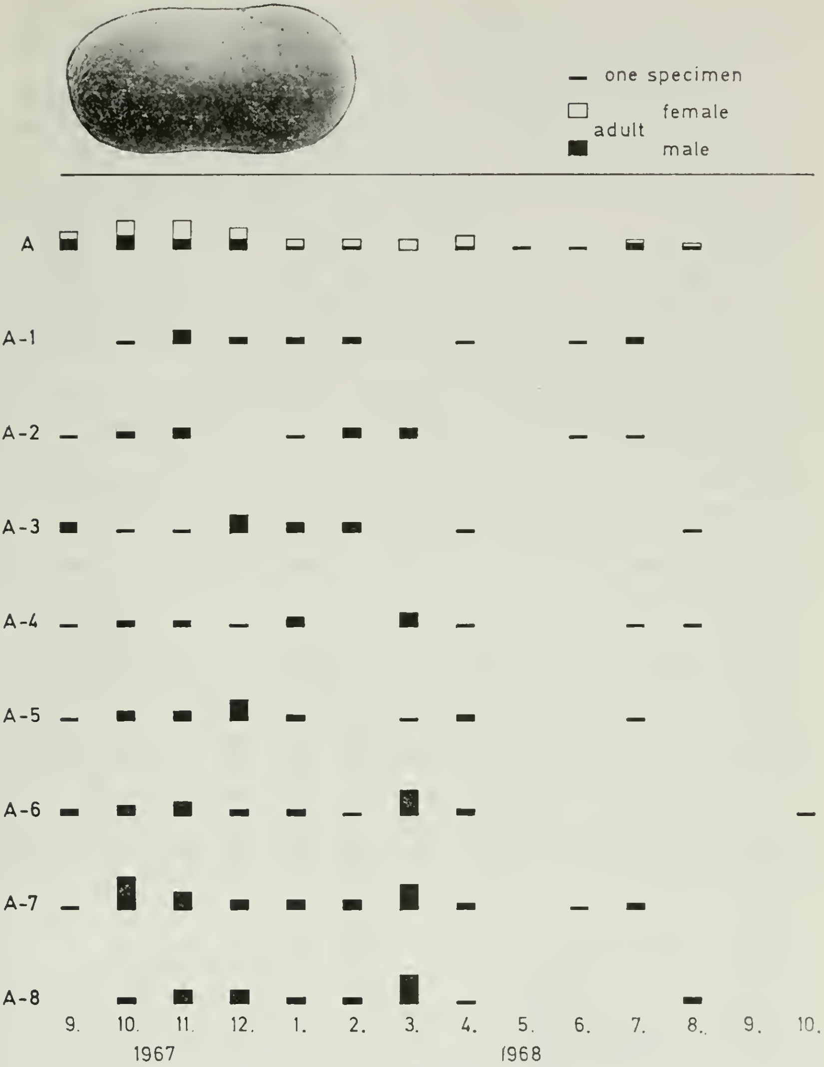
Five (5) groups of perennial forms may be distinguished:

1) *Species which seem to be aperiodic.*

Five species — so far as we can see from a collecting period of 14 months — show no periodic distribution.

Cytherella sp. (Text-fig. 2) (for description see Uffenorde, 1972, p. 50) which is closely related to the fossil species *Cytherella vulgata* Ruggieri, 1962, is found under normal conditions both as juveniles and adults.

During May, June, and August until October, 1968, the population density was extremely low. In an area of 273 cm^2 only a few specimens were present, in September there were none. This apparent, not real, low abundance is caused in part by dragnet fishing in April. Because of this fishing method,



Text-figure 2. *Cytherella* sp. Seasonal distribution of instars, females, and males on the basis of 215 living specimens.

the sediment of the eastern and western regions of the inner Limski kanal is stirred up and displaced, burying the ostracode fauna. It takes approximately two months for the ostracode fauna to reconcentrate on the sediment surface. The reason for the decline in August is unknown.

Cytherella sp. was the only species observed with ovigerous females throughout the year. A maximum of eight eggs was observed, four on each side of the individual. The ratio between ovigerous and non-ovigerous females was on the average about 4 to 1, the sex-ratio nearly five females to four males.

Propontocypris setosa (G. W. Müller, 1894) (Text-fig. 3) is included in this group, too, although the generation that passed the larval stage A-6 from November to February appeared in higher number.

This generation seems to have a relatively high mortality rate in the later larval stages so that no more adults are found. Unfortunately this development is concealed by the destruction of the microenvironment by fishing after the April sampling as well.

Pseudopsammocythere similis (G. W. Müller, 1894) and a *Loxoconcha* species, which is closely related to the fossil *Loxoconcha dertobrevis* Ruggieri, 1967, seem to belong to this group as well as:

Carinocythereis antiquata bairdi (Uliczny, 1969) (Text-fig. 4), although its population density is so low that there are no readings for many of the larval stages. The average sex-ratio is about four females to one male.

Species with long periodic life-cycles have not been found in the area studied.

2) *Species with long periodic dynamics (?) but short life-cycles.*

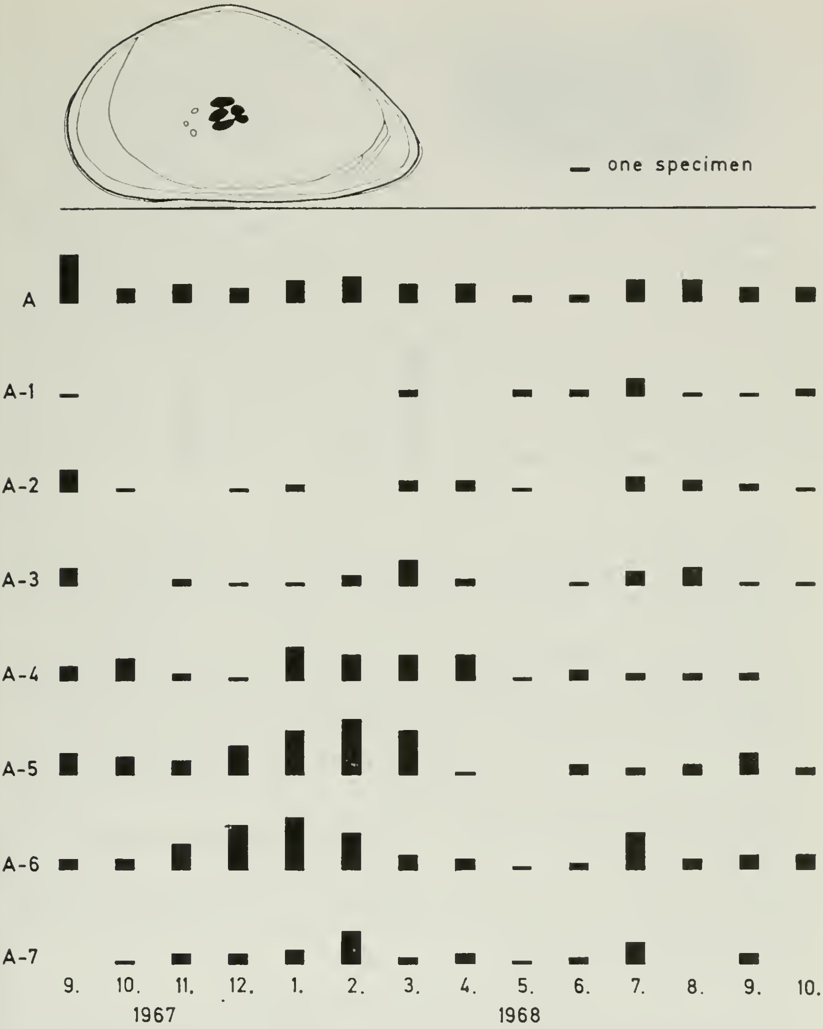
Cytheropteron rotundatum G. W. Müller, 1894 (Text-fig. 5) possibly represents a species with a long periodic population dynamic, the undulations of which last longer than the collecting period and obviously take some generations. Larvae were common in September, 1967, and October, 1967. It seems that a high mortality rate reduced their number so that only a few adults were found in fall 1967. The larvae of the winter generation were, therefore, smaller in number, those of the spring generation were again smaller in number. This interpretation, as well as the dotted line drawn between the winter and the spring generation, tentatively indicating the general trend of the growth rate, should be taken with caution. More material needs to be sampled and studied before we may reach any definite conclusions.

3) *Species with distinct seasonal life-cycles.*

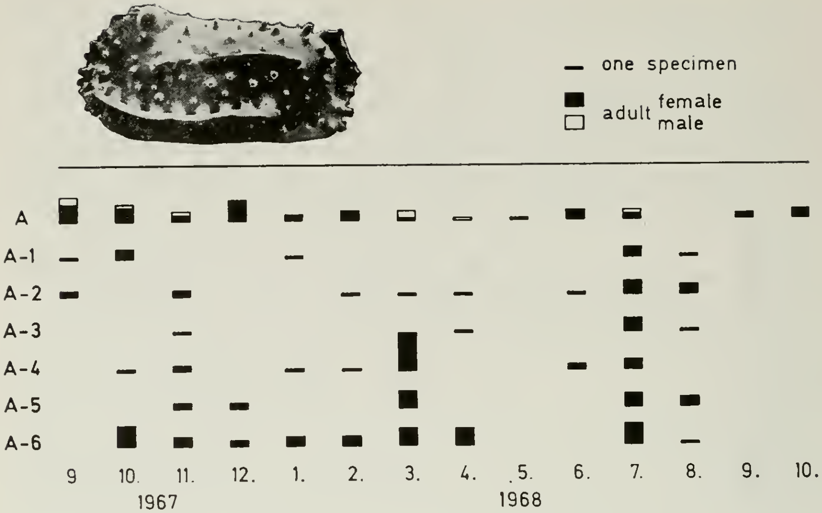
Six species have revealed a distinct seasonal population change.

Leptocythere ramosa (Rome, 1942) (Text-fig. 6) is one of the best examples for this group. From September, 1967, until March, 1968, the generation I was observed, consisting, with two exceptions, of only adults. The average sex ratio was about four females to one male. Generation II first appeared in limited number. The stage A-7 reached its highest abundance in March, reaching maturity first in July. For *Cytherois* sp. C, another good example, see Uffenorde (1972, p. 103).

Four species with lower population densities also seem to produce only one generation per year.



Text-figure 3. *Propontocypris setosa* (G. W. Müller, 1894). Seasonal distribution of instars on the basis of 398 living specimens.



Text-figure 4. *Carinocythereis antiquata bairdi* (Uliczny, 1969). Seasonal distribution of instars, females, and males on the basis of 143 living specimens.

With *Hiltermannicythere turbida* (G. W. Müller, 1894) (Text-fig. 7) first individuals of A-6 appeared in January, and became adults in July. Judging from the long period of occurrence of instars of A-6, it may be assumed that the species has a hatching period of more than half a year. *Pterygocythereis jonesii* (Baird, 1850) (Text-fig. 8) passed the stages A-6 and A-5 in winter and reached adulthood from July onwards, the average growth rate being approximately one instar per month.

A similar life-cycle is shown by *Cytheridea neapolitana* Kollmann, 1960 (Text-fig. 9).

Bassleriles berchoni (Brady, 1869) (Text-fig. 10) develops later in the year, passing the middle larval stages during summer, fall, and winter and being adult from September onwards.

4) *Species with weaker seasonal undulations in abundance.*

A less distinct seasonal population change was observed with *Cytheroma variabilis* G. W. Müller, 1894 (Text-fig. 11) which has higher numbers of larvae in winter and more adults from March to July. During the latter time a few males were found, and it is believed that during these months copulation takes place.

5) *Species with short periodic dynamics.*

Shorter undulations may be seen in the following histograms of *Leptocythere bacescoi* (Rome, 1942) and *Cytherois* aff. *C. fischeri* (Sars, 1866).

With *Leptocythere bacescoi* (Text-fig. 12) three or perhaps four generations developed during the collecting period. There was an undulation between a higher proportion of older larvae and adults (in September, 1967, February and August to October, 1968) and younger larvae (in November, 1967, March, 1968, and July, 1968). The samples disturbed by fishing unfortunately prevent a clearer picture.

This is also true for *Cytherois* aff. *C. fischeri* (Text-fig. 13). In this histogram a second hiatus is visible. Nevertheless two generations seem to exist.

Most of the species studied are perennial forms. Species with strictly seasonal occurrence of adults and larvae are rare in the biotope studied and data are very limited.

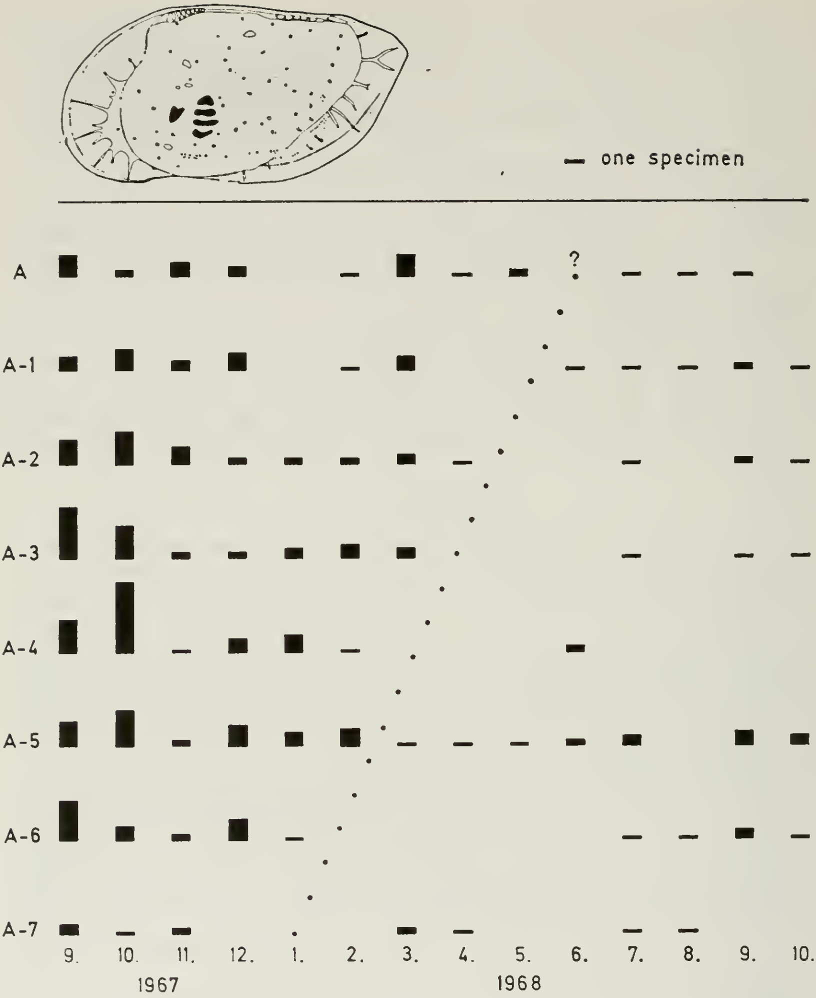
Cytherois frequens G. W. Müller, 1894 (Uffenorde, 1972, p. 101) is one of the relatively more common species, the occurrence of which is seasonally restricted. Larval stages were observed between December and July, adults between February and July. Until resting eggs are found, the seasonal occurrence might also be explained by a seasonal immigration from a neighbouring habitat.

CONCLUSIONS

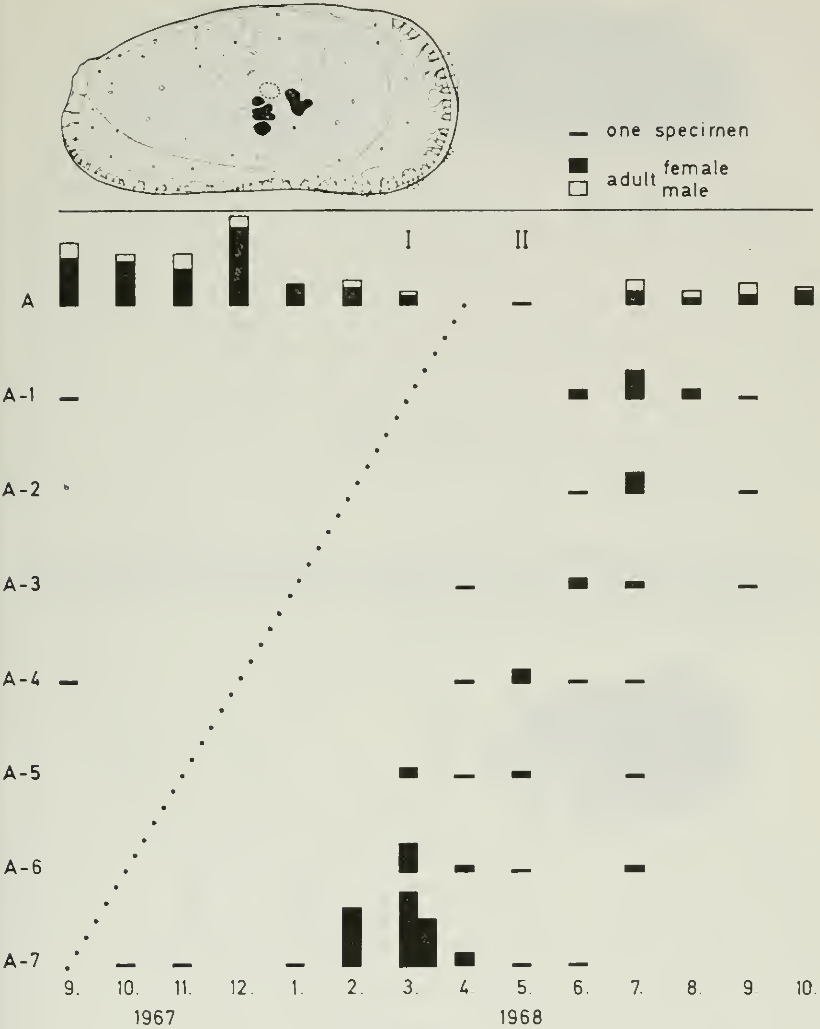
In summarizing the results of this brief study on the seasonal distribution of 12 marine ostracode species, the following conclusions may be drawn:

1. In accordance with the results of studies done by Elofson (1941, pp. 383 ff.), Theisen (1966), and others in northern European marine environments most benthonic ostracode species were found throughout the year as adults and as juveniles or as juveniles. That means in practice that an adequate sample (in the sense of Kaesler, 1966, p. 23) taken at any time of the year, gives correct information for presence/absence records, if we take all individuals (adults and juveniles) into account.
2. Even in a biotope of a low energy level, as the soft bottom of the Limski kanal, certain temporal differences are visible between the perennial ostracodes. The dynamics of the population differ considerably in the course of the year. In consequence, frequency counts have to be done seasonally if one intends to get an adequate representation of the complete living ostracode fauna of a marine environment (*e.g.* Wagner, 1957, p. 107); this applies to biotopes of high as well as low energy levels at least nearshore.
3. Within one and the same ostracode assemblage a wide spectrum in temporal abundance may occur from an obviously aperiodic to a distinct periodic population dynamic. The ostracode associations — although as a whole being in an equilibrum with the environment — react in its elements in different ways according to their special situation in the ecosystem.
4. The more or less distinct periodical abundance dynamic may either be longperiodical, seasonal, or shortperiodical, which applies to distinct generations as well as the total amount of individuals from different generations living at the same time.

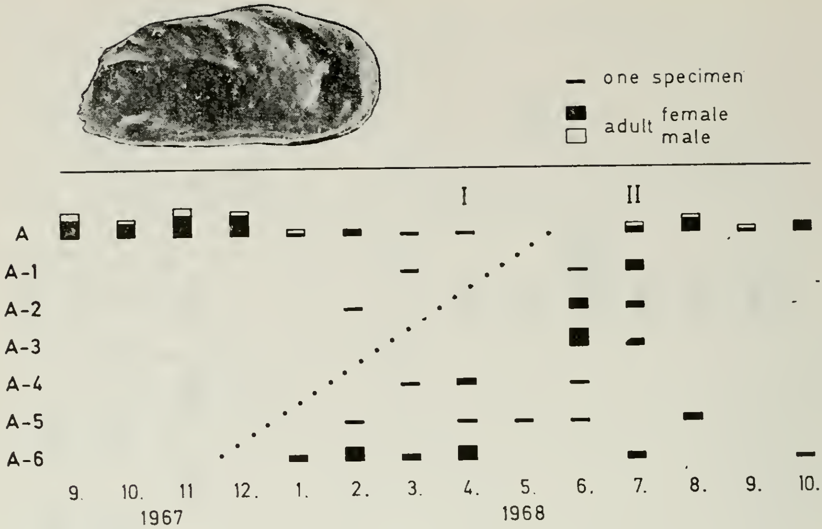
   Species with long-periodic life-cycles, as for instance *Philomedes globosus* (see Elofson, 1941, pp. 396, 397), have not been observed.



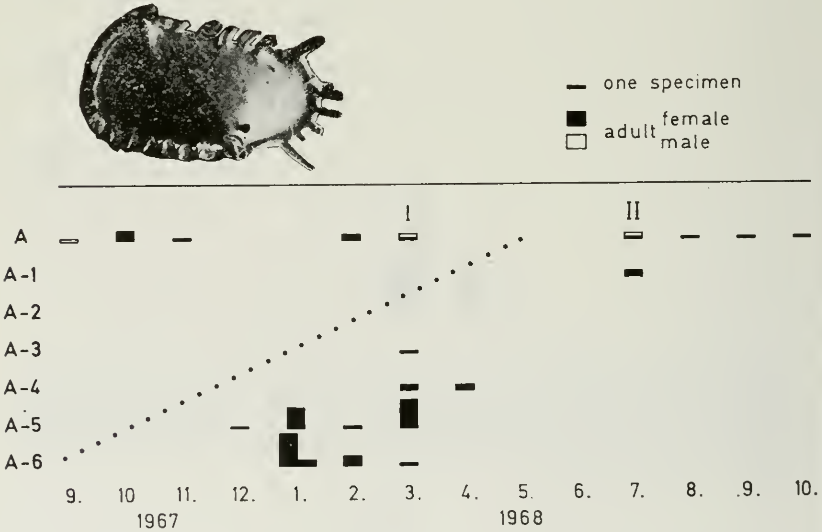
Text-figure 5. *Cytheropteron rotundatum* G. W. Müller, 1894. Seasonal distribution of instars on the basis of 263 living specimens. The dotted line tentatively indicates the border between two generations and the general trend of the growth rate.



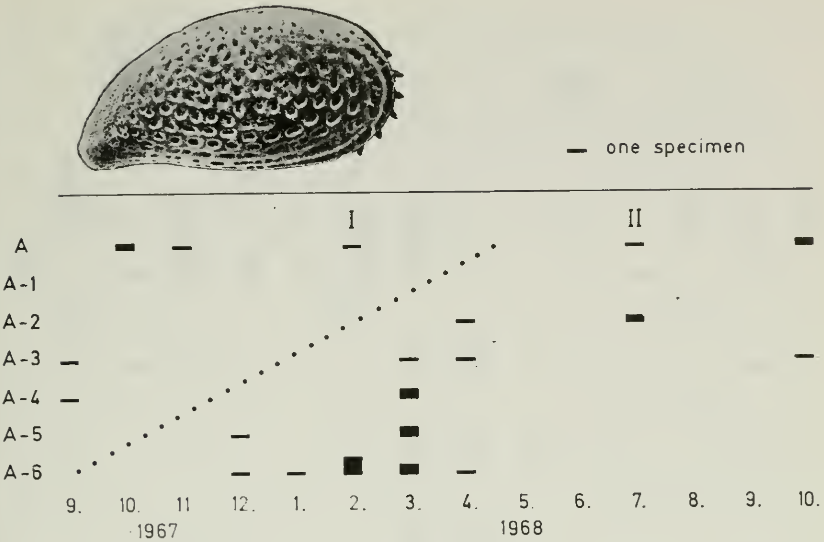
Text-figure 6. *Leptocythere ramosa* (Rome, 1942). Seasonal distribution of instars, females, and males on the basis of 226 living specimens. The dotted line indicates the border between generation I and generation II and the general trend of the growth rate.



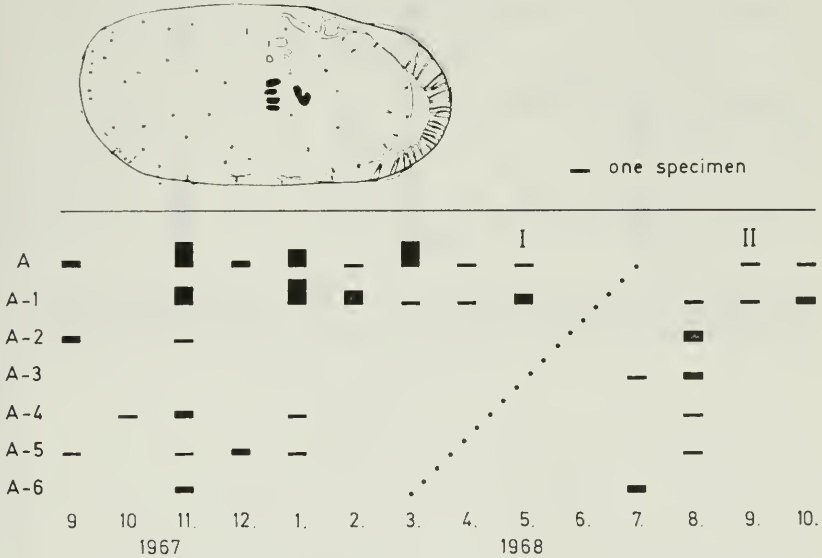
Text-figure 7. *Hiltermannicythere turbida* (G. W. Müller, 1894). Seasonal distribution of instars, females, and males on the basis of 89 living specimens. The dotted line indicates the border between generation I and generation II and the general trend of the growth rate.



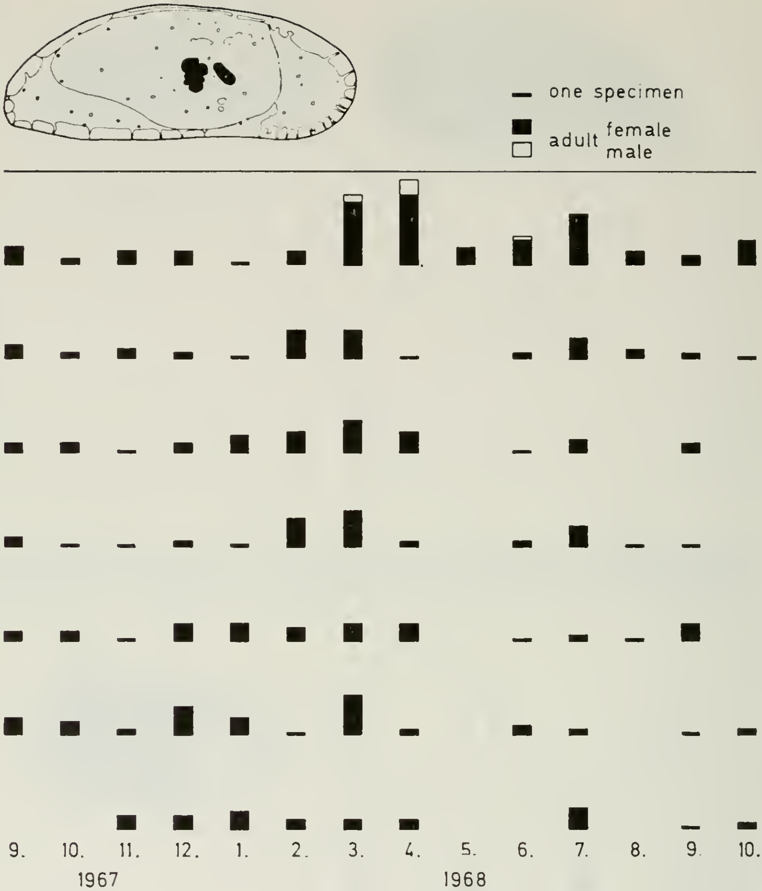
Text-figure 8. *Pterygocythereis jonesii* (Baird, 1850). Seasonal distribution of instars, females, and males on the basis of 52 living specimens. For dotted line see explanation Text-figure 7.



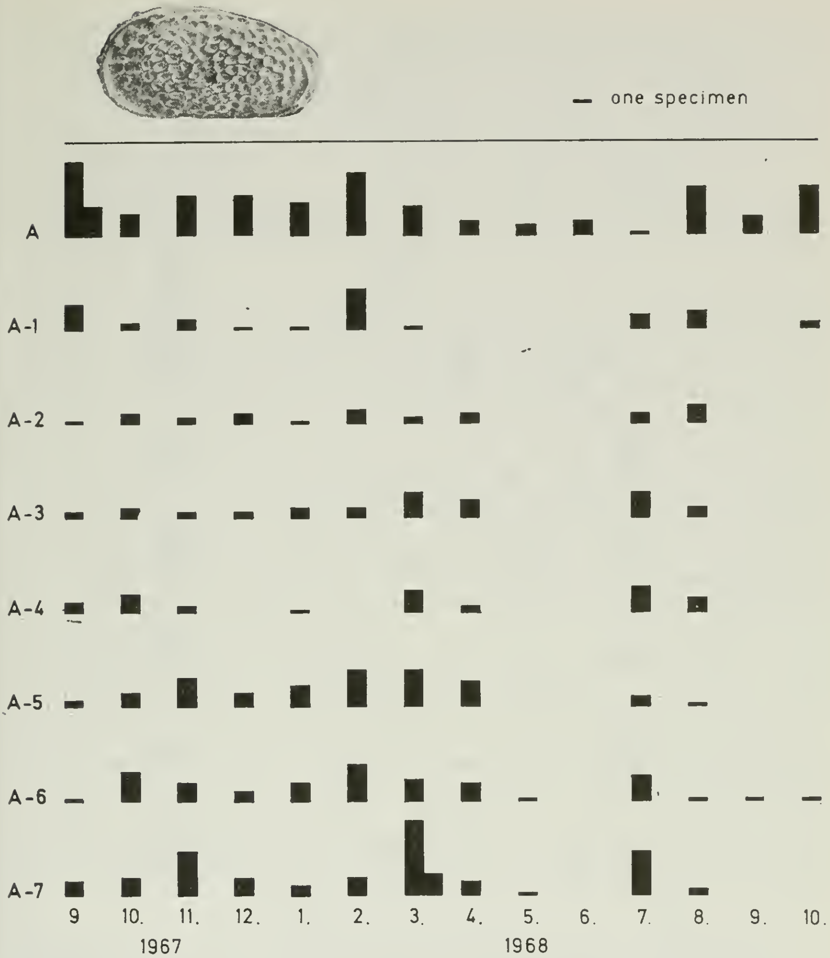
Text-figure 9. *Cytheridea neapolitana* Kollmann, 1960. Seasonal distribution of instars on the basis of 33 living specimens. The dotted line indicates the border between generation I and generation II.



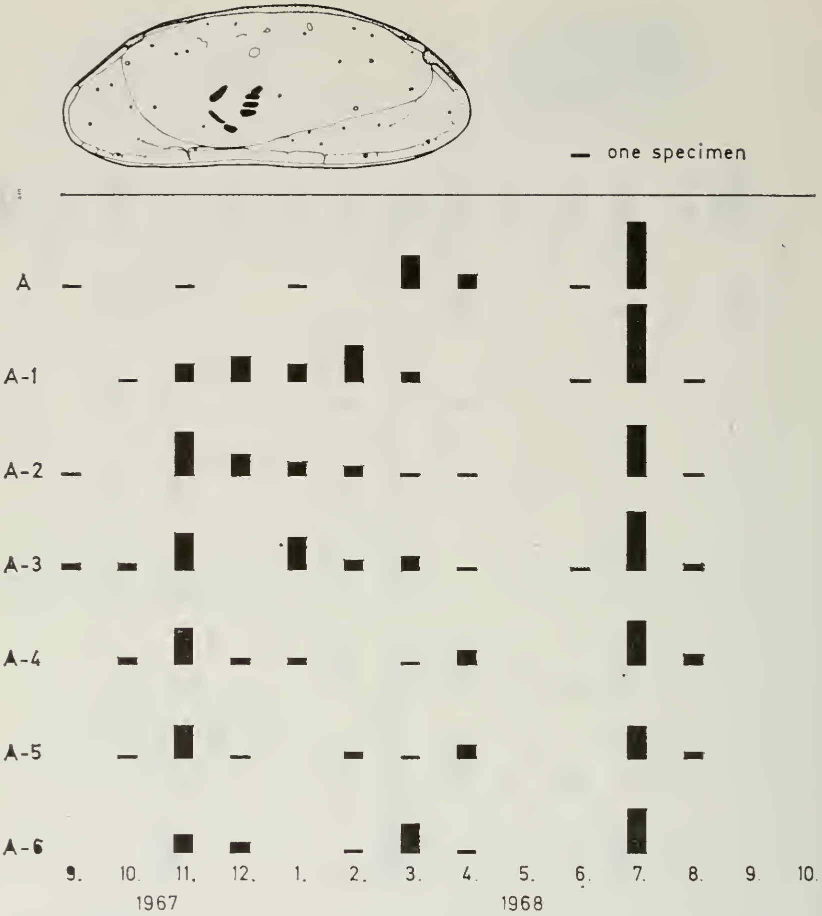
Text-figure 10. *Basslerites berchoni* (Brady, 1869). Seasonal distribution of instars on the basis of 77 living specimens. For dotted line see explanation Text-figure 9.



Text-figure 11. *Cytheroma variabilis* G. W. Müller, 1894. Seasonal distribution of instars, females, and males on the basis of 352 living specimens.



Text-figure 12. *Leptocythere bacescoi* (Rome, 1942). Seasonal distribution of instars on the basis of 352 living specimens.



Text-figure 13. *Cytherois* aff. *C. fischeri* (Sars, 1866). Seasonal distribution of instars on the basis of 277 living specimens.

5. Most perennial species with distinct seasonal life-cycles seem to have similar reproductive periods and duration of development. Thus larvae of the stages A-7 to A-5 of *Leptocythere ramosa, Cytheridea neapolitana, Hiltermannicythere turbida,* and *Pterygocythereis jonesii* appear most frequently in winter and early spring. This generation reaches maturity mainly in summer and early fall.
   According to Theisen (1966, p. 261) ". . . normally copulation occurs immediately after the last moulting . . .". This would mean that copulation takes place during the period of the warmest water temperatures in the area studied.
   As no eggs have been found along with the species studied, and as the first larval stages were not observed, the reproductive period is difficult to determine. It can roughly be estimated that hatching takes place in fall and winter, which means that hatching, in this case, is not dependent upon water temperatures, because these lie above thermopathic levels throughout the year.
6. As assumed by Theisen (1966) food seems to be one of the major controlling factors for the seasonal occurrence. In the area studied food supply for the young larvae is guaranteed in fall and winter by the high amount of decomposed organic material which settles chiefly in areas of minimal currents, such as the Limski kanal. A reduction of this material is prevented by convection currents which start in fall, bringing surface water rich in oxygen to the seafloor.
7. There is no proof that the few observed species with strictly seasonal occurrence belong to the autochthonous assemblages.
8. I may not end without emphasizing that these results and conclusions are preliminary in many ways and that further field work and, in particular, laboratory experiments, as recently done by Theisen (1966) and Hagermann (1969a, 1969b) with euryhaline ostracodes, and statistical treatment are needed to verify them. These results and conclusions, however, may encourage the study of population dynamics of Ostracoda in other marine environments, especially those which are still undisturbed by man.

REFERENCES

Alm, G.

1916. *Monographie der schwedischen Süsswasser-Ostracoden nebst systematischen Besprechungen der Tribus Podocopa.* Zool. Bidr. Uppsala, 4 (1915), pp. 1-247.

v. Daniels, C. H.

1970a. *Jahreszeitliche ökologische Beobachtungen an Foraminiferen im Limski kanal bei Rovinj/Jugoslawien (nördliche Adria).* Geol. Rdsch., 60 (1), pp. 192-204.

1970b. *Quantitative ökologische Analyse der zeitlichen und räumlichen Verteilung rezenter Foraminiferen im Limski kanal bei Rovinj (nördliche Adria).* Göttinger Arb. Geol. Paläont., 8, pp. 1-109.

v. Daniels, C. H., Meischner, D., and Uffenorde, H.

1970. *Ein verbesserter quantitativer Bodengreifer nach H. Krumm.* Meyniana, 20, pp. 1-3.

Elofson, O.

1941. *Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks.* Zool. Bidr. Uppsala, 19, pp. 215-534.

Hagerman, L.

1969a. *Environmental factors affecting Hirschmannia viridis (O. F. Müller) (Ostracoda) in shallow brackish water.* Ophelia, 7, pp. 79-99.

1969b. *Respiration, anaerobic survival and diel locomotory periodicity in Hirschmannia viridis Müller (Ostracoda).* Oikos, 20 (2), pp. 384-391.

Hinze, C., and Meischner, D.

1968. *Gibt es rezente Rot-Sedimente in der Adria?* Marine Geol., 6, pp. 53-71.

Kaesler, R. L.

1966. *Quantitative re-evaluation of ecology and distribution of Recent Foraminifera and Ostracoda of Todos Santos Bay, Baja California, Mexico.* Univ. Kansas Paleont. Contr., Pap. 10, pp. 1-50.

Lutze, G. F.

1964. *Zum Färben rezenter Foraminiferen.* Meyniana, 14, 43-47.

Paul, J.

1970a. *Sedimentgeologische Untersuchungen im Limski kanal und vor der istrischen Küste (nördliche Adria).* Göttinger Arb. Geol. Paläont., 7, pp. 1-75.

1970b. *Sedimentologische Untersuchungen eines küstennahen mediterranen Schlammbodens (Limski kanal, nördliche Adria).* Geol. Rdsch., 60 (1), pp. 205-222.

Schwerdtfeger, F.

1968. *Ökologie der Tiere.* Bd. II. Demökologie. (Verl. P. Parey), Hamburg and Berlin, pp. 1-448.

Theisen, B. F.

1966. *The life history of seven species of ostracods from a Danish brackish-water locality.* Medd. Kommiss. Danm. Fisk. -og Havunders., N.S., 4 (8), pp. 215-270.

Uffenorde, H.

1970. *Zur Ostracoden-Fauna eines marinen Schlammbodens an der istrischen Küste (Limski kanal, NW-Jugoslawien).* Geol. Rdsch., 60 (1), pp. 223-234.

1972. *Ökologie und jahreszeitliche Verteilung rezenter benthonischer Ostracoden des Limski kanal bei Rovinj (nördliche Adria).* Göttinger Arb. Geol. Paläont, 13, pp. 1-121.

Vatova, A.

1931. *La fauna bentonica del Canal di Leme in Istria.* R. Com. Talassogr. Ital., Mem., 181, pp. 1-10.

Vatova, A., and Milo di Villagrazia, P.

1948. *Sulle condizioni chimico-fisiche del Canale di Leme presso Rovigno d'Istria (Nota preliminare).* Boll. Pesca, Piscicolt. Idrobiol., XXIV, 3, n.s., (1), pp. 5-27.

1950. *Sulle condizioni idrografiche del Canal di Leme in Istria.* Nova Thalassia, 1 (8), pp. 1-68.

Wagner, C. W.

1957. *Sur les ostracodes du Quaternaire Récent des Pays-bas et leur utilisation dans l'étude géologique des dépôts Holocènes.* Pp. 1-259, (Mouton & Co.) 's-Gravenhage.

Walton, W. R.
1952. *Techniques for recognition of living Foraminifera.* Contr. Cushman Found. Foram. Res., 3, pp. 56-60.

Henning Uffenorde,
Geol.-Paläont. Institut,
Berliner Str. 28,
D-3400 Göttingen,
Germany

DISCUSSION

Dr. R. A. Reyment: I notice that your sample sizes were not very large judging from the scale on your bar diagram. Is that because you only analyzed small quantities of material? Could you get more material of each species? I am asking this because with more material you would be able to back up your study by computing life tables of each species, which would give you a quantitive rate of assessing the performance of each of them.

Dr. Uffenorde: After having tested the original KRUMM-grab at the sampling stations in spring 1967, an enlarged and improved sampler was built, modeled after the device by v. DANIELS et al. (1970) in order to enable a quantitative study not only of the living foraminiferal fauna but also of the ostracode fauna. In order to keep its unproblematic technique and its easy handling on a rubber boat there is a limit in size.
On the other hand, sampling at one station several times could lead to the result that the first sample only reveals the natural conditions and that the others are samples of a more and more disturbed environment.
The samples taken at one station were indeed too small to study seasonal variations of single species. For the present study I therefore united the counts of 10 stations, which belong to the same biotype. That makes an amount of sediment of more than 500 ccms per month, for most of the species.

Dr. Reyment: It would, I think, be useful and interesting to expend this type of investigation to the production of life tables. This would require samples of about ten times of these figuring in Dr. Uffenorde's study. But inasmuch as he has developed efficient observational and sampling techniques, this should not prove difficult to realize.

Dr. Uffenorde: These are my intentions, too. But although I have samples from 18 further stations, I can't sum them all together, because 1) most of them came from environments more or less different than the investigated one, and 2) to pick one single sample of most of these stations would take quite a lot of time (on the average, I think, more than a week) depending on the amount of the sediment fraction $>$ 63 microns.

Dr. A. Lieubau: *Cytheropteron* needs more than one year for a generation.

Dr. Uffenorde: No, with *Cytheropteron rotundatum* it seems that we have to distinguish between a short change of the generations and a stronger long ranging natural undulation of the whole population. I estimate the duration of development at five to seven months, roughly. As my study only comprised a period of 14 months this was too short a time to evaluate the long periodic undulations of this species.

VARIATIONS IN FRESH-WATER OSTRACODE POPULATIONS FROM LAKES IN ST. LOUIS COUNTY, MISSOURI

DOROTHY J. ECHOLS, L. GREER PRICE, AND MARY ANN RAFLE
Washington University

ABSTRACT

During 1962-1963, seasonal collections of living fresh-water ostracodes were made from six lakes in St. Louis County, Missouri. At that time, the effects of seasonal changes on the occurrence of species and relative abundances of young and mature forms were noted. Now, nearly ten years later, four of these lakes have been sampled during the winter, spring and summer months, and the conditions noted previously were recorded. The combined ostracode fauna of the lakes sampled consisted of species of *Cypria, Candona, Potamocypris,* and *Cypridopsis*. The compositions of the ostracode faunas collected in 1962-63 and 1971-72 show a net increase in faunal diversity and exhibit distinct seasonal variation.

VARIATIONS DANS LE POPULATIONS D'OSTRACODE D'EAU DOUCE DANS DES LACS DU COMTÉ DE SAINT-LOUIS DANS LE MISSOURI

RÉSUMÉ

Pendant l'année 1962-1963, on rassembla à différentes saisons des ostracodes d'eau douce vivants qui ávaient été pêchés dans six lacs du comté de Saint-Louis dans le Missouri. On enregistra chaque fois les effets des changements dus aux saisons sur la présence des espèces et sur l'abondance relative des spécimens jeunes et adultes. Maintenant, près de dix ans plus tard, on a rassemblé des spécimens obtenus dans quatre de ces mêmes lacs pendant les mois d'hiver, de printemps et d'été et on a noté à nouveau le conditions déjà observées auparavant. La faune ostracode rassamblée dans ces lacs se composait d'espèces de *Cypria, Candona, Potamocypris* and *Cypridopsis*. On a constaté qu'il y avait une augmentation nette dans le diversité des faunes ostracodes recueillies en 1971-72 comparées à celles de 1962-63, ainsi qu'une variation saisonnière marquée.

INTRODUCTION

Although studies on Recent fresh-water ostracodes have contributed considerable information to the overall knowledge of ostracode life history and the variables that determine their distribution, many more field observations on permanent, natural, or man-made lakes are needed for meaningful interpretations to be made. The present investigation was undertaken to augment the information obtained from a similar study completed nearly ten years ago.

During 1962-63, R. P. Frey and D. J. Echols made seasonal collections from six lakes in St. Louis County, Missouri. At that time they hoped to determine (1) whether genera and species of ostracodes vary seasonally, (2) whether seasonal changes affect their relative abundances, (3) whether the laying of eggs and the development of young are related to seasonal changes, and (4) whether environmental conditions influence their geographical distribution. Although results of this study did not answer all of the questions asked, they were significant enough to warrant a reinvestigation of at least some of the collecting sites.

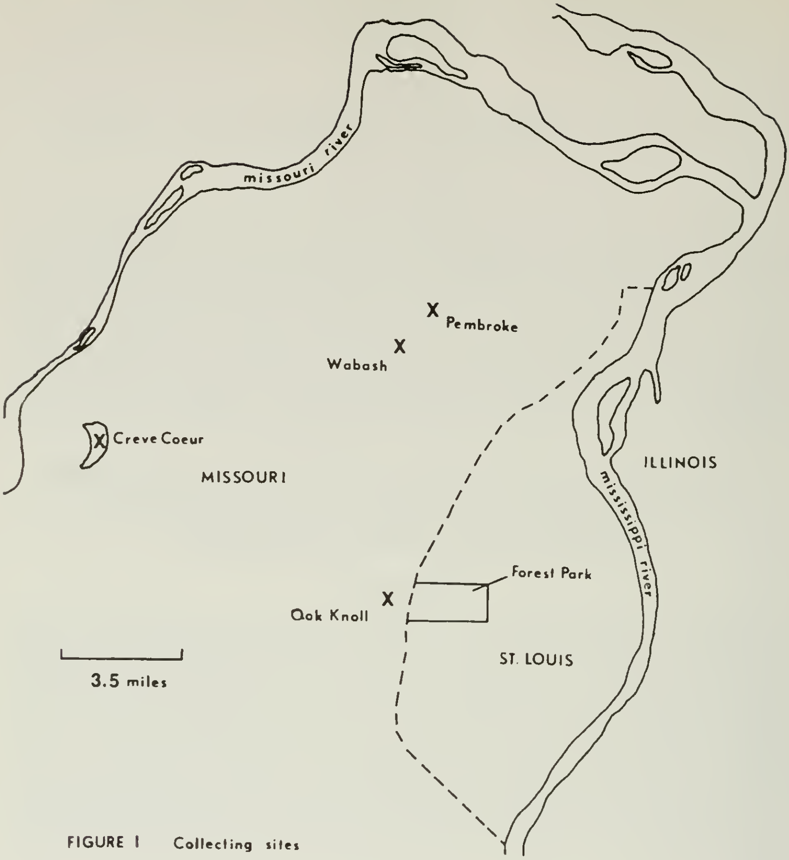


FIGURE 1 Collecting sites

In this second study, we hoped not only to correct operational error and eliminate interpretive bias, but also to answer two other important questions, namely the relationship between faunal variety and the age of the lake, and the effect of man's induced environmental changes on the faunal composition. Text-figure 1 is a schematic map of St. Louis and vicinity which shows the approximate locations of the lakes from which collections were made.

For the present study, four of the lakes sampled in 1962-63 were recollected during the winter, spring and summer months. Samples of 3 to 4 cubic centimeters of material were collected by means of a conical 200 mesh plankton net at various stations and depths within each lake. When the collections were made in 1962-63 and again in 1971-72, the following conditions were noted: (1) the general appearance of the lake (*i.e.* size, water level, amount and distribution of aquatic vegetation), (2) temperature, (3) pH, and (4) bottom conditions. Table I summarizes the physical conditions recorded from the three lakes in which live standing crops of ostracodes were recovered and the relative seasonal abundances of the species identified. The fourth lake collected was Creve Coeur lake, a natural cut-off meander of Missouri River, and

TABLE I

	1962-63												1971-72								
	WABASH				PEMBROKE				OAK KNOLL				WABASH			PEMBROKE			OAK KNOLL		
Surface Area (sq. ft.)	200,000				75,000				8,500				(same)			(same)			(same)		
Water Depth	8-18"				3-5'				10"												
Water Temperature (centigrade)	5-30				5-30				4-30												
pH	8.5				8.1				7.1				9.1			7.9			7.5		
Aquatic Vegetation	None				None				<u>Lemna</u>				<u>Lemna</u> <u>Jussiaea</u>			<u>Lemna</u> <u>Jussiaea</u>			<u>Lemna</u> (decreased)		
Bottom Material	Sandy				Silt & Mud				Black organic mud				(same)			(same)			(same)		
Seasonal Collections	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	W	S	S	W	S	S
<u>Candona</u> <u>acuta</u> Hoff 1942	x	x											R			R	R				
<u>C.</u> <u>caudata</u> Kaufmann 1900	x	x			x	x							R			R					
<u>C.</u> <u>suburbana</u> Hoff 1942	x			x	x			x					R	R		R	R		R	R	
<u>Cypria</u> <u>ophthalmica</u> (Jurine 1820)		x		x	x	x	x	x	x	x	x	x	C	A	C	C	C	.C	A	A	A
<u>Cypridopsis</u> <u>vidua</u> (O.F. Muller 1776)				x	x		x							C	A	R	C	A	R	C	A
<u>Potamocypris</u> <u>smaragdina</u> (Vavra 1891)	x	x	x	x	x								A	A	C	C	A	A			

A=abundant, 75-100% C=common, 25-75% R=rare, less than 25% x = present contained no living ostracode populations in either 1962-63 or 1971-72, although corroded carapaces of *Candona* and *Potamocypris* were found. This appears to be one case in which man's environmental changes have directly affected the ostracode populations. Urbanization within the drainage basin has increased the sediment yield, and the great quantities of suspended silt and mud, as well as the continuing lack of organic material, make this environment unfavorable for the development of a diverse aquatic community. The composition of the ostracode fauna collected from Oak Knoll pond in 1962-63 and 1971-72 shows a net increase in faunal diversity.

SEASONAL DISTRIBUTION OF THE OSTRACODES

Candona acuta Hoff, 1942, *C. caudata* Kaufmann, 1900 and *C. suburbana* Hoff, 1942, showed consistent seasonal distribution. They were conspicuously absent in the late spring and summer collections in both 1962-63 and 1971-72. A few immature forms were found in the fall collections, but the larger, mature forms, both males and females, were found only in the winter and spring collections. Females carrying eggs were most abundant in the December sampling. Hoff's findings (1942) show that many species of *Candona* in Illinois vary in much the same way. Sharpe also noted in 1897 that the species of *Candona* which he studied were absent during the summer months and reappeared in the fall.

Although they occurred in varying abundances, mature and immature forms of most of the other species were found in at least one collection every season. *Cypria ophthalmica* (Jurine, 1820), Brady and Norman, 1889, was by far the most abundant and cosmopolitan form found in the lakes studied in all seasons, with the peak productivity occurring in the spring. Not only was there an enormous increase in numbers but most mature forms and those gravid with eggs were recorded in April. That these are hardy forms is evidenced by the fact that they appeared early in the order of succession and are still a dominant form in Oak Knoll. No males were found in any of the collections.

Potamocypris smaragdina (Vavra, 1891), Daday, 1900, is a common form, especially in permanent bodies of water. It is generally believed to have a seasonal occurrence in the spring, becoming most abundant in the summer months. Ferguson (1944), in collections from Round Lake in Forest Park, St. Louis, Missouri, concluded that *P. smaragdina* attains a primary peak of adult abundance in June, August, and October and is a spring-summer-fall form. He further stated that the normal seasonal population decline occurred in the month of November, and that the absence of adults from December to March suggests that this species passes the winter in the egg state. In contrast with this, both young and mature forms were found in our winter collections. In 1963 it was found in Wabash in all seasons, Pembroke in the fall and winter. In 1972 it was found in Wabash in the winter, spring and summer, and in Pembroke in the winter and summer. However, the relative abundances, the number of young, and mature forms gravid with eggs do suggest that it is predominantly a spring, summer and fall form but may be sporadic in occurrence as reported by Alm (1916). This species is not yet established in Oak Knoll.

Cypridopsis, which is generally considered one of the most common of North American ostracodes in permanent lakes, river backwaters and vernal ponds, was represented in our collections by the single species *C. vidua* (O. F. Müller, 1776), Brady, 1867. Although it appeared in many of the collections, it was present in surprisingly low numbers. This is particularly puzzling because we have on many occasions collected random ponds for the purpose of laboratory culture and have found after a period of a few weeks to months great numbers of this species. Their scarcity in our field collections may possibly be explained by the dominance of *Cypria* and the competition with that genus.

Previous workers have shown that *C. vidua* is a summer-fall form (Hoff, 1943; Ferguson, 1944), present in limited numbers in April and May and very abundant June through October. Ferguson also stated that specimens reaching the adult stage in October could live through the winter into April, and Furtos (1933) reported occasional occurrences of *C. vidua* in February and March. In our collections, this species appeared once in February, became a prominent member of the fauna in May, and adults were most abundant during the summer months. We concur, therefore, with the observations of other authors that this species is a summer-fall form.

In summary, the seasonal distribution of the faunas collected for this study shows that the species of *Candona* recovered from the lakes are absent during summer months, present in small numbers in the fall, and attain full growth in the winter months. *Cypridopsis* is generally absent in the winter months and present in increasing numbers from May through October. *Cypria* and *Potamocypris* are most uniformly distributed throughout the year, both having a peak in abundance in the late spring.

There is a definite relationship between faunal variety and the age of a lake. The appearance of *Candona* and *Cypridopsis* in the 1971-72 collections from Oak Knoll pond is a significant increase in diversity over the ten year span. No change was noted in the bottom material from 1962 to 1972. Hoff (1942) stated that ostracode distribution appears to be random as far as the type of bottom is concerned. This is found to be the case, as changes in distribution appear to be more a function of time than of bottom type.

REFERENCES

Alm, G.
1916. *Monographie der Schwedischen Susswasserostracoden.* Zoolog. Bidrag Uppsala, 4, pp. 1-249.
Ferguson, E.
1944. *Studies on the seasonal life history of three species of freshwater Ostracoda.* American Mid. Nat., 32, pp. 713-727.
Frey, R. P.
1963. *Studies on some recent freshwater ostracodes of Saint Louis County, Missouri.* Unpublished MA thesis, Washington University, St. Louis, Missouri.
Furtos, N. C.
1933. *The Ostracoda of Ohio.* Ohio Biol. Sur., 5, pp. 413-524.

Hoff, C. C.

1942. *The ostracods of Illinois, their biology and taxonomy.* Illinois Biol., Mon. 19, (1 & 2), pp. 1-196.

1943. *Seasonal changes in the ostracod fauna of temporary ponds.* Ecology, 24, pp. 116-118.

Mason, C. B.

1971. *The origin and history of Creve Coeur Lake.* Unpublished MA thesis, Washington University, St. Louis, Missouri.

Needham, P. R.

1940. *Trout streams.* Comstock Publishing Co., Ithaca, N.Y., 233 pp.

Sharpe, R. W.

1897. *Contribution to a knowledge of the North American freshwater Ostracoda included in the families Cytheridae and Cyprididae.* Bull. Illinois St. Lab. Hist., 4, pp. 414-484.

1918. *The Ostracoda.* Ward and Whipple, *Freshwater biology,* John Wiley and Sons, New York, N.Y., pp. 790-827.

Dorothy J. Echols,
L. Greer Price,
Mary Ann Rafle
Department of Earth Sciences,
Washington University,
St. Louis, Missouri 63130

DISCUSSION

Dr. G. Hartmann: Could you explain your identifications of species of *Candona*?

Mr. G. Price: I think that probably it was *C. acuta* and perhaps *C. suburbana.*

Dr. Hartmann: You see there are different types of *Candona,* some with maximum development in the summertime, some maximum in winter.

Dr. Sohn: Did you find males and females of your candonas?

Mr. Price: Yes, we did, but we did not with the other genera.

THE RELATIONSHIP BETWEEN OSTRACODA AND ALGAE IN LITTORAL AND SUBLITTORAL MARINE ENVIROMENTS

R. C. Whatley
Universidad Nacional de La Plata, and
University College of Wales, Aberystwyth, Great Britain

D. R. Wall
Burmah Oil Co. of Australia

ABSTRACT

The importance of algae in influencing the distribution of Ostracoda has been demonstrated by such workers as Colman (1940), Dahl (1948), Wieser (1952-1959), Chapman (1955), Ohm (1964), Reys (1963), and latterly by Hagermann (1966, 1968, 1969), Whatley and Wall (1969), and Williams (1969).

The following statistics further emphasize the importance of this relationship. In a recent study of the podocopid Ostracoda of Cardigan Bay in the southern part of the Irish Sea, involving several hundreds of samples, 95% of the living ostracodes encountered were from samples of littoral and sublittoral algae. The remaining 5% of live individuals were from a much larger number of samples from sediments of various types, both from the littoral and sublittoral and from offshore stations.

The present paper is in the form of a semi-quantitative and largely seasonal study of Ostracoda recovered from various species of algae at a number of stations along the Welsh Coast. A total of 23 species of podocopid Ostracoda were recovered from a total of more than 29 species of algae. (In some cases it was not possible to identify various members of the Rhodophyceae, which were, therefore, collected and considered together at this level.)

The eulittoral and sublittoral are treated separately and conclusions are drawn concerning the significance of seasonal changes in the specific nature and population structure of the ostracode faunas of the two and of seasonal faunal migrations between them. It is further concluded that the nature of the relationship between Ostracoda and algae is a most complex one but that the major factors governing this relationship include: the morphology of the plants and the nature of the shelter or protection which they afford from physical and biological pressures; the position of the plant, both macro and micro-environmentally within the zones studied; whether the relationship to food supply is direct or indirect; the type and amount of sediment enclosed within the plant; and the seasonal development of the plant.

The final part of the paper deals with a comparison of the present results with those of previous workers within this field and with similar studies which one of the authors (RCW) is currently undertaking along the coast of the Argentine Republic.

RÉSUMÉ

L'importance des algues quant à leur influence sur la répártition des Ostracoda a été démontrée par des chercheurs tels que Colman (1940) ; Dahl (1948) ; Wieser (1952, 1959) ; Chapman (1955) ; Ohm (1964) ; Reys (1963) ; et plus récemment par Hagermann (1966, 1968, 1969) ; Whatley et Wall (1969) et Williams (1969).

Les statistiques suivantes mettant l'accent sur l'importance de la relation entre Ostracoda et algues. Dans une récente étude sur les Ostracoda Podocopida de la Baie de Cardigan dans la région sud de la Mer d'Irlande, étude englobant plusieurs certaines d'exemplaire échantillons, 95% des ostracodes vivantes trouvés provenaient d'échantillons d'algues littorales ou sublittorales. Les 5% restant individus vivants provenient d'un plus grand nombre d'échatillons de sédiments de types variés, littoraux et sublittoraux, et de lieux éloignés du Rivage.

L'article suivant est une étude semi-quantitatif et pour la plupart saisonnier sur des ostracodes en provenance d'espèces variés effective d'algues sur un certain nombre de stations de la côte galoise. Un total de 23 espèces de Podocopida fut recueillie sur un total de plus 29 espèces d'algues étudiés. (Dans certains cas il ne fut possible d'identifier plusieurs membres des Rhodophycaea qui furent, par cette raison, rassemblés considéreés ensemble à ce niveau).

L'eulittoral et sublittoral sont traités séparément et des conclusions sont tireés quant à la signigication des changements saisonniers de la nature spécifique et de la structure de la population des faunes ostracodes des deux et des migrations saisonniers de la faune entre elles. Un conclusion plus avant que la nature de la relation entre les Ostracoda et les algues est extrêmement complexe mais que les facteurs les plus importants gouvernant cette relation comprennent: la morphologie de la plante et la nature de l'abri ou protection quel tire des pressions physiques et biologiques; la position de la plante, des macro et microenvironnements à l'intérieur des zones étudiés; si la relation avec l'apport de nourriture est direct ou indirect; le type et la quantité de sédiments que contenant la plante et le developpment saisonnier de la plante.

La partie finale de l'etude traite des résultats actuels comparés à ceux de cherchaurs anteneurs et aux études semblantes que l'un des auteurs (RCW) est actuellment en train d'effectuer sur la côte de la République Argentine.

RESUMEN

La importancia de las algas como factor influyente sobre la distribución de los Ostracoda, ha sido demostrada por varios autores; Colman (1940), Dahl (1948), Wieser (1952, 1959,); Ohm (1964), Reys (1963); y más recientemente por Hagermann (1966, 1968, 1969), Whatley y Wall (1969); y Williams (1969).

Las estadísticas siguientes enfatizan aún más la importancia de la relación entre Ostracoda y algas. En un estudio reciente de los Ostrácodos podocópidos de la Bahía de Cardigan, en la parte meridional del Mar de Irlanda, considerando varios centenares de muestras, un 95% de los Ostrácodos vivientes fué encontrado en muestras de algas litorales o infralitorales El 5% de individuos vivos restantes fué obtenido a partir de un número mucho mayor de muestras, de sedimentos de varios tipos, tanto litorales como infralitorales, y de estaciones de mar abierto.

El presente trabajo tiene la forma de un estudio semi-cuantitativo, y mayormente estacional, de los ostrácodos recuperados en muestras de varias especies de algas en un número de estaciones a lo largo de la Costa de Gales. De un total de más de 29 especies de algas estudiado, se recobraron 23 especies de Ostrácodes podocópidos. (En algunos casos no fué posible identificar varios miembros de las Rhodophycaea, las cuales fueron entonces consideradas colectivamente a dicho nivel taxonómico).

Los ambientes eulitorales e infralitorales son tratados separadamente extrayéndose conclusiones concernientes al significado de los cambios estacionales en la naturaleza específica y estructura de la población de las faunas de Ostrácodos en ambos, así como tambien a las migraciones faunísticas entre ellos. Se concluye, además, que la naturaleza de la relación entre algas y Ostrácodos es sumamente compleja, y que entre los factores principales que gobiernan esta relación se incluyen: la morfología de la planta, y la naturaleza de la protección que ésta brinda contra las presiones físicas y biológicas; la posicion de la planta dentro de las zonas estudiadas, considerando tanto su macro como su microambiente; si la relación de alimentos es de carácter directo o indirecto; calidad y cantidad de los sedimentos incluídos dentro de la planta; y por último, el desarrollo estacional de la planta.

La parte final de esta publicación está dedicada a una comparación de los resultados presentes con aquellos previamente obtenidos por otros autores dentro de este campo, y con estudios similares actualmente en ejecución por uno de los autores (RCW) a lo largo de la costa de la República Argentina.

INTRODUCTION

There have been relatively few studies concerning the faunas inhabiting seaweeds, and the majority of these have tended to neglect the Ostracoda. Colman (1940), Dahl (1948), Wieser (1952, 1959), Chapman (1955), and Ohm (1964) all studied the total fauna of algae and quoted the numbers of Ostracoda occurring but generally did not identify the species concerned. Reys (1963) collected 37 live ostracode species from algae in the vicinity of Marseille and commented on the influence of the form of the algae on the ostracode populations. Hagermann (1966) studied the total fauna of *Fucus vesiculasus* and identified 17 species of Ostracoda, and later (1968) discussed the general ecology of 14 species of podocopids from *Corallina officionalis*. The same author published a further, more detailed study of *Hirschmannia viridis* (O. F. Müller) in 1969, which was largely concerned with the relationship of the species to various green and brown algae. Whatley and Wall (1969) and Williams (1969) published studies of Ostracoda from the coast of Wales which also treated the problem of the relationship between algae and Ostracoda.

The importance of this relationship became apparent to us when, in a recent study of the Ostracoda from the southern Irish Sea, involving many samples from the littoral and Continental Shelf, we obtained 95% of the live individuals from algal samples which represented only a small percentage of the total number of samples studied.

A general summary of the climatic, physiographic, and oceanographic conditions of the area under discussion have already been given in Whatley and Wall (1969).

ACKNOWLEDGMENTS

The authors wish to thank Dr. Lars Hagermann and Dr. John Whittaker for valuable discussions, and various colleagues at U.C.W., Aberystwyth, particulary Dr. John Haynes, Dr. Don Boney, and Dr. Max Dobson for much assistance. D. R. Wall was supported by a NERC Studentship during this work, and R. C. Whatley was supported during part of it by the Argentine Consejo Nacional de Investigaciones Científicas y Técnicas, both are gratefully acknowledged.

METHODS

Algae were collected by means of placing a plastic bag over the plant and, detaching it in such a way as to obtain, not only the plant (roots were not included unless the term "holdfast" is used), but also the immediately surrounding water. Either in the lab or in the field, the contents of the bag were emptied into a large container and a 10% solution of formalin was added. After approximately 15 minutes, the sample was agitated vigorously and then washed with a strong jet of water. The contents of the container, from which the washed alga had been removed, were then collected on a 200 mesh/inch sieve, from which, after being allowed to dry, the Ostracoda were picked manually. The study was semi-quantitative in that each alga was identified and weighed wet, and at the stations where seasonal samples were taken, the same weight was examined for each algal species at each collection. The imperfection of this method from a statistical standpoint is fully acknowledged by the authors, who realise that in terms of potential habitat, 50 grams of say the stem of *Laminaria* bears no relationship to an equal weight of densely intergrown *Cladophora.*

Many of the algae are small or occurred sparsely in the area and this factor accounts for the low weights examined in the case of some species.

In certain cases, after processing in formalin, the alga was examined under the microscope to ensure that all the Ostracoda had been removed. In not one case were ostracodes found on the processed weed. Additionally, several algae were picked manually without being put through the formalin process in order to control the results from the above method. This not only proved time consuming but also yielded a consistently slightly lower number of ostracodes.

Chemical and physical methods are as outlined in Whatley and Wall (1969). Only living ostracode specimens were studied. Individual ostracodes are considered live if they contain appendages.

The usage of the terms "littoral fringe", and "eulittoral" and "sublittoral" zones is based on Lewis (1964); and the terms "upper" and "lower" sublittoral zones are based principally on the observations of one of the authors (DRW). The "upper" sublittoral zone is defined as extending from just above E.L.W.S. to a depth of approximately 2 fathoms, the depth below which wave or surf action is presumed to exert negligible effect on the bottom fauna and the "lower" sublittoral zone as extending out from 2 fathoms to the limit of light penetration (or depth to which algal growth is supported).

THE OSTRACODA

The following 23 species of cytheracean ostracodes were recovered live from algae during the course of this study:

Cythere lutea (Müller, 1785)
Aurila convexa (Baird, 1850)
Heterocythereis albomaculata (Baird, 1850)
Hemicythere villosa (Sars, 1866)
Carinocythereis antiquata (Baird, 1850)
Hirschmannia viridis (Müller, 1758)
Loxoconcha tamarindus (Jones, 1856)
Loxoconcha rhomboidea (Fisher, 1835)
Neocytherideis subulata (Brady, 1868)
Leptocythere tenera (Brady, 1868)
Callistocythere badia (Norman, 1862)
Paradoxostoma ensiforme (Brady, 1868)
Hemicytherura cellulosa (Norman, 1862)
Microcytherura fulva (Brady and Robertson, 1874)
Semicytherura striata (Sars, 1866)
Semicytherura sella (Sars, 1866)
Semicytherura ? concentrica (Brady and Norman, 1889)
Paradoxostoma variabile (Baird, 1835)
Paradoxostoma subelliptica (Wall, 1972)
Paradoxostoma abbreviatum Sars, 1866
Paradoxostoma bradyi Sars, 1928
Paradoxostoma normani Brady, 1868
Paradoxostoma flexuosum Brady, 1868

TAXONOMIC NOTE

It is thought necessary to explain the usage of the following:

Semicytherura? concentrica. The material we have, together with the original, may in fact represent instars of *Hemicytherura cellulosa.* Dr. John Whittaker is working on this problem currently.

Loxoconcha tamarindus: this species is removed from *Hirschmannia* and returned to *Loxoconcha* because the antennae are long and slender and have six podomeres and the penis is very different from that of *H. viridis* and more similar to *Loxoconcha.* The hinge, although more similar to that of *Hirschmannia* is here considered less important than the soft part characteristics mentioned above.

Paradoxostoma subelliptica Wall, nom. nov. is for *P. hibernicum* sensu Sars (1928) which is not conspecific with the original material of Brady (1868).

The majority of the species are well known as being phytal, whilst others such as *Hemicythere villosa* and *Loxoconcha rhomboidea* are also frequently encountered in other environments. The occurrence of such species as *Neocytherideis subulata, Leptocythere tenera* and *Carinocythereis antiquata* living amongst algae, albeit rarely, is unusual.

COLLECTING LOCALITIES

Algal samples were collected at the following stations: From the 'lower' sublittoral zone at stations 105, 106, 107, 108, 109, 110, 111, 556, 647, 931, 932, 939, and 940; from the 'upper' sublittoral zone, eulittoral zone and littoral fringe at stations 736, 745, and 933.

A general description of the stations and of the algae and ostracod fauna collected from them is given below:

Station 736:

This is at Monk's Cave, on the coast some 4½ miles SSW of Aberystwyth (Lat. 52° 21′ N. Long. 4° 07′ W. and NGR 556748). At this station a study of the seasonal and areal variation of Ostracoda was made in the littoral and 'upper' sublittoral zones. Algae were collected from three intertidal rock pools, one in the littoral fringe, one in the eulittoral zone and one in the 'upper' sublittoral zone on six dates (November 14, 1966; April 26, 1967; September 18, 1967; March 2, 1968; May 14, 1968; and August 9, 1968) during low water of Spring Tides.

The shape, surface area and general expression of the plants and their seasonal growth and development, their growth situation relative to various critical tidal levels and their position within the pools, was found to exert a great influence upon their ostracod fauna.

A detailed description of the locality, particularly of the three pools from which the samples were collected is given in Whatley and Wall (1969: 294-296).

Fucus serratus (75 grams wet weight)

This large plant, with flat serrated fronds, was collected from each of the three pools although it occurs in greatest abundance on rock platforms in the upper part of the eulittoral zone, often as dense 'mats'.

a. From the pool in the littoral fringe, this plant was collected from around the periphery where it grew with its fronds partly submerged. Only 9 live ostracodes were collected during the 6 collections, and these in fact were from epiphytes, mainly *Ectocarpus*:

Hemicytherura cellulosa one female, November 14, 1966
Aurila convexa one adult, April 26, 1967
Loxoconcha rhomboidea one female and one juvenile, September 18, 1967
Paradoxostoma variabile one juvenile, August 9, 1968
Heterocythereis albomaculata three females, August 9, 1968

The absence of Ostracoda on two of the collecting dates (March 2, 1968 and May 14, 1968) may possibly be related to the fact that on these dates the *Fucus* did not bear epiphytes.

b. In the eulittoral, *Fucus serratus* only occurred on exposed rock platforms where, despite the common occurrence of epiphytes, ostracodes were not encountered.

c. In the sublittoral, this alga occurs but rarely and generally lacks epiphytes. Only five ostracodes were recovered: three adult *P. bradyi* on April 26, 1967, and further adult on May 14, 1968 together with one female *L. rhomboidea.*

The small number of ostracodes recorded from this weed is probably a reflection of the fact that the large flat fronds afford little protection from turbulence or dessication and this is further aggravated by the fact that the plant frequently inhabits exposed parts of the sea shore.

Hagermann (1966) has shown that in the Øresund large numbers of Ostracoda frequently occur on this plant. Colman (1940) quoted a mean number of only three specimens per 100 grams of damp weed, although his maximum is 1,480. Williams (1969) recorded variable numbers of ostracodes from this weed from localities around the coast of Anglesea. All these authors remarked on the correlation between high numbers of Ostracoda and the degree of epiphytic development. It would seem that the number of Ostracoda on *Fucus serratus* is influenced by whether or not the plant is growing in a sheltered situation. The relatively quiet waters of the Øresund contrast with the exposed coast of Anglesea and Cardiganshire where very few ostracodes occur, although Williams found relatively high numbers at Church Island in the more sheltered waters of the Menai Straits. Similarly the fluctuations in numbers at Wembury recorded by Colman, may also be a product of the situation of the weed. This factor can be seen in minuscule in our samples from Monk's Cave. In the littoral fringe and in the sublittoral, the plant occurs in relatively sheltered situations and contained a fauna, albeit a meagre one. In the relatively more exposed eulittoral, the weed is barren of Ostracoda.

Fucus spiralis (60 grams wet weight)

This weed was collected from the littoral fringe and from the eulittoral only. At this station it always occurs in exposed positions and did not yield any ostracodes. It was noted that this species was, at certain times coated with a slimy secretion, presumably to inhibit the attachment of epiphytes, especially in its reproductive season. It is thought that this substance, together with the rather flat and open form of the weed, its lack in this locality, of epiphytes and its occurrence in exposed situations, could all be contributory factors to the absence of ostracodes.

It is worthy of note that Colman (1940) recorded very few ostracodes from this species with a mean of 0.5 specimens per 100 grams and a maximum of 2. Similarly Williams failed to find any living Ostracoda on this weed in his more exposed localities, although a small number were present in the Menai Straits.

Ulva sp. (30 grams wet weight)

This flat membranous and fronded member of the Chlorophyceae was found in the littoral fringe and in the eulittoral zone, although in the latter not in sufficient abundance to enable a collection to be made. Specimens were collected from beneath an overhang in the pool in the littoral fringe. Many more ostracodes were encountered during the spring and summer than in the winter collections. *Heterocythereis albomaculata, C. lutea,* and *H. viridis* were virtually restricted to the spring and summer, whilst *H. cellulosa, A. convexa, L. tenera. L. rhomboidea,* and *H. villosa* occurred intermittently throughout the year.

The small amount of shelter and protection provided by this weed seems to be compensated by the fact that it frequently occurs in sheltered micro-environments at some depth within the rock pools.

Cladophora rupestris (35 grams wet weight)

This dark green, densely tufted weed occurred commonly in rock pools in the littoral fringe and eulittoral. Whilst ostracodes were relatively abundant in the littoral fringe, in the eulittoral zone, this plant occurs in more exposed situations and yielded very few. During spring and summer it is particularly abundant near the surface of the pools in the littoral fringe, usually beneath a covering of *Fucus* spp. In the winter, however, it 'dies back' and loses its green colour. In the winter sample (November 14, 1966), only four live ostracodes were recovered, but spring and summer samples yielded substantially more (141 on April 26, 1967, 115 on March 2, 1968, and 159 on May 14, 1968). The principal three species found in association with this weed were: *H. viridis, C. lutea,* and *H. albomaculata.* A further nine species occurred in smaller numbers.

The tufted nature of *C. rupestris,* its occurrence in sheltered situations within the rock pools and the fact that it usually contains some amount of sediment, are obviously contributory factors to its providing a favourable habitat for Ostracoda. The increase in ostracode numbers in the spring may be correlated not only with the beginning of the reproduction of these animals with the commencement of favourable temperature conditions, but also with the renewed growth of the plant.

Wieser (1952) also noted the abundance of Ostracoda in association with this plant from the littoral of the Plymouth area and Williams (1969) also found substantial numbers inhabiting the closely related species, *Cladophora sericea,* from his Church Island locality in the Menai Straits. He recorded no less than 7,959 specimens from 100 grams of the weed.

Enteromorpha clathra (30 grams wet weight)

A green weed with long flat, unbranching fronds which, in some specimens, form a dense network. This plant occurs commonly in the littoral fringe and in the eulittoral during spring and summer but 'dies back' and becomes white in the winter. In the littoral fringe it occurs in shallow but sheltered pools often in association with *C. rupestris.* As with the latter, numbers of ostracodes present in the spring and summer are relatively high, whilst in the winter they are very low. The number of ostracodes recorded from *E. clathrata* is less than from *C. rupestris* but slightly more than from *Ulva.* This is presumably a function of the form of these three algae, with *Cladophora* forming a dense and enclosed intergrowth, the flat fronds of *Ulva* providing few opportunities of attachment and relatively little shelter, and *Enteromorpha* being intermediate in this respect. The same three most abundant ostracodes as for *C. rupestris* occurred on this weed. Whilst Ostracoda were common in the littoral fringe, only four live individuals were recovered from the eulittoral samples in which zone the plant occurs in more exposed situations.

Hagermann (1969) demonstrated the attraction of *Enteromorpha* to Ostracoda (as well as to other animals). After removing all the fauna from nine stones, each with a 1 dm^2 patch of *Enteromorpha,* a faunal count was made of successive stones at regular intervals. After four hours there were 15 ostracodes and progressively more until after 120 hours, 815 specimens were counted, only slightly less than that of the control stone. This work affords a most convincing demonstration of the suitability of the microhabitat provided by this weed and of the migratory ability of benthonic Ostracoda. Williams (1969) recorded 176 specimens belonging to six species from 100 grams of the closely related *E. compressa* from Porth Swtan, Anglesea.

Dictyoma dichotoma (18 grams wet weight)

This member of the Phaeophyceae, with flat and rather limp dichotomous fronds in an open network, was collected from the littoral fringe and the eulittoral zone where, in both cases, it occurs in the shallower rock pools or in the shallow fringes of the deeper pools. From the littoral fringe one specimen of *N. subulata* was recorded, all the other samples being barren.

Polysiphonia nigrescens (20 grams wet weight)

This member of the Rhodophyceae, with thin branching fronds, was only collected in the littoral fringe. Although occurring in sheltered localities its open network offers little shelter and this is thought to be the main reason why only four specimens, all female *H. albomaculata,* were collected from this weed (September 18, 1967).

Dumontia incrassata (10 grams wet weight)

A member of the Rhodophyceae which occurred rarely in pools in the littoral fringe and sublittoral. No live ostracodes were encountered on this weed, presumably because its open network of long thin, tubular fronds do not offer a suitable habitat.

Chondrus crispus (25 grams wet weight)

Abundant in the eulittoral, this small member of the Rhodophyceae, with short, flat dichotomously branching fronds in an open network, also occurs more rarely in the littoral fringe and sublittoral zone. The samples from the latter zone were barren although three *Heterocythereis albomaculata* and one *H. viridis* were recovered on September 18, 1967 from the littoral fringe and a total of 7 species in small numbers from the eulittoral at various dates.

Halidrys siliquosa (50 grams wet weight)

A medium-sized member of the Phaeophyceae which is frequently but openly branched and rather stiff. This is a common weed of the sublittoral and eulittoral, although it also occurs rarely in deep pools in the littoral fringe.

a. From the littoral fringe the following were recovered:

H. cellulosa 1 female	*H. viridis* 1 penultimate instar
C. lutea 2 females	*P. ensiforme* 1 female
L. rhomboidea 1 male, 1 female	

b. From the eulittoral, all the samples were barren, probably due to the exposed position of the weed.

c. The sublittoral collections yielded the following:

H. cellulosa 1 female	*H. albomaculata* 2 females
P. bradyi + females	

Williams (1969) records much larger numbers of Ostracoda from this weed at his Church Island locality in the Menai Straits. (5,121/100 grams)

Pelvetia canaliculata (22 grams wet weight)

This weed occurs as tufted bunches of flat fronds on the edge of rock pools in the littoral fringe and eulittoral zone. No live Ostracoda were recovered from it due presumably to its occurrence in exposed situations and its unfavourable morphology. It is interesting to note that of all the algae studied by Colman, (1933, 1940) this was the one with the smallest number of animals and did not yield ostracodes.

Porphyra sp. (55 grams wet weight)

This red alga with a large single, flat membranous frond, was collected only from the deepest part of a rock pool in the littoral fringe, and only two female *L. rhomboidea* were collected, both on September 18, 1967. Wieser (1952) failed to recover ostracodes from this species in the Plymouth area.

Ectocarpus sp. (15 grams wet weight)

This is a common epiphyte on a large number of seaweeds, especially *Fucus serratus,* throughout the littoral of N. W. Europe. At Monk's Cave, however, it does not occur in great abundance, and although a small number of live ostracodes were collected from this alga growing on *F. serratus*, surprisingly none were found where *Ectocarpus* grows on the rocky substrate in the littoral fringe. This is not explicable in terms of the plant not providing sufficient shelter or suitable attachment area for ostracods because the plant forms a dense network and contains large amounts of sediment. Possibly the factor in the littoral fringe would be dessication because the plant at collection was noted to be very dry and rather brittle.

Hagermann (1966, 1969) demonstrated the importance of this plant in providing suitable environments for Ostracoda in areas of dense growths of *Fucus*.

Corallina officionalis (20 grams wet weight)

This alga with a hard 'skeleton' of calcium carbonate grows densely in shallow pools in the littoral fringe and eulittoral. Although failing to yield a fauna during the winter, at other seasons it yielded 18 and 10 specimens from the littoral fringe and eulittoral respectively.

Hagermann (1968) recorded 14 species of ostracods from this plant in Western Norway, the greatest numbers occurring in summer and autumn.

Rhodophyceae (80 grams wet weight)

A number of species of red algae are here considered together because their form is so similar as to render doubtful accurate identification even to the generic level. Amongst these however, *Brogniartella, Gymnogongrus, Ahnfletia,* and *Cystoclonium* were recognized, all of which are of medium size, branching and with thin fronds which generally display a rather open network. In the deep rock pools of the littoral fringe and eulittoral zone, ostracodes were collected in moderate numbers, but in the sublittoral, only nine specimens were recovered.

Ceramium sp. (18 grams wet weight)

Various species of this small red alga with an open network of fine dichotomous fronds occurred in the eulittoral, on rock platforms, and in shallow pools. Samples from the former were barren, whilst one sample from the latter situation, on September 18, 1967, yielded four female *H. albomaculata*.

Laurencia hybrida (23 grams wet weight)

This small red alga, with an open network of small delicate branches, occurs on the bottom of pools in the eulittoral zone, and yielded the following:

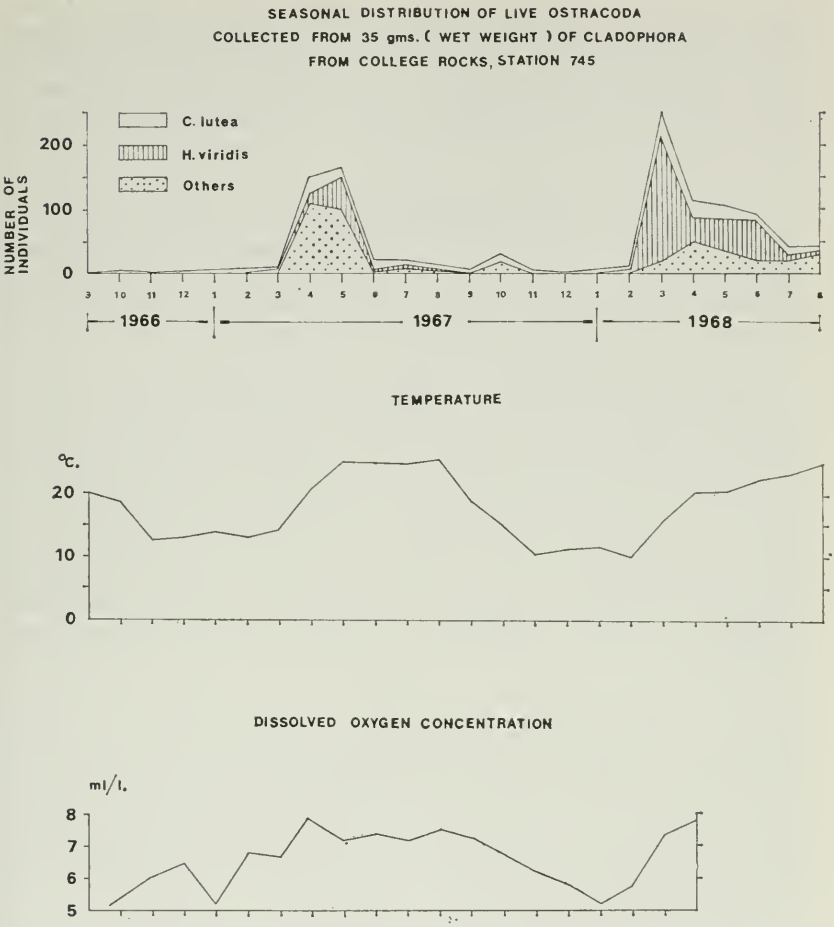
P. variabile	2 females (November 14, 1966)	*H. villosa*
P. bradyi	2 females (April 26, 1967)	(November 14, 1966)

Laurencia pinnatifida (15 grams wet weight)

This species with very similar morphology to the above, was collected from eulittoral rock pools but failed to yield Ostracoda.

Chaetomorpha sp. (28 grams wet weight)

This genus which has a close network of brittle threads, which are un-



Text-figure 1. Seasonal distribution of live Ostracoda collected from 35 grams (wet weight) of *Cladophora* from College Rocks, Station 745.

branched, is usually found only in the eulittoral and littoral fringe. At this station it was also encountered in the upper part of the sublittoral, where it yielded only four specimens of *H. albomaculata* on April 26, 1967 however, two samples collected in the littoral fringe on May 14, 1968, and August 9, 1968 (not shown in Table) yielded 151 and 57 ostracods respectively belonging to *C. lutea, H. viridis* and *H. albomaculata.*

Furcellaria fastigiata (35 grams wet weight)

A red alga with rigid dichotomous branches in an open network and attached by a small holdfast. It was only found in the 'upper' sublittoral and whilst the fronds were barren, the holdfasts collected on August 9, 1968, contained 13 adult *H. albomaculata* and one instar each of *H. viridis* and *P. variabile.*

Laminaria spp. (75-95 grams wet weight)

Two species of the genus, *L. hyperborea* and *L. digitaris,* were collected. Because the fronds did not contain ostracodes, and because the form of the holdfasts and their contained fauna were so similar, they are considered together. The ostracodes contained in the holdfasts of the plant from deep pools in the lower part of the eulittoral zone, were the same as those from the 'upper' sublittoral. Fifty individuals occurred being dominated by *P. bradyi H. albomaculata, H. cellulosa, A. convexa,* and *L. rhomboidea,* which occurred throughout the year, whilst *C. lutea* was only present during the winter. *N. subulata, S. striata,* and *P. variabile* occurred only rarely and irregularly.

Station 745

This is at College Rocks, Aberystwyth, Lat. 52°24′55″N, Long 4°05′10″W. and NGR SN 584815. At low tide, immediately to the west of the Old College buildings, a large rock platform, with a distal seawards extension is exposed. From a rock pool in the upper part of the eulittoral zone, algal and sediment samples were collected at intervals between September 1966, and August 1968. The bottom sediment yielded only dead specimens of *L. rhomboidea, C. lutea, H. viridis, P. variabile, H. villosa, A. convexa,* and *H. albomaculata.*

Of the rock pool algae, *Fucus serratus* failed to yield live ostracodes; *Corallina afficionalis* contained a few as did *Ulva* sp. and *Ascophyllum nodosum.* The largest concentrations of living ostracodes were obtained from tufted growths of *Cladophora* and *Enteromorpha,* especially those plants situated near the surface of the pool but overhung by a layer of larger algae, such as *Fucus serratus.* The same algae, and others situated at the bottom of the pool, yielded significantly lower numbers of Ostracoda, especially during spring collections. This is thought to be the product of small temperature differences; *e.g.* in March, 1967, the bottom of the pool was 9°C. and the top 11°C., whilst the temperatures in August of the same year were 16°C. and 17°C., respectively.

The seasonal distribution of living ostracodes from approximately 25 grams (wet weight) of *Cladophora* sp. taken from all parts of the pool is given in

Text-figure 1. The population is generally dominated by *H. viridis* and *C. lutea.* During the winter of 1966 and the early months of 1967, the two species were absent but in the April 1967 sample they occurred in abundance, being represented almost exclusively by adults, although a few -1 instars of *C. lutea* were collected and a number of -1 and -2 instars of *H. viridis.* The May 1967 sample was similarly dominated by adults of the two species, although *H. viridis* increased in numbers at the expense of *C. lutea.* From this spring maximum, the numbers of the two species declined with *H. viridis* being last recorded in September and *C. lutea* in November. The next appearance of the two species was in March 1968, one month earlier than in the preceding year. This earlier occurrence can probably be correlated with the fact that the water temperature of the pool in March 1968 was, at 16.5°C., ten degrees higher than in the same month of the preceding year. In 1968, *H. viridis* appeared before *C. lutea* and again consisted principally of adults with only a few -1 instars, and gradually decreased in numbers throughout the summer. *C. lutea,* however, was represented in March by -4 instars. In April, adults, -1 and -2 instars were collected and the species was represented throughout the summer by adults and -1 instars with very occasional younger moults.

The sudden appearance of the two species in the spring may perhaps be related to temperature, especially if the species had wintered in the pool as eggs. In 1967, there was a gap in the sampling interval between the 3rd of March and the 6th of April, and it is perhaps feasible that the eggs could have hatched and the species reached maturity during this period of time. In 1968, in order to investigate this possibility, the sampling interval between January and April was reduced to two weeks. This revealed earlier instars of *C. lutea* but not of *H. viridis* and additional samples from *Cladophora* in surrounding pools, taken at the same time, exhibited the same population structure. It would appear that either the ontogenetic development to the adult stage can take place within two weeks or, more probably, that the adults and the -1 instars are able to migrate into the pool from nearby, possibly sublittoral population. There is some direct evidence to support the latter suggestion, in that the adults of *C. lutea* were commonly encountered during the winter in holdfasts of *Laminaria,* and *H. viridis* has also been found associated with other sublittoral weeds. This problem of migration is discussed below.

On March 27, 1968, a large collection of weeds was made at this station, all from the upper part of the eulittoral, the results of which are given below:

Cladophora rupestris (35 grams wet weight)
    H. viridis 207 adults, 8 instars
    H. albomaculata 4 adults, 26 instars
    L. rhomboidea 1 instar
    C. lutea 11 instars
    H. cellulosa 2 adults
    S. striata 3 adults
Halidrys siliquosa (210 grams wet weight)
    H. viridis 9 adults
    H. villosa 2 adults
    C. lutea 7 instars
    H. albomaculata 1 adult

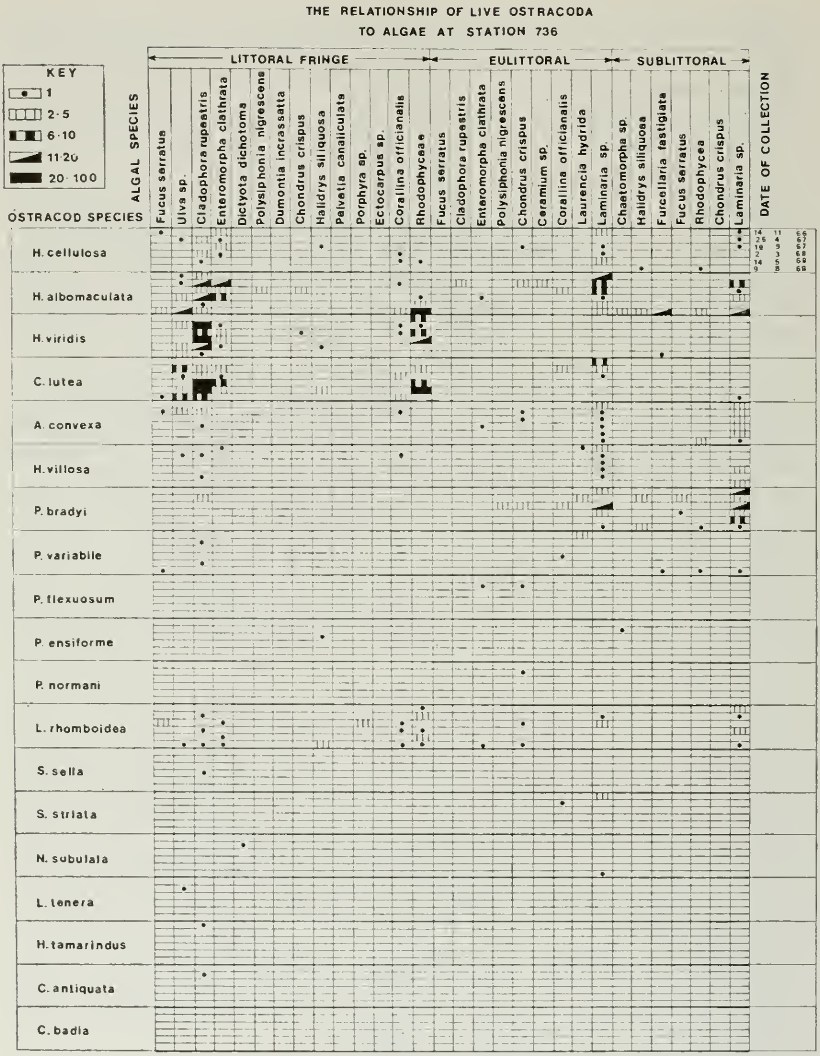


Table 1. The relationship of live Ostracoda to algae at station 736.

---

*Authors now reassign *H. tamarindus* to *Loxoconcha* (see p. 177).

Rhodophyceae (65 grams wet weight)
H. viridis 42 adults
H. albomaculata 2 adults
P. bradyi 1 adult
C. lutea 32 adults
H. cellulosa 1 adult
P. variabile 1 adult, 5 instars

Ulva sp. (44 grams wet weight)
H. viridis 2 adults
P. variabile 1 adult, 1 instar
C. lutea 5 instars
H. albomaculata 2 instars

The number of Ostracoda recovered from these samples was higher than those of the March sample at station 736. The two stations are environmentally very similar except that 745 is close to the joint mouth of the Rheidol and Ystwyth Rivers and hence has a slightly lower mean salinity (30-33o/oo) than station 736 (34-35o/oo).

The relationship between species of plant and ostracode numbers was very similar to that recorded at station 736. Densely intergrown algae, such as *Cladophora* contained large numbers, whilst those with an open network, such as *Halidrys siliquosa* contained many fewer. This is further emphasised by the fact that *Fucus serratus* (50 grams wet weight), *Ascophyllum nodosum* (170 grams), *Dilsea carnosa* (132 grams) and other algae, such as *Chorda filum,* were collected from the same pool on the same date but were all barren.

At the seaward extremity of College Rocks, a rock ledge extends obliquely out to sea. Holdfasts of *Laminaria* were collected from the 'upper' sublittoral, on both the seaward and landward sides of this ledge, with the following results:

	Landward Side		*Seaward Side*	
Date	Wet weight weed (grams)	No. Ostracoda	Wet weight weed (grams)	No Ostracoda
Dec. 6, '66	70	21	80	0
March 3, '67	52	36	61	17
June 7, '68	86	46	42	10
Aug. 27, '68	27	27	80	1

The consistently higher number of ostracodes recorded from the landward side is attributed to the holdfasts there being more sheltered from the waves. A further example of the importance of this factor is provided by the following data: On March 2, 1968 two approximately equal weight samples (35 grams), of *C. rupestris* were collected from the eulittoral. The first sample was from immediately below an 'overhang' in a rock pool where the plant occurred beneath a dense mat of *Ascophyllum nodosum*. The second was collected near the surface of the same pool without a protective covering. The first sample yielded 256 live ostracodes, and the second only 22.

Station 933 (Lat. 52°13′33″ N., Long. 4°27′ W.)

At this station, situated between New Quay and the Teify Estuary, a nearly vertical cliff face extends down to a depth of 2 fathoms below OD, and the vertical zonation of the littoral as expressed by algae, is extremely compressed. Several collections were made at this station, the results of which are quoted below:

Mixture of *Ulva* and *Cladophora* (45 grams wet weight) from the littoral fringe:

H. villosa 1 adult
H. viridis 1 adult
H. albomaculata 1 instar
L. rhomboidea 1 adult
C. lutea 1 instar
P. variabile 1 adult, 4 instars

Laminaria Holdfast (25 grams) from the lower part of the eulittoral zone.

H. viridis 1 adult
H. albomaculata 2 adults
C. lutea 1 instar
H. villosa 1 instar

Laminaria (2 holdfasts total 58 grams) from the sublittoral.

A. convexa 4 adults
C. lutea 1 instar
S.? concentrica 2 adults
H. albomaculata 1 adult, 1 instar
H. viridis 1 adult

Although the number of Ostracoda was very small, it is interesting that in this extremely exposed part of the coast the algae should provide sufficient protection for ostracodes to survive.

Ostracoda collected from algae in the 'lower' sublittoral zone

Between 1962 and 1964, a number of algal samples were collected by dredging from the sublittoral along the coast of Cardiganshire, The algae were unfortunately not identified nor weighed. The Ostracoda recorded from them are given below:

Station 556 (52°14′61″ N., 04°18′53″ W.) Depth 23 feet, June 24, 1968, off the town of Aberarth, large boulders with weeds and many live Foraminifera.

L. rhomboidea 7 females
H. villosa 2 female, 12 juv.
P. bradyi 2 female
L. tenera 1 female
P. ensiforme 1 female
L. tamarindus 10 female, 1 male
H. cellulosa 9 female, 4 male, 5 juv.
M. fulva 2 female
P. normani 2 male
S.? concentrica 2? juv.

Station 647 (52°16′36″ N., 04°12′37″ W.) Depth 21 feet, September 28, 1964, Cadwag Reef off Llanrhystyd.

L. rhomboidea 8 female, 5 male
H. cellulosa 4 female
H. villosa 3 female, 2 juv.
P. bradyi 3 females

Station 105 (52°39′48″ N., 04°7′55″ W.) Depth 21 feet, April 4, 1962.

L. rhomboidea 56 female, 20 male
H. villosa 6 female, 1 male, 1 juv.
H. cellulosa 1 female
P. ensiforme 2 female, 1 juv.
A. convexa 3 female
H. albomaculata 2 females, 6 juv.
H. viridis 7 juv.

Station 106 (52°27'17" N., 04°07'32" W.) Depth 30 feet, April 12, 1962.
L. rhomboidea 29 female, 16 male *A. convexa* 1 female, 2 juv.
H. albomaculata 1 female, 2 juv. *P. ensiforme* 1 female
H. villosa 1 juv.

Station 107 (52°75'44" N., 04°40'00" W.) Depth 40 feet, April 12, 1962.
L. rhomboidea 29 female, 16 male *H. villosa* 1 female, 2 juv.
H. albomaculata 2 female, 9 juv. *H. cellulosa* 2 female, 2 male
A. convexa 1 female *H. viridis* 1 juv.
P. variabile 1 juv.

Station 108 (52°26'40" N., 04°19'45" W.) Depth 52 feet, April 12, 1962.
L. rhomboidea 9 female, 4 male *A. convexa* 3 female
H. albomaculata 1 female, 1 juv. *H. villosa* 1 male

Station 109 (52°25'45" N., 04°40'20" W.) Depth 45 feet, April 12, 1962.
L. rhomboidea 13 female, 10 male, 2juv. *H. albomaculata* 2 female, 1 male
A. convexa 1 female, 1 juv. *H. villosa* 1 female, 1 juv.

Station 110 (52°26'25" N., 04°35' W.) Depth 22 feet, April 12, 1962.
H. albomaculata 1 female

Station 111 (52°30'31" N., 04°59'42" W.) Depth 40 feet, April 12, 1962.
L. rhomboidea 5 female, 1 male

After studying these samples, collected before either of the authors worked at Aberystwyth, it became evident that, because sublittoral sediment samples contained few or no ostracodes, further weed samples from this zone would be required. Accordingly, in 1968, further samples were collected by SCUBA divers. The results from which are given below:

Station 931 (52°14'15" N., 04°17'48" W.) Depth 16-20 feet, April 28, 1968.
Between Aberayron and New Quay.

Halidrys siliquosa (with epiphytes, 28 grams wet weight)
P. variabile 1 juv. *P. normani* 9 juv.
P. abbreviatum 1 juv. *S. contortus* 1 juv.

Laminaria sp. (holdfast, 50 grams wet weight)
A. convexa 1 female

Station 932 (52°14'20" N., 04°17' W.) Depth 15 feet, April 28, 1968.
Between Aberayron and New Quay.
Rhodophyceae (20 grams wet weight)
L. rhomboidea 1 female, 2 male *L. tamarindus* 2 juv.
S.? concentrica 1 ? juv. *P. variabile* 1 juv.
P. bradyi 1 juv. *H. villosa* 1 male
A. convexa 1 female

Chondrus crispus (35 grams wet weight)
P. normani 7 juv.
A. convexa 1 female
P. variabile 7 juv.
L. rhomboidea 1 female
Laminaria sp. (holdfast, 21 grams wet weight)
P. variabile 2 female

Station 939 (52°24′54″ N., 04°14′30″ W.) Depth 30 feet, June 16, 1968.
Sarn Wallog, off Clarach.

Spermothamnium thurneri (130 grams wet weight)
H. albomaculata 30 juv.
P. abbreviatum 5 female, 1 male, 1 juv.
S.? concentrica 1 juv.
P. variabile 2 female, 4 male, 5 juv.
H. viridis 5 juv.
H. cellulosa 1 female, 1 male
Rhodomela conferoides (14 grams wet weight)
H. albomaculata 7 juv.
S.? concentrica 1 ? juv.
P. flexuosum 1 male
L. rhomboidea 2 juv.
H. viridis 4 juv.
Furcellaria fastigiata (130 grams wet weight)
H. albomaculata 2 female, 1 male, 22 juv.
H. cellulosa 7 female, 6 male
P. hibernicum 7 juv.
P. variabile 1 female, 2 male, 3 juv.
H. viridis 8 juv.
S.? concentrica 1 ? juv.
Chorda filum (120 grams wet weight)
H. albomaculata 15 juv.
P. abbreviatum 1 female, 2 male, 1 juv.
H. cellulosa 1 male
S. striata 1 female
P. variabile 11 juv.
H. viridis 5 juv.
L. rhomboidea 2 juv.

Station 940 (52°25′10″ N., 04°14′12″ W.) Depth 20 feet, June 16, 1968.

Chondrus crispus (190 grams wet weight)
P. variabile 1 female, 4 male, 11 juv.
H. cellulosa 5 female, 1 male
P. abbreviatum 6 female, 4 juv.
L. rhomboidea 1 juv.
H. albomaculata 16 juv.
H. viridis 9 juv.
P. flexuosum 1 male
Chorda filum (380 grams wet weight)
P. variabile 17 females, 17 male, 32 juv.
P. subelliptica 2 female, 35 juv.
S.? concentrica 5 ? juv.
H. cellulosa 4 female, 2 male
P. abbreviatum 45 female, 11 male
H. viridis 3 juv., 74 juv.
H. albomaculata 1 female, 65 juv.
Ceramium arborescens and *Brogniartella byssoides* (intergrown and not possible to separate, 260 grams wet weight)
H. albomaculata 24 female, 4 male, 22 juv.
P. abbreviatum 24 female, 4 male, 22 juv.
H. cellulosa 8 female, 5 male
S.? concentrica 2 ? juv.
P. variabile 26 female, 11 male, 46 juv.
P. *hibernicum* 21 juv.
H. viridis 8 juv.

Three major factors emerge from these figures:

1. The large number of ostracodes on the 'lower' sublittoral algae relative to the much smaller numbers encountered in littoral and 'upper' sublittoral phytal environments.

2. The difference in the composition of the ostracode faunas of the 'lower' sublittoral algae and that of those of the intertidal and 'upper' sublittoral zones. The former contains, for example, *P. abbreviatum, P. subelliptica,* and *S. ? concentrica,* which are not recorded from the latter. The Paradoxostomatinae are also much better represented and more dominant in the former.

3. The sublittoral algae, whatever their morphology, contain a relatively large ostracode fauna. For example, the "boot-lace alga", *Chorda filum,* yielded 314 individuals at the "lower" sublittoral station 940 whereas the same weed at station 745, from the eulittoral, was barren. Similarly, the open branched red algae, *Brogniartella byssoides* and *Ceramium arborescens,* yielded 274 ostracodes and the open network of *Chondus crispus* 68. In the intertidal zones, such algae rarely, if ever contain ostracodes.

These results seem to indicate that the shelter and protection provided by the algae, whilst being a major controlling factor in the higher zones of turbulence and dessication, is of lesser importance in the lower energy "lower" sublittoral environments.

MIGRATION OF OSTRACODA

The possibility that ostracodes may migrate seasonally was first suggested by Colman (1940). From samples of *Ascophyllum nodosum* he recovered a varying number of Ostracoda in a traverse across the littoral. At the landward end of his traverse, he obtained maximum numbers in the summer and minimum in the winter whilst, at the seaward end the reverse was true. He did not, unfortunately, identify the species concerned although Lowndes (in Colman, 1940) stated that some at least were *Xestoleberis aurantia* nor did he discuss the population age structure.

Tressler and Smith (1948) found on the basis of monthly samples taken from the North East Coast of the United States, that in the spring, large numbers of adult *L. rhomboidea* appeared without the previous occurrence of instars. During September, large numbers of late stage instars were observed but which had, by December disappeared. These authors noted the similarity of their results to those given by Elofson (1941) on the same species and concluded (p. 41) "The most reasonable explanation is that migration of the late larval stages or young adults takes place and is followed by a wintering over in deeper waters where more even temperatures prevail. This would also explain the sudden appearence of adults in the spring without the appearence of larvae".

The most detailed evidence so far presented to demonstrate migration in littoral and sublittoral Ostracoda is that presented by Hagermann (1966, 1969). In the second paper, he demonstrated by field observations and experiment that the degree and rate of migration of cytheracean ostracods is much greater than hitherto thought. This work to a large extent also explains and accounts for the discrepancies between the ontogenetic development and seasonal geographical distribution observed by many authors. The repopulation, in a very short time, of areas in which the faunas had been wiped out by natural disasters, and the rapid rate with which areas from whence Ostracoda had been removed artificially were repopulated, is eloquent evidence of the ability of these animals to migrate. Whatley and Wall (1969:293) also invoked seasonal migration to account for seasonal population age structure anomalies in littoral populations.

Similar anomalies in the seasonal distribution at Monk's Cave (Station 736) may also be partly explained by migration. In the spring, there is a substantial increase in the number of ostracodes inhabiting *Cladophora, Enteromorpha,* and *Ulva* in the littoral. This spring increase has been documented by all the above mentioned authors and also by Kornicker (1964). All correlate this increase in numbers with increase in temperature and have also noted the absence of early instars. *H. albomaculata, H. viridis,* and *C. lutea* all increase in number in the spring, principally represented as -1 and -2 instars and all being without earlier instars. In the spring sample of the same weed *H. viridis* and *C. lutea* are absent. This seasonal occurrence is unusual and contrasts with the data of Elofson and of Hagermann, especially with respect to *H. viridis*. The latter author (1966, p. 15) stated: "The reproductive period of *H. viridis* started in late May to early June when the first larvae of stages 1-4 were found. In August no adults were found but only larvae of stages 5-7. They then entered the 8th in the autumn and became adults in the following April or May. Thus, this ostracode is annual and dies immediately after reproduction in June".

Our results differ in the absence of early instars in the spring and in the absence of *H. viridis* and *C. lutea* in the littoral zone during the winter. Both these phenomena may be explained by migration in that *C. lutea* appears to overwinter as adults in *Laminaria* holdfasts in the sublittoral. This species was almost always present in holdfasts in the winter, whilst with rare exceptions, it was not encountered in the same microenvironments during the summer. During the winter, *H. viridis* was encountered live from only one sample in the intertidal zones, although relatively large populations occurred throughout the year in the "lower" sublittoral. Of these latter, the winter collections revealed penultimate instars and adults (stations 105-111) and those of the summer, mainly early instars (stations 931-932-939-940). This evidence, together with that quoted above for station 745, would tend to suggest a systematic seasonal migration of *H. viridis* into the "lower" sublittoral zone for the winter and a return to the intertidal zone in the spring. The same may also be postulated for *C. lutea,* with migration between the intertidal area and the upper sublittoral zone, and also probably for *H. albomaculata*. The only other feasible explanation for the observed facts, is that ontogenetic development could take place in less than the period of the sampling interval. Whilst this could perhaps be possible in the case of station 736, where only three spring collections were made, it is exceedingly unlikely at station 745, where samples were taken monthly for two years and at two week intervals during the spring in 1968. In any case the evidence put forward by Hagermann (1969) that *H. viridis* is an annual species would effectively argue against any such possibility.

With the exception of the Chlorophyceae, algae yielded few ostracodes in the intertidal zone, and these almost always occurred as adults. Of the 160 specimens collected from other than green algae at station 736 only 11 occurred in the winter sample (November 14, 1966), 57 in the two autumn collections (September 18, 1967) and (August 9, 1968), and 92 in the three spring/early summer collections (April 24, 1967; March 2, 1968; May 14, 1968). The low number of individuals, and the overwhelming preponderance of adults, is probably a reflection of the fact that they do not provide suitable environments for ontogenetic development. Some of the species encountered appeared to be "accidental" in that they occurred outside their normal ecological niches. *C. antiquata, N. subulata,* and *L. tenera* are more usually encountered in association with inner shelf sediments. *P. ensiforme* is more properly a phytal species of the sublittoral and other species derived by passive or active migration from large sublittoral populations are *P. bradyi* and *A. convexa.* Both these species inhabit *Laminaria* holdfasts in the winter, but in the other seasons may be found on other adjacent sublittoral weeds and, more rarely, also in the eulittoral. The distribution of *H. viridis* is essentially similar.

The intertidal and "upper" sublittoral weed yielded four *L. rhomboidea* in the winter sample, 21 in the three spring and 28 in the two summer samples, being almost exclusively adults. It is tempting to suggest that these adult *L. rhomboidea* were derived by migration from the large sublittoral population of this species.

In the "lower" sublittoral, the ostracode populations consist of both adults and instars and stations 939 and 940 yielded virtually complete age group populations, with, for example, –7 to adult in *H. albomaculata,* and –6 to adult in *P. abbreviatum, P. variabile,* and *H. viridis.* This population age structure is evidence of ontogenetic development taking place *in situ.* Unfortunately, due to inclement weather and to many other problems inherent in sampling the sublittoral, detailed and regular seasonal sampling was not possible in the 'lower' sublittoral and the exact nature of its fauna as a source of supply by migration to the higher littoral zones can only be surmised. The overwhelming conclusion is, however, that such species as referred to above do exhibit regular seasonal migrations between the sublittoral and the higher intertidal littoral zones. It is not implied that the total populations of such species as *H. viridis, C. lutea,* and *H. albomaculata* undertake this migration nor that it is necessary to the life cycle of the species. We have abundant evidence that a large, if not the largest percentage of the population complete their life cycle within the sublittoral. The fact that a large proportion of these populations does migrate seems to us irrefutable.

FACTORS GOVERNING THE NATURE OF THE RELATIONSHIP BETWEEN OSTRACODA AND ALGAE

Several factors are thought to be fundamental to the observed dependence of Ostracoda on algae in high energy environments. These are listed below, not necessarily in order of importance, and although they are treated separately, the authors realise that they are all to varying degrees interrelated and interdependent.

1. *The morphology of the plant.* — The form of the alga has been emphasized as a controlling factor in the density of its epifauna by such workers as Colman (1940), Wieser (1952), Reys (1963), and Hagermann (1966, 1969). Tufted algae, such as *Cladophora* with a close dense network, contain the largest number of ostracodes by providing a high degree of protection against turbulence and dessication. On the contrary, algae with an open network of branches or flat fronds, such as *Dictyota dichotoma* and *Pelvetia canaliculata* contain few or no Ostracoda. This relationship is very apparent in the eulittoral and "upper" sublittoral zones, and even in the littoral fringe, where wave action is only active at high Spring Tides, the effect of the form of the algae is very noticeable. Along the Cardiganshire coast, in the "upper" sublittoral, the only effective protection is provided by the holdfasts of *Laminaria* and *Furcellaria,* the fronds of these plants, other algae and the sediments being barren of living ostracodes. A similar situation exists along the exposed parts of the southern coasts of Argentina and Chile where, in the "upper" sublittoral, Ostracoda are virtually restricted to the holdfasts of *Macrocystis* which are, apart from being much larger, very similar in their morphology to those of *Laminaria.*

2. *The seasonal development and degree of epiphytation of the algae.* — Hagermann (1966, 1969) discussed the importance of both of these factors with regard to the provision of suitable substrate for ostracodes. Generally speaking, the greater the density of epiphytes, the greater the density of the ostracode epifauna. Also, the more mature the plant, the better environment it provides, with the exception of certain times when such plants as *Fucus serratus* are, during their reproductive period, covered with a slimy secretion which seems to inhibit ostracodes.

Those plants with luxurious summer and little winter growth must be expected to contain quite different epifaunas, at least in terms of density at these seasonal extremes. The present authors have noticed that many algal species, such as *Cladophora rupestris* and *Enteromorpha clathrata* "die back", become white, and also lose their dense network of branches during the winter months. This close network is replaced by a much more open mesh of "woody" branches which appears much less favoured by the ostracodes. This factor may be equally responsible, together with falling temperatures, for the migration of certain species out of the eulittoral into the sublittoral for the winter.

3. *The overall situation of the algae within the intertidal and sublittoral zones.* — Colman (1933) and Evans (1947) used the term "critical level" in attempting to isolate and define those levels, particularly in the intertidal area, which are most critical in relation to the vertical distribution of plants and animals. Wieser (1952), who prefers the term "critical zones", stated that the microfauna will be greatly influenced by the vertical distribution of that of algae which support an epifauna. Evans recognised five critical levels within the eulittoral zone and Wieser recognised three critical zones, two within the eulittoral and the other at the eulittoral/littoral fringe boundary. The present authors are able to recognise in the area studied, a critical level at the boundary of what we call the "upper" and "lower" sublittoral on the basis of the distribution of the Ostracoda. Although many species are common to the two parts of the sublittoral, others, such as *P. abbreviatum, P. subelliptica* and *S. ? concentrica,* occur in the "lower" sublittoral but are absent in the higher zones. Equally, such species as *P. bradyi* and *C. lutea* are common in the higher zones but absent in the "lower" sublittoral. This critical level seems to mark the lower limit of certain intertidal forms and the upper limit of certain "lower" sublittoral forms. Above this level, the morphology of the plant exerts a marked influence on the density of its epifauna, whilst below it this factor is much less operative. This would appear to indicate that the critical level is determined by one major observable factor, that of turbulence. The only physical factor which we know to radically change at this level is that of surf action, in that wave base of breaking waves is, at low tide, at about the two fathoms mark, depending of course of the strength and direction of the wind. In the "lower" sublittoral, surf action is only operative during the coincidence of extreme low tide and extreme storm and this could well explain the negligible effect that the form of the alga has on the density of its ostracode epifauna in this zone. Above this level however, surf action is effective and ostracodes inhabit only those algae which afford the greatest degree of shelter and protection. The exact depth below OD. at which this level occurs cannot be determined with accuracy. Perhaps it should be more properly referred to as a critical zone, the position of which varies conditionally upon the configuration of the sea bed and the direction and strength of the prevailing winds. The position of this zone may even vary seasonally since, for example on the Cardiganshire coast, storms are more common in the winter months than in the summer. On exposed coasts, this zone will be at a lower level than on more sheltered ones whilst in very sheltered areas with little tidal range, it may well not be recognisable.

If the lower level of surf action delimits a critical zone or level, it is not unreasonable to suppose that the upper limit may do the same. This to a certain extent seems to be true. Surf action affects the eulittoral and "upper" sublittoral zones during a large part of the tidal cycle, whereas the littoral fringe is only notably affected during high Spring Tides and storms. *Enteromorpha* and *Cladophora* from the eulittoral zone at station 736 yielded only occasional ostracods in the eulittoral, whereas the same weed at the same station produced some 800 from the littoral fringe. The decreasing effect of surf action at the eulittoral zone/littoral fringe boundary is marked by a change in the population density rather than in the specific composition of the fauna.

Species such as *H. albomaculata, A. convexa,* and *H. villosa* occur in all parts of the intertidal and sublittoral zones and are evidently able to withstand surf action and also the various physico/chemico vissiscitudes which correspond to the intertidal environments, such as diurnal changes in temperature, salinity, pH, O_2 concentration, dessication, and turbulence. Other species, such as *P. abbreviatum* and *P. subelliptica* may be restricted from entering the higher littoral zones by any one or more of these factors.

4. *The micro-situation of the algae.* — It has been shown that at station 745, *Laminaria* holdfasts and *Cladophora,* collected from the same zone and pool respectively, contained many more ostracodes if the plant were situated in a sheltered position than if it were from a more exposed site. Although we have no further evidence, this is thought to be a general rule and is supported by Hagermann's (1968) work in which he emphasised the fact that *Corallina officionalis* contains a very rich epifauna when it is covered by various red and brown algae.

5. *The relationship to food supply.* — The nature of the food supply of small animals such as Ostracoda, especially in the sea, is always difficult to determine. The genus *Paradoxostoma* has a styliform mandible which is generally accepted as an adaptation for obtaining nutriment in the form of plant 'juices'. The virtual restriction of the genus to phytobenthic enviroments is evidence of an undoubted relationship with algae. However, since the genus has not, to the knowledge or ourselves, been seen "sucking" plants and since it can also be found, albeit rarely, in non phytal environments, its direct relationship upon plants for nourishment must be considered conjectural. Brady (1868:457) states: "Although it appears to me more fully conformable with what we know of the general habits of the Crustacea and more fully explanatory of the peculiarities of the Paradoxostomatinae if we suppose their diet to consist of microscopic animalicula rather than the juices of algae or of animals much higher in organization than themselves". It seems impossible to us that the specimens of *Paradoxostoma* frequently encountered in *Corallina* or in old and "woody" holdfasts of *Laminaria,* could possess such a relationship with the host of direct nourishment. We feel it is much more probable that, without ruling out the possibility that certain members of the genus may have a direct food source relationship with the host alga, that the principal food of this genus is diatoms, bacteria etc. which are themselves associated with the algae.

Many other well-known phytal species, such as *H. viridis, C. lutea* and *H. albomaculata,* do not have specialised mouth parts and neither do such species as *L. rhomboidea, H. viridis, A. convexa,* and *H. cellulosa* which are found in a variety of other habitats as well as the phytal. This is ample evidence that to live in association with algae, it is not necessary for the ostracode to obtain its food directly from the plant.

Elofson (1941), considered that microscopic algae, associated with the larger plants, were the major food source and quoted as evidence the frequent occurrence of diatoms in the gut of ostracodes, a view supported by Hagermann (1966). Dr. R. Williams (verbal communication) suggests that proteinaceous antibiotic sustances secreted by certain algae, presumably to prevent the attachment of epiphytes, may provide an important food source for their associated epifauna. Both authors have independently observed *C. lutea* and *H. albomaculata* apparently "grazing" or "browsing" on *Cladophora rupestris* and *Ulva intestinalis*. R. C. Whatley has also seen *Loxoconcha elliptica* (Brady, 1868), prescribing an advancing spiral browsing action on the branches of *Enteromorpha,* and *Parakrithella hanaii,* a common phytal species from the Argentine littoral, apparently doing the same on *Enteromorpha, Cladophora,* and *Ceramium.* In all of these cases the authors have not been able to observe on what the animals were feeding. However, we are of the opinion that small diatoms and bacteria are the most obvious possibility.

With the possible exception of the Paradoxostomatinae, algae do not seem to serve as a primary food source for ostracodes. There does not seem to be any evidence that the epifauna favour any particular weed, therefore this cannot be invoked as a possible factor in explaining the observed preference of certain plants by ostracodes over others.

6. *The sediment content of the plant.* — Dahl (1948) noted an increase in the density of the microfauna on algae related to an increase in the amount of contained detritus. Wieser (1959) found that the number of nematodes increased with increase in the amount of sediment, whilst the number of creeping and clinging animals decreased. Hagermann (1966, 1969) also noted this effect, and in the former paper pointed out that the amount of sediment contained within the plant is to a large extent a function of the degree of turbulence. The present authors have also noted this relationship which they regard as further evidence of the supreme importance of turbulence in affecting the distribution of animal life, in the sense of a fundamental factor, within the littoral zones. An analysis was made of the sediment content in the previously described collection of *Laminaria* holdfasts, from a sheltered and from an exposed situation at station 745: (weights in grams)

	Sheltered			Exposed		
Date	Weight of Laminaria	Weight of Sediment	No. of Ostracoda	Weight of Laminaria	Weight of Sediment	No. of Ostracoda
Dec. 6, '66	70	22	21	80	15	0
Mar. 3, '67	52	18	36	61	8	17
June 7, '68	86	19	46	42	6	10
Aug. 27, '68	47	7	27	80	15	1

Those holdfasts from the sheltered station contain more sediment and more ostracodes that those from the exposed site. From this it might be suggested that an increase in sediment is accompanied by an increase in Ostracoda.

However, if the results from the exposed site are considered alone, the reverse is true. The results from the sheltered site considered alone, seem to indicate little relationship between population density and amount of sediment. It might even be said in respect of the latter, that the number of ostracodes increase in spite of the increase in sediment, not because of it.

The authors have noticed that whilst strictly phytal Ostracoda are not greatly influenced by the amount of sediment in the algae other species, which are more commonly found in sedimentary environments, are normally only found in association with those weeds which contain large amounts of sediment. One of the authors (R. C. Whatley) is currently engaged in studying the Ostracoda inhabiting the holdfast of *Macrocystis* from the southern coasts of Argentina and Chile. Here, although the data are as yet incomplete, there seems to be a notable relationship between the density and specific composition of the ostracode fauna and the particle size of the entrapped sediment. In the more exposed areas, the sediment is usually of large size, often in the form of shell fragments. In these cases the density of ostracodes is very low, whereas in more sheltered environments, such as within the Ria at Puerto Deseado, Province of Santa Cruz, the sediment is of mud and silt, and the holdfasts contain many more species and individuals. Very few species are common to the two.

We realise that there are many other important factors capable of influencing this relationship between the plant and its epifauna, such as the role of the plant in preventing dessication, in providing oxygen, and in providing protection from extreme temperature change, and probably as many others, which we are unable to consider here. We believe, however, that the major factors are those six which we have considered above.

A COMPARISON OF THE PRESENT RESULTS WITH THOSE OF PREVIOUS WORKERS

Colman (1940) counted the numbers of Ostracoda per algal sample from the littoral of Church Reef, Wembury. He did not identify the species but stated (p. 143): "Recently (April, 1939) I collected some from Church Reef which Mr. A. G. Lowndes was kind enough to examine; he found that they were all *Xestoleberis aurantia* (Baird). They were not abundant, however, and during the summer there is certainly more than one species present". Since *X. aurantia* has not been found along the Cardiganshire coast (and this in itself is a problem of some interest since it is one of the most common phytal species in British waters), it is only possible to compare the results from the two areas in terms of numbers per 100 grams of wet algae.

	Colman (1940)	Present Study
Pelvetia canaliculata	0	0
Fucus spiralis	0.5	0
Lichina pygmaea	0	–
Fucus vesiculosus	0	–
Ascophyllum nodosum & *Polysiphonis lanosa*	353.3	0
Fucus serratus	3.0	1.7
Gigartina stellata	0.5	–
Laminaria digitata (holdfasts)	7.5	33.5

The number of ostracodes from both areas is small, probably due to the fact that they are exposed coasts. With the single exception of *Laminaria,* the Welsh algae contained less Ostracoda. At all our stations, *Ascophyllum nodosum* was barren of ostracodes, whereas a dense population was found on this weed at Wembury. This may be possibly due to some special selection on the part of *X. aurantia,* although this is not evident in the work of other authors. Williams (1969), however, recorded more of this species on *Ascophyllum nodosum* at his Port Castell locality than on other weeds. This latter author also demonstrated that this plant in Anglesea, especially in the Port Castell locality, (339/100 grams), provides a favourable habitat for ostracodes. The absence of ostracodes on this weed in our area of study may perhaps be due to the fact that this coast is exposed to frequent storms from the west and southwest.

Wieser (1952) studied the fauna occurring on weeds in front of the Marine Biological Station at Plymouth. He divided the algae here into "leaf-like" forms, such as *Porphyra laciniata,* and *Nitophyllum punctatum,* and "tufted" forms such as *Ceramium* sp., *Cladophora rupestris,* and *Lomentaria articulata,* each of which type contained its own particular fauna. This author collected ostracodes on a transect from MHW to MLW but was unable to find any relationship between density and tide level. The numbers ranged between 7 and 280 per 1 gram dry weight of weed. He stated (p. 150) "In my opinion the most important factor is the silt content". As in the present study, *Porphyra,* which was encountered in the littoral fringe only, did not contain ostracods. *Nitophyllum,* with similar "leaf"-like form, contained between 34 and 60 specimens per 100 grams and was collected at 0.7, 1.20 and 3.0 metres below Chart Datum. The fact that ostracodes are able to inhabit "leaf"-like algae in the "upper" sublittoral zone at Plymouth is probably due to the protection afforded by the extensive breakwaters and Drakes Island from the full force of the waves. The higher numbers of Ostracoda collected from the eulittoral weeds by Wieser, may also be attributed to the same factor.

Hagermann (1966) studied the total fauna of *Fucus vesiculosus* and associated epiphytes in the Øresund. He reported 6,000 ostracodes in summer and 2,000 in winter from 200 grams wet weight of this weed. The dominant species were *H. viridis, S. nigrescens* (Baird), *H. cellulosa, X. aurantia, P. abbreviatum,* and *P. variabile.* The distinction between this area and the Cardiganshire coast is considerable in hydrographic terms. The former has a tidal range of only a few cms and is largely sheltered from major storms, whilst the latter has a maximum range of 7 metres and is open to frequent westerly and southwesterly storms. The same author in his (1968) study of the ostracode epifauna of *Corallina officionalis*, from a slightly reduced saline environment in western Norway, found many ostracodes, especially in summer and early autumn. The weed was collected as an undergrowth of *Fucus* and was thus well protected from turbulence and dessication. Four of the species, *Elofsonella concinna* (Jones), *Semicytherura nigrescens* (Baird), *Xestoleberis depressa* (Sars), and *Paradoxostoma pulchellum* (Sars) were permanent annual inhabitats of the weed and reproduced in it. Others, such as *Semicytherura inconspicua* (Klie), *Xestoleberis pusilla* Elofson, were probably accidental, *Cythere lutea* occurred only as a winter migrant in the adult stage. In summer this species was present in the sublittoral at three metres and this seasonal migration, in the opposite direction to that noted by the present authors, was attributed to the fact that the eulittoral was at a temperature too high to support the species during the summer. A further work by this author (1969) demonstrated that the type of algae and the seasonal development of the plant and epiphytation were very important factors in the distribution of *H. viridis* in brackish waters of the Øresund.

The work of Williams (1969), who studied five intertidal localities from Anglesea, contains results which, in general conform with those presented by us.

CONCLUSIONS

Whilst there are many regional differences, due to hydrographic and climatic factors and also to the faunal and floral provincial differences in the Ostracoda and the algae, whilst in different areas different ostracods inhabit the same weed, or the same ostracodes inhabit different weeds; the factors fundamental to the relationship between the animal and the plant are thought to be those outlined above. These factors have been arrived at from our own studies and from those of other workers.

Most of the data we have concerning this relationship is from Europe and to a lesser extent from the United States, and it is important, to test the universality of these factors, to have data from other parts of the world. Very preliminary results from the Argentine suggest that the same factors are operative as in the North Atlantic and adjacent seas. Perhaps the dependence of Ostracoda upon the algae, to provide attachment and protection on this exposed and stormy South Atlantic coast, is even more pronounced. Of the 160 species isolated to date in a study of the Argentine continental shelf and littoral, approximately 80% are restricted to the latter where, with the exception of certain muddy tidal lagoons and estuaries, there is an almost 100% dependence upon algae. The form of the plant, its vertical position within the littoral as well as its micro-situation and contained sediment, all seem to be important controlling factors in the selection of the weed by its ostracode epifauna. It is also worthy of note that in the eulittoral and sublittoral, sedimentary environments are, with very rare exceptions, not inhabited by ostracodes and moreover, the genera which would normally be encountered in these and inner shelf sedimentary environments of Europe, are here found in association with algae. Many examples could be given. For example, the Leptocytheridae (Whatley and Moguilevsky in this publication) are much more phytal in habit here than elsewhere. Also, other genera such as *Argilloecia, Paracypris, Macrocypris,* and the great majority of the Hemicytheridae, are found commonly, and often exclusively, on algae together with well-known phytal genera such as *Parakrithella, Xestoleberis,* and *Paradoxostoma.*

REFERENCES

Brady, G. S.

1868. *A mongraph of the Recent British Ostracoda. Linn. Soc. London,* Trans. 26 (2), pp. 353-495, pls. 23-41.

Chapman, G.

1955. *Aspects of the fauna and flora of the Azores, VI. The density of animal life in the coralline zone.* Ann. Mag. Nat. Hist., 12th ser., 8, pp. 801-805.

Colman, J.

1933. *The nature of the intertidal zonation of plants and animals.* Jour. Mar. Biol. Ass., United Kingdom, 18, pp. 435-476.

1940. *On the faunas inhabiting intertidal seaweeds.* Jour. Mar. Biol. Ass., United Kingdom, 24, pp. 129-183, 23 tables.

Dahl, E.

1948. *On the smaller Arthropoda of marine algae, especially in the polyhaline waters off the Swedish west coast.* Dissertation, Lund. Undersokn over Øresund, vol. 35, pp. 1-193.

Elofson, O.

1941. *Zur Kenntnis der marinen Ostracoden Schwedems mit Besonderer Berucksichtigung des Skageraks.* Zool. Bidr. Uppsala, 19, pp. 215-534.

Evans, R. G.

1947. *The intertidal ecology of Cardigan Bay.* Jour. Ecol., 34, pp. 273-309, 10 text-figs., 5 tables.

Hagermann, L.

1966. *The macro- and microfauna associated with Fucus serratus L., with some ecological remark. Ophelia,* 3, pp. 1-43.

1968. *The Ostracod fauna of Corallina officionalis L. in western Norway.* Sarsia, 36, pp 49-54.

1969. *Environmental factors affecting Hirschmannia viridis (O. F. Müller) (Ostracoda) in shallow brackish water.* Ophelia, 7, pp. 79-99.

Kornicker, L. S.

1964. *A seasonal study of living Ostracoda in a Texas Bay (Redfish Bay) adjoining the Gulf of Mexico. In Ostracods as ecological and palaeecological indicators.* Pubbl. staz. Zool. Naples, 33 suppl., pp. 45-60.

Lewis, J. R.

1964. *The ecology of rocky shores.* English Universities Press, London. 323 pp.

Ohm, G.

1964. *Die Besiedlung der Fucus-Zone der Kieler Bucht und der westlichen Ostsee unter besonderer Berücksichtigung der Mikrofauna.* Kieler Meeresforsch., 20, pp. 30-64.

Reys, S.
1963. *Ostracods des peuplements algaux de l'etage infralittoral de substrat rocheux.* Recl. Trav. Stn. mar. Endoume, 28 (43), pp. 33-47.

Tressler, W. L., and Smith, E. M.
1948. *An ecological study of seasonal distribution of Ostracoda, Solomon Island, Maryland region.* Contr. Chesapeake Biol. Lab., 71, pp. 1-57.

Whatley, R. C., and Wall, D. R.
1969. *A preliminary account of the ecology and distribution of Recent Ostracoda in the southern Irish Sea.* In J. W. Neale ed. *The taxonomy, morphology and ecology of Recent Ostracoda.* Oliver and Boyd, Edinburgh, pp. 268-298.

Wieser, W.
1952. *Investigations on the microfauna inhabiting seaweeds on rocky coast. IV. Studies on the vertical distribution of the faunas inhabiting seaweeds below the Plymouth Laboratory.* Jour. Mar. Biol. Ass. U. K., 31, pp. 145-174.
1959. *Zur Okologie der Fauna mariner Algen nit besonderer Beruchsichtingung des Mittelmeeres.* Int. Revue. ges. Hydrobiol., 44, pp. 137-180.

Williams, R.
1969. *Ecology of the Ostracoda from selected marine intertidal localities on the coast of Anglesea.* In J. W. Neale ed. *The taxonomy, morphology and ecology of Recent Ostracoda.* Olivier and Boyd, Edinburgh, pp. 299-327.

R. C. Whatley,
División Micropaleontología,
Facultad de Ciencias Naturales
y Museo,
Universidad Nacional de la
Plata,
Paseo del Bosque,
La Plata, Argentina.
and
Department of Geology,
University College of Wales,
Aberystwyth, Great Britain.

D. R. Wall,
Burmah Oil Co.
of Australia,
10 Stirling Highway,
Nedlands, Perth,
W. Australia.

DISCUSSION

Dr. R. L. Kaesler: You mention the importance of protection the algae provided in the case of some of the tufted algae. How important is the surface area? I would think that as the surface area increases, there would simply be more room for the ostracodes.

Dr. Whatley

This is extremely important but how does one go about measuring surface area of algae. Hagermann used a formula in his 1967 paper which we tried at one stage to employ but found to be extremely unsatisfactory. The major problem was always to separate out the epiphytes and in some cases the microepiphytes and the residual organic and inorganic material contained within the plant to arrive at some reasonable estimation of its surface area. This, in the very tufted plants with a great deal of epiphytic growth and contained sediment, proved difficult if not impossible. As a result of this we abandoned a consideration of surface area in favour of that of wet weight of algae. However I am certain that available surface area must exert a considerable influence on the density of ostracod occupation of various species of algae and this is a factor which should be given more consideration in future studies.

Anonymous: What's the maximum depth of your sub-littoral zone?

Dr. Whatley
We consider that the sub-littoral zone in the context in which we have used the term extends out to about 5 fathoms and this depth marks the outward limit of our algal collections.

Dr. J. W. Neale: I covered this to some extent in the Naples Symposium of 1963 and in littoral environments it seems that surface area is less important than what one might call tuftiness and ability to retain moisture. This comes out very well in the work of Colman (1940) and Wieser (1952). I was particularly interested in your mention of die back in the winter coupled with the migration of Ostracoda because Tressler and Smith (1948) found this phenomenon of migration in their Solomon Island work. They attributed this to change in temperature and suggested that the ostracods sought the more equable temperatures of the deeper waters during the winter. How would you rate the importance of cover as a factor compared with that of changing temperature?

Dr. Whatley
As we have stated in the paper, we regard the "die back" of algae and the causative fall-off of temperature in late autumn, as being of equal importance in causing a migration of ostracods from the eulittoral to the sub-littoral for the winter.

The reverse migration in the spring is also thought to be due equally to renewed algal growth and increased temperature.

Hagermann (1968) has recorded that Ostracoda migrate out of the eulittoral into the sublittoral in western Norway during the summer months and concludes that this migration is to escape extreme high summer temperatures although we have not observed this phenomenon.

Dr. Neale: Yes, but is there not the factor of constancy or equability involved as well?

Dr. Whatley: It could well be.

TO THE PROBLEM OF NODING ON *CYPRIDEIS TOROSA* (JONES, 1850)

Bernd Vesper

Zoologisches Institut und Zoologisches Museum, Hamburg

ABSTRACT

Among Ostracoda *Cyprideis torosa* is the best known example for the development of nodes on their shells. *Cyprideis torosa,* which lives in slack waters, was collected by the author in different areas on the coastal region of the North Sea (not directly in the North Sea but in ditches behind the dike) and in slack waters along the shore of the Baltic Sea in Schleswig-Holstein. Smooth as well as noded specimens occur in the sampling area. The results: The salinity of 5o/oo, which Schäfer fixed in 1953 as the upper limit for the occurrence of *Cyprideis torosa* is by far too low, since the nodes appear in a range of salinity from 1.8 to 14.5o/oo.

The intensity of the nodes differs in the various ranges of salinity. At higher salinity the intensity of the nodes is distinctly weaker than at middle or very low salinity.

Moreover the intensity of the nodes is different in the different regions studied, in spite of nearly the same salinity.

The nodes may occur differently strong on both valves.

As to the number of the nodes, different combinations of nodes may be developed, whereas their location seems to be constant.

ZUSAMMENFASSUNG

Unter den Ostracoden ist *Cyprideis torosa* für die Ausbildung von Schalenbuckeln wohl das bekannteste Beispiel.

Cyprideis torosa, der ja ein Stillwasserbewohner ist, wurde vom Autor in verschiedenen Gebieten im Bereich der Nord- und Ostseeküste Schleswig-Holsteins gesammelt. In dem Untersuchungsgebiet wurden sowohl glatte als auch gebuckelte Exemplare der oben genannten Art angetroffen.

Dabei ergaben sich folgende Resultate:

Der Salzgehalt von 5o/oo, den Schäfer (1953) als obere Grenze für das Vorkommen von gebuckelten Exemplaren angibt, ist als erheblich zu niedrig angesetzt, denn gebuckelte Tiere treten in einem Salzgehaltsbereich von 1.8 bis 14.5o/oo auf.

Die Intensität der Buckel ist in den einzelnen Salzgehaltsbereichen verschieden. Bei höherer Salinität ist der Ausbildungsgrad der Buckel deutlich geringer als bei mittlerem oder sehr niedrigem Salzgehalt.

Ferner ist der Ausbildungsgrad der Buckel trotz annähernd gleichem Salzgehalt in den verschiedenen untersuchten Gebieten unterschiedlich.

Die Buckel können auf beiden Schalenhälften unterschiedlich stark ausgeprägt sein.

Was die Anzahl der Buckel anbetrifft, können verschiedene Buckel-Kombinationen ausgebildet werden, wobei die Lage der Buckel konstant zu sein scheint.

INTRODUCTION

Among Ostracoda *Cyprideis torosa* (Jones, 1850) is the best known example for the development of nodes on their shells under certain conditions.

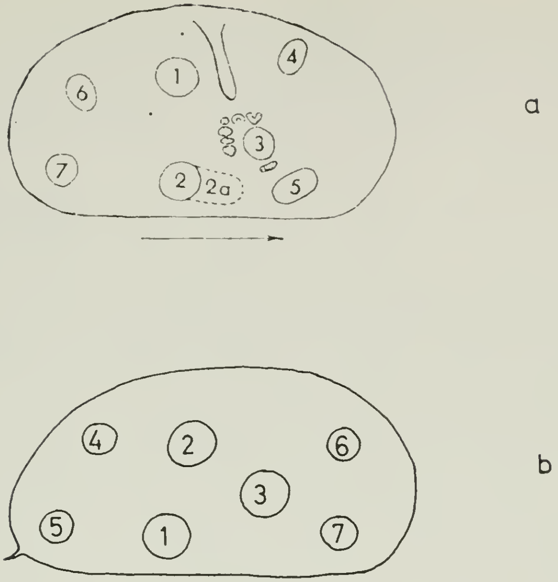
According to available data from the literature, generally the shells of individuals of *Cyprideis torosa* living in low salinity develop a row of nodes, but individuals in higher salinity have a smooth shell. The named species is called "*Cyprideis torosa*", the unnoded form should correctly be cited as "*Cyprideis torosa* forma *litoralis*", and the noded form as "*Cyprideis torosa* forma *torosa*".

Text-figure 1. Study areas in Schleswig-Holstein.

OBSERVATIONS BY THE WRITER

I have collected *Cyprideis torosa,* which lives in slack waters, on the coast of the North Sea and the Baltic Sea in corresponding waters (Text-fig. 1). On the coast of the Baltic Sea, there are numerous lagoons along the shore; in the area of the North Sea there are ditches behind the dike. All localities contain brackish water and are in constant or fluctuating spatial continuity with the marine living space.

About the noded forms of *Cyprideis torosa* a general statement can be made, concerning the distribution of the single nodes on the shells. Sandberg (1964) stated that the total number of nodes known to occur in the genus *Cyprideis* is seven, but that no species has yet been observed to have exhibited



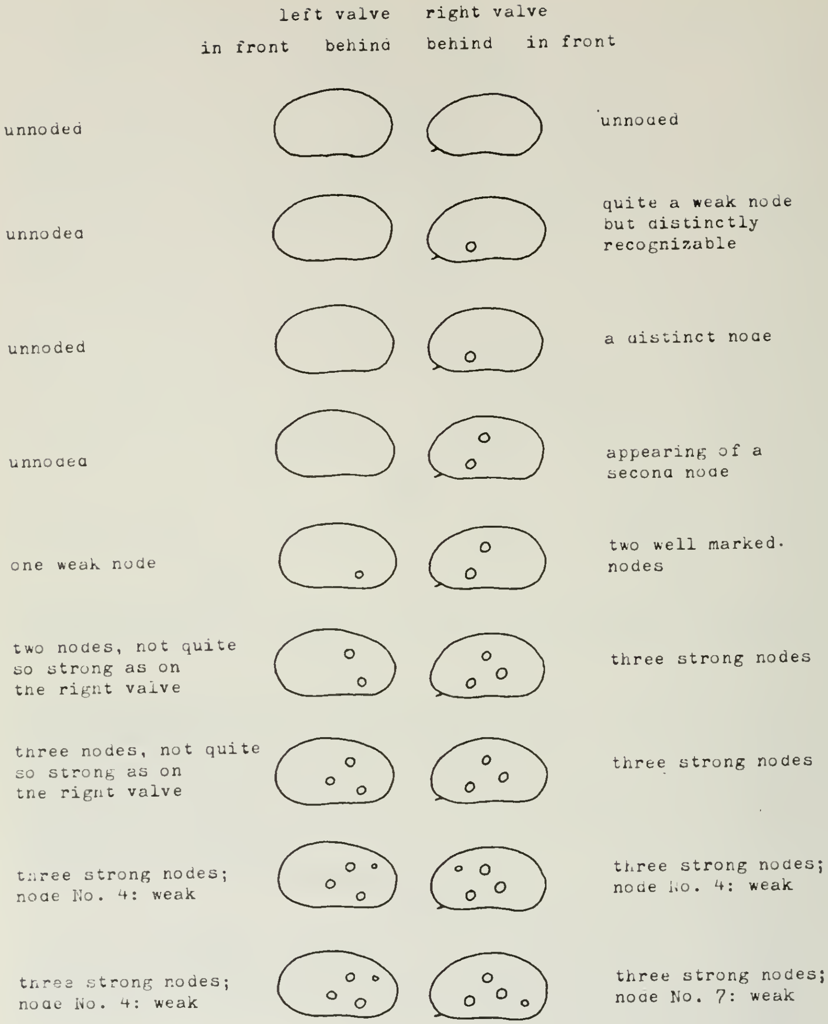
Text-figure 2. *Cyprideis torosa,* right valve: location and designation of the nodes, (a) usage of Sandberg, 1964, (b) usage herein.

all seven. In a general scheme (Text-fig. 2a) he showed the distribution of the nodes on the surface of the valve. I have numbered the nodes differently from those by Sandberg and have done this in succession of their appearance (Text-fig. 2b). It can be stated that in all samples which contained noded forms, if only one node is present it is mostly the node which Sandberg called number two (= my node no. 1). Node number one of my scheme always appears first; in the presence of two nodes, node number three may possibly appear before number two, but this is an exception.

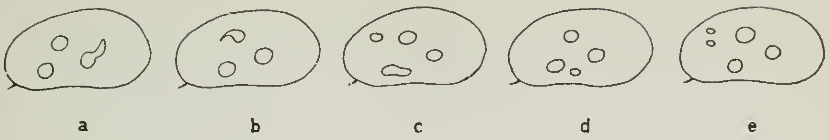
As to the distribution of the nodes on the valve surface, different combinations are possible. In one sample, I could observe variations of completely unnoded to heavily noded specimens. Text-fig. 3 shows some of possible combinations of nodes on the females in one sample of a sampling area. The same condition exists in the males.

A number of general statements were also made by Sandberg (1964):

1. Nodes are nearly always stronger on the right valves.
2. Nodes may be limited to the right valve.
3. No specimen had been observed in which the left valve was noded and the right valve was unnoded.
4. The females commonly are more strongly noded than the males.
5. The right valve seems to be distinctly preferred with regard to noding.



Text-figure 3. Combinations of the nodes occurring on the valves of females of *Cyprideis torosa.*



Text-figure 4. Peculiarity in the forming of the nodes.

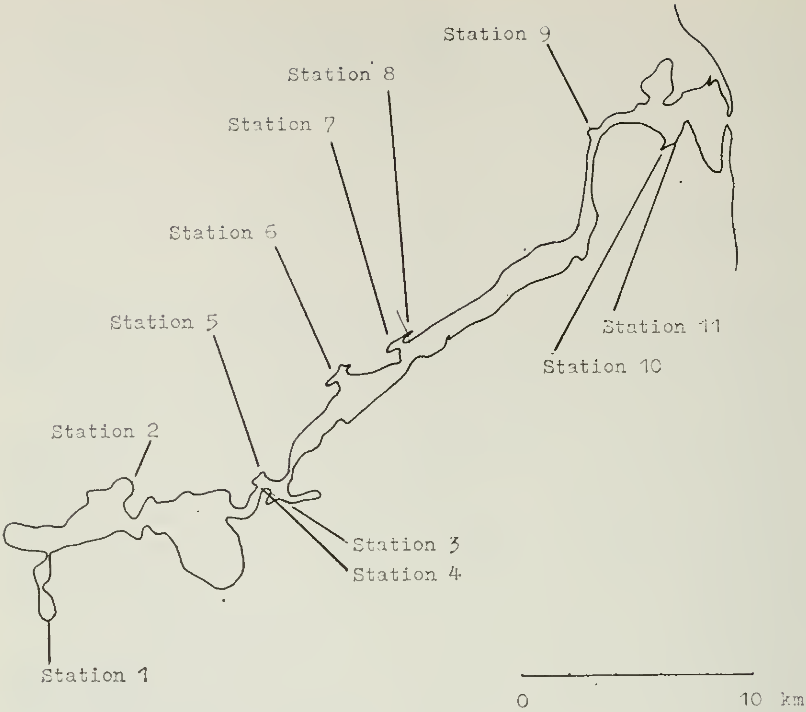
In general the nodes have a round extension. Divergences as can be seen in Text-fig. 4 are possible. Node number three and number two may respectively show an upward and backward hooklike extension, or node number one is long and not round as it is common. Other than node number one, there may appear two small nodes which are distinctly separated from one another.

To clarify the findings mentioned above, that the unnoded forms of *Cyprideis torosa* appear in high salinity and the noded forms in low salinity a study area which shows a slow graduation of salinity would be desirable. Such an ideal area which can scarcely be found on European shores in such a form and extension is the "Schlei". The Schlei is suitable for examinations in respect to the influence of different salinities on the animals. It is seldom like another water on the shore of Schleswig-Holstein, because salinity decreases more or less regularly on the entire length of the Schlei.

The Schlei (Text-fig. 5) extends about 40 km inland from the Baltic Sea and is a narrow, commonly 500-800 m wide, relatively shoal indented water with a water-way of 4 to 5 m depth; the salinity decreases more or less regularly on its entire length from 14o/oo to respectively 2o/oo. According to the classification of the "Venice system" there is always mesohaline water in the entire Schlei region.

Schäfer (1953) from observations based on his data, and also those taken from the literature, thought the upper limit for the existence of the noded form to be a salinity of 5o/oo. Such a condition is not substantiated by my samples of the Schlei. I observed the noded form in the entire region of the Schlei that is also beyond the 5o/oo limit, even in the outer Schlei where there is an average salinity of 13 to 15o/oo.

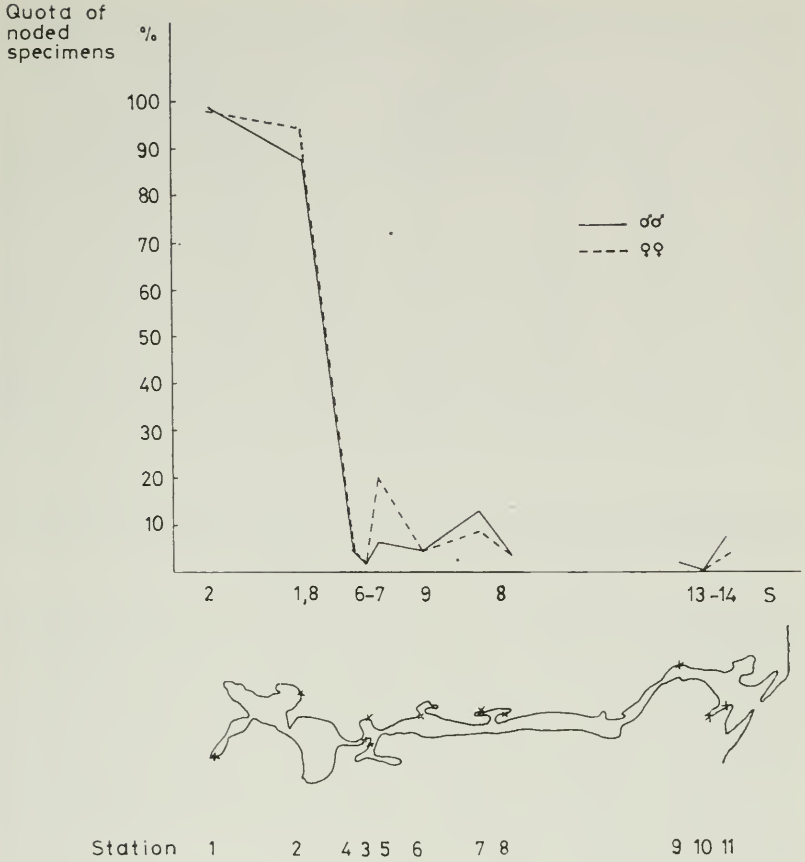
Text-fig. 6 shows the distribution of the noded and unnoded forms within particular stations. There are noded and unnoded forms in all stations, station 10 excepted. Text-fig. 6 shows also that the proportion of noded to unnoded specimens shifts with increasing distance from the Baltic Sea in favour of the noded form. Suddenly in the range of 5o/oo (station 1 and 2) 99o/oo of the males and 98o/oo of the females here are noded, whereas in the other stations 3 to 11 (middle and outer Schlei-region) the unnoded form of *Cyprideis torosa* predominates in both sexes. The course of the curves for both sexes is approximately the same as to the decrease at about 5o/oo salinity and the increase



Text-figure 5. Location of sampling stations in the Schlei.

which is repeated twice in the range of 6 to 9‰ and the increase at station 11. The ranges of salinity at about 5‰ and between 6 to 9‰ seem to be critical ranges.

The table (Table 1) shows the numerical relation of males and females, of noded and unnoded individuals, and serves for completion of the curve shown in Text-fig. 6. As seen from the Text-fig. and the Table the noded specimens can be observed in the entire region of the Schlei. But number and intensity of the nodes are different in the single regions of the Schlei. In the outer region of the Schlei, the noded specimens of station 11 (both males and females) have node number one very weakly developed only on the right valve, whereas the left valve is unnoded. Station 10 had only unnoded specimens. The males at station 9 have only node number one either on both valves or only on the right valve. The same is true for the females, and node number one may only be developed very weakly on the left valve so that it looks as if this node is rising. Station numbers 8 to 1 of the middle and the inner Schlei are distinguished, unlike stations 11 to 9 of the outer Schlei just discussed, by generally stronger noded specimens.



Text-figure 6. Percentage distribution of males and females of the noded form of *Cyprideis torosa* within the sampling stations of the Schlei. (July, 1969). Salinity values are in parts per thousand.

Table 1. Distribution of males and females of the noded and unnoded form of *Cyprideis torosa* within the sampling stations of the Schlei (July, 1969).

		Males			Females		
Station	Salinity ‰	unnoded quantity	noded quantity	%	unnoded quantity	noded quantity	%
11	13,2	214	18	8	478	16	3
10	13,1	all	—	0	all	—	0
9	14,5	666	13	2	639	13	2
8	7,7	57	2	3	115	4	3
7	8,0	198	29	13	421	41	9
6	9,3	162	8	5	703	36	5
5	6,2	57	4	7	120	30	20
4	6,9	235	11	4	693	29	4
3	7,7	151	3	2	988	9	1
2	1,8	20	140	88	19	303	94
1	2,1	5	396	99	15	711	98

In stations 8 to 1, there appear still weakly noded forms, represented by weak node number one and smooth left valve, as this is also true in the specimens of the outer Schlei.

It could be summarized for the Schlei region that:

1. In the entire Schlei region from 2 to 14‰ there appear noded and unnoded specimens.
2. Above the limit of 5‰ salinity the unnoded form predominates, below the 5‰ limit almost exclusively the noded form of *Cyprideis torosa* is present.
3. Number and intensity of nodes in the stations of the outer Schlei (station 11 to 9) are lower than those in the middle and inner Schlei (station 8 to 1), although in both latter regions animals with a lower number of nodes and weaker nodes may appear.
4. A complex of station 11 to 9 in which the noded specimens have developed weak and few nodes, mostly only one node, is opposed to a complex of station 8 to 1, in which the noded specimens mostly have developed several and strong nodes. The extent to which one can speak of an increase of the number of nodes and the intensity of the nodes on decreasing salinity is obscure; in any case there is no straight rise.

Another of my study areas on the shore of the Baltic Sea was the lake "Kleiner Binnensee". This lagoon is protected by two dikes against the Baltic Sea and drains through an outlet (waste-pipe with a flood-gate) into the Baltic Sea. The salinity is never above 4o/oo; this is supported by the data from the literature, and it is relatively constant as the salinity fluctuations are rather low.

Unnoded and noded specimens of *Cyprideis torosa* also appear in the Kleiner Binnensee. It is striking that the noded specimens of both sexes have in most cases developed only one node (number one). In general this is confined to the right valve, it also appears on both valves. In any case, it is very weak, sometimes even weaker than in regions of the just mentioned outer Schlei with its salinity of 13 to 15o/oo. Sporadically, node number three instead of node number one appears. It is striking that extremely weakly noded specimens appear in a salinity of never more than 4o/oo and in relatively constant conditions which are present in the Kleiner Binnensee. In respect to the stations of the Schlei with similar salinity, one should expect considerably stronger noded specimens.

In the region of the shore of the North Sea, ditches of the Friedrichskoog and the Neufelder Koog behind the dike had been investigated. These ditches have a water-surface of about 4.50 m breadth. The salinity of these ditches is about 4o/oo, and therefore is similar to some regions of the Schlei and of the Kleiner Binnensee. In the stations examined in the ditches, all specimens of *Cyprideis torosa* are unnoded, although, the salinity only is about 4‰ as mentioned above. In consideration of some stations of the Schlei and those of the Kleiner Binnensee, one should expect both unnoded and noded animals.

In summary:

1. Nodes appear in a range of salinity between 2 and 15o/oo. The upper limit for the existence of noded specimens at the 5o/oo limit mentioned by Schäfer is by far too low.
2. The intensity of the nodes is different in the particular salinity ranges. At higher salinity, the intensity of the nodes is distinctly weaker than at middle or very low salinity, although animals with weak nodes may also appear in the latter two. Moreover the intensity of the nodes is different in the different regions studied, in spite of nearly the same salinity. While in the Schlei at a salinity of 4o/oo noded and unnoded specimens appear, the noded specimens of the Kleiner Binnensee only have one weak node on the right valve at about the same salinity; all specimens living at the same salinity in the North Sea ditches, contrary to expectation, are unnoded. The nodes may occur differently strong on both valves. They are nearly always stronger on the right valve than on the left; they may be limited only to the right valve.
3. As to the number of the nodes, different combinations of nodes may be developed, although their location seems to be constant. Some nodes repeatedly show different extensions.

DISCUSSION

Extensive consideration has been given to explanations of this phenomenon. The possible causes of this feature range from physiological to genetic fixation.

While Triebel (1941) supposed that the nodes increase the cavity (volume) between the two shells and, therefore, noding is to be regarded as an adaption to the lower specific gravity of brackish or freshwater, Sandberg (1964) considers this theory insufficient, for nodes would have to lie within the area of the muscle scars what does not always prove right. Moreover the nodes examined by Sandberg were not filled with body tissue but were reflected internally by corresponding depressions of equivalent size. Sandberg concludes "that noding in brackish-water and in freshwater species has different causes", but does not realize "why the nodes must be regarded as functional structures (*e.g.,* regulators of specific gravity). The nodes may well be nonfunctional responses to an altered, perhaps abnormal, environmental factor" (p. 41).

According to Sandberg, noding is negatively correlated with salinity. Due to the decrease of salinity the chemical constituents (organic as well as inorganic) of the environment are in lesser amounts; perhaps occasionally they are nearing a critical minimum level. Sandberg thinks it possible that noding is a physiologically controlled, abnormal but not pathological reaction to a deficiency in the changed environment. The variation in strength of noding, let us suppose, results from each animal showing different reactions to the environment. According to the results cited herein that noded forms appear below a salinity of 5o/oo, noding on *Cyprideis torosa* has to be considered, according to Hartmann (1964), as modificatively produced phenotypical characteristic. According to Hartmann it is surprising (translated by the writer) that "the unnoded form also appears in water with low salinity and in nearly freshwater where, if such a concentration of salinity has a modifying effect, the noded form would be expected. Beside the modifying effect of low salinity other factors are due to participate in the occurrence of noding". A long continuing conservation argues against a phenotypical modification of long duration. "Perhaps modificative and genetic fixation effect in the same direction" (Hartmann, 1964, p. 65).

During the symposium at Pau (France, 1970) Kilenyi expressed the opinion (personal communication from Hartmann) that noding is a genetically fixed dominant characteristic. Opposed to this assumption, however, is the proportion of the unnoded and noded individuals in the different populations found during this study. It would be difficult to imagine how a characteristic which is only genetically and not (also) influenced by the milieu should be used in palaeontology as an indicator of marine coastal area. If noding is a genetically controlled phenomenon, it will most probably be a polygene system. One or several specifically effecting gene-complexes and components influenced by the milieu lead to the formation of a phenotypic characteristic, in which not the characteristic but the norm of reaction to the milieu is inherited.

Although I could state that noding does not appear, as so far believed, in a fixed salinity of 5o/oo but that this phenomenon occurs slowly, and if correlated with decreasing salinity, then the question of the causality of noding goes unanswered. As discussed earlier in this paper, noding does not appear in all types of waters regularly with decreasing salinity (respectively at the same low salinity).

A decisive factor could particularly be the content of $CaCO_3$ of the particular waters. The table (Table 2) shows how the amount of $CaCO_3$ is distributed at the stations studied. Thereafter at higher concentration of

Table 2. Amount of calcium (mg/l) in the different regions

Schlei

station	
11	205
10	181
9	182
8	132
7	135
6	141
5	124
4	125
3	133
2	94
1	78

Kleiner Binnensee

station	max.	min.	mean
1	113	91	108
2	119	32	90
3	115	36	87

region of the shore of the North Sea
Neufelder Koog

station	max.	min.	mean
1	183	85	137
2	171	87	138

Friedrichskoog

station	max.	min.	mean
1	268	145	196
2	296	123	165
3	205	117	148
4	153	75	122

$CaCO_3$ only weakly noded specimens appear, at lower concentration strong noded examples appear.

A physiological control of noding, *i.e.* an influence of environmental factors, either salinity or the amount of $CaCO_3$, within sensitive periods of the animals could be imagined.

REFERENCES

Hartmann, G.
1964. *Das Problem der Buckelbildung auf Schalen von Ostracoden in ökologischer und historischer Sicht (Mit Bemerkungen zur Fauna des Trasimenischen Sees)*. Mitt. Hamburg. Zool. Mus. Inst. (Kosswig-Festschrift), pp. 59-66.

Sandberg, P.
1964. *The ostracod genus Cyprideis in the Americas*. Stockholm Contr. Geol., 12, pp. 1-178.

Schäfer, H. W.
1953. *Über Meeres- und Brackwasserostracoden aus dem Deutschen Küstengebiet mit 2. Mitteilung über die Ostracodenfauna Griechenlands.* Hydrobiologia, 5, pp. 351-389.

Triebel, E.
1941. *Zur Morphologie und Ökologie der fossilen Ostracoden. (Mit Beschreibung einiger neuer Gattungen und Arten).* Senckenbergiana, 23, pp. 294-400.

Bernd Vesper
Zoologisches Institut
und Zoologisches Museum
2000 Hamburg 13
Papendamm 3
Germany

DISCUSSION

Dr. P. A. Sandberg: What about the possibility of a genetic fixation of the nodes as suggested by Kilenyi?

Dr. Vesper: I think that the position of the nodes is genetically fixed but the intensity of the nodes will be controlled by environmental factors.

Dr. R. Reyment: I found in our work in the Niger Delta that one has to be very careful about ecological measurements. In upper littoral sediment, you have one set of ecological conditions, that is in the interstitial pore water; in the water immediately overlying the sediment, results that differ quite considerably are obtained. The ostracods living in the sediments are subject to quite different environments from those that live on the surface.

Dr. H. Löffler: I think you really could prove your ideas by culturing the species.

Dr. Vesper: Yes, I am making experiments in culturing the species.

Dr. M. C. Keen: I take it from your diagrams that you didn't sample higher salinities?

Dr. Vesper: No, I did not.

Dr. Keen: I ask this because Kilenyi (Tax., Morph., and Ecol. of Recent Ostracoda, Ed. J. W. Neale, 1969, p. 91) mentioned an increase in nodosity from marine waters down to a salinity of 20 o/oo, then a decrease in nodosity going into lower salinities. In other words, not a simple relationship between nodosity and decrease in salinity.

VARIATION IN PREDATION BEHAVIOR OF OSTRACODE SPECIES ON SCHISTOSOMIASIS VECTOR SNAILS[1]

I. G. Sohn and L. S. Kornicker
U.S. Geological Survey; Smithsonian Institution

ABSTRACT

Laboratory experiments using 1- to 3-day old *Biomphalaria glabrata* (Say, 1818) and species of ostracodes belonging to the genera *Cypretta, Cypridopsis, Heterocypris,* and *Cypricercus* indicate that the rate of of predation varies with the ostracode species used.

RÉSUMÉ

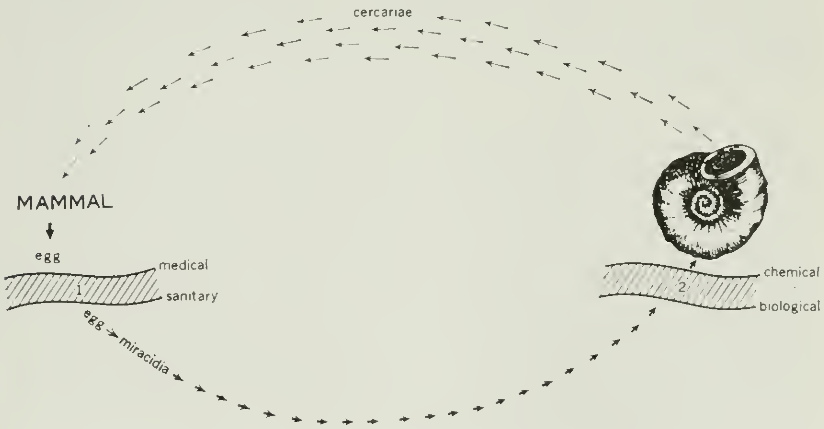
Les expériences de laboratoire utilisant des *Biomphalaria glabrata* (Say, 1818) agés d'un à Trois jours et des espèces d'ostracodes appartenant aux generes de *Cypretta,* de *Cypridopsis,* de *Heterocypris* et de *Cypricercus* indiquent que la fréquence de prédation varie entre les especès d'ostracodes employées.

INTRODUCTION

The life cycle of the blood fluke that causes schistosomiasis (bilharziasis) in humans and other mammals is shown in Text-figure 1.

Diseased animals excrete eggs, which develop in water into free-swimming miracidiae. These miracidiae enter the body of vector snails where they metamorphose into sporocysts which in turn produce many cercariae (free-swimming blood flukes) that leave the snail. After contact and penetration of the skin or hide of mammals, the cercariae invade certain organs where they multiply.

Text-figure 1 suggests two stages during which the life cycle of the blood fluke may be interrupted: 1) The miracidiae may be eliminated through sanitary methods that prevent the eggs from developing in waters that contain the vector snail, and the development of worms in the infected animal may



Text-figure 1. Life cycle of the blood fluke that causes schistosomiasis. Four methods which may cause an interruption in the life cycle are indicated.

---

[1] Publication authorized by the Director, U. S. Geological Survey.

be prevented by drugs; 2) the vector snails may be controlled by chemical or biological means. Ostracodes have been suggested as one of many potential biological controls.

Many laboratories breed vector snails to obtain cercariae in order to infect laboratory animals for testing the effectiveness of drugs. Bruce and Radke (1971, p. 2) reported that the Walter Reed Army Institute of Research established a Composite Drug Screening Unit in Japan in which to test 8,000 to 10,000 drugs per year against *Schistosoma mansoni* in rodents and primates. During 1969, that facility alone produced about 40,000 snails (*ibid,* p. 65, fig. 25). These snails produced 15 to 20 million cercariae per week. Ostracodes have been found to be a pest in the snail-breeding operation because they decimate aquarium snail populations (Van der Schalie, 1970, p. 6)). Thus, ostracodes have a negative effect in this phase of schistosomiasis research, and studies have been made to eliminate ostracodes from snail aquaria.

HISTORICAL REVIEW

The first published record of ostracodes killing snails was by Deschiens, Lamy, and Lamy (1953); they described how *Cypridopsis hartwigi* Müller, 1900, attacked and killed snails in laboratory aquaria maintained for breeding snails to be used in the study of schistosomiasis. The following year, Deschiens (1954) described how the ostracodes attacked the snails *Bulinus contortus* (Michaud, 1829) and *Planorbis glabratus* Say, 1818 (= *Biomphalaria glabrata*) like a swarm of bees, and speculated that this ostracode could be used for the biological control of these schistosomiasis vector snails. Watson (1958, p. 868), quoting Wright (personal communication, 1957) stated "*Cypridopsis* is normally a detritus-feeder. If no other food is available in an aquarium it will eat the faecal pellets of the snails present, even going so far as to nibble them from the snail's anus. The irritation thus produced causes the molluscs to retract and cease feeding. The impression is thus created that the crustaceans are actually attacking the snails when in fact they are merely seeking their faeces as food".

Lo (1967) experimented with *Cypridopsis vidua* (O. F. Müller, 1776) collected near Ann Arbor, Michigan, and 2-day-old *Biomphalaria glabrata* and found that the ostracodes kill the snails in the laboratory. He reported that snails in eight additional genera were affected by the ostracodes and that the snail species varied in their tolerance to the ostracodes. He concluded, however, that ostracodes could probably not be used in nature as a biological control. Kawata (1971) noted that in his cultures of *B. glabrata,* an ostracode species [*Cypretta kawatai* Sohn and Kornicker, 1972b] was an efficient predator on young snails. The ostracodes so irritated adult snails that the snails left the water, then weakened, and either died or returned to the water and were killed by the ostracodes. Sohn and Kornicker (1972a) reported on the basis of laboratory experiments that *Cypretta kawatai* is an effective predator on 1- to 3-day old *Biomphalaria glabrata.*

EXPERIMENTAL DATA

We experimented with *Heterocypris incongruens* (Ramdohr, 1808) and *Cypridopsis* cf. *C. vidua* (O. F. Müller, 1776) from Lover's Lane Pond, Dumbarton Oaks, Washington, D.C., and *Cypricercus* sp., probably new, grown in our laboratory since June 1969 from dry mud collected in Lake Colombo, Ceylon, by Dr. A. S. Mendis, Department of Fisheries, Sri Lanka. We used 1- to 3-day old snails of the red mutant (albino) strain of *Biomphalaria glabrata.* Our experimental procedures have been described previously (Sohn and Kornicker, 1972a, p. 1258, paragraph 2). The results of additional experiments are shown in Table 1; these are combined with previous experiments in Text-figure 2.

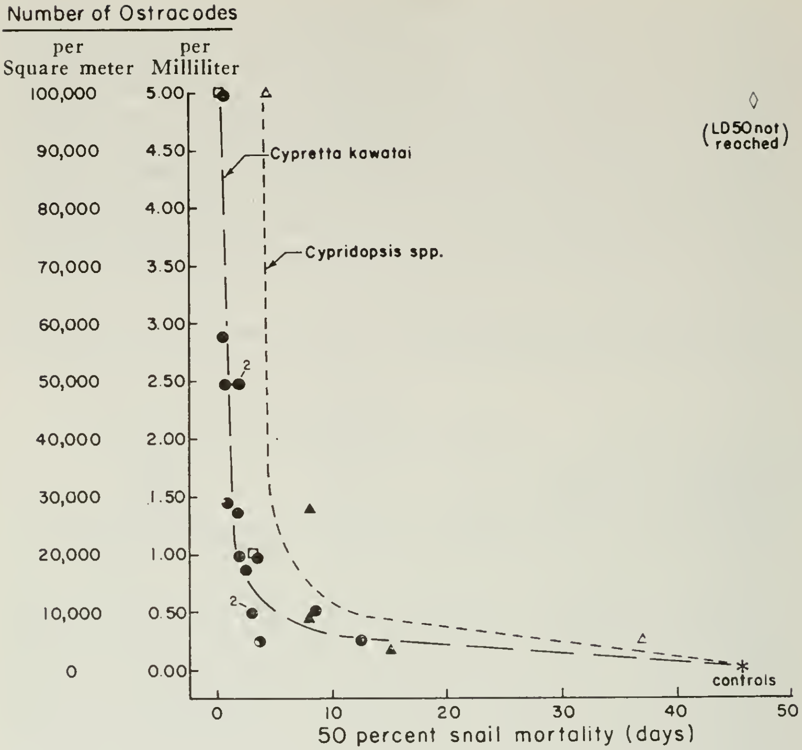
Table 1. Number of days to 50 percent mortality of snails, using *Heterocypris, Cypridopsis,* and *Cypricercus.*

Species of Ostracoda	Number of ostracodes	Days to 50 percent snail mortality
Heterocypris incongruens	500	0.50
Cypridopsis cf. *C. vidua*	500	3.28
Cypricercus sp.	500	47[a]

[a] No dead snails and more than 600 ostracodes; experiment discontinued.

Text-figure 2 includes data on *C. vidua* derived from Lo (1967). We calculated the abundance of ostracodes from Lo's data on the basis of culture dishes 90 mm in diameter (G. M. Davis, Philadelphia Acad. Science, oral communication on size of dish, July, 1972), and an estimated water depth of 20 mm. "Equivalent number of ostracodes/m^2" was calculated by dividing the number of ostracodes in each experiment by the area of the dish, and the quotient was extrapolated to a square meter. The data on *Cypretta kawatai* are from Sohn and Kornicker (1972a). Because the ordinate on the graph in our previous study (1972a, fig. 1) represented the number of ostracodes used, we did not include on it experiments with parameters other than five snails and dishes with 80-mm diameters. These data (1972a, table 1) are included in Text-figure 2.

On this graph we use population density as the ordinate in order to compare roughly the laboratory data with population densities in nature. In our experiments we used the equivalents of 5,000 to 100,000 ostracodes/m^2. These are within the ranges of some abundances recorded in nature. Luferova (1968) cited a peak of 18,000 specimens/m^2 of *Cypridopsis vidua* in September, 1965 in the Rubinsk Reservoir, USSR, and quoted references to Mordukai-Boltovskoi (1937) who recorded 50,000 ostracodes/m^2 as usual in Taganrog Bay in the Sea of Azov and as many as 230,000 ostracodes/m^2 during periods of maximum development. Dr. M. N. Gramm, Vladivostock, USSR, informed us (letter, Aug. 17, 1972) that the species involved is *Cyprideis littoralis* (Brady, 1868 [1869]). Barthelmes (1965) recorded as many as 9,000 to 22,000 specimens/m^2 of *H. incongruens* in certain carp ponds at Schwerin, Germany.



Text-figure 2. Number of days to 50 percent mortality of snails. Square — *Heterocypris incongruens,* circle — *Cypretta kawatai,* open triangle — *Cypridopsis* cf. *vidua,* filled in triangle — *Cypridopsis vidua,* diamond — *Cypricercus* sp., LD50 = live-dead ratio. Second column should read "per Milliliter."

The data on *C. kawatai* and the controls represent experiments that were duplicated 5 or more times, with 5 to 50 snails, 25 to 500 ostracodes, and dishes 80 to 190 mm in diameter. The number of snails in the experiments had no effect on the rate at which they died; the death rate was controlled primarily by the ostracode density. The curve for *Cypridopsis* spp. is based on our experiment with *C.* cf. *C. vidua* and those by Lo (1967). This curve was drawn subparallel to the curve for *C. kawatai.* Although we performed only two experiments with *Heterocypris incongruens,* the results suggest a curve very close to that of *C. kawatai.* Our single experiment with 500 specimens of *Cypricercus* sp. was terminated after 47 days, at which time all the snails were alive; the average number of days for the snails to reach 50 percent mortality in the controls was 46.

The results of the experiments shown on Text-figure 2 suggest that *Heterocypris incongruens* may be as effective a predator as *C. kawatai,* that *Cypridopsis* spp. may be slightly less effective, and that *Cypricercus* sp. may have no effect on snail mortality. Additional experiments are necessary to support this hypothesis.

REFERENCES CITED

Barthelmes, Detlev

1965. *Heterocypris incongruens (Ramdohr) 1808 (Crustacea, Ostracoda) als fakultativer Räuber und seine mögliche Bedeutung in Karpfenteichen.* Fischerei, Band 13, N.F., Heft ½, pp. 1-2.

Bruce, J. I., and Radke, M. G.

1971. *Cultivation of Biomphalaria glabrata and maintenance of Schistosoma mansoni in the laboratory, Part I,* in *Culturing Biomphalaria and Oncomelania (Gastropoda) for large-scale studies of schistosomiasis.* U.S. Army Medical Depart. Activity, Japan, Bio-Medical Report, 19, 406th Medical Laboratory, pp. 1-84.

Deschiens, R.

1954. *Mechanisme de l'action lethale de Cypridopsis hartwigi sur les mollusques vecteurs de bilharzioses.* Soc. Pathologie Exotique, Bull. 47, pp. 399-401, 2 figs.

Deschiens, R., Lamy, L., and Lamy, H.

1953. *Sur un ostracode prédateur de Bullins et de planorbides.* Soc. Pathologie Exotique, Bull. 46, pp. 956-958, 2 figs.

Kawata, Kazuyoshi

1971. *Survival studies of Biomphalaria glabratus in polluted waters.* Rockefeller Foundation grant GA MNS 6846, Technical Report, 44 pp., 10 figs.

Lo, C.-T.

1967. *The inhibiting action of ostracodes on snail cultures.* Amer. Micros. Soc., Trans. vol. 86, No. 4, pp. 402-405.

Luferova, L. A.

1968. *K faune Ostracoda Rybinskogo Vodokhranilischa.* Akad. Nauk SSSR, Inst. Biologii Vnutrennikh Vod, Trudy No. 17, pp. 76-81, "Nauka," Leningrad (Translated, 1959, by R. H. Howland, Bureau of Sport Fisheries and Wildlife, Washington, D.C., 9 mimeographed pages).

Mordukai-Boltovskoi, F.

1937. *Composition and distribution of the benthos in Taganrog Bay.* [Sostav i raspredelinie bentosa v taganrogskom zalive]. Raboty Dono-Kubansk. nauchn. rybn. stantsii, No. 5. Rostov (not seen).

Sohn, I. G., and Kornicker, L. S.

1972a. *Predation of schistosomiasis vector snails by Ostracoda (Crustacea).* Science, vol. 175, pp. 1258-1259, 1 fig., 1 table.

1972b. *Cypretta kawatai, a new species of freshwater Ostracoda (Crustacea).* Biol. Soc. Washington, Proc., vol. 85, No. 26, pp. 313-316, 3 figs.

Van der Schalie, Henry

1970. *Studies of the intermediate snail hosts of Oriental and African schistosomiasis.* U.S. Army Medical Research and Development Command, contract DA-49-193-MD-2651, Annual Progress Report, 28 pp., 31 figures.

Watson, J. M.

1958. *Ecology and distribution of Bulinus truncatus in the Middle East.* World Health Organization Bull., 18, pp. 833-894.

I. G. Sohn,
U.S. Geological Survey,
Washington, D.C. 20244

L. S. Kornicker
National Museum of
Natural History,
Smithsonian Institution,
Washington, D.C. 20560

DISCUSSION

Dr. R. H. Benson: Greg was good enough to give me some specimens of his *Cypretta* species, of which I showed a diagram of the marginal structure this morning. The species *Cypretta,* which all have marginal septa, have an interesting distribution in that they are rather disjunct throughout the world. *Cypretta* is very much like *Cypridopsis* except that it has an unusually thin shell. It's identified primarily by the fact that it has accessory struts or septa in and along the margin. To bring a taxonomic query to this discussion, I'm suggesting that *Cypretta* may not be taxonomically distinct. The important diagnostic character, that is the presence of struts, is simply a mechanical adaptation near the margin for increasing the strength of a very thin shell in order to provide resistance against buckling in this sensitive area. So that, in fact, this disjunct distribution of *Cypretta* may be an expression of a very simple mechanical adaptation which is morphologically convergent in many parts of the world.

Dr. Sohn: I believe that the present geographic distribution of *Cypretta* is partly explained by the fact that the genus is a member of the highly adaptable ricefield biota. Dr. Kornicker and I have ample evidence that *Cypretta* was introduced with the snail *Biomphalaria glabrata* (Say, 1818) to laboratories in Washington, then to laboratories in Baltimore, and later to our laboratory. I recently saw an adult *Cypretta* feeding inside the gelatinous cluster of snail eggs. Because some of the species in *Cypretta* can reproduce parenthogenetically, it is conceivable that they, as well as other ostracodes could have attained considerable geographic distribution through the water casks of sailing ships.

The septate anterior is not the sole character that differentiates *Cypretta* from *Cypridopsis,* these genera differ primarily in the development of the furca. This session is not the appropriate time to discuss how much weight to place on what character for generic discrimination. This topic may profitably serve as a basis for a future symposium.

The suggestion that the development of septate structures in *Cypretta* is simply a mechanical adaptation for increasing the strength of a very thin shell is not convincing because there are no precise measurements on the relative shell thickness of *Cypretta* and *Cypridopsis*. *Oncocypris* Müller, 1898, appears to have a thicker shell than *Cypridopsis,* and this genus also has septate margins. *Stenocypris* Sars, 1889, has septate margins, and this genus is architecturally and morphologically quite different from *Cypridopsis.*

Discussion of Film by I. G. Sohn and L. S. Kornicker showing Ostracodes feeding on Schistosomiasis Vector Snails

Dr. L. D. Delorme: Have you removed the mucus from the snails and placed it with the ostracodes to see if this is what attracts them?

Dr. Sohn: No.

Anonymous: Would they go after dead snails just as they do after live snails?

Dr. Sohn: Yes. Ostracodes are known to eat dead snails. The unresolved question is whether or not ostracodes actually kill snails. Research in cooperation with Dr. J. I. Bruce, Schistosomiasis Research Unit, Department of Medical Zoology, Walter Reed Army Institute of Research, may answer that question. We plan to tag snails by feeding them C-14 glucose. The snails will then be starved in order to eliminate fecal pellets which ostracodes are known to eat. We will then introduce ostracodes into the snail container, and will remove dead snails. Should the ostracodes become tagged, we will know that they kill snails.

Dr. L. E. Petersen: What are the possibilities that the ostracodes are attracted to the snail by the movement of the snail?

Dr. Sohn: You may have noticed that the elongate ostracode (*Cypricercus* sp.) did not behave as though he was attracted by the snails, and that the fat ostracode (*Cypretta kawatai*) was more interested in the snails. As I said yesterday, we have just barely scratched the surface of ostracode-snail predation, and that there is a great deal of research to be done. We will gladly supply starter colonies of ostracodes that are available to us to any laboratory interested in additional experiments.

Mr. J. H. Baker: Do you get a growth of algae on the gastropods which could attract the ostracodes? Their movement around the gastropod would disturb it, causing it to retract, and thus eventually death.

Dr. Sohn: We did not see algae on the 1- to 3-day old snails used in our experiments. We used also older snails for making the motion pictures in order to see whether or not the ostracodes behaved differently.

MORPHOLOGY OF *CYPRIDOPSIS VIDUA* (O. F. MÜLLER): VARIATION WITH ENVIRONMENT

ROGER L. KAESLER
The University of Kansas

ABSTRACT

Study of the correlations of six morphological characters of *Cypridopsis vidua* (O. F. Müller) with parameters of the physical and chemical environment was based on repeated sampling of five farm ponds in eastern Kansas. Morphological data were analyzed by nested analysis of variance and Student-Newman-Keuls *a posteriori* tests. Relationships among the environmental parameters and between morphological characters and the environment were analyzed using correlation coefficients, distance coefficients, and cluster analysis. The statistical analyses showed that many of the very subtle correlations between morphological characters and environmental parameters, though slight, are highly significant in a statistical sense. Evidence suggests that both antagonistic and synergistic effects of environmental parameters on each other may influence the response of morphology to differences in the aquatic environment.

Cypridopsis vidua is interpreted as a morphologically very plastic species. If morphological plasticity is an indicator of physiological adaptability, the success of *C. vidua* in populating the freshwater environment could be accounted for readily. Moreover, ignoring for the moment problems of speciation one encounters with parthenogenetic organisms, if the morphological characters that have been used to discriminate species of *Cypridopsis* show as much variation as the characters used in this study, some of the many species in the genus may be synonyms. Such high variability within a species has important implications for its use in the study of plate tectonics and continental drift.

RÉSUMÉ

L'étude des corrélations des six caractères morphologiques du *Cypridopsis vidua* (O. F. Müller) avec les paramèters de l'environnement physique et chimique s'est fondée sur l'échantillonnage répété de cinq étangs du Kansas oriental. On a analysé des données morphologiques par l'analyse emboîtée du désaccord et par des épreuves Student-Newman-Keuls *à posterior.* On a analysé les rapports parmi les paramètres environnants et entre les caractères morphologiques et l'environnement. en employant les coefficients de corrélation et les coefficients de distance aussi bien que l'analyse d'un groupe. Les analyses statistiques ont montré qu'un grand nombre de corrélations subtiles entre les caractères morphologiques et les paramètres environnants, bien que peu considérables, sont très significatives au sens statistique. L'évidence suggère que les effets antagoniques et synergistiques, tous deux, sur les paramètres environnants l'un sur l'autre, peut influencer la réaction de la morphologie aux différences dans l'environnement aquatique.

On interprète *Cypridopsis vidua* morphologiquement comme une espèce très plastique. Si la plasticité morphologicale indique la faculté d'adaptation physiologique, on pourrait facilement se rendre compte de la réussite du *C. vidua* à peupler l'environnement d l'eau douce. De plus, en ne tenant pas compte pour le moment des problèmes de détermination des espèces que l'on rencontre avec des organismes parthenogenetiques, si les caractères morphologiques que l'on a employés, afin de distinguer des espèces du *Cypridopsis,* montrent aussi de variation que les caractères employés dans cette étude, il se peut que quelques-unes de ce grand nombre d'espèces dans le genre soient synonymes. Une telle grande variabilité dans une espèce tient des implications importantes pour son emploi dans l'étude de plaques tectoniques et des apports continentals.

INTRODUCTION

The study of the ecology and paleoecology of Ostracoda has been directed primarily toward determining the presence or absence of species of ostracodes in an area, the relative abundances of species, and the tolerances of species to various parameters of the physical and chemical environment. Studies of these kinds, along with increasingly refined taxonomy and biogeography, have marked our science and have accounted for most of its considerable progress during the past century. While this progress has been underway, one aspect of the study of Ostracoda has received significantly less attention until very recently than the kinds of research mentioned above, enough less, in fact, that it could be regarded as a neglected dimension of our science. I refer, of course, to the study of intraspecific variation of morphology.

The existence of variability within species has long been recognized. Indeed, it is inherent in ostracodes which we very properly study as organisms rather than as sedimentary particles. Nevertheless, except for sexual dimorphism, intraspecific variation of morphology has usually received only passing mention rather than systematic study, and its discussion has often been limited to effects of neoteny or postmatural molting (see Szczechura, 1971, for an interesting evaluation). Notable exceptions to this rule are the stimulating discussions of salinity and nodosity in *Cyprideis* (*e.g.*, Sandberg, 1964; Kilenyi, 1971). Several other examples could serve nearly as well, such as *Leptocythere* or *Ilyocypris bradyi* and *I. gibba.*

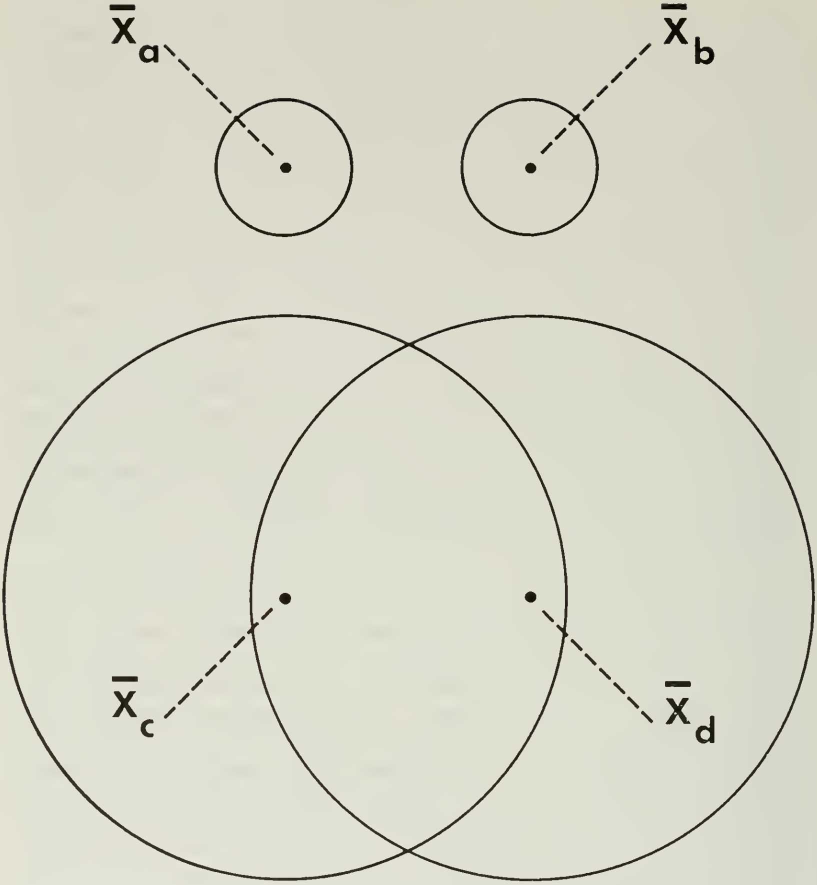
The study of intraspecific variation of morphology is one aspect of the growing field of population biology. As population biology has ascended, it is not surprising that students of the Ostracoda have concerned themselves more in recent years than ever before with intraspecific variation of morphology (Barker, 1963; Kilenyi, 1971; Szczechura, 1971; Kaesler, 1971a, 1971b; Cadot and Kaesler, 1973). For greatest success, such research should be founded on careful study of the fundamental unit of evolution, the biological population. Moreover, it should consider both the *sources* and the *causes* of the variation under study.

The purpose of my study is to test the hypothesis that morphology of local populations of *Cypridopsis vidua* varies consistently with differences in parameters of the physical and chemical environment. The results will show, first, statistically significant differences among some local populations of the species; second, variations in the aquatic environments of the ponds; and, third, correlations of morphological characters with environmental parameters. Finally, brief mention will be made of possible synergistic and antagonistic effects between chemical constituents of the water in which the ostracodes lived.

To speak of biological populations of an obligate parthenogenetic organism such as *Cypridopsis vidua* is somewhat irregular. The population of *C. vidua* in a single pond is in no sense a quasi-isolated, intrabreeding biological population. One of the primary advantages parthenogenesis gives its practitioners is the ability for a single individual accidentally carried to a new locality or accidentally left behind in an old one to generate a new colony (White, 1970). It is possible, then, but not certain, that all the individuals in a given locality are genetically identical. Reasons for lack of genetic identity are presence of clones within the pond from two or more genetically different founders, mutation within a clone subsequent to founding of the colony by one or more genetically identical founders, and heterozygosity of the founder leading to genetic segregation — if the species is an automictic one (*i.e.,* having meiosis with doubling of the number of chromosomes later in life; see White, 1970). In the area studied, it seems unlikely that the colony in any pond represents only a single clone, and one can never rule out mutation. Moreover, it is too early to speculate on the importance of heterozygosity of *C. vidua* because little is known about its genetics, although it is difficult to conceive of sustained heterozygosity since the Oligocene other than that reintroduced by mutation, unless *C. vidua* shows polyploidy. For this research it has been necessary to make the reasonable but untested assumption that individuals within a pond are on the average more similar to each other genetically than to individuals from other ponds. It has not been possible, however, to ascribe the morphological differences observed either to *annidation* — "an adaptive correspondence between the various genotypes present in the population and the alternative ecological niches present in the environment" (White, 1970, p. 238; Ludwig, 1950) — or simply to the effect of the evironment on the phenotype.

As was mentioned earlier, both the *sources* and the *causes* of observed morphological differences should be determined if possible. Here *sources* refers to the relative magnitudes of variation within populations and among populations. For example, if all local populations — here the individuals within a pond — have a very small variance, then differences among ponds will be readily apparent. On the other hand, if the populations within ponds are highly variable, detecting differences among ponds will be very difficult. Text-figure 1 demonstrates the importance of this concept for two studies involving two populations each, one study with small variances within populations and the other with large variances within populations. Although the mean differences between populations are the same in both examples, the differences are much less easily detected when the variation within ponds is great. The analysis of variance is a statistical tool that is well suited for partitioning variances, and it has been used in this study.

Determining *causes* of variation is much more difficult and usually requires the controlled conditions possible only in a laboratory study. Just as it is impossible to ascribe morphological variation to genotypic or phenotypic differences without study of the genetics, so it is not possible to separate causes of variation from correlations among effects without eliminating the vageries that nature has introduced into the natural setting. In this research, I have studied correlations of morphological characters with environmental parameters rather than trying to attribute the variation to particular aspects of the environment. Clearly, the understanding of variations in morphology in response to preset differences in the environment under controlled laboratory conditions requires further study in the future.



Text-figure 1. Diagrammatic representation of two studies of two populations each. Members of populations *a* and *b* with no overlap in morphologic characters are easily discriminated; members of populations *c* and *d* with a great deal of overlap are difficult to discriminate. Means of populations indicated by $\bar{X}$.

ACKNOWLEDGMENTS

I am indebted to Richard B. Koepnick and Johnny A. Waters who assisted me with field, laboratory, and computational work. Arch H. Layman, Jr. drafted the illustrations. Mr. Waters' and Mr. Koepnick's participation in the research was made possible by support from the Wallace E. Pratt Research Fund of the Paleontological Institute, The University of Kansas. The research was also supported by the Kansas Geological Survey, a General Research Grant from The University of Kansas, and Biomedical Sciences Support Grant FR07037 from The University of Kansas. All computation was done at The University of Kansas Computation Center using the Honeywell 635 computer. Specimens studied have been entered in the collections of The University of Kansas Museum of Invertebrate Paleontology.

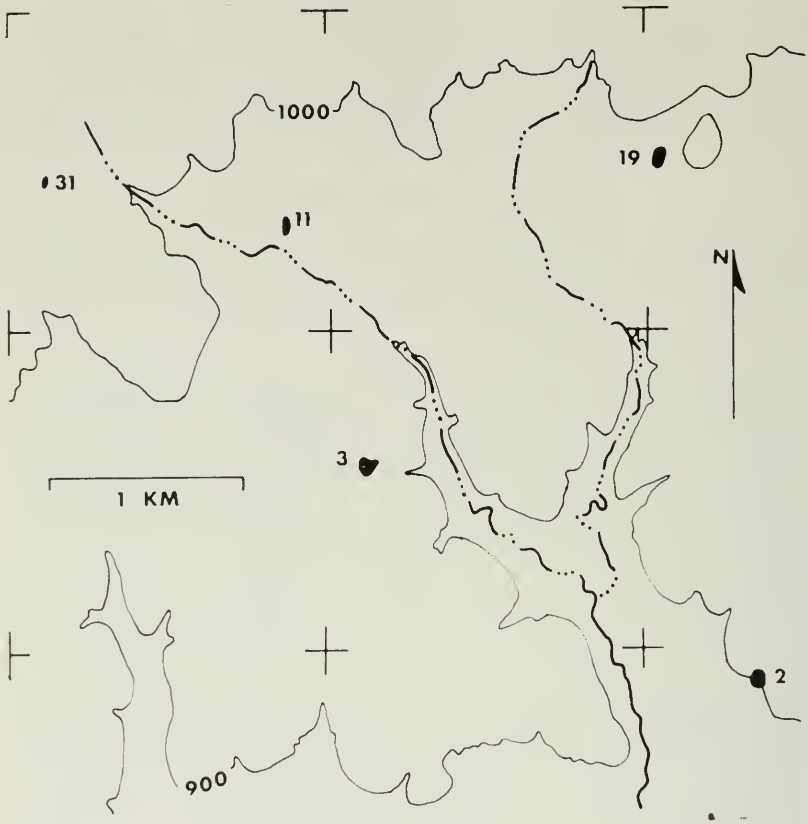
MATERIAL AND SAMPLING

Cypridopsis vidua was chosen for study because it has been intensively studied in other ways previously and is a well understood, geographically widespread species (Kesling, 1951). It also occurs in great abundance in some of the ponds in the study area, the Yankee Tank Creek drainage basin (Text-figure 2).

The study area, occupying about 10 square kilometers near the city of Lawrence in eastern Kansas, is the site of a multiphase environmental monitoring program being conducted by the Kansas Geological Survey. The drainage basin is now primarily upland brome-grass farming land and pasture, and it contains more than 30 small to moderate-sized, man-made ponds used primarily for watering cattle. The area was chosen for environmental monitoring because it lies in the path of expansion of Lawrence, Kansas, one of the fastest growing cities in the state. The area will almost certainly be completely urbanized during the next ten years. Already it is the site of a sanitary land fill, and some of the farmers have begun to sell lots for houses. This study of the ostracodes from the area is a part of the environmental monitoring program.

Field work was done in early July of 1970 during a nine-day interval in which no rain fell in the area. Five of the ponds (Text-figure 2) were each sampled on alternate days until they had been sampled five times. At the same time, the chemical and physical parameters of the environment listed in Table 1 were measured. Temperature, pH, conductivity, dissolved oxygen, and dissolved CO_2 were determined in the field, the latter three by using the Hach DR-EL system. The water samples were then refrigerated, and the other 12 parameters were determined within 24 hours after they were collected, also using the Hach system.

Ostracodes were sampled by passing pond water and floating and attached filamentous algae through 20 mesh and 100 mesh sieves. Most algae were retained on the 20 mesh sieve, and ostracodes and other small invertebrates were retained on the 100 mesh sieve. After concentrating the biological material in this way, the ostracodes were placed into a small jar. The first living specimens seen swimming were collected, up to a maximum of 15 specimens per sample. Pond 31 was barren of ostracodes, although during the previous summer it had yielded abundant *C. vidua*. The ostracodes that were selected for study were then opened and were drawn using a camera lucida. The six morphological characters shown in Text-figure 3 were measured from the drawings. A total of 225 ostracodes were measured, distributed among samples as shown in Table 2.



Text-figure 2. The Yankee Tank Creek drainage basin near Lawrence, Kansas, showing locations of the five ponds sampled.

METHODS OF ANALYSIS AND RESULTS

VARIATION OF MORPHOLOGY

The first phase of the analysis was to determine if any of the six morphological characters studied vary significantly, either from sample to sample within a pond or from pond to pond. As was pointed out in reference to Text-figure 1, the problem is to determine if either the variation between samples from the same pond or the variation among ponds is sufficiently larger than the variation within a sample to enable one to detect significant differences. Alternatively, the differences that are observed may be ascribed solely to the chances of sampling.

The analysis of variance is a statistical method that enables one to subdivide or partition the variance in a set of samples in order to test hypotheses about differences in mean values of the samples. Here a nested model was chosen in order to test the null hypothesis that all samples were collected from the same *statistical population* and, hence, no significant differences exist either between samples from the same pond or between ponds. Recall that the significance of the differences is measured by the amount of variance within samples as compared to the amount among samples from the same pond or among ponds (Text-figure 1). It is here that partitioning the variance is important. The nested model is shown verbally in Table 3.

Use of a parametric statistical method such as the analysis of variance is based on the assumption that the sampling and the data meet several conditions. Three of the most important of these conditions for the analysis of variance are that sampling was random, that the data within any sample are normally distributed, and that the variances of all samples are the same. Several other assumptions are also required, but these were not tested. Sampling was not strictly random as is required, but neither was it purposive in any way because of the small size of the ostracodes. Any bias of the samples was introduced by the ostracodes themselves since only swimmers were collected. This bias is not believed to be appreciable. Most of the samples yielded normally distributed data. Sokal and Rohlf (1969) pointed out that small departures from normality usually have little effect on the statistical tests used here. That is, the analysis of variance is said to be a *robust* method with respect to nonnormality of the data. It is more sensitive to unequal variances. Three of the morphological characters showed heterogeneity of variance — length, height, and posterior radius of curvature. For each of these, two additional tests were computed: 1. an equality of means test that takes into consideration the differences in variances and 2. a Kruskal-Wallis nonparametric test that is distribution free. The results of these two tests support the results obtained from the analysis of variance which, however, must be regarded as an approximation only, because the data failed to meet the assumptions.

Table 4 shows the percent of the variance that resides at each of the three levels in the analysis of variance. For length, for example, 67 percent

Table 1. Parameters of the physical and chemical environment measured and the units for each.

Parameter	Units
Temperature	°C
pH	
Conductivity	mg/l as NaCl
Turbidity	Jackson Turbidity Units
Color	APHA Platinum-Cobalt Standard
Dissolved carbon dioxide	mg/l of CO_2
Dissolved oxygen	mg/l of O_2
Alkalinity	mg/l as $CaCO_3$
Total hardness	mg/l as $CaCO_3$
Calcium hardness	mg/l as $CaCO_3$
Magnesium hardness	mg/l as $CaCO_3$
Iron	mg/l of Fe
Chloride	mg/l of Cl
Total nitrogen	mg/l of nitrate and nitrite
Phosphate	mg/l of orthophophate
Silica	mg/l of SiO_2
Sulfate	mg/l of SO_4

Table 2. Number of specimens of *Cypridopsis vidua* measured from each sample.

	Pond			
Date	2	3	11	19
July 1, 1970	9	10	12	15
July 3, 1970	10	10	15	12
July 5, 1970	11	10	15	2
July 7, 1970	9	10	14	8
July 9, 1970	10	14	14	14

Table 3. Nested analysis of variance model.

Level	Variance	Explanation
2	Among ponds	Differences between ponds 2, 3, 11, 19
1	Among samples, within ponds	Differences between any of the 5 samples from any one pond
0	Within ponds (error variance)	Differences between any of the 2 to 15 ostracodes in any one sample.

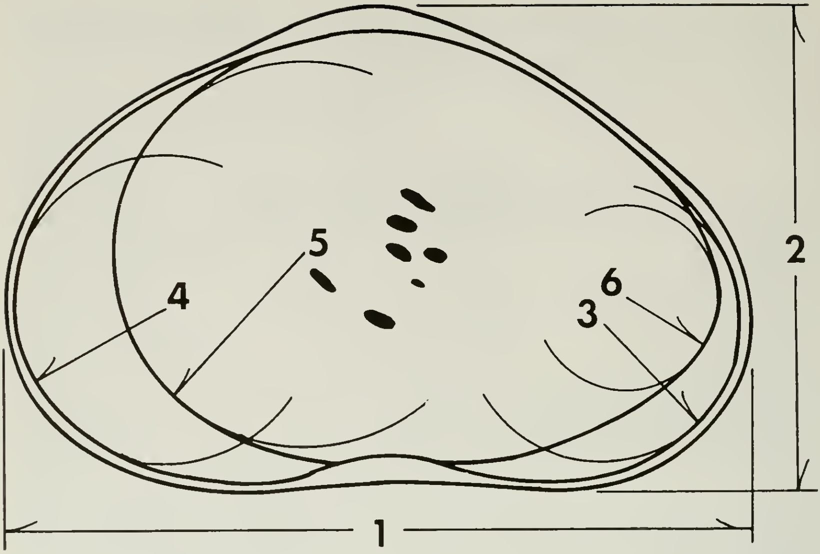
Table 4. Percent of each variance component after partitioning. Asterisks indicate level of statistical significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; tests of top three morphological characters approximate because assumptions of method not fully met.

	Percent of Variance		
Character	Among ponds	Among samples within ponds	Within ponds (error variance)
Length	22**	11**	67
Height	19*	19***	62
Posterior radius of curvature	1	17***	82
Anterior radius of curvature	13**	4	83
Anterior radius of curvature, inner lamella	13**	1	88
Posterior radius of curvature, inner lamella	0	2	98

of the variance is *error variance,* the variance in length of ostracodes within samples. Only 11 percent of the variance is accounted for by variance among the 5 samples all collected from the same pond, and 22 percent is variance among ponds.

Also shown in Table 4 by asterisks are the levels of significance of the differences observed between mean values in the study. Again using length as an example, the significance level for *among ponds* is less than 0.01 and for *within ponds among samples* is less than 0.001. This means that if all samples had been drawn from the same statistical population, the probability of obtaining *by chance alone* due to sampling, differences *among ponds* as great or greater than those observed is less than 0.01. In biological work, 0.05 is ordinarily regarded as an appropriate significance level. It is appropriate, therefore, to reject the null hypothesis that all samples were drawn from the same normal distribution. Similarly, the probability of obtaining differences as great as or greater than those observed among samples from the same pond is less than 0.001. Recall that the analysis of variance of length, height, and posterior radius of curvature must be considered an approximation because the data do not meet the assumption of homogeneity of variances. Nevertheless, the test of equality of means (given unequal variances) and the Kruskal-Wallis test both indicated very highly significant differences ($P < 0.001$) when all samples are considered together.

The results in Table 4 indicate that populations of ostracodes from the different ponds are statistically significantly different from each other in length, height, anterior radius of curvature, and anterior radius of the inner lamella. Neither the posterior radius of curvature nor the posterior radius of the inner lamella differ significantly. It appears either that the ostracode populations differ in their genetics, being separate biological populations in



Text-figure 3. Outline of *Cypridopsis vidua* showing the six characters studied: 1. length; 2. height; 3. posterior radius of curvature; 4. anterior radius of curvature; 5. anterior radius of inner lamella; 6. posterior radius of inner lamella.

the sense discussed earlier, that they respond differently to different environments in the various ponds, or some combination of these two possibilities.

Much more difficult to explain are the highly significant differences that occur among samples within ponds. Although Kaesler (1971b) found some evidence for temporal changes in morphology among populations of adult *Cypridopsis vidua,* the changes were neither so dramatic nor did they occur over such a short time as these changes. In order to attempt to interpret these differences as well as to find out which samples differ from each other, Student-Newman-Keuls (SNK) *a posteriori* tests were computed for each morphological character (Sokal and Rohlf, 1969). Note that the assumptions of the SNK test are the same as those of the analysis of variance, so the same reservations should be applied to interpretation of results for the first three morphological characters.

The SNK test is a means of determining which groups of samples are statistically significantly different from each other. Only three of the characters studied showed any significant differences at all by this test, which considers all samples simultaneously. These were length, height, and radius of curvature of the anterior inner lamella. Results are summarized in Table 5 in which samples are ranked and arranged in nonsignificant subsets. Considering length, for example, samples 3-3 through 2-1 are not significantly dif-

Text-figure 4. Q-mode dendrogram showing euclidean distances between samples as determined by the seventeen parameters of the physical and chemical environment studied. P indicates pond number; W indicates day sampled in sequence. Cophenetic correlation coefficient = 0.781; clustering method UPGMA.

ferent from each other. If sample 2-2 is added to the subset, statistically significant differences occur within the new subset. Similarly, samples 3-1 through 19-3 form a nonsignificant subset and are not to be regarded as statistically significantly different from each other.

VARIATION OF ENVIRONMENT

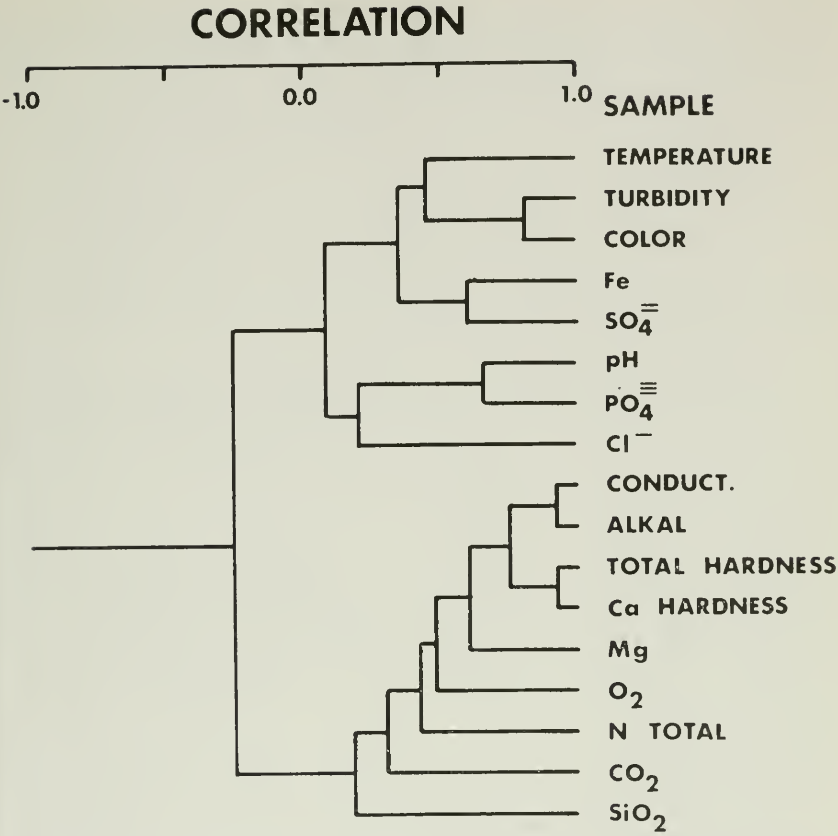
Text-figure 4 is a dendrogram computed by Q-mode cluster analysis showing average euclidean distances between samples on the basis of all physical and chemical parameters of the environment that were measured. Note that for the most part samples from the same pond are closely similar and lie in the same cluster, especially samples from ponds 11 and 19. Samples from ponds 2 and 3 are mixed in the dendrogram, but most of the samples from pond 3 are in the same cluster. Lack of identity of successive samples from the same pond indicates change in the environment over the time when the sampling was done. The most notable change observed was an algal bloom underway in pond 3 during the sampling interval, but clearly other, less apparent changes must have taken place in other ponds as well in order to account for the differences shown in Text-figure 4.

CORRELATIONS OF MORPHOLOGY AND ENVIRONMENT

In a study of variation of morphological characters with environmental parameters, it is helpful to deal first with intracorrelations of both the morphological characters and the environmental parameters. Where a large number of characters or parameters is used, this is particularly useful in order to reduce the number of individual correlations that must be discussed.

Text-figure 5 shows results of R-mode cluster analysis of 17 chemical and physical parameters of the aquatic environment. It is apparent from the dendrogram that many parameters are highly correlated with each other. For example, turbidity and color, conductivity and alkalinity, and total hardness and calcium hardness show strong pairwise intracorrelations. If both members of any of these three pairs of parameters are strongly correlated with morphology of the ostracodes, then only one of them need be discussed because of the strong, pairwise correlations. It should be pointed out that some other parameters may be either more or less highly correlated than shown in the dendrogram because of distortion introduced during averaging in the clustering process. Nevertheless, the dendrogram gives a close approximation to the real situation.

Table 6 shows correlations among the six morphological characters studied. The highest correlation is between length and height, a not unexpected result given the relative constancy of shape of ostracode species. It is perhaps a little surprising that the correlation between these two characters is as low as it is ($r = 0.751$). Other characters have comparatively low correlations, some of



Text-figure 5. R-mode dendrogram showing correlations between parameters of the environment. Cophenetic correlation coefficient = 0.839; clustering method UPGMA.

them not significantly different from zero. Results of principal components analysis in which three principal components were computed are shown in Table 7. The first principal component is strongly correlated with both length and height and may be regarded as a general size factor. The second principal component correlates strongly with posterior radius of the inner lamella; and the third shows no really strong correlation, although it is closest to anterior radius of the inner lamella. These three principal components together explain 72 percent of the variance in the data. To the extent that the three principal components are represented by the characters length or height, posterior

Table 5: Nonsignificant subsets of samples from Student-Newman-Keuls test. In each test, samples are ranked from smallest to largest; lines join nonsignificant subsets.

Character	Samples in nonsignificant subsets																				
Length	Pond	3	3	2	3	11	2	2	3	3	2	2	19	11	11	19	11	19	11	19	19
	Sample	3	1	4	2	2	5	3	4	5	1	2	2	4	1	4	3	1	5	5	3
Height	Pond	3	11	3	3	2	2	3	3	19	2	2	2	11	19	11	11	11	19	19	19
	Sample	3	2	1	2	5	4	5	4	4	1	3	2	4	2	1	5	3	1	5	3
Anterior radius	Pond	2	2	2	2	3	3	19	3	3	19	3	2	11	11	11	11	19	19	19	11
of inner lamella	Sample	1	5	2	4	2	4	3	1	5	4	3	3	4	2	1	3	2	5	1	5

Table 6. Correlation coefficients computed between all pairs of morphological characters studied.

	1.	2.	3.	4.	5.	6.
1. Length	1.000					
2. Height	0.751	1.000				
3. Post. Rad. Curv.	0.332	0.429	1.000			
4. Ant. Rad. Curv.	0.294	0.433	0.241	1.000		
5. Ant. Rad. In. Lam.	0.246	0.260	0.169	0.204	1.000	
6. Post. Rad. In. Lam.	0.060	0.162	0.200	0.068	–0.067	1.000

Table 7. First three principal components computed from correlations between morphological characters.

Character	I	II	III
Length	–0.809	–0.100	0.356
Height	–0.888	0.010	0.242
Posterior radius of curvature	–0.629	0.279	–0.193
Anterior radius of curvature	–0.605	–0.097	–0.007
Anterior radius of inner lamella	–0.443	–0.534	–0.683
Posterior radius of inner lamella	–0.227	0.844	–0.330
Percent variance explained	40.90	18.25	13.29
Cumulative percent explained	40.90	59.15	72.44

radius of the inner lamella, and anterior radius of the inner lamella, these three characters alone could account for most of the variance in the data.

Table 8 gives the values of correlation coefficients between the six morphological characters and the 17 environmental parameters. The correlations are all very weak ones, being without exception less than 0.4. Nevertheless, because of the large sample sizes, any value with an absolute value greater than 0.134 is significant at the 0.05 level, and absolute values greater than 0.2203 are significant at the 0.001 level. The correlations, then, though of low value are highly significant in a statistical sense, suggesting a very real relationship between the aquatic environment and the morphology of *Cypridopsis vidua.*

Five environmental parameters will be considered in more detail: conductivity, calcium hardness, magnesium hardness, chloride, and sulphate. Conductivity is a measure of the electrical resistance of the pond water. This resistance may be affected by temperature, dissolved gases, dissolved salts, and chemical reactions within the water. Conductivity may be thought of as a kind of composite measurement of all the other chemical parameters and is more useful in monitoring the environment than in studying ostracode morphology. Nevertheless, conductivity was very highly significantly correlated

Table 8. Product-moment correlation coefficients between morphological characters and parameters of the environment. Absolute values > 0.1314 significantly different from zero at $P < 0.05$, indicated *; absolute values > 0.1726 significantly different from zero at $P < 0.01$, indicated **; absolute values > 0.2203 significantly different from zero at $P < 0.001$, indicated ***

Character	Length	Height	Post Rad.	Ant. Rad.	Ant. Rad. In. Lam.	Post. Rad. In. Lam.
Temperature	-0.023	-0.033	-0.070	-0.094	-0.138*	0.075
pH	-0.177**	-0.198**	-0.047	-0.198**	-0.115	0.074
Conductivity	0.332***	0.281***	0.133*	0.291***	0.241***	0.015
Turbidity	0.002	0.047	0.060	-0.147*	-0.150*	0.082
Color	-0.030	0.027	0.114	-0.122	-0.134*	0.077
CO_2	0.156*	0.145*	-0.016	0.208**	0.129	0.138*
O_2	0.062	-0.035	0.093	0.121	0.073	-0.062
Alkalinity	0.214**	0.176**	0.056	0.241***	0.182**	0.009
Total hardness	0.334***	0.306***	0.102	0.256***	0.236***	-0.039
Calcium hardness	0.224***	0.187**	0.067	0.190**	0.135*	-0.064
Magnesium hardness	0.389***	0.393***	0.121	0.263***	0.321***	0.028
Iron	0.067	0.063	0.013	-0.060	0.026	0.054
Chloride	-0.350***	-0.356***	-0.177**	-0.223***	-0.232***	-0.022
Total nitrogen	0.208**	0.149*	-0.023	0.106	0.275***	-0.017
Phosphate	-0.319***	-0.308***	-0.028	-0.228***	-0.153*	-0.005
Silica	-0.019	-0.024	-0.029	0.087	0.030	0.087

($P < 0.001$) with length, height, and the two measures of anterior curvature. It is less strongly correlated ($P < 0.05$) with posterior radius of curvature margin and is uncorrelated with posterior curvature of the inner lamella.

Calcium hardness and magnesium hardness are the concentrations of those two cations expressed as milligrams per liter of $CaCO_3$ and $MgCO_3$ respectively. They are positively correlated with the same morphological characters (Table 8), but magnesium hardness is generally more strongly correlated with all characters. These positive correlations indicate that as the concentration of calcium or magnesium increases in the water, the size of the ostracodes increases.

The two anions, chloride and sulfate, are highly correlated ($P < 0.01$ or $P < 0.001$) with all morphological characters except posterior radius of the inner lamella. Chloride content, however, is negatively correlated with the morphological characters, whereas sulfate is positively correlated. The difference in sign means that as chloride content increases, the measurements of morphological characters decrease, quite the opposite from the relationship with the sulfate radical.

POSSIBLE SYNERGISTIC AND ANTAGONISTIC EFFECTS

A factor that may contribute to the low correlations between morphological characters and some environmental parameters and that certainly complicates their interpretation is the existence of synergistic and antagonistic effects between many pairs or groups of ions. Calcium, for example, reduces the toxicity of many chemical compounds (McKee and Wolf, 1963).

Interaction of ions is strongly suggested here by the fact that correlation coefficients between pairs of chemical parameters are generally much higher than correlations between morphological characters and the environment. Such relationships are difficult to detect under natural conditions and point further to the need for controlled laboratory study of the response of ostracode morphology to various environmental conditions.

DISCUSSION AND CONCLUSIONS

Piecing together all the relationships that have been mentioned above into a coherent story about the morphology of *Cypridopsis vidua* and its differences in different environments would be a virtually impossible task. This is particularly true in light of intercorrelations and interactions between morphological characters and environmental parameters and given the absence of experimental data from the laboratory. We have observed variations in morphology that may be partitioned into variations within samples, variations among samples but within ponds, and variations among ponds. The variations among samples within ponds, a temporal variation, were found to be statistically significant for the characters length, height, and posterior radius of curvature. Variations among ponds were found to be statistically significant for all characters except those that measure posterior curvatures. We have also observed appreciable differences between all samples when compared on the basis of parameters of the physical and chemical environment of the ponds at the time the samples were collected.

It is reasonable to assume that some of the variation in morphology is due to differences in the environment of the ponds. This contention is supported by the highly significant correlation coefficients computed between morphological characters and environmental parameters. Length and height, for example, were found to be significantly positively correlated with concentrations of all dissolved chemicals studied except O_2, a highly variable parameter with a diurnal cycle; iron; silica, which is not used in the ostracode carapace; and chloride ion, with which all morphological characters had a negative correlation (Table 8). Other characters that were not so strongly related to overall size of the carapace had fewer significant correlation or correlations significant only at a higher level of probability.

Patterns of similarity among samples of the morphological characters length and height are such that samples from ponds 2 and 3 nearly always form nonsignificant subsets with each other, whereas samples from ponds 11 and 19 show greatest similarity to each other (Table 5). When one examines overall similarity of the samples based on all parameters of the environment that were studied, one sees a different picture (Text-figure 4). Samples from ponds 2 and 3 are indeed quite similar to each other, but samples from ponds 11 and 19 are highly dissimilar. This result suggests that rather than being controlled by similarities in the overall environment (as expressed in Text-figure 4), length and height are affected by only a subset of the parameters of the environment, thus yielding a pattern of similarity based on these morphological characters that is different from the pattern of similarity of the overall environment.

Based on the six characters chosen for study, *Cypridopsis vidua* is interpreted as a morphologically very plastic species. If morphological plasticity is an indicator of physiological adaptability, the success of *C. vidua* in populating the freshwater environment could be accounted for readily. Moreover, ignoring for the moment problems of speciation introduced by parthenogenesis, if characters that have been used to discriminate species of *Cypridopsis* show as much intraspecific variation as the characters used in this study, some of the many species in the genus may be synonyms.

The use of freshwater ostracodes in the study of plate tectonics and continental drift has been suggested in recent years by Krömmelbein (1970 and earlier papers), McKenzie (1971), and Kaesler (1971b). It is indeed tempting to envision continents as rafts moving about on the surface of the earth, each carrying with it its respective ostracode fauna. According to this model, as two continents approach each other, migration and gene flow between continents may increase, resulting in increased similarity in morphology between conspecific populations of the two continents. If, however, other species of freshwater ostracodes are morphologically as plastic as *Cypridopsis vidua* is in the area studied, one will need to be careful to develop a nested model of the variation in order to test for significant changes in morphology with movement of the continents.

REFERENCES CITED

Barker, Dennis
1963. *Size in relation to salinity in fossil and Recent euryhaline ostracodes.* Jour. Mar. Biol. Assoc. United Kingdom, vol. 43, pp. 785-795.
Cadot, H. M., and Kaesler, R. L.
Variation of carapace morphology of bairdiacian and cytheracean Ostracoda from Bermuda. University Kansas Paleont. Contr. Paper 61, 10 p.
Kaesler, R. L.
1971a. *Preliminary report: morphological variation of Ostracoda from the Yankee Tank Creek drainage basin, Douglas County, Kansas.* Kansas Geol. Sur., Bull. 202, pt. 1, pp. 5-7.
1971b. *Morphological variations of Cypridopsis vidua (Ostracoda) from eastern Kansas (abstr.).* Abstracts with Programs, Geol. Soc. America, vol. 3, No. 7, p. 616.
Kesling, R. V.
1951. *The morphology of ostracod molt stages.* Illinois Biol. Monographs, vol. 21, No. 1-3, 324 pp.
Kilenyi, T. I.
1971. *Some basic questions in the palaeoecology of ostracods. Paléoécologie des Ostracodes* (H. J. Oertli, ed.). Bull. Centre de Recherches Pau, S.N.P.A., vol. 5 suppl., pp. 31-44.
Krommelbein, Karl
1970. *Non-marine Cretaceous ostracods and their importance for the hypothesis of "Gondwanaland".* Second Gondwana Symposium, Council for Scientific and Industrial Research, Scientia, Pretoria, South Africa, pp. 617-618.
Ludwig, W.
1950. *Zur Theorie der Kondurrenz. Die Annidation (Einnischung) als fünfter Evolutionsfaktor.* Neue Ergebn. Probleme Zool. Kl. Festschr., pp. 516-537.
McKee, J. E., and Wolf, H. W.
1963. *Water quality criteria.* 2nd ed., Resources Agency of California; State Water Quality Control Board, 548 pp.
McKenzie, K. G.
1971. *Palaeozoogeography of freshwater Ostracoda. Paléoécologie des Ostracodes* (H. J. Oertli, ed.). Bull. Centre de Recherches Pau, S.N.P.A., vol. 5 suppl., pp. 207-237.
Sandberg, Phillip
1964. *Notes on some Tertiary and Recent brackish-water Ostracoda.* In *Ostracods as ecological and paleoecological indicators* (H. S. Puri, ed.). Pubbl. Staz. Zool. Napoli, vol. 33, suppl., pp. 496-514.
Sokal, R.R., and Rohlf, F.J.
1969. *Biometry.* W. H. Freeman and Company, San Francisco, 776 pp.

Szczechura, Janina
1971. *Seasonal changes in a reared fresh-water species, Cyprinotus (Heterocypris) incongruens (Ostracoda), and their importance in the interpretation of variability in fossil ostracodes. Paléoécologie des Ostracodes* (H. J. Oertli, ed.). Bull. Centre de Recherches Pau, S.N.P.A., vol. 5 suppl., pp. 191-205.

White, M. J. D.
1970. *Heterozygosity and genetic polymorphism in parthenogenetic animals. Evolution and genetics in honor of Theodosius Dobzhansky* (M. K. Hecht and W. C. Steere, eds.). Appleton-Century-Crofts, New York, pp. 237-262.

Roger L. Kaesler
Department of Geology
The University of Kansas
Lawrence, Kansas 66045

DISCUSSION

Dr. R. A. Reyment: The study I made some years ago with B. Brännstrom on *Cypridopsis vidua* was certainly only a laboratory study of populations. We had three environments, the so-called normal one, the one in which calcium carbonate was in excess, and one in which we kept the Eh at stagnation environment.

Dr. Kaesler: Do you find in the stagnant environment that the ostracodes were smaller?

Dr. Reyment: They became smaller: For the other two, we could not pick up differences in environmental effects. I must say a word in defense of Prof. Krommelbein. He hadn't only based his conclusions on the ostracods he also has very strong geological information, such as structural and sedimentalogical data backing up his work.

Dr. Kaesler: I would agree that Prof. Krommelbein has presented a very compelling case. Neither he nor McKenzie studied geographic variation in the sense used here. My point is that if one should decide to apply studies of ostracode variation to tests of plate tectonics, he would need to be very careful to eliminate local variations due to differences in environments.

One of the interesting aspects of the study of effects of water chemistry on the morphology of Ostracoda is that there are many interactions between dissolved constituents of the water. For example, in studies with *Daphnia* it has been found that an increase in concentration of calcium reduces the toxicity of copper. I have some ponds that have limestone outcrops in them, so there is an abundance of calcium carbonate in the water. This could have a marked influence on the effects of the other substances dissolved in the water.

MORPHOLOGICAL VARIATION IN *LEGUMINOCYTHEREIS ? HODGII* (BRADY), OSTRACODA (CRUSTACEA), FROM JAPAN

Kunihiro Ishizaki
Tohoku University

ABSTRACT

During studies of the ostracodes from shallow marine waters around Japan, it was recognized that the specimens of *Leguminocythereis ? hodgii* (Brady) show differences in reticulate ornamentation and valve size depending on factors prevailing in the regions in which the forms lived.

To testify the significance of those differences, samples taken from three regions of Uranouchi Bay, Kochi Prefecture, Nakanoumi Estuary, Shimane Prefecture, and Aomori Bay, Aomori Prefecture are treated by a non-parametric statistical method of Mann-Whitney's u test because of unfavourable conditions of samples.

As the result, in the moulting stages of the adult-1 and adult-2, the differences of ornamentation of reticulation are suggested to be significant among the samples from the three regions by 98 percent confidence intervals of their means. The differences in dimensions of valve length and height, are significant between the samples from Uranouchi Bay and the Nakanoumi Estuary, and Uranouchi Bay and Aomori Bay throughout the moulting stages of the adult-2 to the adult instars, although that between the specimens from the Nakanoumi Estuary and Aomori Bay seems to be questionable.

Judging from the data recorded, such difference may be caused by the differences in water temperature in the regions in which the forms lived, and zoogeographical variations of the Ostracoda between the Japan Sea and Pacific side of Japan.

ZUSAMMENFASSUNG

Während Studien der Ostracoden aus den Bucht en um Japan herum, es hat gekannt, das die Formen der *Leguminocythereis ? hodgii* (Brady) unter Stücken von andere Regionen sich in den Vollkommenheit der gitterartige Skulptur unterscheiden.

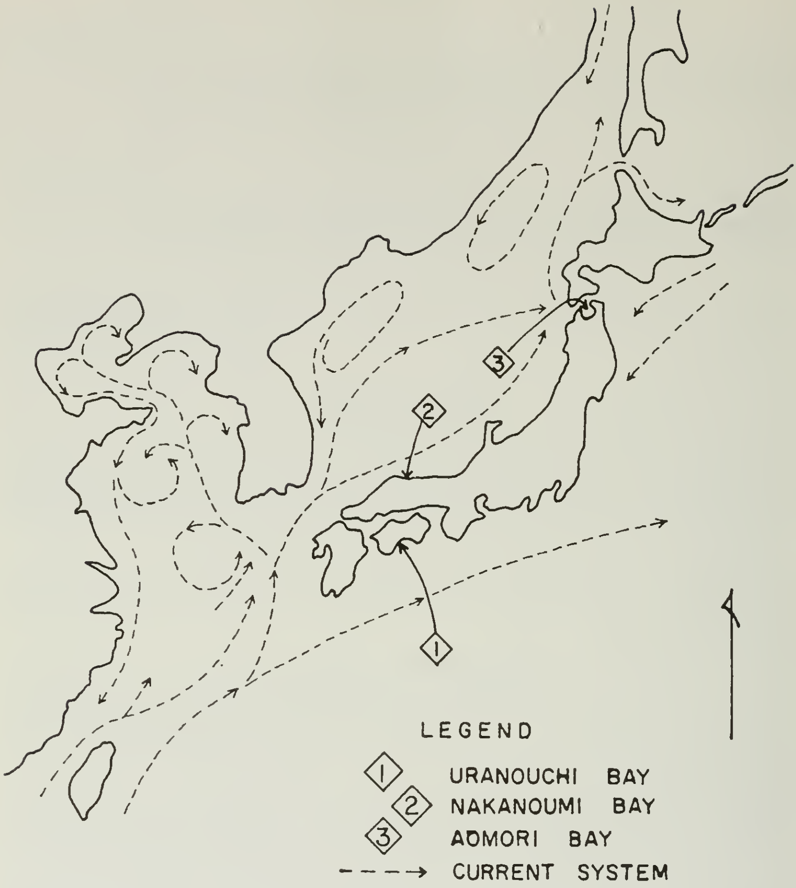
Diese Abhandlung ist in Klappengröße und Verhältnisse der gitterartige Skulptur um Verschiedenheiten klar zu machen mit nichtparametrische Methode, U Test von Mann-Whitney und 98 Prozent Verlassensintervall, für Stücken durch 3 Stufen aus Erwachsenen bis Erwachsenen-2 aus 3 Regionen.

Das Resultat zeigt daß die Klappengröße sich unterscheiden zwischen Stücken von Uranouchi Bucht und Nakanoumi Mündung, und Uranouchi Bucht und Aomori Bucht, aber die Verschiedenheit ist unklar zwischen Nakanoumi Mündung und Aomori Bucht; daß die Verhältnisse der dunkle gitterartige Skulptur unterscheidet sich zwischen Ontogenie Stufen und zwischen Stücken von Uranouchi Bucht und Aomori Bucht klar.

Diese Unterschiede mag auf Temperatur oberem order unterem Grenzpunkte des Meerwasser beruhen, darin Ostracoden wohnen, und auf physischen und chemischen Bedingungen verschieden zwischen das Pazifik und das Japanische Meer.

INTRODUCTION

During studies of the ostracodes from shallow marine waters, especially embayed areas around Japan, it was recognized that in the Nakanoumi Estuary, Shimane Prefecture (lat. 35°30′ N and long. 133°10′ E), and Aomori Bay, Aomori Prefecture (lat. 40°53′ N and long. 140°50′ E), the valve sur-



Text-figure 1. Main current system around Japan (after Uda, 1934), and the approximate locations of (1) Uranouchi Bay, (2) Nakanoumi Estuary, and (3) Aomori Bay.

face of *Leguminocythereis* ? *hodgii* (Brady) has obscure reticulation (termed "obsolete" by Brady, 1880) anteriorly in younger moulting stages. In the adult instar, however, reticulation completely covers the valve surface. On the other hand, those from Uranouchi Bay, Kochi Prefecture (lat. 33°32′ N and long. 133°30′ E) are completely reticulate even in younger moulting stages (Pl. 1, figs. 1-5, figs. 7-11; Pl. 2, figs. 1-4, figs. 6-9).

The purpose of this work is to clarify the morphological variation among the samples from the three regions. Because of the number of individuals and inadequate distribution of many samples, judgments were made only on the three moulting stages of the adult instar to the adult-2 (Tables 3, 4), using a non-parametric method, Mann-Whitney's u test.

All the samples treated in this work were washed with tap water through a 200 mesh sieve.

The writer takes this opportunity to express his sincere gratitude to Prof. Frederick M. Swain of the University of Delaware for his continuous encouragement and critical reading of the manuscript.

SYNOPSIS OF LEGUMINOCYTHEREIS ? HODGII (Brady)

Leguminocythereis hodgii was first described by Brady (1866) under the name of *Cythere hodgii* based on only one valve from Levant in the north-central Mediterranean Sea, and subsequently by Brady (1880) from a dredging in the Inland Sea (Setonaikai), Japan (15 fms depth). In his second report, he mentioned that the European specimen differs from that of Japan in the valve being sparingly sculptured and with obscure reticulation except for the posterior part.

As mentioned by Brady (1880), it is still uncertain whether the European and Japanese specimens belong to the same species. Under the circumstances, it is noteworthy that such variations in valve ornamentation are great, even among regions within Japan, and specimens of Brady (1880) may be morphologically identical with the ones from Uranouchi Bay.

As a detailed description and clear illustrations have been given by Brady (1880), only a few characters necessary for measurement for statistics and some new details will be given.

Sexual dimorphism in this species is great: the valve of the male is longer and oblong in lateral outline; that of the female is shorter and ovate. Thus measurement for the statistics should be done on either sex.

The hinge structure is holamphidont: the left valve is slightly larger than the right valve because of the so-called hinge ears developed.

At 1,000 magnification, rather regular flute structure (a sort of caperation in Sylvester-Bradley and Benson, 1971) could be seen on the slope of muri (valve in the adult instar from Nakanoumi Estuary, Pl. 2, fig. 10).

The normal pore canals, scattered near the base of muri, and surrounded by moderate rims are situated near the center of a low mound slightly elevated above sola, and probably free from the flute structure mentioned above (Pl. 2, fig. 10). At about 10,000 magnification, the normal pore canals are only sieve type. The normal pore canal in the adult instar from Uranouchi Bay is an "irregularly perforate sieve plate in a circular depression" (referable to *Callistocythere* sp. from the Pliocene of Italy fig. 12 in Sandberg and Plusquellec, 1969) (Pl. 2, fig. 5).

PLATE 1

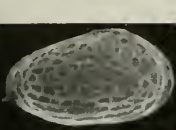
All figures are scanning electron micrographs.

Figure

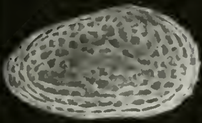
1-6. Serial moulting stages of right valve and normal pore canal of *Leguminocythereis ? hodgii* (Brady) from Uranouchi Bay (St. 79 of Ishizaki, 1968), all × 95 except for figure 6.
1. Smaller specimen of adult-3 stage, ornamented by complete reticulation over entire valve surface. 2. Larger specimen of adult-3 stage. 3. Specimen of adult-2 stage. 4. Specimen of adult-1 stage. 5. Specimen of adult instar. 6. Highly enlarged micrograph of normal pore canal of figure 4, × 10,000.

7-12. Serial moulting stages of right valve and hinge structure of specimens from Aomori Bay (St. 14 of Ishizaki, 1971), all × 100 except for figure 12.
7. Specimen of adult-3 stage, ornamented by complete reticulation only on posterior third of valve. 8. Specimen of adult-2 stage, also obscure reticulation occupying more than anterior half of valve. 9. Specimen of adult-1 stage, obscure reticulation still discernible on anterior third of valve. 10. Inner view of right valve of adult instar. 11. Lateral view of right valve of adult instar, ornamented by complete reticulation throughout valve surface. 12. Inner view of left valve of adult instar showing the details of hinge structure, × 190.

13. Highly enlarged micrograph of normal pore canal of figure 9 (adult instar from Nakanoumi Estuary), × 10,000.

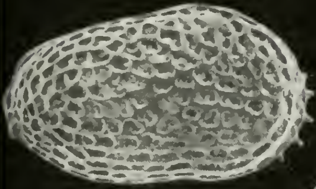


1

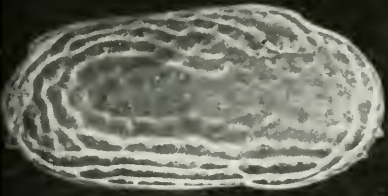


2

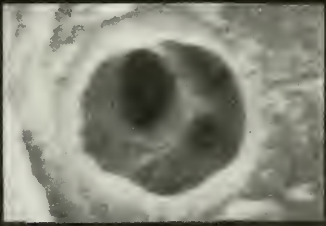
3



4

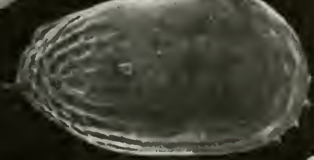


5

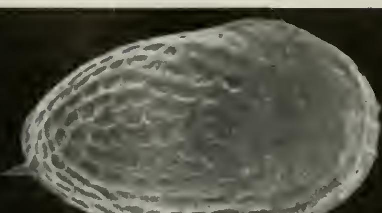


6

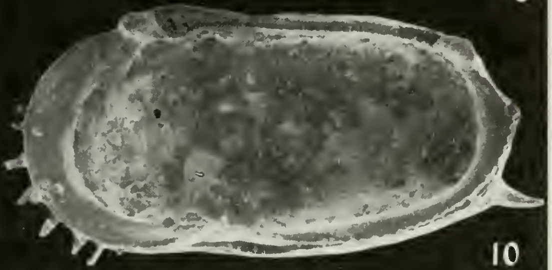
7



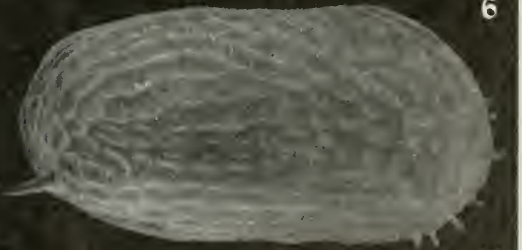
8



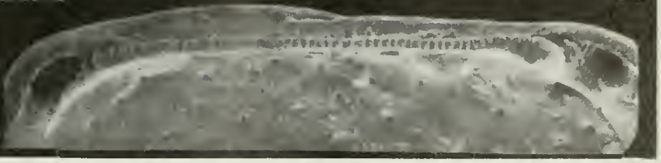
9



10



11



12

13

Table 1. Average surface water temperature of each month for Esashi (representative of Aomori Bay), Saigo (near the Nakanoumi Estuary), and Ashizuri (representative of Uranouchi Bay) (after Meteor. Agency, 1969, 1970).

Station	Month			
	February	April	August	December
Esashi	4.9°C	8.0°C	21.3°C	6.4°C
Saigo	10.8°C	14.2°C	27.2°C	14.0°C
Ashizuri	16.5°C	19.0°C	27.1°C	18.0°C

Table 2. t value and its probability between left valve and right valve of 38 complete carapaces from Aomori Bay. Calculation was made after the pair comparison.

	t	p
length	6.045	<0.001
height	6.689	<0.001
O. R. ratio	0.133	<0.200

Table 3. See p. 251.

Table 4. Calculated probabilities by Mann-Whitney's u test. Probabilities less than 0.01 are taken in significant difference between samples compared.

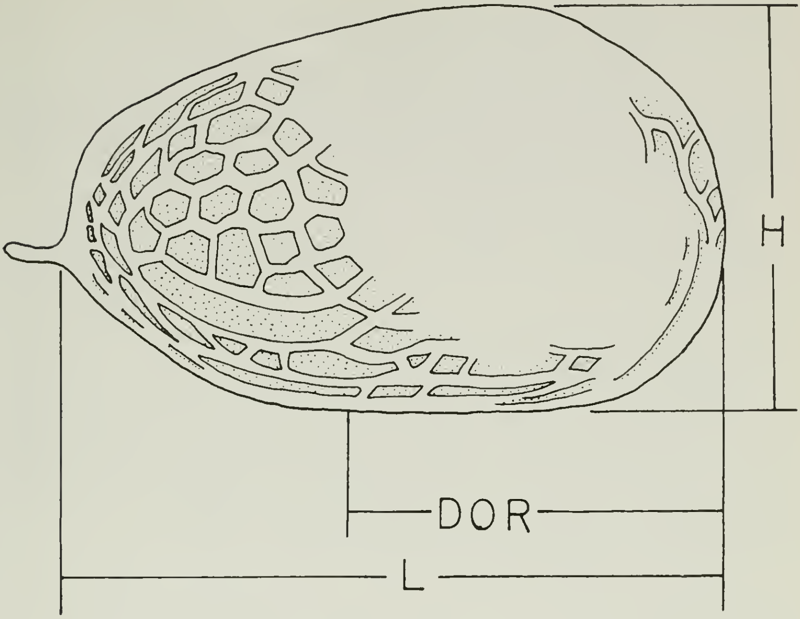
		Adult-2		Adult-1		Adult	
		Aomori Bay	Nakanoumi Estuary	Aomori Bay	Nakanoumi Estuary	Aomori Bay	Nakanoumi Estuary
Nakanoumi Estuary	length	<.0100		.0688		<.0100	
	height	<.0100		.1936		.2584	
	O.R. ratio	<.0100		<.0100			
Uranouchi Bay	length	<.0100	<.0100	<.0100	<.0100	<.0100	<.0100
	height	<.0100	<.0100	<.0100	<.0100	<.0100	<.0100

Table 3. Properties of samples: means of three characters, 95% confidence intervals for length and height, and 98% confidence interval for obscure reticulation ratio when frequency distributes in normal, standard deviations, calculated x^2 and its probability corresponding degree of freedom.

Locality	Moulting stage	N	Length					
						Normality		
			Mean	95% conf. interval	S. D.	X^2	p	D. F.
Aomori Bay	Adult	52	.842	±.007	.0267	3.246	>.500	3
	Adult-1	63	.656	±.004	.0159	7.893	>.050	4
	Adult-2	53	.503	±.004	.0141	2.048	>.500	3
	Adult-3	9	.382					
Nakanoumi Estuary	Adult	52	.866		.0338	10.881	<.050	4
	Adult-1	60	.651		.0194	14.430	<.010	4
	Adult-2	56	.491		.0165	13.618	<.010	4
	Adult-3	21	.385					
	Adult-4	2	.302					
Uranouchi Bay	Adult	52	.688	±.010	.0357	3.063	>.250	3
	Adult-1	52	.544		.0240	20.223	<.005	4
	Adult-2	52	.415		.0172	27.294	<.005	4
	Adult-3	8	.327					

Table 3. continued

Height						O. R. Ratio					
			Normality						Normality		
Mean	95% conf. interval	S. D.	X^2	p	D.F.	Mean	98% conf. interval	S. D.	X^2	p	D.F.
.447		.0186	9.686	<.050	4	.000					
.387		.0124	10.654	<.050	4	.314	±.020	.0669	6.247	>.100	4
.315		.0108	7.977	<.025	2	.496	±.037	.1127	5.240	>.250	4
.243						.690					
.451	±.005	.0175	3.761	>.250	4	.000					
.384	±.003	.0130	9.046	>.050	4	.099		.0836	31.465	<.005	3
.304	±.003	.0115	9.062	>.050	4	.179		.1187	16.398	<.005	4
.238						.493					
.200						.706					
.354	±.006	.0226	5.036	>.250	4	.000					
.306		.0140	10.471	<.050	4	.000					
.246		.0114	10.349	<.050	4	.000					
.194						.383					



Text-figure 2. Three characters considered in this work; total length of valve, height, and obscure reticulation ratio. L: total length of valve, H: height, D. O. R.: dimension of obscure reticulation area at mid-height. Obscure reticulation ratio is given by D. O. R. / L.

In all the three regions, the species is prolific on muddy bottoms not much affected by water current and shows an abrupt decline toward areas affected by currents. Therefore, it is impossible to examine the variation of this species in a certain bay, because of the difficulty in obtaining sufficient specimens from different biotopes.

METHODS

To detect morphological variation, measurement was made on valve length, height, and dimension of obscure reticulation (Text-fig. 2).

As already stated, the left valve is more or less larger than the right valve in length and height. This difference is believed to be significant at a very low level, after tests on 38 complete carapaces from Aomori Bay, using the pair comparison (Simpson, *et al.,* 1960) which is a sort of t test for the difference between the means of paired samples. The notation is,

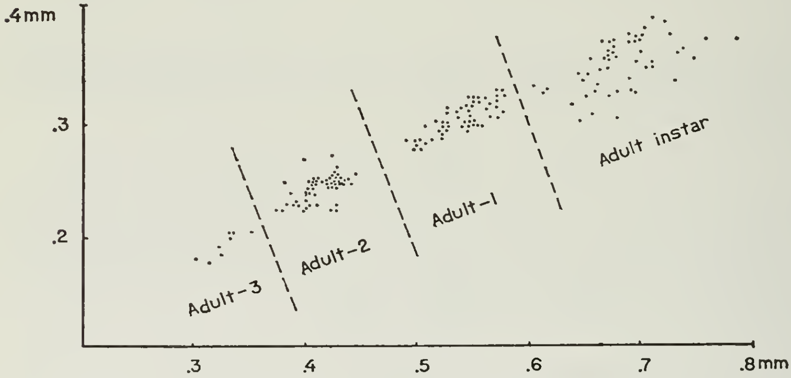
$$t = \frac{\bar{d}}{\sqrt{\frac{Sd^2}{N}}}$$

where, $\overline{d}$ = the mean difference between paired measurements,
Sd^2 = variance of these differences,
N = number of specimens of either left or right valve.
The result are tested at the degree of freedom of (N - 1) and judged as shown in Table 2. Thus the differences of length and height between both valves are significant, and that of obscure reticulation ratio (dimension of obscure reticulation / length) is not significant.

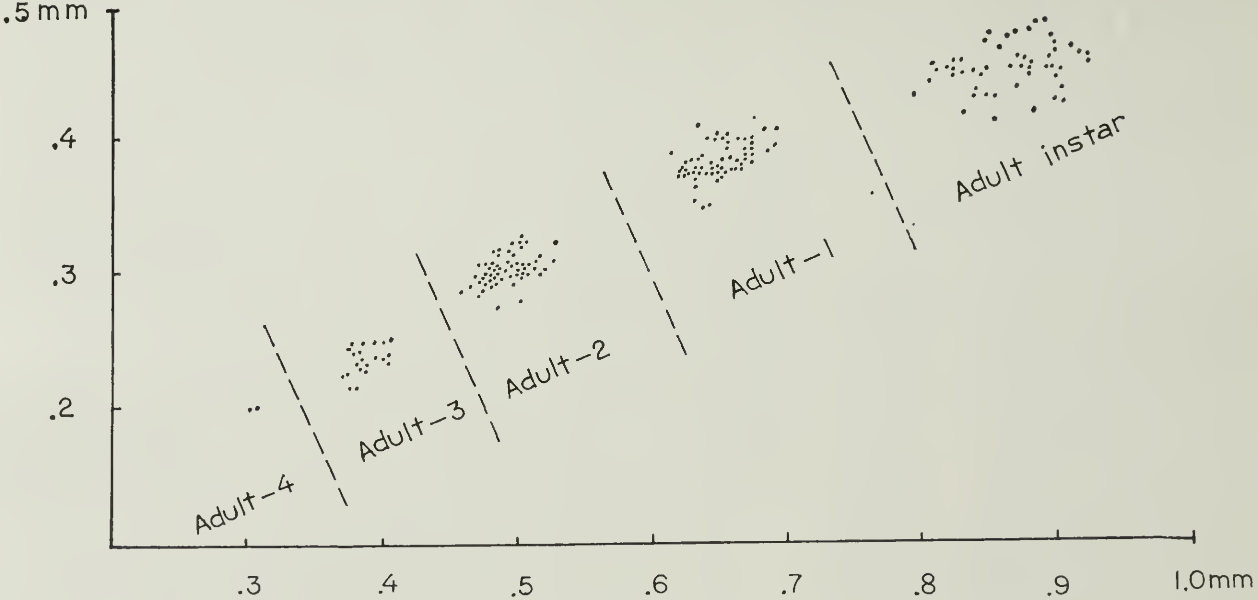
Moreover, the sexual dimorphism of this species is fairly great, and is commonly the case, the number of male specimens is fewer than that of the female.

In spite of an endeavour to prepare samples sufficient for statistical study for each moulting stage from the three regions, specimens younger than adult-3 are very few, and only few valves could be found.

With the unfavorable limitations mentioned above, measurement was made on right valves of the female alone, using a binocular microscope equipped with a micrometer scaled 25 microns. The measurements on length, height, obscure reticulation ratio are listed in Table 3. A total of 598 valves was measured, but further consideration will be given to only 492 valves in three moulting stages of the adult-2 to the adult instar.



Text-figure 3. Length-height graph of the sample from Uranouchi Bay.



Text-figure 4. Length-height graph of the sample from the Nakanoumi Estuary.

In general, the discrimination of effects among the regions, and moulting stages may easily be carried out by the two-factor analysis of variance in levels of 3 x 3. This method, however, depends on the samples being the same or nearly so in variance and normal distribution. As shown in Table 3, the results from x^2 test show that in nearly half of the samples their frequencies are far from the normal distribution. Therefore, these samples may not be adequate for analysis of variance.

Therefore, further consideration was based on the results from the non-parametric method, Mann-Whitney's u test which has been somewhat revised for lower probability cases. The method is a sort of test by rank of variables and the equation is

$$CR = \frac{|U - E(U)| - 0.5}{\sqrt{Var\ (U)}}$$

where $U = n_1 n_2 + [n_1 (n_1 + 1)/2] - R_1$
or $n_1 n_2 + [n_2 (n_2 + 1)/2] - R_2$

n_1: number of specimens in sample 1
n_2: number of specimens in sample 2
R_1: sum of rank in sample 1
R_2: sum of rank in sample 2
$E(U) = n_1 n_2 / 2$, stands for expected value of U when $p(x = y) = 1/2$,

$$\sqrt{Var\ (U)} = \left(\frac{n_1 n_2}{N (N - 1)} \right) \left(\frac{N^3 - N}{12} - T \right)$$, stands for expected variance when $p(x = y) = 1/2$.

$N = n_1 + n_2$

$T = \Sigma (t_i^3 - t_i) / 12$

t: number of rank in which variables more than 2 referred,
i: number of variables in any above case.

The results are listed in Table 4. In this work, the datum of significance is taken as 1 per cent.

Concerning valve length, significant differences are indicated through the three moulting stages between the samples from Uranouchi Bay and Nakanoumi Estuary, and Uranouchi Bay and Aomori Bay. On the other hand, between the ones from Nakanoumi Estuary and Aomori Bay, differences can be seen in two stages of adult-2 and the adult instar, but not significant in adult-1 stage. As to valve height, significant differences are also indicated between the samples from Uranouchi Bay and Nakanoumi Estuary, and Uranouchi Bay and Aomori Bay through the three moulting stages. Between the ones from Nakanoumi Estuary and Aomori Bay, the difference is significant only in adult-2 stages, but not in the adult-1 and adult instar stages. Therefore, it can be briefly said that between Uranouchi Bay and the other two regions, there exist significant differences in valve size (length and height); on the other hand, between Nakanoumi Estuary and Aomori Bay, significant difference in valve size seems to be questionable.

All the specimens in the adult instar stage are ornamented by complete reticulation entirely over the valve surface. Concerning the obscure reticulation ratio, significant differences are detected only in the adult-2 and adult-1 stages, between the samples from the Nakanoumi Estuary and Aomori Bay, using the u test. Most specimens from Uranouchi Bay do not have obscure reticulation and show zero obscure reticulation ratio. In this case, the u test is not adequate for such samples because the rank is not in continuity. Fortunately, the frequencies of obscure reticulation ratio of the samples from Aomori Bay show near-normal distribution (Table 3) in the adult-1 and adult-2 stages, when the datum is taken as the probability of 0.05. Therefore, these samples can be judged by their confidence intervals by the following formula,

$$X \pm t \left(\frac{S}{\sqrt{N}} \right),$$

t: value of t for N-1 degree of freedom corresponding to the confidence interval desired,

N: number of specimens in sample.

Calculation by this formula indicates their confidence intervals in 98 per cent probability, as

$$0.314 \pm 0.020 \text{ for adult-1 stage and}$$

$$0.496 \pm 0.037 \text{ for adult-2 stage.}$$

In the confidence interval, the obscure reticulation ratio of the sample of Uranouchi Bay (zero) should be significantly different from those of the other regions.

As shown in Plate 1 and Plate 2, the obscure reticulation ratio decreases gradually as maturity is approached except for the samples from Uranouchi Bay where the ratio is nearly zero through all the moulting stages. Such a tendency is also seen from the u test for the samples from the Nakanoumi Estuary and Aomori Bay between adult-1 and adult-2 stages.

PROBABLE CAUSE OF VARIATIONS

The main ocean current system around Japan, according to Uda (1934), is shown in Text-figure 1. The coastal regions south of central Honshu (Choshi) facing the Pacific are washed by the Kuroshio current and the northern half by the Oyashio current. These currents are said to meet near the central part of Honshu. Thus, a rather sharp boundary can be seen there between the subtropical and temperate faunas (Horikoshi, 1962). On the other hand, no sharp boundary is found along the coast of the Japan Sea side, and the characteristic faunas of the southern areas are found prevailing in more northern areas (Horikoshi, 1962). On the other hand, he suggested that the inner sublittoral zone is, in general, sheltered from the direct main current, and the faunas are distributed widely from Kyushu to Hokkaido. The ostracodes under consideration, in the case of the inner sublittoral zone, are expected to be widely distributed as stated by him. But some characteristic genera as *Finmarchinella, Urocythereis, Hemicytheria,* and *Howeina* seem to be restricted to the Japan Sea side.

The average surface water temperature for each month at the stations near the regions from where ostracodes were collected is shown in Table 1 (Japan Meteor. Agency, 1969, 1970). Esashi, Hiyama County, southwestern Hokkaido is near to Aomori Bay, and its surface water temperature is shown to be lowest among the regions: the lowest average temperature is 4.9°C during February and the highest of 21.3°C during August. Saigo, Okijima, Shimane Prefecture is near to the Nakanoumi Estuary, and its lowest average temperature is 10.8°C during February and highest 27.2°C during August. Ashizuri, Kochi Prefecture is near to Uranouchi Bay, and its surface water temperature is the highest among the regions studied: the lowest average temperature is 16.5°C during February and the highest 27.1°C during August.

From the records, there exist, in general, a distinct difference in average water temperature between the three regions throughout the year, except for the summer (August).

Among possible environmental factors that are responsible for the variation in valve morphology in these regions, the following three may be considered.

1) The main oceanic current system is thought to have no bearing on the variations of the ostracode valves, because none of the three regions is in the northern half of the Pacific side of Japan where the Oyashio current has direct effects.

2) Even in the inner sublittoral zone, some distinct differences are evident between ostracode faunas of the Pacific side and those of the Japan Sea side.

3) The surface water temperatures are distinct between the three regions, especially during winter.

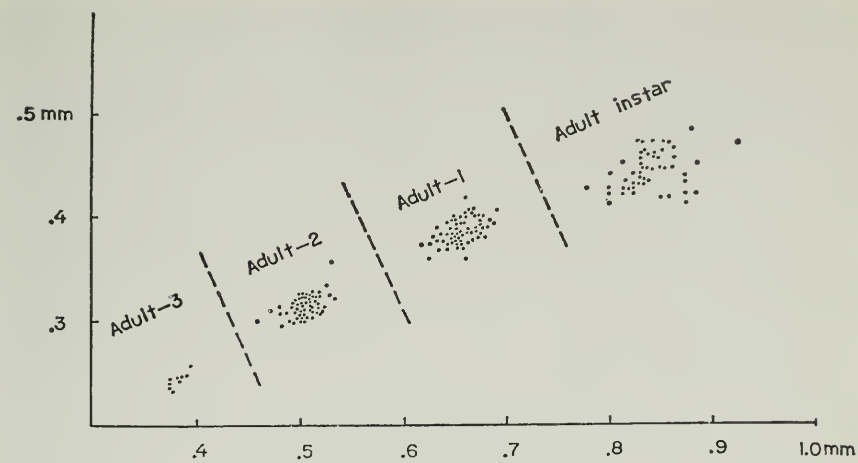
Therefore, it is thought that 2) and 3) cited above may have the most probable bearing on the variation of ostracode morphology.

REMARKS

From the observations and measurements made on the ostracode samples from Uranouchi Bay, Nakanoumi Estuary, and Aomori Bay, the following remarks can be made.

1) The valve size is clearly different between the samples of Uranouchi Bay and the Nakanoumi Estuary, and Uranouchi Bay and Aomori Bay. The specimens of Uranouchi Bay are much smaller than those of the other regions. It can not be considered that the valve size depends upon the water temperature where the ostracodes live because no sharp distinction could be found between the specimens of the Nakanoumi Estuary and Aomori Bay. Therefore, the following two working explanations are proposed.

a) The first, the variation of the valve size may be due to the temperature above or below a critical point; that is, the valve becomes smaller when the temperature is higher and larger when lower.



Text-figure 5. Length-height graph of the sample from Aomori Bay.

b) The physico-chemical conditions may be fatally distinct for ostracode life between the Pacific side and the Japan Sea side. Judging from the fact that some characteristic ostracode genera are restricted to the Japan Sea side, distinction may be expected, at least, in terms of ostracode zoogeography.

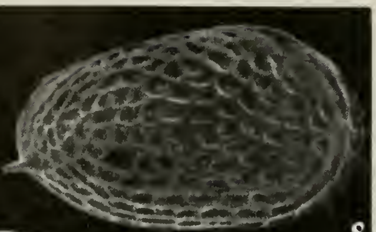
At the present, the writer prefers the latter explanation as more suitable for explaining the difference of valve size.

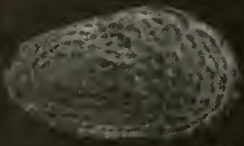
2) The obscure reticulation ratio decreases evidently through ontogeny, in general.

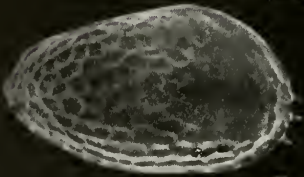
3) The obscure reticulation ratio is significantly different in the three regions. It becomes lower when the ostracode is taken from warm water, and higher from the cold water in the corresponding moulting stages. Thus, it may be that the change of this ratio takes place in correspondence to the gradient of water temperature.

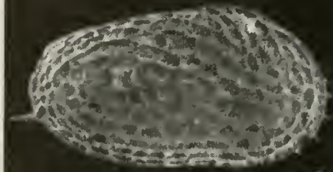

1


6

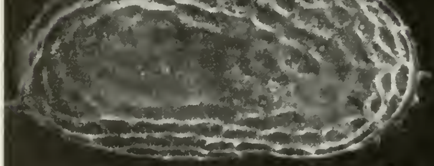

8


2


7


3


9


4


5

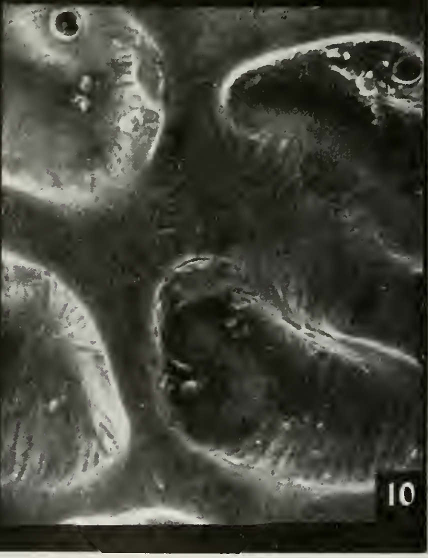

10

PLATE 2

All figures are scanning electron micrographs.

Figure

1-5. Serial moulting stages of right valve and normal pore canal of specimens from Uranouchi Bay (St. 67 of Ishizaki, 1968), × 93 except for figure 5.
1. Lateral view of specimen of adult-3 stage, ornamented by complete reticulation over valve surface. 2. Lateral view of specimen of adult-2 stage. 3. Lateral view of specimen of adult-1 stage. 4. Lateral view of adult instar. 5. Highly enlarged micrograph of normal pore canal of figure 4.

6-10. Serial moulting stages of right valves and details of reticulation of specimens from Nakanoumi Estuary (St. 4 of Ishizaki, 1969), × 93 except for figure 10.
6. Lateral view of specimen of adult-3, obscure reticulation occupying nearly anterior half of valve. 7. Lateral view of specimen of adult-2, slightly obscure reticulation discernible at anterior part of valve. 8. Lateral view of specimen of adult-1, complete reticulation prevailing nearly over entire surface. 9. Lateral view of specimen of adult instar, complete reticulation covering entire surface. 10. Enlarged micrograph of reticulation of the valve of figure 9, flute structure developing downward from top of wall of reticulating ridges, × 1,000.

REFERENCES

Brady, G. S.

1866. *On new or imperfectly known species of marine Ostracoda.* Zool. Soc., London, Trans., vol. 5, pp. 359-393, pls. 57-62.

1880. *Report on the Ostracoda dredged by H. M. S. Challenger during the years 1873-1876.* Zool., vol. 1, pt. 3, Ostracoda, 184 pp., 44 pls.

Horikoshi, M.

1962. *Warm temperature region and coastal-water area in the marine biogeography of the shallow sea system around Japanese Islands.* Quart. Res., vol. 2, Nos. 2-3, pp. 117-124 (in Japanese with English summary). Japan Meteor. Agency, Tokyo.

Japan Meteor. Agency

1969. *The results of marine meteorological and oceanographical observations.* No. 39, Japan Meteor. Agency, Tokyo, 349 pp.

1970. *The results of marine meteorological and oceanographical observations. Ibid.,* No. 40, 336 pp.

Sandberg, P. A., and Plusquellec, P. L.

1969. *Structure and polymorphism of normal pores in cytheracean Ostracoda (Crustacea).* Jour. Paleont., vol. 43, No. 2, pp. 517-521, 12 figs.

Simpson, G. G., Roe, Anne, and Lewontin, R. C.

1960. *Quantitative zoology.* rev. ed., Harcourt, Brace and Co., New York-Burlingame. 440 pp., 64 figs., 5 tables.

Sylvester-Bradley, P. C., and Benson, R. H.

1971. *Terminology for surface features in ornate ostracodes.* Lethaia, vol. 4, No. 3, pp. 249-286, 48 figs.

Uda, M.

1934. *Hydrographical studies based on simultaneous oceanographical survey made in the Japan Sea.* Rec. Ocean. Works, Japan, vol. 6, pp. 19-107, 36 figs., 13 tabs.

Kunihiro Ishizaki,
Institute of Geology and Paleontology,
Faculty of Science,
Tohoku University,
Sendai, Japan.

OSTRACODES CENOMANIENS DU BASSIN DE PARIS: QUELQUES RESULTATS D'ORDRE PALEOECOLOGIQUE ET PALEOGEOGRAPHIQUE

Renée Damotte
Centre National de la Recherche Scientifique

RÉSUMÉ

Le faunes d'Ostracodes du Cénomanien, récoltées en différentes régions du Bassin de Paris, sont comparées. Certaines faunes déposées dans des milieux similaires, mais provenant de diverses localités, ne sont pas toujours identiques, alors que certaines déposées en milieu différent le sont. L'importance de la localisation géographique des affleurements à l'intérieur d'un même bassin est mise en évidence. De même la composition faunistique de certains gisements peut donner des renseignements intéressants concernant la paléogéographie du bassin.

ABSTRACT

The Cenomanian ostracode fauna collected in different parts of the Paris Basin are compared. Some faunas deposited in same environments, but localised in separate places, are not always identical, then some deposited in different environments are identical. The importance of the geographical position of the outcrops in a basin is rendered evident. In the same way, the ostracode association of certain deposits can give some interesting information about the paleogeography of the basin.

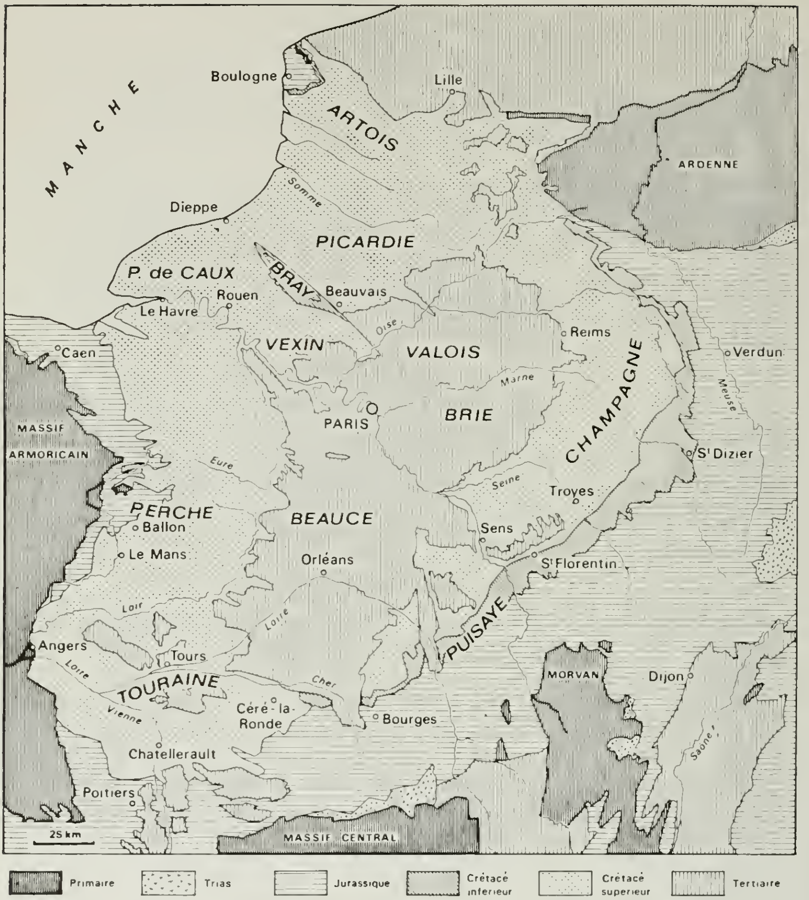
INTRODUCTION

Le Bassin de Paris occupe la plus grande partie du Nord de la France, et mesure environ 580Km du Cotentin à l'Ardenne et 440Km du Boulonnais au Massif Central (Fig. 1).

Au point de vue géologique, ce Bassin est constitué de terrains tertiaires et secondaires entourés par des massifs anciens séparés par des seuils. Le centre est occupé par les terrains tertiaires, les terrains secondaires dessinant des auréoles concentriques, mieux visibles dans l'Est du Bassin. Les terrains d'âge crétacé inférieur ont une aire d'affleurement très réduite, située dans l'Est et le Sud-Est du Bassin: Marne, Haute-Marne, Yonne, Aube et un peu au Nord dans le Pays de Bray. Le Cénomanien, qui a été très transgressif, est visible dans des régions plus étendues : Touraine, Sarthe, Ardenne, Boulonnais . . . Dans la région du Mans, région type de l'étage, on peut distinguer dans le Cénomanien des argiles et sables glauconieux (10m environ), les marnes sableuses de Ballon, les sables et grès du Mans (40 à 50m d'épaisseur), parfois agglutinés en bancs gréseux à *Acanthoceras rothomagense;* les sables du Perche (20 à 30m) souvent agglutinés en blocs ou bancs à *Acanthoceras naviculare* et par places à très nombreuses Huîtres: *Exogyra columba* et *Ostrea biauriculata*. Les dépôts de la Sarthe sont des dépôts littoraux, indiquant la proximité du rivage de la mer cénomanienne.

Dans l'Aube et l'Yonne, le Cénomanien devient crayeux: craie marneuse à la base, puis craie plus massive et au sommet la craie de Saint-Parres, craie sèche en plaquettes. On a ici des dépôts de mer de plate-forme et assez éloignés des zones côtières.

En Touraine, au Cénomanien se sont déposés des sables glauconieux alternant avec des bancs gréseux ou calcaires et surmontés par des marnes à Ostracées. Comme dans la Sarthe les dépôts sont littoraux et le rivage de la mer cénomanienne peu éloigné.



CARTE GEOLOGIQUE SCHEMATIQUE DU BASSIN DE PARIS

Text-figure 1.

Au Turonien et au Sénonien, les dépôts se sont effectués dans l'ensemble du Bassin de Paris.

PRINCIPAUX GISEMENTS ETUDIES DANS CE TRAVAIL

Aube - Yonne: Au Nord de Saint-Florentin (Yonne), environs du Mont Avrelot, le Cénomanien affleure principalement le long de la route départementale 30, en particulier une carrière montre la craie du Cénomanien moyen à *Schloenbachia varians, Acanthoceras mantelli, Inoceramus concentricus.* La craie marneuse du Cénomanien inférieur est mieux visible le long de la route départementale 20, un peu à l'Ouest de la carrière précédente.

Bairdia pseudoseptentrionalis MERTENS
Cytherella ovata (ROEMER)
Cytherella parallela (REUSS)
Cytherelloïdea stricta (J. & H.)
Cythereis larivourensis D. & G.
Cythereis hirsuta D. & G.
Cythereis aff. matronae D. & G.
Protocythere lapparenti D. & G.
Protocythere sp. aff. consobrina TRIEBEL
Neocythere vanveeni MERTENS
Veenia ballonensis D. & G.
Schuleridea jonesiana (BOSQUET)
Dolocytheridea bosquetiana (J. et H.)
Paracypris sp.
Cythereis religata DAM.
Cythereis dordoniensis DAM.
Cythereis petrocorica DAM.
Platycythereis minuita DAM.
Platycythereis sp.
Protocythere terera DAM.
Dolocytheridea crassa DAM.

CENOMANIEN INFERIEUR

	Saint-Florentin Mont - Avrelot	Ballon Saint-Mars-sous-Ballon	Boulonnais Petit-Blanc-Nez	Région de Chatellerault
Bairdia pseudoseptentrionalis MERTENS	= = = = =	+ + + + +	+ + + + +	
Cytherella ovata (ROEMER)	= = = = =	+ + + + +	+ + + + +	+ + + + +
Cytherella parallela (REUSS)	--------	--------	--------	
Cytherelloïdea stricta (J. & H.)	--------	--------	--------	
Cythereis larivourensis D. & G.	+ + + + +	+ + + + +	--------	
Cythereis hirsuta D. & G.	+ + + + +	+ + + + +	+ + + + +	
Cythereis aff. matronae D. & G.		--------	--------	--------
Protocythere lapparenti D. & G.	+ + + + +	+ + + + +	--------	
Protocythere sp. aff. consobrina TRIEBEL		--------	--------	
Neocythere vanveeni MERTENS	+ + + + +	+ + + + +	= = = = =	--------
Veenia ballonensis D. & G.	+ + + + +	+ + + + +		
Schuleridea jonesiana (BOSQUET)	--------	+ + + + +	+ + + + +	
Dolocytheridea bosquetiana (J. et H.)			--------	
Paracypris sp.	--------			
Cythereis religata DAM.				+ + + + +
Cythereis dordoniensis DAM.				--------
Cythereis petrocorica DAM.				+ + + + +
Platycythereis minuita DAM.				+ + + + +
Platycythereis sp.				--------
Protocythere terera DAM.				--------
Dolocytheridea crassa DAM.				--------

= = = = : abondant ; + + + + : fréquent ; - - - - : rare.

Tableau 1

Région du Mans: Le Cénomanien inférieur sableux, à niveau de minerai de fer n'a pas montré d'Ostracode. Les marnes sableuses de Ballon, au sommet du Cénomanien inférieur, ont été prélevés en particulier à Ballon et à Saint-Mars-sous-Ballon, elles sont très fossilifères pour les Ostracodes. Les sables du Perche ne contiennent que très rarement des Ostracodes (Greez-les-Rocs, Courgenard. . .).

Touraine: Les sables glauconieux sont généralement azoïques pour les Ostracodes, quelques prélèvements ont montré une faune pauvre (Ciran, Huismes . . .). Les marnes, surtout celles recueillies dans le sondage de Céré-la-Ronde, contiennent une riche et variée faune d'Ostracodes. Dans le Sud de la Touraine (environs de Chatellerault, Vienne) le Cénomanien inférieur est assez rarement fossilifère (Saint-Genest-d'Ambière). Le Cénomanien moyen par contre renferme de nombreux Ostracodes, en particulier à Noirpuis, Port-de-Piles. . .
Boulonnais: La craie marneuse du Cénomanien inférieur du Petit-Blanc-Nez, et la craie blanche du Cénomanien supérieur du Cran d'Escalles contiennent de nombreux Ostracodes. Il est à signaler que le Boulonnais n'appartient pas au Bassin de Paris selon la conception stricte du terme, car il est situé au Nord de l'axe de l'Artois; mais les sédiments cénomaniens appartenant à la même transgression que ceux de l'ensemble du Bassin, ils seront examinés ici.

CONTENU FAUNISTIQUE DES DIFFERENTS GISEMENTS ETUDIES

Il nous a paru plus simple et plus clair de présenter le contenu faunistique des gisements sous forme de tableau par niveau stratigraphique. Des impossibilités matérielles (en particulier des difficultés pour échantillonner à nouveau certains niveaux) nous ont empêché de faire des comptages précis et la notion de fréquence des espèces sera indiquée par les seules notations de rare (— — —) fréquent (+ + +) et abondant (= = =).

COMPARAISON ENTRE LES FAUNES DES DIFFERENTES REGIONS

CENOMANIEN INFERIEUR (TABLEAU 1)

L'examen du Tableau 1 montre que la faune est homogène dans trois régions: Yonne (Saint-Florentin, Mont-Avrelot), Sarthe (Ballon et Saint-Mars-Sous-Ballon) et Boulonnais (Petit-Blanc-Nez). Une seule espèce *Veenia ballonensis* n'a pas été retrouvée dans le Boulonnais, où par contre *Dolocytheridea bosquetiana* a été reconnue; deux espèces ne sont pas présentes dans l'Yonne: *Cythereis aff. matronae* et *Protocythere aff. consorbrina.* Dans le Sud de la Touraine (environ de Chatellarault) la faune est presque totalement différente au point de vue spécifique, seules trois espèces sont communes à l'ensemble des régions citées ici: *Cytherella ovata, Neocythere vanveeni* et *Cythereis aff. matronae.*

CENOMANIEN MOYEN (TABLEAU 2)

Un fait s'impose au premier examen du Tableau 2, il y a une différence très grande entre le contenu faunistique de la Touraine et celui des autres régions, cette différence se situe au niveau spécifique. Seules trois espèces *Cytherella ovata, Cythereis larivourensis* et *Neocythere vanveeni* sont présentes dans l'ensemble des gisements, *Bairdia pseudoseptentrionalis* est également connu dans presque toutes les régions, excepté le Sud de la Touraine. Les nombreuses espèces qui semblent confiner à la Touraine sont en réalité des espèces connues ou décrites dans le Nord de l'Aquitaine: Dordogne (DAMOTTE, 1971): *Cythereis begudensis, Cythereis dorsospinata, Cythereis religata, Cytherei fournetensis, Cythereis dordoniensis, Cythereis cereensis, Cythereis praetexta arta, Cythereis petrocorica, Cythereis sp. 1970, Cytherella dordoniensis, Dolocytheridea crassa, Dordoniella strangulata, Dumontina cenomana, Oertliella ingerica, Platycythereis minuita, Parexophthalmocythere oertlii. Pterygocythere rati, Schuleridea tumescens.* Certaines de ces espèces sont même connues en Provence (Sud-Est de la France): en particulier: *Cythereis begudensis, Cythereis fournetensis, Parexophthalmocythere oertlii, Pterygocythere rati.*

REMARQUES D'ORDRE PALEOECOLOGIQUE ET PALEOGEOGRAPHIQUE

Le Cénomanien moyen est le niveau le plus intéressant à étudier du point de vue écologie des associations et paléographie du Bassin de Paris.

Dans l'Yonne le Cénomanien moyen est crayeux, sédiment qui a dû se déposer dans une mer peu profonde, épicontinentale, aux eaux probablement calmes.

Les marnes sableuses de Ballon indiqueraient un milieu de dépôt littoral, un peu agité, milieu néritique côtier. Les sables du Perche sont également des dépôts de faciès littoraux assez agités.

Le milieu de dépôt des sables glauconieux de Touraine était similaire à celui des sables du Perche: milieu littoral assez agité. Les marnes à Ostracées ont dû se déposer dans un milieu plus calme à sédimentation argileuse fine, milieu néritique côtier vraisemblablement.

L'ensemble de ces espèces du Cénomanien moyen vivait dans un milieu peu profond, néritique et côtier, à l'exception peut-être de l'Yonne, et elles préferaieient un milieu calme, car elles sont moins abondantes dans les sables. Les espèces recueillies dans la craie de l'Yonne, vivaient dans un milieu également peu profond, mais non côtier, milieu plus ouvert (mer de plate-forme).

Les milieux de dépôt des sédiments cénomaniens moyens de la Sarthe sont de même type que ceux de la Touraine, et différents de ceux de l'Yonne or c'est entre l'Yonne et la Sarthe que les similitudes de faune existent.

La localisation géographique des gisements sarthois, tourangeaux et de l'Yonne est donc également à envisager, car elle peut nous aider à comprendre les différences entre les faunes de ces régions.

Bairdia pseudoseptentrionalis (
Cytherella ovata (ROEMER)
Cytherella parallela (REUSS)
Cytherelloïdea stricta (J. et H
Cythereis larivourensis D & G
Cythereis hirsuta D & G
Protocythere lapparenti D & G
Protocythere aff. consobrina
Schuleridea jonesiana (BOSQU
Neocythere vanveeni MERTE
Cythereis aff. matronae D & (
Veenia ballonensis D & G
Cythereis sp. 1970 DAM.
Cythereis petrocorica DAM.
Pterygocythere rati DAM.
Cythereis glabrella TRIEBEL
Cythereis begundensis BABIN
Cythereis dorsopinata DAM.
Cythereis religata DAM.
Cythereis fournetensis DAM.
Cythereis dordonensis DAM.
Cythereis cereensis DAM.
Cythereis praetexta arta DAM
Platycythereis minuita DAM.
Parexophtalmocythere oertlii
Oertliella ingerica DAM.
Dolocytheridea crassa DAM.

Dordoniella strangulata APOS
Schuleridea tumescens DAM.
Cytherella dordonensis DAM.
Dumontina cenomana DAM.

CENOMANIEN MOYEN

	Saint-Florentin Mont-Avrelot	Région du Mans	Boulonnais Cran d'Escalles	Touraine		Région de Chatellerault
				Ciran Huismes	Céré-la-Ronde	
Bairdia pseudoseptentrionalis (MERT.)	= = = = =	+ + + + +	= = = = =	+ + + + +	+ + + + +	
Cytherella ovata (ROEMER)	= = = = =	+ + + + +	= = = = =	= = = = =	+ + + + +	--------
Cytherella parallela (REUSS)	--------	--------	--------			
Cytherelloïdea stricta (J. et H.)	--------	--------				
Cythereis larivourensis D & G	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+ + + + +	--------
Cythereis hirsuta D & G	+ + + + +	+ + + + +	+ + + + +			
Protocythere lapparenti D & G	+ + + + +	+ + + + +	+ + + + +			
Protocythere aff. consobrina TRIEBEL		--------	--------			
Schuleridea jonesiana (BOSQUET)	--------	+ + + + +	--------			
Neocythere vanveeni MERTENS	+ + + + +	--------	--------	+ + + + +	+ + + + +	--------
Cythereis aff. matronae D & G		--------	--------			
Veenia ballonensis D & G	+ + + + +					
Cythereis sp. 1970 DAM.				+ + + + +	+ + + + +	+ + + + +
Cythereis petrocorica DAM.				+ + + + +	+ + + + +	+ + + + +
Pterygocythere rati DAM.				+ + + + +	+ + + + +	+ + + + +
Cythereis glabrella TRIEBEL					--------	
Cythereis begundensis BABINOT					--------	
Cythereis dorsopinata DAM.					+ + + + +	+ + + + +
Cythereis religata DAM.					+ + + + +	+ + + + +
Cythereis fournetensis DAM.					+ + + + +	
Cythereis dordonensis DAM.						+ + + + +
Cythereis cereensis DAM.					+ + + + +	+ + + + +
Cythereis praetexta arta DAM.					+ + + + +	+ + + + +
Platycythereis minuita DAM.					+ + + + +	+ + + + +
Parexophtalmocythere oertlii (BAB.)					+ + + + +	
Oertliella ingerica DAM.					+ + + + +	+ + + + +
Dolocytheridea crassa DAM.					--------	--------
Dordoniella strangulata APOST.					+ + + + +	+ + + + +
Schuleridea tumescens DAM.					--------	--------
Cytherella dordonensis DAM.						+ + + + +
Dumontina cenomana DAM.						--------

= = = = : abondant ; + + + + : fréquent ; - - - - : rare.

Tableau 2

Pour les niveaux du Cénomanien moyen de l'Yonne, on a à la fois différence de milieu de dépôt et éloignement géographique par rapport à la Sarthe et à la Touraine, l'éloignement géographique entre la Sarthe et l'Yonne est même plus important qu'entre la Sarthe et la Touraine.

De ces faits, il se dégage l'idée que l'emplacement géographique des gisements à l'intérieur d'un même bassin est un facteur à ne pas négliger.

La localisation géographique de la Touraine explique l'allure particulière de la faune, il y a eu influence du Bassin Aquitain, avec apport de faune différente plus méridionale, faune de mer plus chaude qui a pu subsister dans la mer tourangelle tempérée par les courants venus du Sud. La communication entre les deux bassins a dû se faire par le détroit du Poitou dés le Cénomanien moyen alors qu'avant cette période les communications entre les deux bassins étaient moins aisées, la mer devant contourner la Vendée et pénétrer en Touraine par la Basse Loire. Toutefois, il ne faut pas oublier que dés le Cénomanien inférieur: la faune des environs de Chatellerault contient quelques espèces connues en Dordogne.

CONCLUSION

Quand on étudie la paléoécologie de faunes appartenant à un niveau stratigraphique semblable et provenant d'un même bassin, la localisation géographique des gisements à l'intérieur du bassin peut influer sur la composition de la faune, le plus souvent par l'intermédiaire d'autres facteurs: climatologique en particulier: courants plus chauds amenant des faunes qui peuvent alors subsister dans des eaux plus tempérées que celles de l'ensemble du bassin.

A l'inverse la présence de faunes différentes dans un secteur du bassin doit faire penser à la possibilité d'apports extérieurs et donc à la communcation avec une autre région.

Ici l'étude de la faune d'Ostracode de la Touraine et de la région de Chatellerault, qui montre de grandes similitudes avec celle du Nord de l'Aquitaine, est un argument supplémentaire en faveur de la large ouverture du détroit du Poitou au Cénomanien moyen et même inférieur.

BIBLIOGRAPHIE SOMMAIRE

Apostolescu, V.

1955. *Un nouveau genre d'Ostracode du Cénomanien de Dordogne: Dordoniella strangulata n. sp.* Cahiers géologiques de Thoiry, No. 33, pp. 329-331.

Babinot, J. F.

1970. *Nouvelles espèces d'Ostracodes du Cénomanien supérieur de l'auréole septentrionale du Bassin du Beausset (Bouches-du-Rhône-Var). 1ère partie.* Rev. Micropaléont., vol. 13, No. 2, pp. 95-106, 3 pl.

1971. *Nouvelles espèces d'Ostracodes du Cénomanien supérieur de l'auréole septentrionale du Bassin du Beausset (Bouches-du-Rhône-Var).* 2 ème partie. Rev. Micropaléont., vol. 13, No. 4, pp. 237-248, 3 pl.

Damotte, R.
1971. *Quelques Ostracodes du Cénomanien de Dordogne et de Touraine.* Rev. Micropaléont., vol. 14, No. 1, pp. 3-20, 3 pl.
1971. *Contribution à l'étude des Ostracodes marins dans le Crétacé du Bassin de Paris.* Soc. Géol. France, nelle série, t. L, mém. No. 113, 152 pp., 8 pls.
Damotte, R.. et Grosdidier, G.
1963. *Quelques Ostracodes du Crétacé de la Champagne Humide. 1 Albien-Cénomanien.* Rev. Micropaléont., v. 6, No. 1, pp. 51-66, 3 pls.
Deroo, G.
1956. *Etudes critiques au sujet des Ostracodes marins du Crétacé inférieur et moyen de la Champagne Humide et du Bas-Boulonnais.* Rev. l'Inst. Fr. Pétrole, vol. XI, No. 12, pp. 1499-1635, 5 pls.
Howe, H. V., et Laurencich, L.
1958. *Introduction to the study of Cretaceous Ostracoda.* Louisiana State University Press. 536 pp.
Juignet, P.
1971. *Modalités du contrôle de la sédimentation sur la marge armoricaine du Bassin de Paris à l'Aptien-Albien-Cénomanien.* Bull. Bureau Recherches Géologiques et Minières, 2éme série, section I, No. 3, pp. 113-126.
Moore, R. C.
1961. *Treatise on Invertebrate paleontology, part. Q. Anthropoda 3. Crustacea Ostracoda.* Geol. Soc. America and Univ. Kansas Press, 442 pp.
Morkhoven, F. P. C. M. van
1962-1963. *Post Paleozoic Ostracoda.* Elsevier Publishing Company, vol. I, 204 pp., vol. II, 478 pp.
Oertli, H. J.
1963. *Faunes d'Ostracodes du Mézozoïque de France.* E. J. Brill éd. — Leiden, 57 pp., XC pls.
Pokorny, V.
1964. *Some palaecological problems in marine ostracode faunas, demonstrated on the Upper Cretaceous ostracodes of Bohemia, Czechoslovakia.* Publ. staz. zool. Napoli, 33, suppl., pp. 462-479.
Pourmotamed-Lachtenechai, F.
1971. *Etude micropaléontologique du Cénomanien dans le Nord du Seuil du Poitou.* Thèse 3ème cycle, Université Paris, 195 pp., 19 pls. ronéotypé, inédit.

Renée Damotte,
Centre National de la Recherche
Scientifique,
Laboratoire de Micropaléontologie,
Université de Paris VI.
Tour 15-E4,
4 Place Jussieu
75 - Paris V - France

DISCUSSION

Dr. H. J. Oertli: Did you have an opportunity to see in greater detail forms of southeastern France and compare them with your Touraine forms? It is also important to demonstrate that Touraine, which is in the southwestern part of the Paris Basin, has common species with the Aquitaine, which are 100% different from the Paris Basin.

Dr. Damotte. On the first slide (map in the text) you can see the position of Touraine in the Paris Basin, and just on the south of "détroit du Poitou" is the North of Aquitaine, the Dordogne.

I know myself the fauna of Dordogne, north of Aquitaine, and I have studied some samples of the Pyrénées and I have seen the same species. Dr. Babinot is working on the Provence fauna, and he found some of my species. We have discussed those problems and he has seen my fauna of Touraine.

Dr. Oertli: We have two biogeographical Cretaceous provinces, a northern part and a southern part, both very well delimited.

Dr. A. Liebau: Could you remark on the lagoonal ostracodes in the Cenomanian.

Dr. Damotte: Yes, but here I speak only of the marine fauna. I know the existence of lagoonal faunal in the Cenomanian, but it is not the subject of this work.

Dr. F. M. Swain: In the middle Atlantic region we have a lagoonal Cenomanian sulcate cytherideid that we (Swain and Brown, 1964) named *Fossocytheridea*. I wonder if either in France or elsewhere you are familiar with, there are any sulcate cytherideids?

Dr. Damotte: I have never seen such a type of form.

Dr. Oertli: But I think there is a lot still to be done with the Cenomanian. In every new sample you find new things. It is a new world that is arising with the Cenomanian.

Dr. Damotte: We have in all Cenomanian samples a lot of species, and especially some new species and genera, so I want to continue the study of this fauna.

Dr. Liebau: Perhaps it is of interest to you that in the Cenomanian of the Ile Madame (Charente Maritime) and of Roquefort (Landes) species of the Provence fauna occur (as described by Babinot). Very typical is a *Cythereis* species and the "*Opimocythere*" *taxyae*-group. These faunas represent a more lagoonal facies.

Dr. Damotte: Yes, but it is marine, . . .

Dr. Liebau: It should be noted that in these lagoonal Cenomanian faunas the oldest known hemicytherids appear — but this depends also on the definition of this family.

THE PALAEOBIOLOGY OF SOME UPPER PALAEOGENE FRESH-WATER OSTRACODES

M. C. Keen
University of Glasgow

ABSTRACT

Two assemblages can be recognised amongst the fresh-water ostracodes of the upper Eocene and Oligocene of western Europe. These are the *Candona-Cypridopsis* Assemblage and the *Moenocypris* Assemblage. The first of these is the more complex and the more widely distributed. It is thought to have characterised lake margins and shallow lakes up to about one metre in depth; a distinct subassemblage is found in limestones, with a striated cyprid of the *Eucypris tenuistrata* (Dollfus) group and *Cypridopsis* spp. The *Moenocypris* Assemblage, absent in the Paris Basin, is thought to have characterised deeper waters. The mode of life of the various species is discussed.

RÉSUMÉ

On a décrit deux associations fauniques d'ostracodes d'eau douce de l'Eocène supérieur et de l'Oligocène inférieur en Europe de l'ouest, à savoir l'ensemble *Candona-Cypridopsis* et l'ensemble *Moenocypris*. La première association se compose de nombreuses espèces, et on l'a reconnu en Angleterre, dans le bassin de Paris, en Alsace, dans le bassin de Mayence, et en Hesse. Une sous-association coincide avec les roches calcaires; elle est representée par un Cyprididae strié et *Cypridopsis*. On a reconnu la deuxième association en Angleterre et dans le basin de Mayence; elle se caractérise par le seule genre *Moenocypris*. Divers critères suggèrent que l'ensemble *Candona-Cypridopsis* témoigne un milieu près de la côte du lac ou un milieu d'eau peu profonde (1m.?); l'ensemble *Moenocypris* témoigne un milieu plus profonde (2-10m.?).

INTRODUCTION

The Palaeogene deposits of western Europe contain many fresh-water horizons; this report however, is only concerned with the upper Eocene and lower Oligocene. In southern England the horizons dealt with are the lower and upper Headon Beds, Osborne Beds, Bembridge Limestone, and the Hamstead Beds. Some authors regard the whole of this succession as Oligocene (*e.g.* Curry, 1966), while others would place the base of the Oligocene at the base of the Hamstead Beds (*e.g.* Cavelier, 1969; Keen, 1972). In the Paris Basin samples have been examined from the Eocene Calcaire de Nogent l'Artaud and the marls underlying the Marnes à *P. ludensis* at Verzy, and from the Oligocene Bande blanche and Calcaire de Brie. Few fresh-water ostracodes have been obtained from Belgian samples. Farther eastwards lower Oligocene fresh-water ostracodes are found in the Couches de Pechelbronn of Alsace and the Mainz Basin, and the Melanienton of Hesse.

The taxonomy of the ostracodes is far from satisfactory. Many species still need describing, and some of the commoner of these are known almost entirely from juvenile moult stages. Generic designation is not always easy, while geographical variation and distribution present difficult problems. Nonetheless, a great deal of work has been carried out in recent years: Stchepinsky (1960), Margerie (1961, 1972), Triebel (1963), Haskins (1968), Carbonnel and Ritzkowski (1969), and Keen (1972).

FRESH-WATER OSTRACODE ASSEMBLAGES

Those samples which yielded ostracodes were divided into two main groups for statistical purposes, and for each group Jaccard's Coefficient of Correlation was calculated for those species occurring in four or more samples. The first group, consisting of 32 samples, was from the Headon, Osborne, and Bembridge Beds of the Hampshire Basin; the second, of 22 samples, was from the Hamstead Beds of the Isle of Wight, and the Sannoisian of the Paris Basin. The separation was necessary because two distinct units are present, with different, although often related, species. The combination of the English and French Sannoisian samples is justified because the fauna is so similar on the species level that the absence of a particular species from one of the areas is itself of importance. Other French localities were not included because they yield different species, while there were not enough samples to warrant statistical treatment. Two distinct faunal assemblages can be recognised (Text-fig. 1, 2; Table 1). These have been discussed briefly in Keen (1972), and it should be noted that *Vecticypris packsoni* Keen is now included in a different assemblage. The assemblages can also be related to sediment-type and to macrofauna.

The Candona-Cypridopsis Assemblage

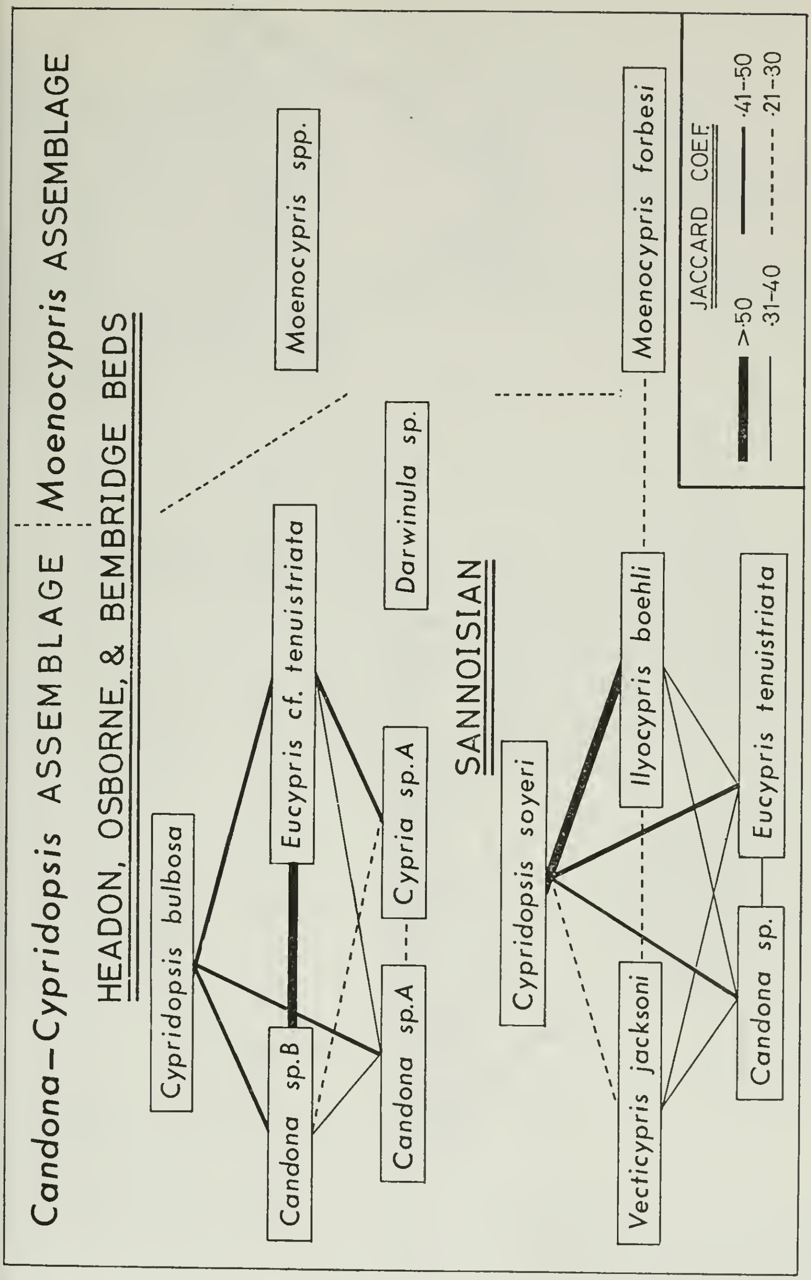
This is the more complex of the two. Associated gastropods are *Galba* and *Planorbina; Chara* nucules are extremely abundant; seeds of water plants are often present. The sedimentary rock may be a green, black, grey, or chocolate-coloured clay, or a buff-coloured limestone with algal "pisolites" and algal laminations. Certain species are more commonly found in the limestones, and these form a subassemblage. The common members of this subassemblage were tested by means of an X^2 test to see if their association with limestones was significant. The following values of p were obtained:

Eucypris cf. *tenuistriata*	0.001
Candona sp. B	0.005
Cypridopsis bulbosa	0.03

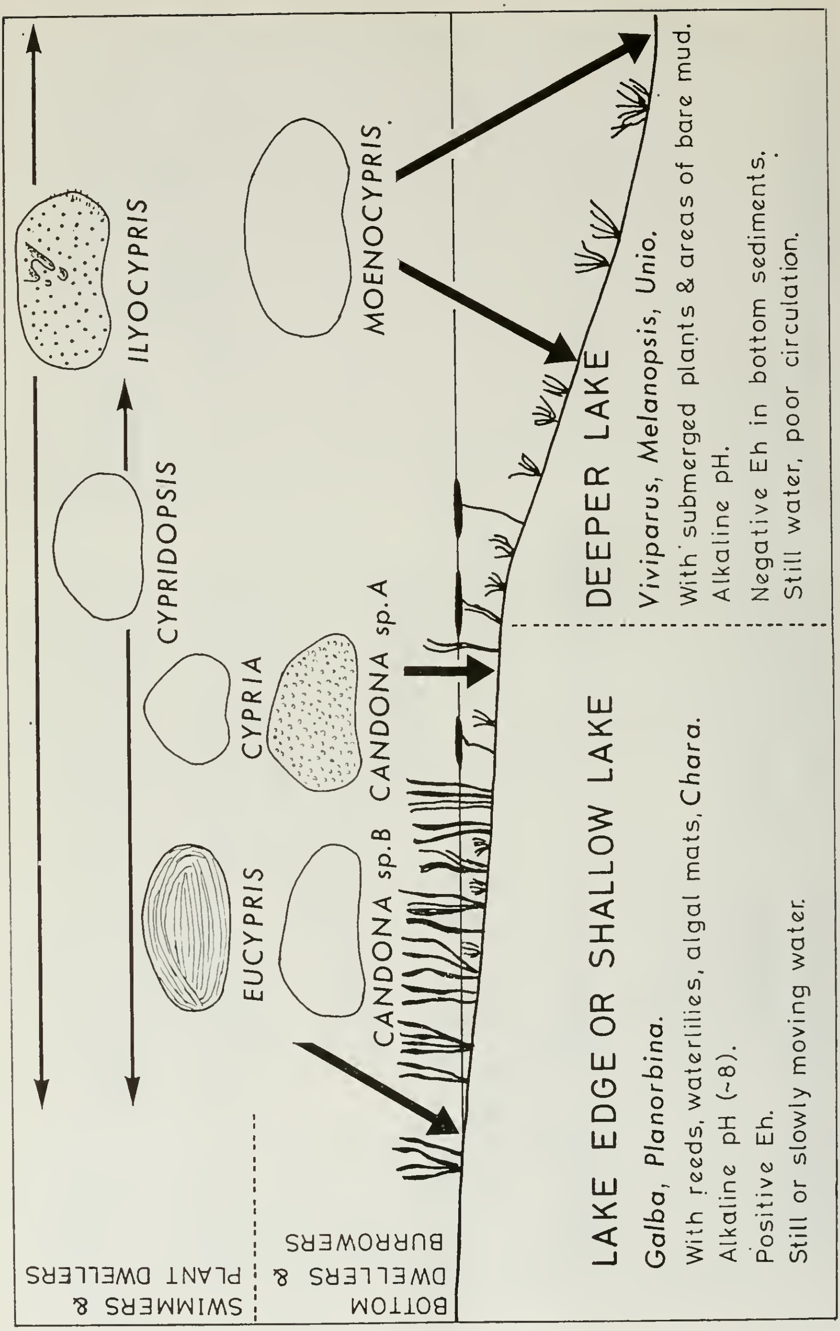
These are all highly significant statistically, well above the 5% level usually applied by modern ecologists. It should be borne in mind however, that the number of samples available for testing was low, 9 limestones and 23 non-limestones. Nevertheless, when the X^2 test was applied to *Candona* sp. A, p was found to be 0.40, indicating a lack of any clear relationship with limestones. To complete the picture, p for *Moenocypris* was found to be –0.08, indicating some significance in its absence from limestones.

The Moenocypris Assemblage

This is much the simpler of the two, *Moenocypris* often comprising the whole of the sample. Associated molluscs are the gastropods *Melanopsis* and *Viviparus*, with the bivalve *Unio*; abundant seeds and leaves of waterplants such as *Stratiotes* and waterlilies are often present. The enclosing sedimentary rock is usually a grey silty clay, occasionally a fine-grained sandstone.



Text-figure 1. Constellation diagram of Jaccard's Coefficient of Correlation.



Text-figure 2. Suggested habitats of the fresh-water ostracode assemblages.

Table 1. Species found in the *Candona-Cypridopsis* Assemblage

OCENE		OLIGOCENE	
Candona (Pseudocandona) sp. A	B	*Candona (Pseudocandona)* sp.	B
Candona (Pseudocandona) sp. B	B	*Cypridopsis soyeri* (Margerie, 1961)	S
Cypridopsis bulbosa (Haskins, 1968)	S	*Eucypris tenuistriata* (Dollfus, 1877)	S
Cypridopsis sp. A		*Ilyocypris boehli* Triebel, 1942	S
Eucypris cf. *tenuistriata* (Dollfus, 1877)	S	*Hemicyprideis montosa* (Jones & Sherborn, 1889)	B
Cypria sp. A	S	****Vecticypris jacksoni* Keen, 1972	S
Darwinula sp.	B	****Cypria* sp.	S
Cypris sp.		****Darwinula* sp.	B
Eucypris sp.	S	*****Herpetocypris nuda* (Dollfus, 1877)	B
Strandesia cf. *spinosa* Stchepinsky, 1960		*****Lineocypris* sp.	B

*Limestone sub-assemblage
**Bembridge Limestone only
**England only
**Paris Basin only

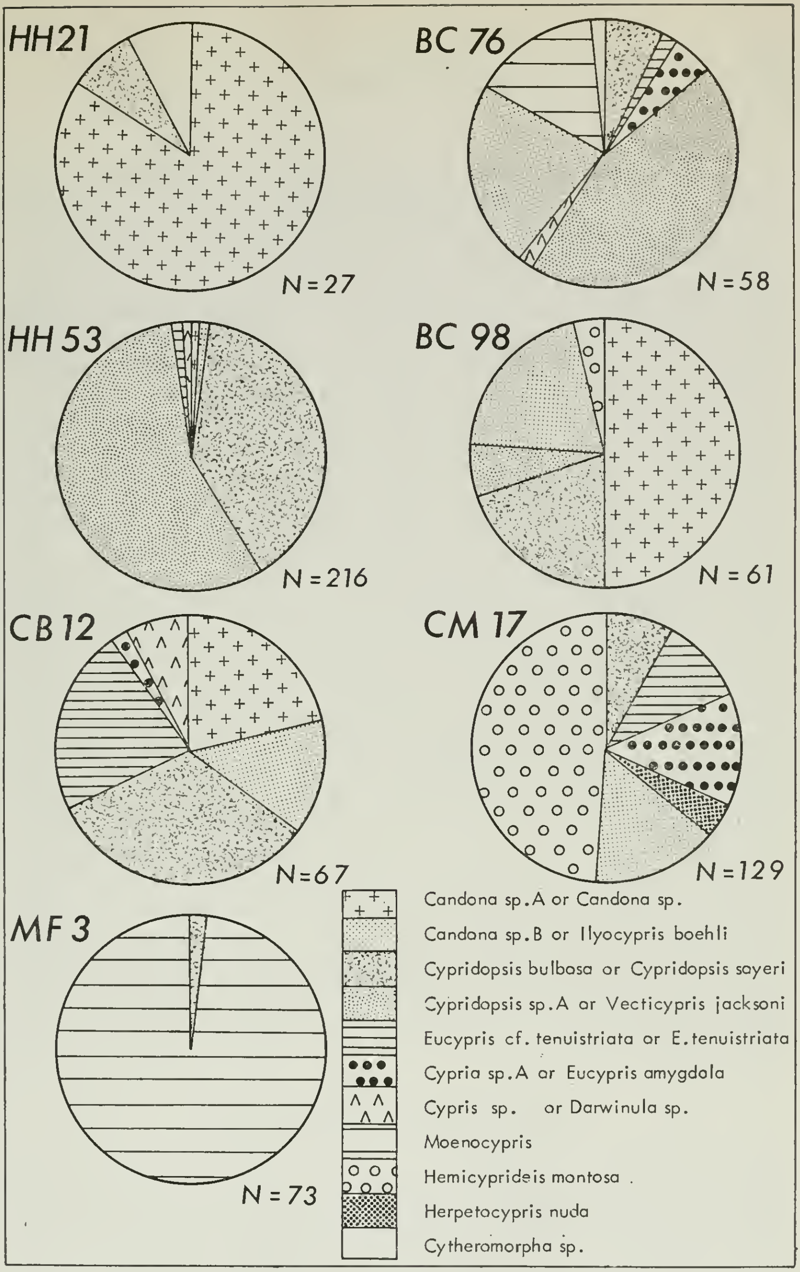
B Bottom dwelling forms
S Swimmers

ENVIRONMENTS AND PALAEOBIOLOGY

The environment envisaged for the *Candona-Cypridopsis* Assemblage is a shallow lake or lake edge, less than a metre deep and perhaps often emergent. Reeds, rooted water plants, *Chara,* and algal mats would have grown in the shallow water (Text-figs. 2). For a more detailed discussion see Daley (1972) and Edwards (1967). *Galba* and *Planorbina* are usually found in water less than 2 metres deep and are capable of living out of water and breathing air (Daley, 1972). In the following discussion of the ostracodes, especially their mode of life, much use has been made of Sars (1928). *Candona (Pseudocandona)* spp. probably burrowed or crawled slowly over the soft bottom sediment as do their modern descendants: *Candona (Pseudocandona)* sp. B where algal lime was accumulating, *Candona (Pseudocandona)* sp. A not being restricted by the type of bottom sediment. The *Eucypris tenuistriata* group of ostracodes probably lived and swam amongst the waterplants but was restricted to areas of carbonate sedimentation. This may reflect a primary control by sediment, the ostracodes living near the bottom in search of food, or a secondary control via the plants. Recent species of *Eucypris* seem to live near the bottom, so the first of the two suggestions may be the more probable. *Cypridopsis* spp. probably swam amongst the waterplants: this is suggested by comparison with living species of the genus, most of which are active swimmers; by its morphology, with rounded anterior and ventral margins (Hartmann, 1965, and Benson in discussion of Hartmann, 1965); and by their greater distribution than other members of the assemblage. *Cypria* is another active swimmer generally found in shallow water.

Going into deeper water (2-10 metres ?), the *Moenocypris* Assemblage would have been found. The vegetation would have consisted of submerged waterplants, drifted and partially rotted shore plants, with areas of bare lake muds. *Melanopsis* and *Viviparus* browse over bare areas, *Viviparus* usually being abundant where the vegetation is abundant (Daley, 1972). Although *Moenocypris* is an extinct genus, there are several reasons for believing it to have been a freshwater bottom crawler. It is a member of the Cyprididae, most of which inhabit freshwater, is found associated with typical fresh-water molluscs, and when found with other ostracodes these are fresh-water genera. Its elongate shape is rare for active swimmers; its numerous and well-developed ventral radial pore canals are characteristic of bottom dwelling crawlers (Hartmann, 1965); and finally its central muscle scars are situated well to the anterior, perhaps indicating poorly developed antennae for swimming, but well-developed posterior appendages for crawling. *Ilyocypris* appeared in the Oligocene and obviously had a broader environmental tolerance than the other ostracodes. Thus it is found in both assemblages and is the only ostracode to have a significant relationship with *Moenocypris* (Text-fig. 2). It was presumably a swimmer, and it is interesting to see that its closest association is with *Cypridopsis soyeri,* another swimmer. However, unlike *Cypridopsis* it was not apparently affected by the depth of water, giving it a wider range. None the less, it is more closely associated with the *Candona-Cypridopsis* Assemblage so presumably was more abundant in the shallower waters. Recent species of *Ilyocypris* are not amongst the most active of the swimming ostracodes, mainly living on the bottom. It is likely that the Oligocene species lived similarly, its swimming power allowing its wide distribution. *Vecticypris* also appeared in the Oligocene; its rounded shape suggests a swimmer, with a range similar to *Cypridopsis* spp. *Hemicyprideis montosa* has been regarded as a euryhaline ostracode, sometimes present as part of the biocoenosis of the *Candona-Cypridopsis* Assemblage (Keen 1971). Its main distribution, however, was in mesohaline salinities.

The two fresh-water assemblages may have inhabited separate areas, or may have been found in a single lake. Certainly there is very little mixing of the two; an exception can be seen in BC 76, Text-figure 3 (and see below). The physical conditions envisaged are indicated on Text-figure 2. The water must have been alkaline as evidenced by the molluscan faunas. The presence of well-preserved leaves and rootlets in the sediments of the *Moenocypris* Assemblage indicates the existence at times of a reducing environment, at least within the sediment if not the bottom waters. The water could only have flowed slowly, if at all, because of the presence of a well-preserved ostracode fauna. This is supported by the types of sediment and the fact that the fragile molluscan shells are usually complete. Salinity must have been less than 3‰ in most cases, again evidenced by the fauna. However the fresh-water environment graded into lagoonal regions with higher salinities, giving distinct ostracode faunal assemblages. *Cytheromorpha bulla* Haskins inhabited waters thought to have had a salinity of 5-9‰ and this ostracode may be present within either of the fresh-water assemblages. However, any rise in salinity much above 3‰ would have killed off the molluscs (Daley, 1972). The temperature is difficult to determine from the ostracodes; evidence from the other fauna and flora, presence of gypsum deposits and laterites, suggest much warmer conditions than today. The climate has traditionally been regarded as subtropical to warm temperate.



Text-figure 3. Diagram to show the percentages of various species in selected examples.
HH 21, lower Headon Beds, Headon Hill; HH 53, upper Headon Beds, Headon Hill; CB 12, upper Headon Beds, Colwell Bay; MF 3, lower Headon Beds, Milford; BC 76 and BC 98, middle Hamstead Beds, Bouldnor Cliff; CM 17, Bande blanche, Cormeilles-en-Parisis. In the key some symbols have two meanings; the first refers to the four Eocene samples on the left hand side of the diagram, the second to the three Oligocene samples on the right. N = number of specimens.

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTIONS

In general terms the *Candona-Cypridopsis* Assemblage is characteristic of the lower and upper Headon Beds, Bembridge Limestone, and a few horizons within the middle Hamstead Beds; while the *Moenocypris* Assemblage characterises the upper Headon, Osborne, and middle Hamstead Beds, although it also occurs in the lower Headon *Unio* Bed of Milford. The *Moenocypris* Assemblage is absent in the Paris Basin. The reason for this is fairly self evident: all the fresh-water deposits which have yielded ostracodes are limestones. Thus, as would be expected, the *Candona-Cypridopsis* Assemblage is often dominated by striated cyprids of the *Eucypris tenuistriata* group. In the Calcaire de Nogent l'Artaud of Nogent l'Artaud, Rosières and Grisy-les-Plâtres it is represented by *E. grisiensis* Margerie (Margerie, 1972); in the marls underlying the Marnes à P. *ludensis* by a closely related form, accompanied by two undescribed species of *Cypridopsis* and rare *Candona (Pseudocandona)*. The fauna of the Bande blanche can be seen in Text-fig. 3, C.M 17.

In Alsace the Couches de Pechelbronn have yielded many examples of the *Candona-Cypridopsis* Assemblage. A sample collected from the type locality yielded: *Eucypris pechelbronnensis* Stchepinsky (30%; cf. *E. amygdala* of the Bande blanche), *Candona (Pseudocandona) fertilis fertilis* Triebel (22%), *Herpetocypris* sp. 1 Stchepinsky (22%; cf. *H. nuda* of the Bande blanche), *Cypridopsis entzheimensis* (Stchepinsky) (17%), and *Ilyocypris* sp. (9%). This was from a clay, so the absence of the striated cyprid is not unexpected; otherwise it is very similar in composition to the fauna of the Bande blanche.

The Couches de Pechelbronn of the Mainz Basin have yielded both assemblages; *Cypridopsis* appears to be rare, while the striated cyprid is absent. Once again, only clays are present. The *Moenocypris* Assemblage is also found in the middle and upper Oligocene and in the Miocene (Triebel, 1963). In Hesse, only the *Candona-Cypridopsis* Assemblage is present, with several species of *Cypridopsis, Candona (Pseudocandona), Strandesia, Ilyocypris,* and the striated cyprid *E. tenuistriata straubi* (Carbonnel and Ritzkowski), (Carbonnel and Ritzkowski, 1969).

POPULATION STRUCTURE

The percentages of the different species are indicated in seven selected samples in Text-fig. 3. The first thing to notice is that the size of the samples is small. Jaccard's Coefficient depends upon the presence or absence of a species in a sample, so it is important that all the species present are recorded. Normally some 300 specimens are needed to satisfy this requirement. Such numbers were impossible to obtain from the size of the samples collected. Fresh-water ostracodes are not often abundant, and a great deal of sediment was searched to obtain the present number of specimens. However, as the number of species is small it is likely that a smaller number of specimens is needed to give a complete faunal analysis, while only the commoner species were used to determine the assemblages.

HH 21 and BC 98 show typical clay assemblages, dominated by *Candona (Pseudocandona)*, and with *Cytheromorpha bulla* as thanatocoenosis in HH 21. A typical limestone assemblage can be seen in CB 12; note that although *Candona (Pseudocandona)* sp. B is characteristic of limestones, *Candona (Pseudocandona)* sp. A is still the more abundant of the two. Some limestones could almost be called *Cypridopsis* limestones (HH 53); in these the ostracods can be seen clearly in the rock, with complete carapaces, although the valves are usually separated during preparation. CM 17 is from the Bande blanche; note the large percentage of *H. montosa*. In the three Oligocene samples illustrated (BC 76, BC 98, CM 17) *Ilyocypris boehli* forms an approximately constant percentage of the fauna, although the other constituents vary. BC 76 is one of the few samples to show a mixture of the two assemblages; this may be due to deepening, or shallowing, of the lake, resulting in one of the assemblages forming a remanié portion of the sample. MF 3 illustrates a *Moenocypris* Assemblage, with small numbers of *C. bulbosa;* in fact *Candona (Pseudocandona)* spp., *E. tenuistriata*, and *Darwinula* are also occasionally found with *Moenocypris*. This is presumably due to postmortem transportation. *Moenocypris*, being a large ostracode, can often be seen in hand specimens, and in the middle Hamstead beds sometimes completely covers bedding planes.

Sexual dimorphism is not readily apparent in many of the species. Margerie (1972) reported it in *E. grisiensis*. Males and females have been recognised in all the *Moenocypris* species and in *E.* cf. *grisiensis* due to the preservation of the imprints of testes and oves, but it is impossible to determine their relative abundance.

The age structure differs from species to species. The most "normal" of the species delt with are those of the *E. tenuistriata* group. Adults and larval stages are usually preserved, and in several samples many different moult stages can be recognised. The samples from Verzy have yielded several hundred specimens, making it possible to differentiate seven moult stages. The latter are not clearly differentiated so it is possible that *E.* cf. *grisiensis* had more than one breeding season per year (Keen, 1972). In the case of the *Cypridopsis* larval stages are rare, while with *Candona (Pseudocandona)* spp. only 2-3% of the specimens are adult. The small size of *Cypridopsis* (.4-.5 mm) may have led to the easy destruction of the even smaller larval stages. The lack of adults is more difficult to explain. It may be preservational, the larger adults being more liable to break; it may be an effect of migration; or it may reflect the true population structure, with few individuals reaching maturity. If the latter is the case then some environmental factor must have been operating, but it is difficult to determine what this may have been.

SOME TAXONOMIC COMMENTS

Haskins (1968) has described and figured some of the species referred to. *Candona (Pseudocandona)* sp. A = *Potamocypris* sp.; *Candona (Pseudo-*

candona) sp. B = *?Candonopsis* sp., the striated cyprid is referred to as *?Scottia* sp.; *Cyclocypris bulbosa* Haskins has been placed in the genus *Cypridopsis,* and *Candona forbesii* Jones into *Moenocypris.*

The generic designation of the striated cyprid is problematical; for a discussion see Margerie (1972). For reasons of uniformity Margerie's conclusion, *i. e.* that *Eucypris* is the nearest genus, has been adopted, although such a designation is still debatable.

REFERENCES

Carbonnel, G., and Ritzkowski, S.
1969. *Ostracodes lacustres de l'Oligocène.* Arch. Sci. Genève, vol. 22, pp. pp. 55-82, pls. 1-5.
Cavelier, C.
1969. *La limite 'Éocène-Oligocène' In Colloque sur 'lÉocène, Paris,* 1968, vol. 3, Mém. Bur. Rech. géol. min., No. 69, pp. 431-437.
Curry, D.
1966. *Problems of correlation in the Anglo-Paris-Belgian Basin.* Proc. Geol. Ass., vol. 77, pp. 437-467.
Daley, B.
1972. *Macroinvertebrate assemblages from the Bembridge Marls (Oligocene) of the Isle of Wight, England, and their environmental significance.* Palaeogeography, Palaeoclimatol., Palaeoecol., vol. 11, pp. 11-32.
Edwards, N.
1967. *Oligocene studies in the Hampshire Basin.* Thesis, University of Reading, pp. 170, unpublished.
Hartmann, G.
1965. *The problem of polyphyletic characters in ostracods and its significance to ecology and systematics.* Pubbl. Staz. zool. Napoli, vol. 33 suppl., pp. 32-44.
Haskins, C. W.
1968. *Tertiary Ostracoda from the Isle of Wight and Barton, Hampshire, England, Part II.* Rev. Micropaléont., vol. 11, pp. 3-12, 2 pls.
Keen, M. C.
1971. *A palaeoecological study of the ostracod Hemicyprideis montosa (Jones and Sherborn) from the Sannoisian of North-West Europe.* Bull. Cent. Rech. Pau, S.N.P.A., vol. 5 suppl., pp. 523-543, 2 pls.
1972. *The Sannoisian and some other Upper Palaeogene Ostracoda from North-West Europe.* Palaeontology, vol. 15, pp. 267-325, pls. 45-56.
Margerie, P.
1961. *Ostracodes de la carrière Lambert à Cormeilles-en-Parisis.* Bull. Soc. amic. Géol. amateurs, No. 2021, p. 1-24, 4 pls.
1972. *Essai de "quantification' 'du contour des ostracodes à l'occasion de la description d'une nouvelle espèce de Cypridinae du Marinesien du Bassin de Paris.* Rev. Micropaléont., vol. 14, pp. 227-234, 1 pl.
Sars, G. O.
1922-1928. *An account of the Crustacea of Norway.* Bergen Museum, vol. 9, 277 pp.
Stchepinsky, A.
1960. *Étude des ostracodes du Sannoisian de l'Alsace.* Bull. Serv. Carte géol. Alsace Lorraine, vol. 13, pp. 11-33, 3 pls.

Triebel, E.
1963. *Ostracoden aus dem Sannois und jungeren Schichten des Mainzer Beckens: 1, Cyprididae.* Senckenberg Leth., vol. 44, pp. 157-207, 12 pls.

M. C. Keen,
University of Glasgow,
Glasgow W2,
United Kingdom.

DISCUSSION

Dr. L. D. Delorme: Where you find *Ilyocypris*, is there any indication of water movement, either a stream entering the lake close by or current movement?

Dr. Keen: There is no evidence of water movement from the sediments containing the ostracodes, so they were probably deposited in fairly still water in flood plain lakes. Small scale current bedding and channeling occur within the succession, but such horizons are devoid of ostracodes.

Dr. H. S. Puri: You referred in your paper to "deeper" and "shallower" and a "hot" lake. I would like to ask what were depths and temperature ranges in the lakes?

Dr. Keen: As regards temperature, the ostracodes offer little information. From other evidence these Tertiary deposits are certainly subtropical, perhaps even tropical, so we are dealing with warm water. I wouldn't like to go any further than that. As for the deep water *vs.* shallow, I hesitate to give any exact figures. For shallow I am thinking of something in the order of a metre or less, for deep around four or five metres. There could thus be two situations, one where a single lake has these two depth zones, the other where there are extensive areas of shallow lakes.

Dr. A. Liebau: You mentioned the gastropod *Melanopsis* as characterizing your fossil freshwater faunas. As far as I know, *Melanopsis* indicates brackish water influences. In Upper Cretaceous faunas I have studied, *Melanopsis* is found from about polyhaline down to oligohaline brackish water. Also the Recent representatives I know live next to the sea (Spain, Morocco) or in the neighbourhood of a salt lake (Tunisia) or get *e.g.* salinity from Miocene gypsum (Spain: Rio Genil).

Dr. Liebau: I cannot imagine that *Melanopsis* lives in true fresh water. But on the other hand besides *Viviparus*, another genus in your list, also *Unio* is said to indicate a salinity less than 3‰ (at least in the Baltic Sea area). Perhaps there were some salinity influences below the 3-per mille mark. I mention this because also such a small difference could be important for the occurrence of some fresh-water ostracodes.

Dr. Keen: *Melanopsis* is one of those gastropods that inhabits both brackish and freshwater. I wouldn't draw any firm conclusions from its occurrence, although it is very common. I draw my evidence from *Viviparus* which is never found in salanities greater than 3‰ at the present day.

(i). By freshwater, I mean less than 3‰, although I believe it to have been less than 0.5‰ in most cases. *Unio* is also present, and, as you mention, provides further evidence for freshwater conditions.

(ii). May I refer you to Daley (1972)? In his discussion of the habitat of *Melanopsis* from the Bembridge Beds, he mentioned its problematical significance with regard to salinity, concluding that while it inhabited freshwater together with *Viviparus,* it may have had a higher salinity tolerance than the latter, as it also occurs in shell concentrates thought to have accumulated in waters transitional from fresh to brackish.

Dr. R. L. Kaesler: Is it possible that the *Moenocypris "assemblage"* is from the hypolimnion and that the other, more diverse assemblage is epilimnetic?

Dr. Keen: I don't believe these terms are applicable to the kind of lake I'm envisaging. Firstly, they were probably subtropical, and secondly they were probably never really deep (*i.e.* $>$ 20m.). So I doubt if there was any marked temperature division. It is more likely that *Moenocypris* would have been found in the lower infralittoral zone (*i.e.,* zone of submerged water plants), while the *Candona-Cypridopsis* Assemblage would have been found in the upper infralittoral zone (*i.e.* zone of emergent water plants).

Dr. Sohn: *Melanopsis* is shallow in the Jordan River, Israel. The striated form looks something like *Zonocypris.*

Dr. Keen: As I've already mentioned, I have not placed much emphasis on *Melanopsis.* The striated ostracode certainly resembles *Zonocypris,* and in fact I first assigned it to this genus. The ornamentation is different, however, being longitudinal rather than concentric as in *Zonocypris.*

Dr. Oertli: We find similar striated forms as far down as Lias. Several other striated species still not described occur also in the Spanish Wealden.

Dr. Keen: (i). I hadn't realised that. Do these show the same smooth and striated forms?

(ii). The taxonomic position of these forms is difficult. Their outstanding characters, *i.e.* striations, appears to be ecologically controlled. According to Dr. Carbonnel temperature may be the controlling factor. So you can hardly define a group upon a phenotypic character. And yet, they do seem to form a distinct group of ostracodes.

Dr. Swain: With regard to the depth of the lakes, the assemblages that you cited composing mostly snails and ostracodes suggest epilimnetic conditions rather than hypolimnetic, perhaps shallower vs deeper parts of the epilimnion. We have a form similar to the striated ostracode in the Green River Formation, and I have the types here if you would care to look at them.

Dr. Keen: What genus do you refer it to?

Dr. Swain: I called it a *Metacypris,* but it probably is not.

Dr. Hazel: I am curious about how many specimens per sample and how big a sample do you have to take?

Dr. Keen: This varies a lot. Some of the limestones are very rich in ostracodes, in fact some could almost be called ostracode limestones. On the other hand, with some samples, you need to sort through several pounds of sediment to find 30 or so specimens. Thus the numbers vary considerably. Some idea of the numbers is given in the text, and in Text-figure 3.

Dr. Sohn: Is *Ilyocypris* a swimmer or a crawler?

Dr. Keen: According to Sars some species are swimmers, some are predominantly crawlers.

Dr. Hartmann: The striated form *(?Eucypris)* may equal *Strandesia,* and the *Moenocypris* may equal *Stenocypris. Strandesia* and *Stenocypris* are warm water forms. All the species are probably calm water forms.

Dr. Keen: I'm not too sure whether this is meant as a taxonomical or ecological synonymy. I wouldn't agree with assigning them to these genera. Ecologically, I don't know about *Strandesia,* except that its a warm water form; *Mocnocypris* is envisaged as having a similar life mode to *Stenocypris.*

LE FACTEUR LISSE CHEZ CERTAINS OSTRACODES TERTIAIRES: UN INDEX DE PALÉOTEMPÉRATURE

G. Carbonnel
Université Lyon1-Claude Bernard

RÉSUMÉ

La disparition de l'ornementation, ou facteur lisse, et ses modalités sont étudiées chez plusieurs espèces marines telles *Leptocythere pentagonalis* Carbonnel et *Elofsonella amberii* Carbonnel ou saumâtres *Cytheromorpha* sp. Kuster-Wendenburg et *Hemicyprideis dacica grekoffi* Carbonnel, enfin lacustres telles *Eucypris? grisiensis* Margerie, *Eucypris? tenuistriata straubi* Carbonnel, Ritzkowski et *Limnocythere* n. sp.

L'observation au microscope électronique à balayage a permis la découverte de nouvelles structures anatomiques exclusives des formes lisses, à savoir *verrucae* et *aréa-polyporée*. Leur signification physiologique est encore inconnue.

La corrélation entre le facteur lisse et l'apparition de tubercules a conduit à la définition des morphotypes lisse et tuberculé (lt), lisse (l) orné tuberculé (ot) et orné (o).

L'analyse de groupe appliquée au déterminisme du facteur lisse exclut la salinité comme agent déterminant. La variation de température du milieu est proposée comme agent responsable du facteur lisse.

ABSTRACT

The disappearance of ornamentation, or smooth factor and its modalities are studied in different marine species such as *Leptocythere pentagonalis* Carbonnel and *Elofsonella amberii* Carbonnel or in brackish species as *Cytheromorpha* sp. Kuster-Wendenburg and *Hemicyprideis dacica grekoffi* Carbonnel and eventually lacustrine species as *Eucypris? grisiensis* Margerie, *Eucypris? tenuistriata straubi* Carbonnel, Ritzkowski and *Limnocythere* n. sp.

The scanning electron microscope observation allowed the discovery of new anatomical structures which are exclusive of smooth shapes, viz *verrucae* and *area polyporea*. Their physiological meaning still remains unknown.

The correlation between the smooth factor and the apparition of tubercules has led to the definition of the smooth and ornate (lt), smooth (1), ornate and tuberculated (ot) or ornate (o) morphotypes.

Cluster analysis applied to the determination of the smooth factor excludes salinity as a determining agent. Variation of temperature in the biotope is taken as the responsible agent for the smooth factor.

INTRODUCTION

L'importance accordée jusqu'à présent dans la description systématique des Ostracodes à l'ornementation justifie en retour celle que l'on doit attribuer à sa régression chez ces mêmes espèces. On entendra par facteur lisse la disparition ou la régression de l'ornementation observée habituellement chez une espèce: côtes, ponctuations, fossettes, réticulations etc. . . Ce concept ne s'appliquera pas à la disparition des tubercules (phénotypiques ou génotypiques, selon les auteurs), éventuellement apparus sous certaines conditions écologiques.

Un nombre trop restreint d'auteurs se sont intéressé jusqu'alors à ce phénomène et à ses modalités. C'est une lacune que ce travail se propose de combler partiellement. On envisagera ici les modifications anatomiques à la suite de la disparition de l'ornementation et sa liaison avec la présence des tubercules (phénotypiques ou génotypiques). L'analyse du déterminisme du facteur lisse conduira à proposer la variation de la température comme agent déterminant.

HISTORIQUE

Dès 1960 V. Stchépinsky signalait l'existence (chez *Cytheridea gilletae*) de valves lisses à côté de valves ornées. Mais la première étude synthétique importante a été celle de Ph. Sandberg (1964). Il a indiqué l'existence de la disparition de l'ornementation chez plusieurs espèces (tabl. 2), invoquant l'abaissement de la salinité comme déterminisme écologique de ce phénomène.

En 1967 G. Carbonnel a montré l'existence du même phénomène chez *Elofsonella amberii*. Il en rendait également responsable une baisse de la salinité du milieu.

Plus récemment, R. H. Benson (1969) soulignait à propos d'un représentant de *Limnocythere* (du Pleistocène ancien de Rita Blanca Lakes) que les espèces de ce genre acquièrent une ornementation plus accentuée, lorsque l'eau douce de leur biotope devient plus salée. Il reconnaissait toutefois, quelques lignes auparavant, que le problème n'était pas résolu!

En 1969 G. Carbonnel (*in* G. Carbonnel et S. Ritzkowski) signalait encore l'existence du facteur lisse chez une forme lacustre de l'Oligocène : *Eucypris* ? *tenuistriata straubi.*

Au dernier symposium sur la Paléoécologie des Ostracodes (Pau, 1971) divers auteurs ont évoqué ce phénomène. En particulier W. Ohmert (p. 611) a constaté, lors de l'étude des formes laguno-marines du Crétacé, une relation entre la réduction de l'ornementation et la diminution de la profondeur.

H. Jordan et M. J. M. Bless (1971, p. 683 et suiv.) ont observé parmi diverses modifications, une réduction de l'ornementation chez une espèce du genre *Cypridea.*

D'après ces quelques renseignements bibliographiques les espèces à facteur lisse sont taxinomiquement variées; elle vivent en milieu lacustre, saumâtre ou marin. Le déterminisme de ce facteur est variable (salinité profondeur, ou autre(s). . . . .), mais mal connu et peu étudié.

RÉPARTITION SYSTÉMATIQUE, GÉOGRAPHIQUE ET ÉCOLOGIQUE DES ESPÉCES ÉTUDIÉES

Elle est indiquée sur la tableaux 1 et 3.

Il ressort de ces répartitions que le facteur lisse est un phénomène général, largement réparti dans le temps et probablement indépendant de la chlorinité du biotope originel de l'espèce.

MODALITÉS MORPHOLOGIQUES DE L'APPARITION DU FACTEUR LISSE

Chez *Limnocythere,* n. sp. (Pl. 2, figs. 10-20)
(environ 500 individus observés)

Le morphotype orné, considéré comme "normal", est très rarement représenté au sein des populations. L'ornementation est essentiellement constituée

Espèces	N échant
Cytheromorpha sp.	1353 à 1353 1353 1353
Elofsonella amberii	1350 1350 1350 1353 à 1353
Eucypris? grisiensis	1353 1353 1353 à 1353 1353
Eucypris? tenuistriata straubi	2 638- 1353
Hemicyprideis dacica grekoffi	1353 à 1353
Leptocythere pentagonalis	1350 1350 1353
Limnocythere n. sp.	
	1353 1353 1353 1353 1353
	135 135
	135 135
	135 135 135

[1] Exemplaires conse
Pasteur, 69-Lyon

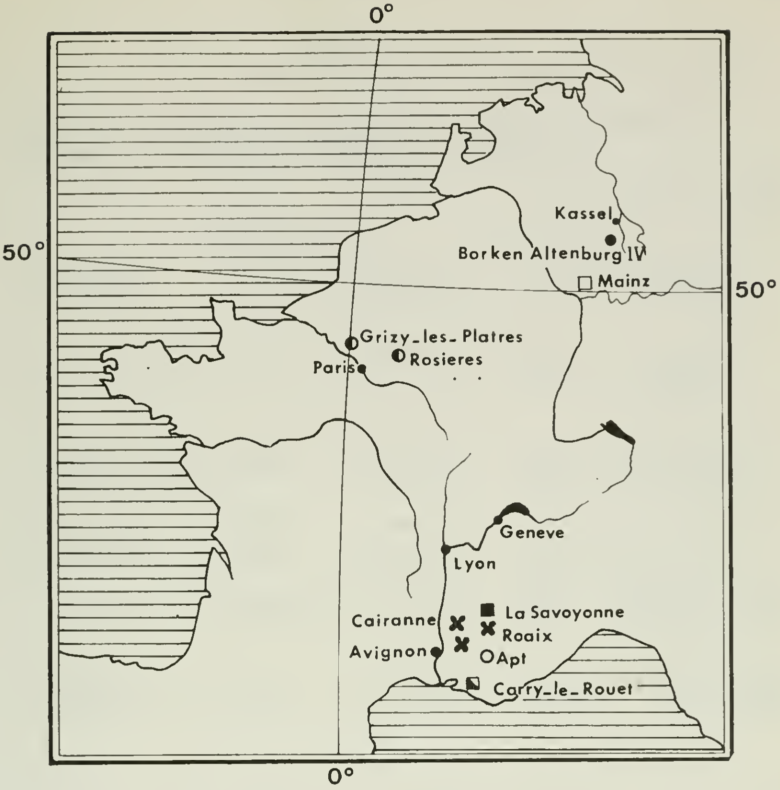
[2] Exemplaires conse
Fédérale.

Tableau 1. Répertoire du Matériel Étudié

Especes	No échantillon	Dénomination de la coupe	Formation	Étage	Commune	Département
Cytheromorpha sp.	135358[1] à 135362 135380[2] 135382		Untere Hydrobien-Schichten	Aquitanien	Mainz	
Elofsonella amberii	135008 135009	la Savoyonne	à *Ostrea crassissima*	Tortonien	Visan	Vaucluse
	135018	Cairanne	"	"	Cairanne	"
	135336 à	Roaix	"	"	Buisson	"
	135338	les Eyssarettes	"	"	Puyméras	"
Eucypris? grisiensis	135339 135340	Grisy-les-Plâtres		Bartonien	Grisy-les-Plâtres	Seine et Oise
	135343 à 135357 135386	Rosières		Bartonien	Rosières	Oise
Eucypris? tenuistriata straubi	[2] 638-142 135341	Borken Altenburg IV	à *Nystia-Melanopsis*	Sannoisien		
Hemicyprideis dacica grekoffi	135326 à 135328	Carry-le-Rouet	pararécifale du Cap des Nautes/ bioclastique de Carry; biodétritique de Sausset-les-Pins	Aquitanien	Carry-le-Rouet	Bouches-du-Rhône
Leptocythere pentagonalis	135046 135047 135363	la Savoyonne	à *Ostrea crassissima*	Tortonien	Visan	Vaucluse
Limnocythere n. sp.		1777		Sannoisien	Caseneuve	Vaucluse
		1577		"	Rustrel	"
		20		"	Apt	"
	135367	27		Stampien	Mallemont-du-Comtat	"
	135368				Fontaine-de-Vaucluse	
	135387			"		"
	135385	49			l'Isle sur Sorgue	Vaucluse
	135384			"		
		52		"	Vénasque	"
		62		Bartonien	Apt	"
		100				
				Ludien	Apt	"
	135369	102				
	135372			Sannoisien	Apt	"
		103		"	"	"
		104		Ludien	Blauvac	"
		106				
				Stampien	Vénasque	"
	135364	122				
	135366			Stampien	"	"
		124		"	"	"
		146				
	135370 135371 135383	926		Oligocène inf.	Gignac	

[1] Exemplaires conservés au Département Sciences de la Terre, Université de Lyon Claude-Bernard, 86, rue Pasteur, 69-Lyon 7eme, France

[2] Exemplaires conservés au Geolog. Paläontol. Institut, 34 Gottingen, Berliner-Strasse 28, Allemagne Fédérale.



○ *Limnocythere*, n. sp.

◐ *Eucypris ? grisiensis*

● *Eucypris ? tenuistriata straubi*

□ *Cytheromorpha* sp.

◪ *Hemicyprideis dacica grekoffi*

■ *Leptocythere pentagonalis*

✖ *Elofsonella amberii*

Text-figure 1.

Tableau 3. Répartition géographique, lithostratigraphique et écologique des espèces étudiées, à facteur lisse

	genre/espèce	localisation géographique	localisation stratigraphique	chlorinité du biotope "normal"	lithofacies du prélèvement
LIMNO-CYTHER-IDAE	Limnocythere, sp.	bassin du Rhone	Oligocène	lacustre	
CYPRIDINAE	Eucypris? grisiensis Margerie, 1971	bassin de Paris	Eocène sup. (Bartonien)	lacustre	sables argileux et calcaires argileux
	Eucypris? tenuistriata straubi (Carb. Ritz, 1969)	bassin de la Hesse	Oligocène inf.	lacustre	
LOXOCON-CHIDAE	Cytheromorpha sp. Kuster-Wendenburg, 1970	bassin de Mayence	Miocène inf. (Aquitanien)	saumâtre	calcaire-argileux
CYTH-ERIDAE	Hemicyprideis dacia grekoffi (Carb., 1969)	bassin du Rhône	Miocène inf. (Aquitanien)	saumâtre à marin	sables argilo-calcaire à argiles
LEPTO-CYTH-ERIDAE	Leptocythere pentagonalis (Carb, 1969)	bassin du Rhône	Miocène sup. (Tortonien)	marin	calcaire argileux
HEMI-CYTH-ERIDAE	Elofsonella amberii (Carb., 1969)	bassin du Rhône	Miocene sup. (Tortonien)	marin	calcaire argileux

par des cellules polygonales, développées de préférence dans la moitié postérieure de la valve (Pl. 2, figs. 10-12).

Le morphotype lisse présente un stade intermédiaire (Pl. 2, fig. 13) avant d'acquérir la structure lisse. Dans ce cas l'ornementation subsiste dans la zone postérieure de la carapace. La facteur lisse est présent chez les larves.

Tableau 2 (•) C
modifié d'après Sandberg

Morphotypes

	Espèces
ETATS-UNIS D'AMERIQUE	Cyprideis ovata (Mincher)
	Cyprideis salebrosa van den Bold
	Cyprideis locketti (Stephenson)
	Cyprideis pascagoulensis (Mincher)
	Cyprideis castus Benson
	Cytheromorpha calva Krutak
	Cytheromorpha ouachatensis Howe et Chambers
	Cytheromorpha paracastanea (Swain)
	Anomocytheridea inornata Stephenson
FRANCE	Cytheridea gilletae Stchépinsky
	Nombre de morphotypes observés

Tableau 2. Ostracodes présentant le facteur lisse
modifié d'après Sandberg (1964, pl. I-III) et Stchépinsky (1960, pl. 3)

	Espèces / Morphotypes	orné tuberculé (ot)	lisse tuberculé (lt)	lisse (l)	orné (o)
	Cyprideis ovata (Mincher)	+			+
ETATS-UNIS D'AMERIQUE	Cyprideis salebrosa van den Bold	+		+	+
	Cyprideis locketti (Stephenson)	+		+	+
	Cyprideis pascagoulensis (Mincher)				+
	Cyprideis castus Benson			+	+
	Cytheromorpha calva Krutak			+	+
	Cytheromorpha ouachatensis Howe et Chambers			+	+
	Cytheromorpha paracastanea (Swain)			+	+
	Anomocytheridea inornata Stephenson			+	+
FRANCE	Cytheridea gilletae Stchépinsky	+		+	+
	Nombre de morphotypes observés	4	0	8	10

Tableau 4. Morphotypes observés chez *Limnocythere*, n. sp. et leur relation avec la salinité et la température du milieu.

No. des prélèvements	morphotype lisse		morphotype orné		% NEOCYPRIDEIS			température déduite des morphotypes	salinité déduite des morphotypes	température, salinité, d'après la sédimentation
	tub. lt	non tub. l	tub. ot	non tub. o	> Limnocythere	< Limnocythere	abs.	is = instable		
147/15		+			+					
1777/3		+				+				
1577/8		+				+				
20 1bis		+					+			
27/23	+	+				+		is	is	is
27/37		+			+					
27/24						+				
27/12		+					+			
27/22	+	+				+		is	is	is
27/72		+		+	+					
49/30		+	+		+			is	is	is
49/18	+		+			+		is	is	is
49/16				+		+				
49/8		+		+	+					
49/19		+				+				
49/29		+			+					
49/26	+	+				+		is	is	is
49/27	+	+		+	+			is	is	is
52/14		+					+			
62/7	+				+			is	is	is
100/12		+		+			+			
100/11		+		+			+			
102/20	+	+				+		is	is	is
102/21		+					+			
103/48		+					+			
104/2c		+				+				
104/2a		+					+			
104/6		+				+				
104/5		+				+				
104/7		+					+			
104/9		+					+			
104/10	+	+			+			is	is	is
104/12							+			
104/13		+				+				
104/15		+				+				
104/18		+					+			
106/9		+			+					
122/	+	+					+	is		is
124/3		+					+			
146/10	+	+			+			is	is	is
146/9		+			+					

Chez *Eucypris ? grisiensis* Margerie, 1972 (Pl. 1, figs. 2-4, 6-10)
(200 individus observés)

Les morphotypes ornés portent des stries longitudinales sur toute la surface. Certains présentent une anastomose de stries (Pl. 1, fig. 2).

Le morphotype orné tend à acquérir, par place (dans la zone dorsale, médiane ou ventrale) une structure lisse. Cette observation est, pour l'instant, limitée aux ostracodes présents dans deux prélèvements du bassin de Paris (coupe de Rosières, Oise, niveau 602). Les morphotypes ornés de côtes anastomosées, ne présentent pas ce stade intermédiaire.

Des morphotypes entièrement lisses ou semi-lisses (Pl. 1, figs. 4, 6-10) existent suivant les lieux de prélèvements. Les morphotypes semi-lisses conservent encore la trace des côtes dans les zones périmarginales antérieure et postérieure. Les larves semblent de préférence aux adultes exprimer le facteur lisse.

Chez *Eucypris ? tenuistriata straubi* Carbonnel, Ritzkowski, 1969. (Pl. 1, figs. 1, 5). La réalisation de l'ornementation du morphotype orné est semblable à celle d'*E. ? grisiensis* (cf. Carbonnel, Ritzkowski, 1969, pl. 2, figs. 1, 2, 6).

Le morphotype semi-lisse, avec costules antérieures et postérieures résiduelles, (*cf.* Carbonnel, Ritzkowski 1969, pl. 2, figs. 4, 5) est le seul observé.

Chez *Cytheromorpha* sp. Kuster-Wendenburg, 1969 (Pl. 2, figs. 4-9).

Le morphotype le plus orné possède un réseau de cellules polygonales très accentuées.

Les morphotypes lisse ou à tendance lisse montrent une régression du réseau, particulièrement sensible dans la moitié postérieure (Pl. 2, figs. 8-9). Dans le cas le plus regressé seules subsistent les fines ponctuations situées à l'intérieur des mailles polygonales du réseau (Pl. 2, fig. 9).

Chez *Hemicyprideis dacica grekoffi* (Carbonnel, 1969).

Les modifications de l'ornementation ont été étudiées précédemment (Carbonnel, *in* P. Andreiff, *et al.,* 1971).

On se bornera à rappeler que l'acquisition du facteur lisse est progressif. (Carbonnel, 1971, pl. 4, figs. 1, 4, 7, 11). La réduction de l'ornementation (chez l'adulte) commence dans la région antérieure.

Chez *Leptocythere pentagonalis* Carbonnel, 1969(Pl. 2, figs. 1-3).

Le morphotype orné est essentiellement observé au stade adulte.

Les morphotypes semi-lisses et lisses sont observés aux différents stades larvaires. La régression de l'ornementation peut se poursuivre jusqu'à la disparition des fossettes (Carbonnel, 1969, pl. 5, figs. 4-6). Elle débute dans la zone médiane et s'étend vers l'arrière et dorsalement.

Chez *Elofsonella amberii* Carbonnel, 1967 (Pl. 1, figs. 11-13).
(185 individus observés)

Le morphotype orné présente une réticulation entre les côtes alors que le morphotype lisse en est dépourvu (pl. 1, figs. 11-2).

CONCLUSIONS

Des stades intermédiaires dans la régression de l'ornementation existent chez tous les exemples étudiés. Leur nombre et l'importance de l'ornementation résiduelle sont variables selon les espèces.

L'acquisition de la structure lisse débute toujours chez une espèce dans le même zone, mais cette dernière est variable suivant les espèces.

Les larves comme les adultes semblent affectés par ce facteur.

MODIFICATIONS ANATOMIQUES CHEZ CERTAINS MORPHOTYPES LISSES

Elles concernent *Eucypris ? grisiensis* Margerie et *Elofsonella amberii* Carbonnel.

Microtubercules ou verrucae (Pl. 1, figs. 8-9).

Des microtubercules supplémentaires, assimilables aux *verrucae*[1], sont visibles dans la région médio-dorsale sur un exemplaire entièrement lisse d'*E. ? grisiensis*. Ils sont dépourvus de pores sétigères. Au grossissement utilisé (x 1100 environ) la surface elle même parait granuleuse.

Les morphotypes semi-lisses, adultes ou larvaires, en sont dépourvus qu'elle qu'en soit la provenance géographique.

Aréa polyporée (Pl. 1, fig. 13).

On note la présence d'une surface percée de nombreux pores de petite taille vers l'extrémité antérieure de la côte médiane chez *Elofsonella amberii,* sur le morphotype lisse. L'aréa polyporée est inconnue chez les autres morphotypes.

Les autres espèces étudiées ici ne présentent pas, jusqu'à présent, de modifications semblables du système porifère ou de la surface des valves.

L'acquisition du facteur lisse influe parfois sur les micro-structures de la carapace de façon variable. La répercussion de ces modifications sur le comportement physiologique nous échappe encore.

LE FACTEUR LISSE ET LES TUBERCULES "PHÉNOTYPIQUES"

Quelques espèces présentant le facteur lisse peuvent également porter, dans certaines circonstances écologiques, des tubercules communément appelés tubercules "phénotypiques". Il s'agit de:

Limnocythere, n. sp.
Cytheromorpho sp. Kuster-Wendenburg
Hemicyprideis dacica grekoffi Carbonnel

L'analyse a porté sur 40 prélèvements ayant fourni des adultes et des larves appartenant à *L.*, n. sp. On a pu constater l'existence: de morphotype à la fois lisse et tuberculé, *lt*[2], (Pl. 2, figs. 16-18) représentant 25% de la population,[3] de morphotype lisse et non tuberculé, *l.*[2] (Pl. 2, fig. 15) repré-

---

[1] Selon la terminologie de P. C. Sylvester-Bradley, 1971.

[2] L'assimilation des formes figurées par Ph. Sandberg 1964 à ces morphotypes est indiquée sur le tableux 2.

[3] La somme en pourcentage peut être supérieure à 100, un prélèvement pouvant présenter simultanément plusieurs morphotypes.

sentant 90% de la population, de morphotype orné et tuberculé, Ot^2 (Pl. 2, fig. 11), représentant 5% de la population et de morphotype orné et non tuberculé O^2 (Pl. 2, figs. 10, 12) repréentant 15% de la population.

On retiendra de ces pourcentages l'indépendance des facteurs lisse et tuberculé. Cette indépendance est confirme chez *Cytheromorpha* sp. Kuster-Wendenburg, espèce chez laquelle les tubercules apparaissent sur des larves très ornées (Pl. 2, fig. 4). Il en est de même chez *Hemicyprideis dacica grekoffi* où les tubercules semblent s'atténuer et même disparaitre sur les morphotypes lisses (*cf.* Carbonnel, 1971, pl. 4, figs. 5, 11). On peut raisonnablement déduire de ces constatations que la disparition de l'ornementation est relativement indépendante de l'apparition des tubercules. Cette déduction acquerra une grande importance dans l'étude du déterminisme de ce phénomène.

ÉTUDE DU DÉTERMINISME DU FACTEUR LISSE

1) Variation de la chlorinité.

La présence temporaire, suivant les prélèvements, du facteur lisse chez une espèce implique probablement un déterminisme écologique. Compte tenu de l'indépendance pressentie entre les facteurs lisse et tuberculé, leurs déterminismes doivent être différents.

La voie expérimentale directe, interdite au géologue, consisterait à faire varier l'amplitude des paramètres réputés actifs sur la biologie des ostracodes: la chlorinité (teneur en NaCl du milieu), la température, la concentration en O_2, le pH, etc. . . On observerait alors les modifications morphologiques éventuelles. On devra toutefois se contenter d'une approche géologique, c'est-à-dire indirecte, du phénomène.

2) Calcul du taux de liaison par l'analyse de groupe (W.P.G.M.) entre le facteur lisse observé chez *Limnocythere*, n. sp. et le genre saumâtre *Neocyprideis*.

On peut étudier par cette méthode, le taux de liaison entre les divers morphotypes précédemment définis (*lt, l, ot, o*) et la présence, l'absence et la dominance du genre *Neocyprideis*. Ce dernier, réputé saumâtre, constitue alors une référence de la chlorinité du milieu. Le dendogramme de la figure 2, obtenu à partir du coefficient de Jaccard, traduit le degré de liaison entre ces "paramètres". On constate que le facteur lisse est associé à une population parmi laquelle le genre *Neocyprideis* n'est pas prédominant. Ce facteur n'est donc pas inféodé à une chlorinité réduite.

3) Calcul du taux de liaison par l'analyse de groupe (W.P.G.M.) entre le facteur lisse observé chez *Hemicyprideis dacica grekoffi* et la chlorinité obtenue par l'analyse sédimentologique.

Dans cet exemple, la chlorinité a été uniquement déduite des études sédimentologiques. (P. Andreiff, R. Anglada *et al.* . . . 1971). L'analyse de groupe permet d'établir le taux de liaison très faible entre la diminution de la chlorinité et le facteur lisse comme le montre le dendogramme de la figure 3, obtenu à partir du coefficient de Jaccard.

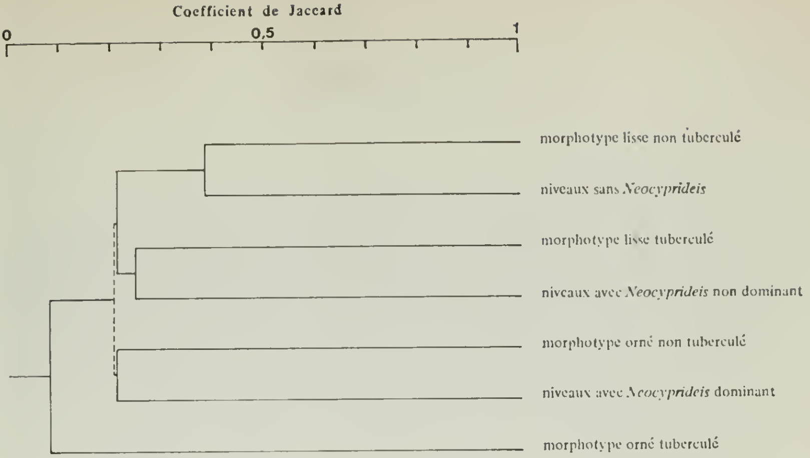


Figure 2. Dendogramme (coefficient de Jaccard, W.P.G.M.) des morphotypes de *Limnocythere*, n. sp. et du genre *Neocyprideis* dans les bassins oligocènes d'Apt, Pernes et Mormoiron.

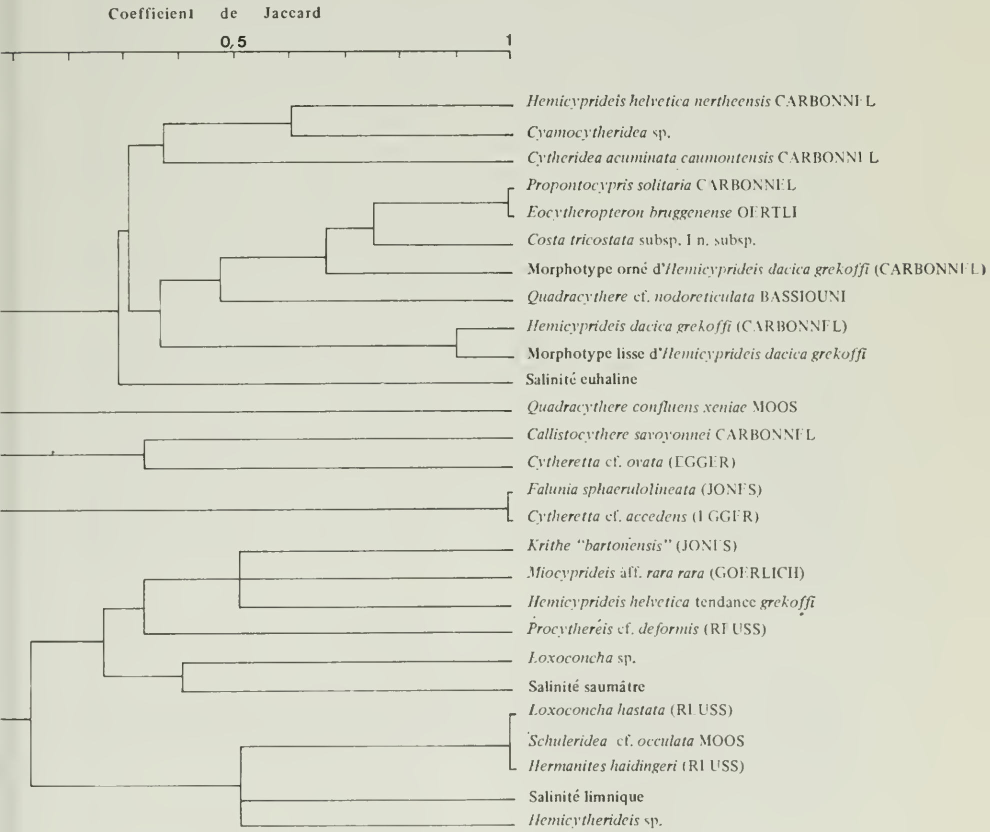


Figure 3. Dendrogramme (coefficient de Jaccard, W.P.G.M.) des ostracodes associés à *Hemicyprideis dacica grekoffi* (Carb.,) (morphotypes lisses et ornés) et de la chlorinité du milieu, dans la coupe de Carry-le-Rouet.

4) Conclusions

Ces deux analyses confirment l'indépendance du facteur lisse (de son apparition et de sa persistance) par rapport à la baisse de la chlorinité de l'eau. Elle avait été pressentie par l'auteur en 1969 à propos des morphotypes semi-lisses d'*E.* ? *tenuistriata straubi* Carbonnel et Ritzkowski (de l'Oligocène de la Hesse). L'observation de ces morphotypes comme de ceux rapportés ici à *E.* ? *grisiensis* (de l'Eocène du bassin de Paris) en *milieu lacustre,* interdit d'envisager une baisse de la chlorinité comme agent déterminant. Le déterminisme de ce facteur doit être recherché dans une autre direction.

5) Variation de la Température

O. Kinne, dans diverses publications (en particulier 1964) a montré l'importance des couples température-salinité-concentration en oxygène du milieu, sur le comportement physiologique des Crustacés. D'après ce qui précède, la chlorinité étant exclue comme agent déterminant, peut-on considérer une variation de la température comme responsable de l'apparition de facteur lisse? En l'absence de mesures de paléo-températures, l'approche de ce problème sera encore indirecte.

Jusqu'à présent aucune indication sur la température ne peut être obtenue à partir des prélèvements ayant livrés *Eucypris* ? *grisiensis*, *E.* ? *tenuistriatus straubi, Elofsonella amberii* et *Leptocythere pentagonalis.*

La majorité des niveaux de la coupe de Carry-le-Rouet ayant livré *Hemicyprideis dacica grekoffi* est caractérisée par une eau tempérée chaude d'après la macrofaune (*pro parte*) et certains foraminifères. On aura garde en outre d'oublier l'existence de formations récifales à plusieurs niveaux de la coupe.

Une seconde preuve de l'influence de l'augmentation de la température nous est fournie par l'environnement des niveaux à *Limmocythere,* n. sp. Il s'agit de prélèvements intercalés au sein d'un complexe évaporitique, gypseux, de l'Oligocène (J. M. Triat, et G. Truc 1972). On exclura, compte tenu de ce qui précède, une baisse de la température comme agent déterminant.

De plus, l'analyse du rapport hauteur/longueur de la valve chez *Elofsonella amberii* et *Eucypris* ? *tenuistriata straubi,* morphotypes lisses et ornés, ne révêle aucune augmentation de taille. En effet, elle devrait se produire dans un milieu à basse température (*cf.* J. Szczechura, 1971 pour l'étude la plus récente de ce phénomène).

L'ensemble de ces arguments tend à accréditer l'hypothèse d'une augmentation de la température de l'eau comme déterminisme du facteur lisse. Des phénomènes analogues concernant la disparition de caractères ornementaux ont été décrits et étudiés expérimentalement chez *Daphnia retrocurva* et *Daphnia galeata* (J. L. Brooks, 1946). La disparition de l'épine sommitale de la tête résulte d'après ces études d'un abaissement de la température, à l'inverse des Ostracodes.

INTERPRÉTATION DES MORPHOTYPES LT, L, OT, O

Il ressort de l'analyse précédente qu'une élévation de la température du milieu peut se manifester par l'apparition du facteur lisse. Il est en outre admis qu'une variation de la salinité peut se traduire par la production de tubercules.

L'observation dans un prélèvement de morphotypes appartenant au groupe:

— *ot*: indiquerait un milieu à chlorinité variable, à température constante

— *lt*: indiquerait un milieu à chlorinité variable, à température variable en hausse

— *l*: indiquerait un milieu à chlorinité constante, à température variable en hausse

— *o*: indiquerait un milieu à chlorinité constante, à température constante.

Application aux prélèvements oligocènes à *Limnocythere* n. sp. Confirmation de la température comme agent déterminant du facteur lisse.

Les 4 premières colonnes du tabl. no. 4 indiquent pour chaquh prélèvement la nature des morphotypes observés. La présence du genre *Neocyprideis* et son abondance, relativement à la population de *Limnocythere,* n. sp., sont inscrites dans les 3 colonnes suivantes. Dans les 2 autres colonnes sont figurées l'interprétation de la température et de la salinité du milieu; elle est déduite des morphotypes présents dans les 4 premières. La confirmation ou l'infirmation de l'interprétation du milieu par l'analyse sédimentologique est mentionnée dans la dernière colonne.

Dans l'ensemble, la confirmation apportée par ces études sédimentologiques nous autorise à proposer la variation de température comme déterminisme susceptible de provoquer, chez certains ostracodes, l'apparition du facteur lisse.

ESSAI D'INTERPRÉTATION PHYSIOLOGIQUE DU FACTEUR LISSE

O. Kinne (1966) a souligné que le degré de résistance des organismes est augmenté lorsque la concentration en calcium des cellules croit corrélativement.

Le facteur lisse correspond, sans doute, à une diminution de la consommation du calcium au profit d'une rétention potentielle plus élevée de cet élément à l'intérieur du liquide cellulaire; cela permettrait d'étendre l'interprétation de O. Kinne à certains Ostracodes.

REMERCIEMENTS

Je tiens à remercier particulièrement P. Margerie (Argenteuil, France), E. Kuster-Wendenburg (Mainz, Allemagne Fédérale) et M. Castel (Montpellier, France) pour l'amabilité avec laquelle ils m'ont permis d'utiliser leur matériel.

Mes remerciements vont également à J. M. Triat (Marseille) et G. Truc (Lyon) pour l'autorisation de mentionner leurs résultats stratigraphiques et sédimentologiques.

BIBLIOGRAPHIE

Andreiff, P., Anglada, R., Carbonnel, G., Catzigras, F., Cavelier, C., Chateauneuf, J. J., Colomb, E., Glintzboeckel, Ch., Jacob, C., Lay, J., Lezeaud, L., Lhomer, A., Lorenz, C., Mercier, H., Parfenoff, A.

1971. *Contribution à l'étude de l'Aquitanien. La coupe de Carry-le-Rouet, Bouches-du-Rhône, France,* Bull. Bur. Rech. géol. min., Paris, Sect. 1, No. 4, 135 p., 17 pls.

Benson, R. H.

1969. *Ostracodes of the Rita Blanca lake deposits.* Geol. Soc. America, Mem., No. 113, pp. 107-115, pl. 21-22.

Brooks, J. L.

1946. *Cyclomorphosis in Daphnia I. Analysis of D. retrocurvata and D. galeata.* Ecol. Monogr., vol. 16, No. 4, pp. 409-447, 18 figs.

Carbonnel, G.

1967. *Variations phénotypiques chez une espèce tortonienne du genre Elofsonella Pokorný. In The taxonomy, morphology, and ecology of recent Ostracoda.* Oliver and Boyd édit., Edinburgh, pp. 85-92, 1 pl., 1 fig.

1969. *Les Ostracodes du Miocène rhodanien. Systématique, biostratigraphie écologique, paléobiologie.* Thèse. Docum. Lab. Géol. Fac. Sci. Lyon, no. 32, fasc. 1-2, 469 p., 48 figs., 57 tabls., 16 pls.

Carbonnel, G., et Ritzkowski, S.

1969. *Ostracodes lacustres de l'Oligocène, (Melanienton) de la Hesse (Allemagne),* Arch. Sc., Genève, vol. 22, fasc. I, pp. 55-82, figs. 1-4, pls. 1-5.

Jordan, H., et Bless, M. J.

1971. *Eine inverse Cypridea aus dem Oberen Jura von Teruel (Spanien).* Bull. Centre Rech. Pau, SNPA, vol. 5, suppl., pp. 683-693, 2 pls., 2 figs.

Kinne, O.

1964. *Non genetic adaptation to temperature and salinity.* Helgol. Wiss. Meeresunters., vol. 9, No. 1-4, pp. 433-458, 8 figs.

1966. *Physiological aspects of animal life in estuaries with special reference to salinity.* Netherl. Jour. Sea. Res., vol. 3, No. 2, pp. 222-244, 9 figs., 2 tabls.

Margerie, P.

1972. *Essai de "quantification" du contour des ostracodes à l'occasion de la description d'une nouvelle espèce de Cypridinae du Marinésien du Bassin de Paris.* Rev. Micropaléontol. Paris. vol. 14, No. 4, p. 227-235.

Ohmert, W.

1971. *Ecology of some Trachyleberididae (Ostracoda) from the Bavarian Upper Cretaceous.* Bull. Centre Rech. Pau, SNPA, vol. 5, suppl., pp. 601-614, 7 figs.

Sandberg, P.

1964. *Notes on some Tertiary and Recent brackishwater Ostracoda.* Pubbl. Staz. zool. Napoli, vol. 33, suppl., pp. 496-514, 3 pls., 1 fig.

Stchepinsky, A.

1960. *Etudes des Ostracodes du Sannoisien de l'Alsace.* Bull. Serv. Carte Alsace-Lorraine, Strasbourg, t. 13, fasc. I, pp. 11-34, 3 pls.

Sylvester-Bradley, P. C. et Benson, R. H.

1971. *Terminology for surface features in ornate ostracodes.* Lethaia, vol. 4, No. 3, pp. 249-286, 48 figs.

Triat, J. M., et Truc, G.
1972. *L'oligocène du bassin de Mormoiron (Vaucluse). Etude paléontologique et sédimentologique.* Docum. Lab. Gélo. Fac. Sci. Lyon, No. 49, pp. 27-52, 1 pl., 2 figs., 1 tabl.

Szczechura, J.
1971. *Seasonal changes in a reared fresh-water species, Cyprinotus (Heterocypris) incongruens (Ostracoda), and their importance in the interpretation of variability in fossil ostracodes.* Bull. Centre Rech. Pau, SNPA, vol. 5, suppl., pp. 191-205, 1 pl., 7 figs., 1 tabl.

Wendenburg, E. K.
1969. *Mikrofaunistiche Untersuchungen zur Stratigrafie und Ökologie der Hydrobienschichten (Aquitan, Untermiozän) im Gebiet der Stadt Mainz-am-Rhein.* Notizbl. hess. L-Amt Bodenforsch., Wiesbaden, vol. 97, pp. 229-242, 2 figs., 2 tabls., pls. 8-10

G. Carbonnel,
Université Lyon 1-Claude Bernard,
Département des Sciences de la Terre,
69 Villeurbanne,
France,

Planche 1

Figure

1, 5. **Eucypris ? tenuistriata straubi** Carbonnel, Ritzkowski (× 55)

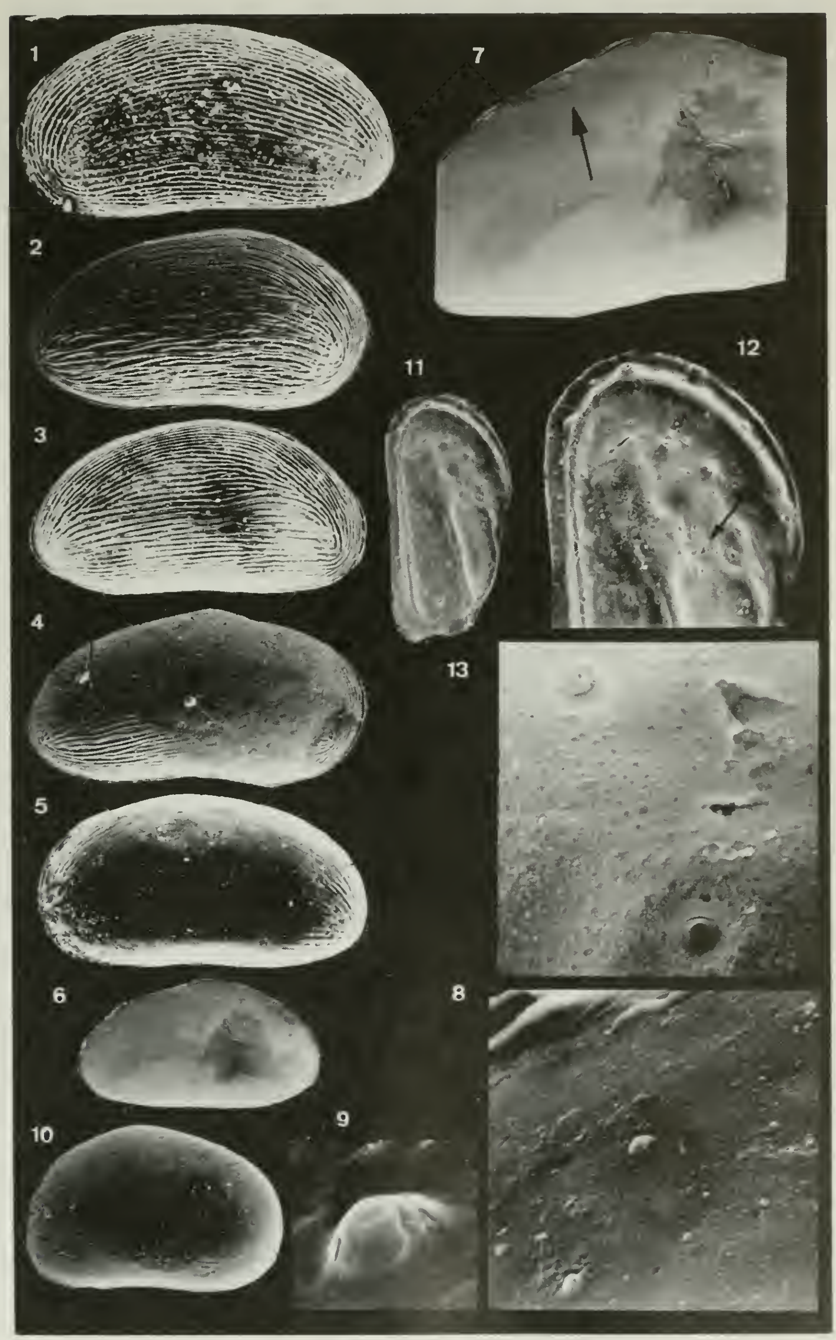
1. vg., paratype No. 135341/1, Borken Tagebau Altenburg IV Melanienton; morphotype orné. 5. vg., paratype No. 135341/2, Borken Tagebau Altenburg IV, Melanienton; morphotype semi-lisse.

2-4, 6-10. **Eucypris ? grisiensis** Margerie (2-4, × 55)

2. vd., No. 135345, Rosières niveau 602/10, Bartonien; morphotype orné à stries anastomosées. 3. vd., No. 135339, Grisy-les-Plâtres, Bartonien; morphotype orné. 4. vd., No. 135344, Rosières, niveau 602/10, Bartonien; morphotype semi-lisse. 6. vd., No. 135386 (× 55), stade larvaire, Grisy-les-Plâtres, Bartonien; morphotype lisse. 7. vd., No. 135386 (× 265). 8. vd., No. 135386 (× 540), détail de la zone médio-dorsale. 9. vd., No. 135386 (× 2700), détail d'un microtubercule ou verrucae.

11-13. **Elofsonella amberii** Carbonnel

11. vg., No. 135337 (× 50), Cairanne, Tortonien; morphotype lisse à côtes. 12. vg., No. 135337. (× 100). 13. vg., No. 135337 (× 800), détail de l'aréa polyporée.


1
2
3
4
5
6
7
8
9
10
11
12
13

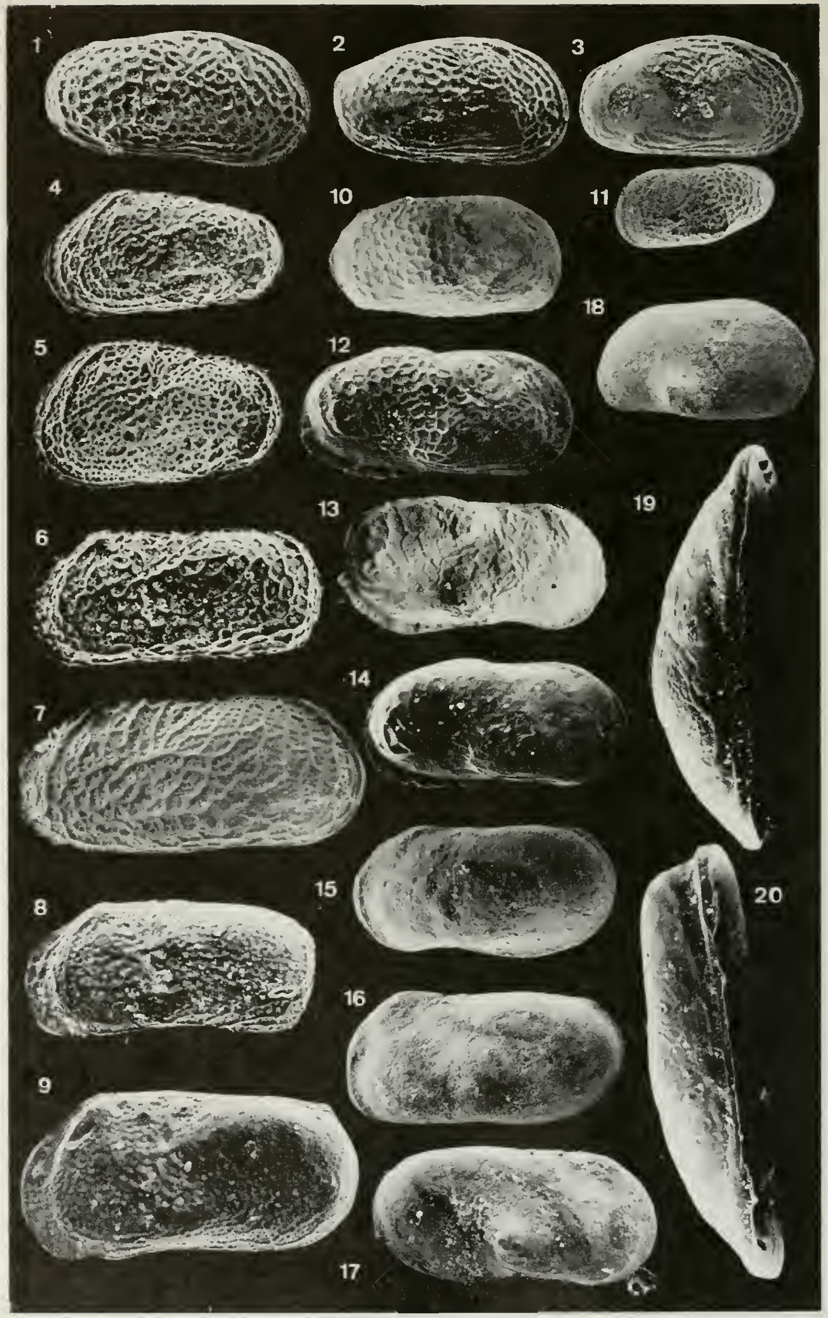

1
2
3
4
10
11
18
5
12
6
13
19
7
14
15
20
8
16
9
17

Planche 2

Figure

1-3. **Leptocythere pentagonalis** Carbonnel (× 70)

1. vd., No. 135363/1, adulte, la Savoyonne niveau 104 f, Tortonien; morphotype orné. 2. vd., No. 135363/2, stade larvaire ?; morphotype à tendance lisse. 3. vd., No. 135363/3, stade larvaire ?; morphotype semi-lisse.

4-9. **Cytheromorpha sp.** Kuster-Wendenburg, Mainz, Aquitanien

4. vg., No. 135380, stade larvaire (× 110); morphotype orné tuberculé. 5. vg., No. 135381, stade larvaire (× 110); morphotype orné. 6. vg., No. 135382, mâle (× 85); morphotype orné. 7. vg., No. 135360, mâle (× 140); morphotype orné, à ornementation atténuée. 8. vg., No. 135359, mâle (× 85); morphotype à tendance lisse. 9. vg., No. 135358, mâle (× 55); morphotype lisse.

10-20. **Limnocythere,** n. sp.

10. vd., No. 135371, femelle (× 65); collection M. Castel niveau 926, Oligocène inférieur; morphotype orné. 11. vg., No. 135369 (× 55); Apt niveau 102/20, Ludien; morphotype orné tuberculé. 12. vd., No. 135368, mâle (× 70); Mallemort-du-Comtat niveau 27/72, Stampien; morphotype orné. 13. vd., No. 135383, mâle (× 60); collection M. Castel, Gignac niveau 926 Oligocène inférieur; morphotype orné à tendance lisse. 14. vd., No. 135367, mâle (× 55); Mallemort-du-Comtat niveau 27/72, Stampien; morphotype semi-lisse. 15. vg., No. 135372 mâle (× 65); Apt niveau 102/20, Ludien; morphotype lisse. 16. vg., No. 135370, mâle (× 70); collection M. Castel; Gignac niveau 926/1, Oligocène inférieur; morphotype lisse avec un tubercule ventral ébauché. 17. vd., No. 135364, mâle (× 70); Blauvac niveau 122, Ludien; morphotype lisse tuberculé. 18. vd., No. 135366, stade larvaire (× 70); Blauvac niveau 122, Ludien; morphotype lisse tuberculé. 19. vg., No. 135385, femelle vue dorsale (× 110), Fontaine-de Vaucluse niveau 49/29, Stampien; morphotype orné. 20. vd., No. 135384, mâle vue dorsale (× 110), Fontaine-de-Vaucluse, niveau 49/29, Stampien; morphotype orné.

MUDLUMP OSTRACODA

H. V. Howe* and W. A. van den Bold
Louisiana State University

ABSTRACT

Mudlumps are intrusive clays that have penetrated into and through bar deposits near the mouths of Mississippi River Passes. They may occur above or below sealevel and about a hundred of them have been mapped. Radiocarbon date on Foraminifera from these deposits is 15,000 years before present, on macrofossils 15,500 years. Ostracoda are listed from three of the mudlumps. Each of the three samples contained more than 50 species, which is well above the number found in any Recent samples from the Gulf of Mexico. The Ostracoda are very well preserved and their distribution suggests deposition at a depth of approximately 100 feet. No formal descriptions are given, but SEM photographs are shown for all but the rarest species (Plates 1-3). Several species indicated in the list as new have been described erroneously under different names by previous workers.

RÉSUMÉ

Les îles de boue du delta du Mississippi à "pied d'oiseau" sont des structures d'argiles diapyriques qui ont pénétré les sediments sableux marginaux des bouches. On en a régistré une centaine. Détermination de l'age de ces dépots à base de C^{14} sur des foraminifères a donné 15000 ans, sur des macrofossiles 15500. Nous présentons une liste des ostracodes de trois de cettes îles de boue. Chacun de ces trois échantillons a fourni plus de 50 spécies, un nombre plus élevé de que l'on a encontré dans aucun échantillon actuel dans le Golfe de Mexique. Les ostracodes sont bien préservés et leur répartition sugère une déposition à une profondeur d'environ 100 pieds. Nous avons évité des descriptions formales, en contraire nous présentons des photographies SEM de toutes les espèces sauf les plus rares (Planches 1-3). Plusieurs espèces représentées dans la liste ont été décrites antérieurement sous des noms différents par des autres auteurs.

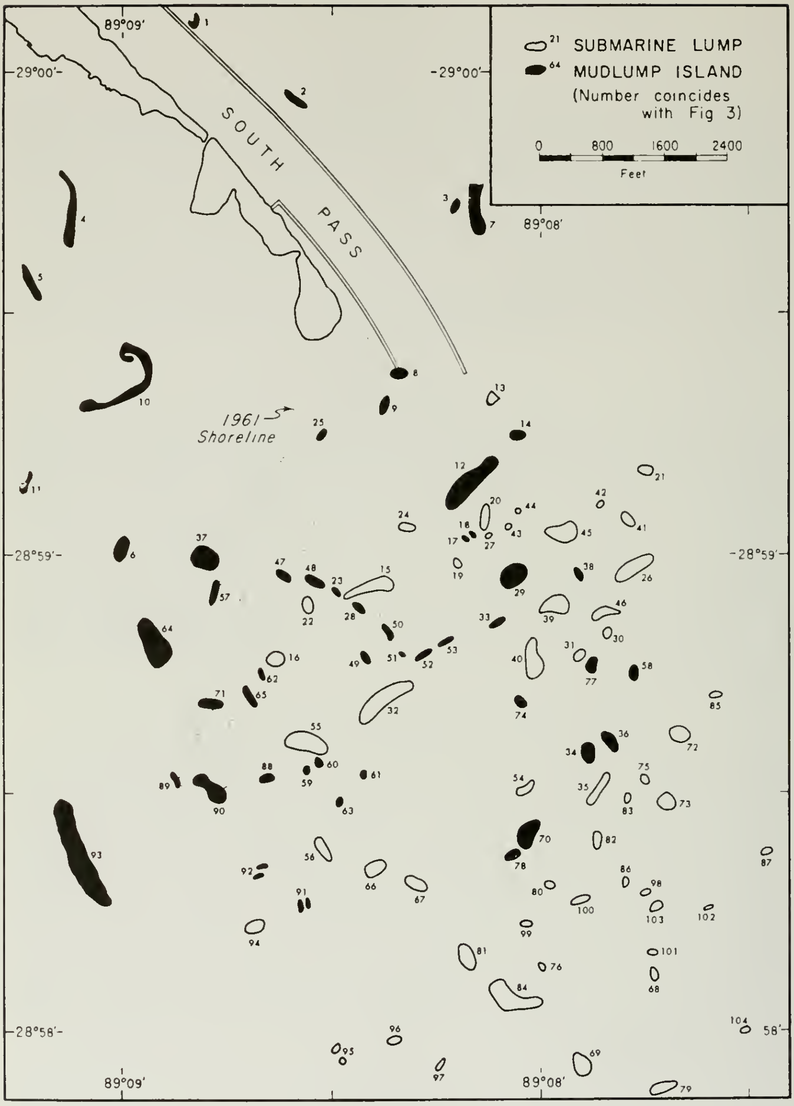
OSTRACODA OF MUDLUMP SAMPLES

The unique "bird's foot" delta of the Mississippi River is characterized, at the tips of its toes, by curious structural features which during the past 200 years have come to be known as "mudlumps." They were well illustrated by Sir Charles Lyell in his *Principles of Geology* (Eleventh Edition, volume 1, pages 442-459). The term "mudlump" is a popular name for the upswellings of clay which occur just beyond the mouths of the Mississippi River passes. They may occur as shoals, or if active, as distinct mud islands. Detailed studies of these mudlumps have been made by J. P. Morgan (1961, 1963) which conclusively show that they are diapiric (intrusive) folds of clay thrust into and through the bar deposits, accompanied by low angle thrust faults, which have displaced the clay units vertically as much as 350 to 400 feet to their present subaerial position.

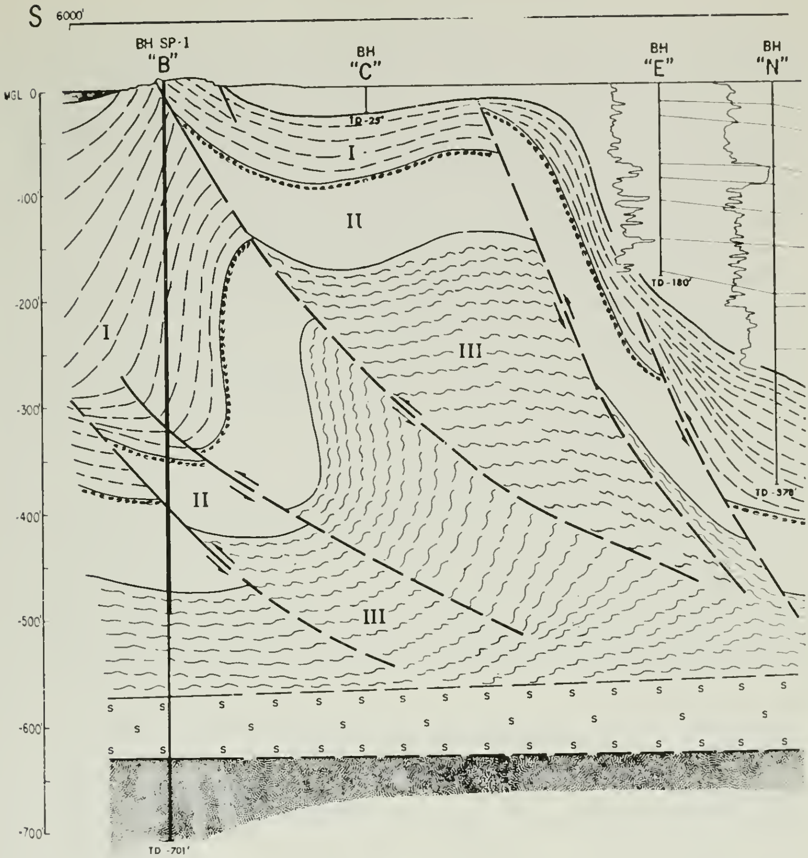
The foraminiferal content of the mudlump clays has been described by H. V. Andersen (1961). In the region of South Pass, Dr. Morgan has mapped the occurrence of over 100 of these mudlumps, here reproduced as Text-figure 1. The structural relationship of the fossiliferous clays, Unit II, is shown on Text-figure 2, from a portion of a section figured by Morgan (1963, fig. 11). Through the kindness of Dr. Morgan, the senior author was supplied with a sample from mudlump 89-90 (now one island) and called SP-1 in Andersen's

---

*Deceased September 27, 1973



Text-figure 1. Mudlump distribution South Pass. Data from 123 maps dated between 1867-1961. (After Morgan, 1963, fig. 2.)



Text-figure 2. Cross section illustrating mudlump structure in South Pass area. (After Morgan, 1963, fig. 11.)

1961 report. He also supplied material from mudlump 94 which has become an island since 1963. Dr. Andersen supplied the junior author with material from his most prolific locality, mudlump SP-5 (No. 91 on Text-fig. 1) which has become a shoal since the map was made.

One of the most interesting features of this fossiliferous, very plastic clay is its extremely fine grain. All of the non-organic material passes a 200-mesh sieve. This is even true of the layer referred to as shell horizon, or "shell hash" in Morgan's report. Gagliano's (1963) report on these clays showed that they were not derived from the Mississippi River, but from the Southern Appalachians. It must be assumed that the Mississippi River, at the time these clays were deposited, was occupying the Submarine Canyon south of the city of Houma, approximately 100 miles west of its present mouth. The radiocarbon date for the deposition of these clays has been set at 15,000 years on Foraminifera, and 15,500 years on the macro-shells of the shell bed according to Dr. Morgan. The preservation of the Foraminifera and Ostracoda is as good as that of living specimens. Whether one considers them to be Recent or Pleistocene in age, it should be noted that Cvancara, *et al.* (1971, p. 172) remarked that "Active glacial ice existed in the general area [of southeastern North Dakota] until about 13,000 years before the present (B.P.)." Delorme described the fresh-water Ostracoda in that report.

Dr. Andersen, during the years 1948-1950, obtained over 200 species of Foraminifera from his mudlump samples. Most of them came from the shell layer on mudlump SP-5 (91). His samples from SP-1 contained brackish water assemblages of Unit I as shown in Text-figure 2 such as are characteristic of the prodelta clays of the present Mississippi. Thrusting has continued at this area and the shell bed, and perhaps 4 feet of overlying very fossiliferous clay of Unit II, are now exposed with mudlumps 89 and 90 united at the present time. The sample described in this report from 89-90 came from soft mud inside the shell of a giant snail *Tonna.*

Ostracoda are naturally not as abundant and diverse as Foraminifera in these samples, but the more than 60 species we have obtained are far more than have been reported from any samples we know of from the northern shelf of the Gulf of Mexico (checklist). This is not a near-shore fauna. However, the abundance and variety of genera and species indicates that it lived within the phytal zone at a depth probably closer to 100 feet than the 450 feet where it is encountered in wells between the mudlumps. We plan to describe the new species later.

ACKNOWLEDGMENTS

We are grateful to Tom Choung for his help with the stereoscan pictures. Philip Larimore and Mrs. Judy Ardoin arranged the plates and figures.

LITERATURE CITED

Andersen, H. V.

1961. *Foraminifera of the mudlumps, Lower Mississippi River Delta.* Louisiana Geol. Sur., Bull. 35, part II, 209 pp, 29 pls.

Gagliano, S. M.

1963. *Clay mineralogy of south pass mudlumps.* Louisiana St. Univ. Studies (Coastal Studies Series No. 10), Appendix C, pp. 73-97.

Morgan, J. P.

1961. *Mudlumps at the mouths of the Mississippi river.* Louisiana Geol. Sur., Bull. 35, Pt. 1, 116 pp, 61 figs.

1963. *Mudlumps at the mouth of south pass, Mississippi River: Sedimentology, Paleontology, Structure, Origin, and Relation to Deltaic processes.* Louisiana St. Univ. Studies (Coastal Studies No. 10), pp. 1-50.

Cvancara, A. M., Clayton, L., Bickley, W. B., Jr., Jacob, A. F., Ashworth, A. C., Brophy, J. A., Shay, C. T., Delorme, L. D. and Lammers, G. F:

1971. *Paleolimnology of late quaternary deposits: Seibold Site, North Dakota.* Science, 171, pp. 172-174.

H. V. Howe
and
W. A. van den Bold,
School of Geoscience,
Louisiana State University,
Baton Rouge,
Louisiana, U.S.A. 70803

CHECKLIST OF OSTRACODA

Checklist of Ostracoda from Mississippi River mudlumps. Columns list numbers of specimens in each of the three samples.

		SP-1 (80-90)	SP-5 (91)	94
1.	Actinocythereis n. sp.?	4	14	21
2.	Ambocythere exilis Bold, 1966			12
3.	Argilloecia sp. 1	70		37
			41	
4.	Argilloecia sp. 2	28		6
5.	Aurila n. sp. (not A. conradi)	105	122	36
6.	Aurila sp. aff. A. amygdala (Stephenson, 1944)			4
7.	Bairdia sp. (fragment)			1
8.	Basslerites minutus Bold, 1958	4	3	14
9.	Buntonia n. sp.	3	6	31
10.	"Bythocypris" ? sp.		1	1
11.	Bythocythere sp.	76	58	28
12.	Bythoceratina sp.			1
13.	Cativella n. sp.	9	16	12
14.	Cytherella n. sp. 1	9		16
15.	Cytherella n. sp. 2		2	4
16.	Cytherelloidea n. sp. 1	37	7	35
17.	Cytherelloidea n. sp. 2			8
18.	Cytheromorpha cf. C. apheles Bold, 1963	24	25	13
19.	Cytheropteron sp. 1	138	69	54
20.	Cytheropteron sp. 2	37	6	13
21.	Cytheropteron horacecoryelli Puri, 1962?	13		
22.	Cytherura sp.	83	54	28
23.	Echinocythereis margaritifera (Brady, 1870)	159	377	91
24.	Echinocythereis spinireticulata Kontrovitz, 1971		3	2
25.	Eucythere sp. aff. E. triangulata Puri, 1954	3	2	5
26.	Eucythere sp. 2			1
27.	Eucytherura sp. 1	49		20
28.	Eucytherura sp. 2	31	6	
29.	Henryhowella ex gr. asperrima (Reuss, 1850)	19	70	53
30.	Hulingsina sp. aff. H. sulcata Puri, 1960		10	26
31.	Hulingsina tuberculata Puri, 1958	145	157	44
32.	Jugosocythereis pannosa (Brady) 1868		1	
33.	Kangarina sp. aff. K. ancycla Bold, 1963	77	18	14
34.	Krithe [at least 2 sp.]	148	115	92
35.	Loxoconcha sp. 1	117	123	86
36.	Loxoconcha sp. 2	39		3
37.	Loxoconcha sp. 3 [? = purisubrhomboidea of Grossman, 1965]	82		16
38.	Loxoconcha fischeri (Brady, 1869)	1		
39.	Luvula sp.	13		2
40.	Machaerina sp.	8		2

41.	Macrocyprissa sp.	21	13	6
42.	Macrocyprina sp.		26	5
43.	Macrocypris? sp.		12	
44.	Microcythere [several sp.?]	45	1	
45.	Munseyella n. sp., aff. M. bermudezi Bold, 1966	120	37	20
46.	New genus? aff. "Cytheromorpha" caudata Bold, 1966	7		1
47.	Paracypris sp.	34	2	13
48.	Paracythere sp.	1		3
49.	Paracytheridea sp.	13	44	55
50.	Paracytherois sp., aff. Paradoxostoma robusta Puri, 1954	31		
51.	Parakrithe sp.		3	
52.	Pellucistoma sp.	49	10	
53.	Polycope sp.		2	
54.	Propontocypris sp.	8	4	
55.	Proteoconcha gigantica (Ed.) Plusquellec & Sandberg, 1969			4
56.	Protocytheretta, n. sp. aff. P. pumicosa (Brady, 1866)	9	7	16
57.	Pseudocythere sp.	23	3	1
58.	Pseudopsammocythere? or Parakrithella? sp.	12	4	5
59.	Pterygocythereis, n. sp., aff. P. americana (Ulrich & Bassler)	74	26	71
60.	Pterygocythereis, n. sp. 2		4	9
61.	Pumilocytheridea sp.	1		
62.	Puriana, n. sp.	55	44	17
63.	Sclerochilus sp. 1	26	7	8
64.	Sclerochilus sp. 2	4	10	
65.	Semicytherura sp. 1	50	8	5
66.	Semicytherura sp. 2	50	11	7
67.	Semicytherura sp. 3	2	3	5
68.	Xestoleberis sp.	25	10	46
	Subtotals	2191	1597	1139
	Total number of specimens		4927	

DISCUSSION

Dr. R. H. Benson: It is interesting that within the particular species of *Echinocythereis,* which you have, one can notice a change in the living form as they go deeper. They become larger and less coarsely spinose. But the most important thing I think is the change in the size of the eye tubercle. As you know, the ones living in shallow waters today have a very large tubercle. As you get material from deeper localities the eye tubercle gets smaller, until about 600 meters, which is deeper than yours, where it completely atrophies. This suggests that not only does *Echinocythereis* originate in this area, but it may be possible to show the depth of the water relative to the ability or need of the animal to see. It may be useful to trace the size and occurrence of the eye tubercles in fossil ostracodes as a means of indicating the amount of light and perhaps the depth of ancient sedimentary conditions.

Dr. H. Howe: You see this is a very much larger fauna than you get in any samples that I know of taken out on the shelf of the Gulf of Mexico at the present time.

Dr. J. E. Hazel: The fauna is actually very similar to what you get along the Atlantic coast south of Cape Hatteras, with some notable exceptions.

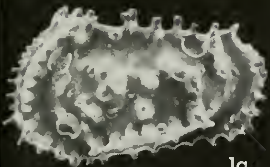
Dr. Howe: Valentine's paper shows this (P. C. Valentine U.S.G.S., Prof. Paper 683-D, 1971).

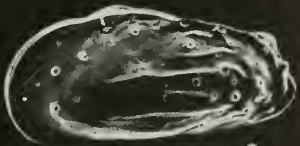
Explanation of Plate 1

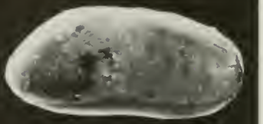
Figure
1a,b. **Actinocythereis,** n. sp. aff. **A. bahamensis** (Brady, 1870) × 50
2. **Ambocythere exilis** Bold, 1966 × 75
3. **Argillcecia** sp. 1. × 75
4. **Argilloecia** sp. 2. × 75
5. **Aurila,** n. sp. aff. **A. conradi** (Howe & McGuirt, 1935) × 50
6. **Aurila,** n. sp. aff. **A. amygdala** (Stephenson, 1944) × 50
7. **Basslerites minutus** van den Bold, 1958 × 75
8. **Buntonia,** n. sp. × 75
9. **Bythocythere** sp. × 60
10. **Cativella,** n. sp. aff. **C. semitranslucens** (Crouch, 1949) × 50
11. **Cytherella,** n. sp. 1. × 50
12. **Cytherella,** n. sp. 2. × 50
13. **Cytherelloidea,** n. sp. 1. × 50
14. **Cytherelloidea,** n. sp. 2. × 50

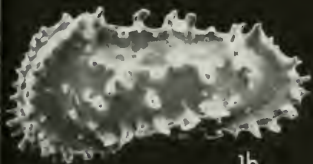
15. **Cytheromorpha** sp. aff. **C. apheles** van den Bold, 1963
16. **Cytheropteron** sp. 1. × 75
17. **Cytheropteron** sp. 2. × 75

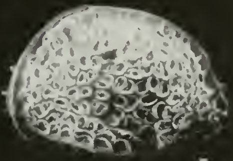
Figured specimens deposited in Museum of Geoscience, Louisiana State University, numbers: HVH 9699-9716.


1a

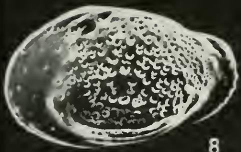

2

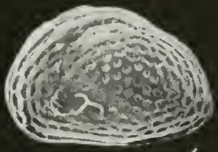

3

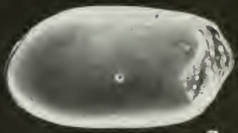

1b

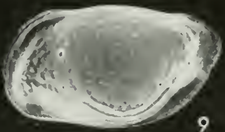

5

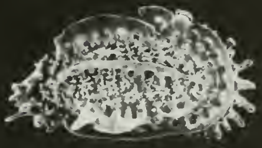

4

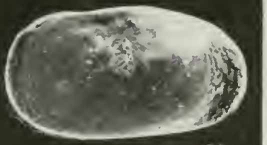

8

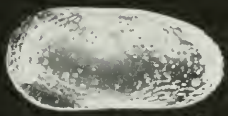

6


7

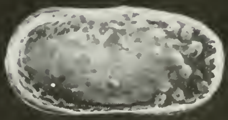

9

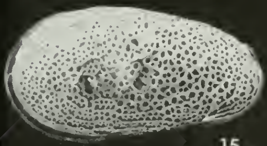

10

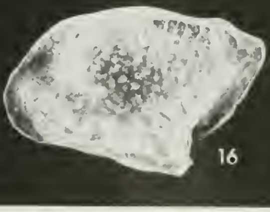

11

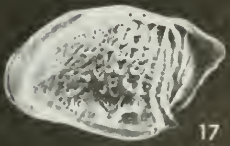

12


14


13


15

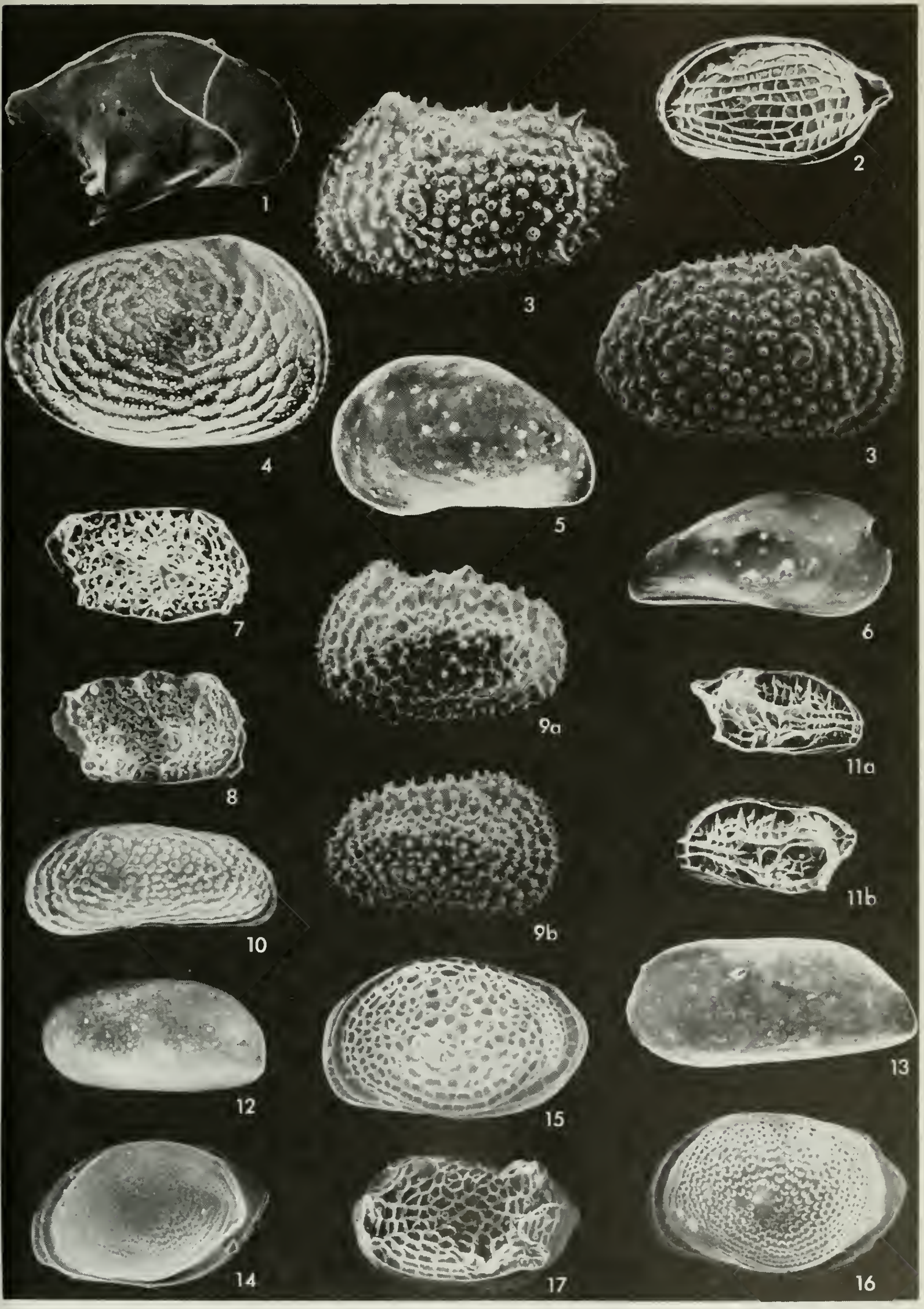

16


17

EXPLANATION OF PLATE 2

Figure
1. **Cytheropteron horacecoryelli** Puri, 1962? × 75
2. **Cytherura** sp. × 75
3a,b. **Echinocythereis margaritifera** (Brady, 1870) × 50
4. **Echinocythereis spinireticulata** Kontrovitz, 1971 × 50
5. **Eucythere** sp. aff. **E. triangulata** Puri, 1954 × 75
6. **Eucythere** sp. × 75
7. **Eucytherura** sp. 1. × 100
8. **Eucytherura** sp. 2. × 100
9a,b. **Henryhowella** ex. gr. **asperrima** (Reuss, 1850) × 50
10. **Hulingsina tuberculata** Puri, 1958 × 50
11a,b. **Kangarina** sp. aff. **ancycla** van den Bold, 1963 × 75
12. **Krithe** sp. 1 × 75
13. **Krithe** sp. 2 × 75
14. **Loxoconcha** sp. 1. × 75
15. **Loxoconcha** sp. 2. × 100
16. **Loxoconcha** sp. 3. × 75
17. **Loxoconcha fischeri** (Brady, 1869) × 75

Figured specimens deposited in Museum of Geoscience, Louisiana State University, numbers: HVH 9717-9736.

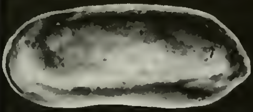

1
2
3
3
4
5
6
7
8
9a
9b
10
11a
11b
12
13
14
15
16
17

Explanation of Plate 3

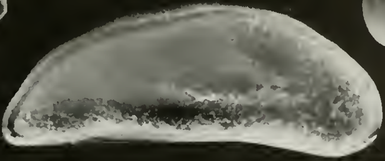
Figure

1. **Luvula** sp. × 75
2. **Macrocyprissa** sp. × 50
3. **Macrocyprina** sp. × 50
4. **Microcythere** sp. 1 × 100
5. **Microcythere** sp. 2 × 100
6. **Munseyella,** n. sp. aff. **M. bermudezi** van den Bold, 1966 × 100
7. New genus? aff. **"Cytheromorpha" caudata** van den Bold, 1966 ×
8. **Paracypris** sp. × 50
9. **Paracytheridea** sp. × 50
10. **Paracytherois** sp. × 50
11. **Pellucistoma** sp. × 75
12. **Propontocypris** sp. × 50
13. **Protocytheretta,** n. sp. aff. **P. pumicosa** (Brady, 1866) × 50
14. **Proteoconcha gigantica** (Ed.) Plusquellec and Sandberg, 1969 × 50
15. **Pseudocythere** sp. × 50
16. **Pseudopsammocythere**? or **Parakrithella**? sp. × 70
17. **Pterygocythereis,** n. sp. aff. **P. americana** (Ulrich and Bassler, 1904) × 50
18. **Pterygocythereis,** n. sp. 2 × 50
19. **Puriana,** n. sp. × 50
20. **Semicytherura** sp. 3 × 75
21. **Semicytherura**? sp. 2 × 60
22. **Xestoleberis** sp. × 75

Figured specimens deposited in Museum of Geoscience, Louisiana State University, numbers 9737-9758.

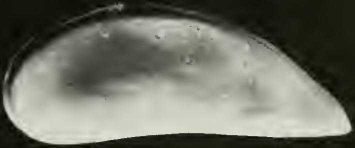

1

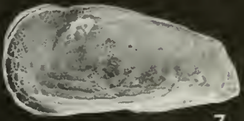

2

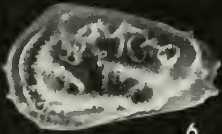

3

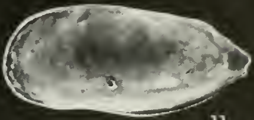

4

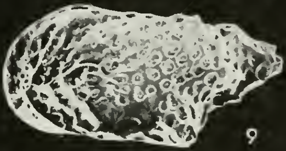

5


8

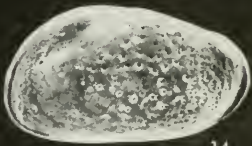

7

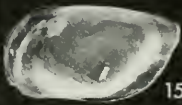

6

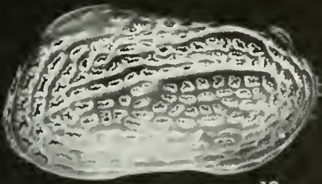

11

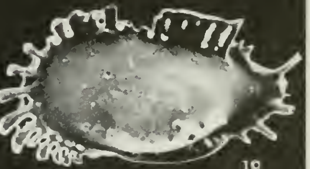

9

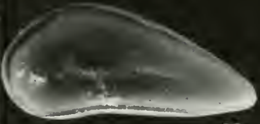

10

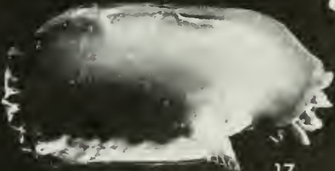

14

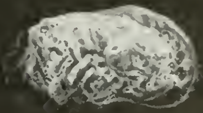

15


13


18


12


17


19


16


21


20


22

OSTRACODE ECOLOGY DURING THE UPPER CRETACEOUS AND CENOZOIC IN ARGENTINA

Alwine Bertels*
Universidad Buenos Aires

ABSTRACT

Upper Cretaceous and Cenozoic marine strata are exposed in Argentina and mostly contain a well-preserved ostracode and foraminiferal assemblage.

This paper is a first attempt to infer some environmental changes from the Upper Cretaceous through the Cenozoic in Argentina by means of ostracodes. Foraminiferal assemblages associated with the ostracodes, well known as paleoecological indicators, were the principal aid for most of the interpretations.

The principal factors that in the past influenced the distribution of marine Ostracoda are analyzed, the most important being water temperature, salinity, and depth.

Temperature is the principal factor that has influenced the latitudinal distribution of the ostracode faunal assemblages; salinity and depth are also important controlling factors: some species show a tolerance to changes in these ecological factors whereas some other species are markedly restricted to definite environments.

As a result of this study some temperature changes are registered during the Cenozoic and salinity and depth variations can be inferred in some basins.

LA PALEOECOLOGIE OSTRACODALE PENDANT LE CRÉTACÉE SUPERIEURE ET LE CENOZOIQUE EN ARGENTINE

RÉSUMÉ

De couches marins cénozoïques et de la Crétacée supérieure se trouvent exposés en Argentine, contenant pour la plupart un assemblage ostracodal et foraminiféral bien préservé.

Le travail est une première tentative dans la direction d'inférer quelques changements paléoécologiques de le Crétacée supérieure à travers le Cénozoïque en Argentine, au moyen des ostracodes. Les assemblages foraminiféraux, associés avec les ostracodes et bien connus comme des indicateurs paléoécologiques, constituait l'aide principale pour la plupart des interprétations.

Les facteurs principaux qui, dans le passé, ont influencé la distribution des ostracodes marins sont analysés, dont les plus importants sont la température de l'eau, la salinité, et la profondeur.

La température de l'eau est le facteur principal qui a influencé la distribution latitudinale des assemblages ostracodaux-faunaux; la salinité et la profondeur sont aussi d'importants facteurs de contrôle: Certaines espèces démontrent une certaine tolérance envers ces facteurs écologiques, lorsque d'autre espèce sont restreintes dans leurs ambients d'une facon marquée.

Comme résultat de cette étude, quelques changements de température sont enregistrés pendant le Cénozoïque, et des variations de salinité et de profondeur peuvent s'inférer dans quelques bassins.

INTRODUCTION

The purpose of the present work is to pursue the two following fundamental objectives:

1) To establish some ecological factors that influenced the distribution of

---

*The paper was read by R. C. Whatley

marine ostracodes during the Upper Cretaceous and Cenozoic, particularly the Tertiary, of Argentina.

2) To show in an approximate integral form the microfaunal assemblages of ostracodes which prevailed during the above mentioned interval and attempt to infer some phylogenetic relations within selected lineages.

From recent literature, it is apparent that Recent benthonic ostracodes are, in many cases, very restricted environmentally. Because of this, they can be used to reconstruct palaeoenvironments. In the upper part of the Cenozoic, to approximately as far back as the Oligocene, these reconstructions are relatively easy to make because these deposits contain the same, or very similar taxa as those living in Recent seas. However, in the early Tertiary and Cretaceous these reconstructions are more problematical because the taxa are less closely related to living forms, and it becomes necessary to guess as to their environmental limitations. This problem to some extent can be resolved by recourse to the known ecology of other microorganisms.

It is intended in this work to demonstrate which microfaunas prevailed during these periods in the Argentine and to show how, with the aid of other tools (such as lithology, Foraminifera, and other microfossils), the ostracodes can be used as chronostratigraphic and palaeoenvironmental indicators. Frequently these are the only elements the author had to use, in many parts of the sedimentary basins discussed below.

It is not the author's purpose to make a detailed systematic review of the fossil forms found up to the present day in our country, because it would be outside the scope of the present work. Nevertheless it is necessary to remark that the fundamental factor underlying both ecologic and palaeoecologic studies is an accurate and consistent taxonomy. This problem is not, in this case, so serious because the greater part of the species are new and in most cases I refer to an assemblage of microfossils which typify each of the separate marine stages and because mostly I refer to one type locality within each basin.

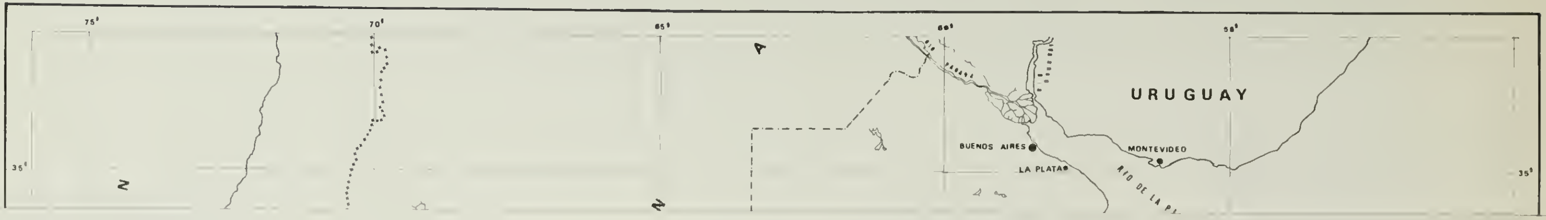
The data on which this work are based were taken from all the works published to date within this field in the Argentine and also those unpublished theses dealing with the same topic.

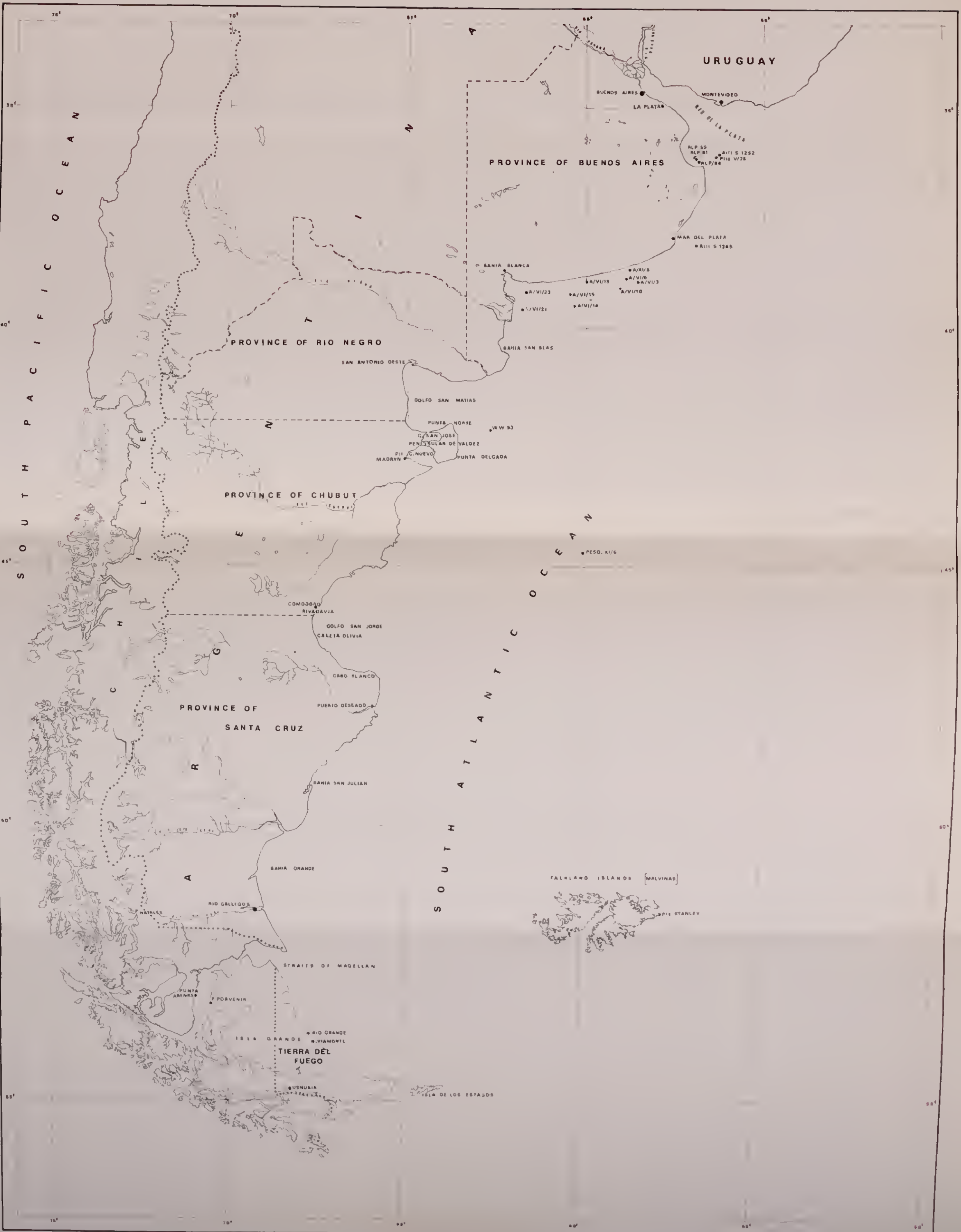
The mentioned and illustrated material was collected by the author and is deposited at the Facultad de Ciencias Exactas y Naturales, Laboratorio de Micropaleontología, under the numbers 588 to 657.

The author has in most cases followed the taxonomic usages of other workers; however, in certain cases changes have been made, mostly at the generic level, which are indicated in parentheses.

ACKNOWLEDGMENTS

The author wishes to express gratitude to the Argentine National Council for Scientific and Technical Research, for economical aid in the realization of


75°
70°
65°
60°
55°
35°
35°
N
A
N
URUGUAY
RIO PARANA
BUENOS AIRES
LA PLATA
MONTEVIDEO
RIO DE LA P


URUGUAY
BUENOS AIRES
MONTEVIDEO
LA PLATA
RIO DE LA PLATA
PROVINCE OF BUENOS AIRES
ALP 65
ALP 81
ALP/84
AIII S 1252
PIII V/25
MAR DEL PLATA
AIII S 1245
BAHIA BLANCA
A/XI/3
A/VI/13
A/VI/6
A/VI/3
A/VI/23
A/VI/15
A/VI/10
A/VI/21
A/VI/18
BAHIA SAN BLAS
PROVINCE OF RIO NEGRO
SAN ANTONIO OESTE
GOLFO SAN MATIAS
PUNTA NORTE
WW 53
G. SAN JOSE
PENINSULAR DE VALDEZ
PTO MADRYN
G. NUEVO
PUNTA DELGADA
PROVINCE OF CHUBUT
PESO. XI/6
COMODORO RIVADAVIA
GOLFO SAN JORGE
CALETA OLIVIA
CABO BLANCO
PUERTO DESEADO
PROVINCE OF SANTA CRUZ
BAHIA SAN JULIAN
BAHIA GRANDE
RIO GALLEGOS
NATALES
STRAITS OF MAGELLAN
PUNTA ARENAS
P. PORVENIR
RIO GRANDE
VIAMONTE
ISLA GRANDE
TIERRA DEL FUEGO
USHUAIA
ISLA DE LOS ESTADOS
FALKLAND ISLANDS [MALVINAS]
PT. STANLEY
SOUTH PACIFIC OCEAN
SOUTH ATLANTIC OCEAN
CHILE
ARGENTINA
76°
70°
65°
60°
55°
50°
35°
40°
45°
50°
55°

the present work, and who generously provided the use of the Jeolco JSM-U3 scanning electron microscope with which the micrographs were taken. Particular thanks are expressed to Mr. Natalio de Vicenzo whose careful work was responsible for the good photographic results.

The writer is also grateful to Dr. Robin C. Whatley for his helpful reading and discussions concerned with the manuscript.

Thanks are equally due to General Motors Argentina, who provided the vehicle which was used to collect most of the samples on which part of this work is based.

I. UPPER CRETACEOUS

The first Atlantic influence in the extra-andean geological history of the Argentina began after the Intersenonian movements or Huantrai-co phase (Stipanicic, *et al.,* 1968).

Although in the southern and extreme western regions of Argentina continuous marine sections are known from the Albian and Barremian respectively, much of the data have not been published because they were obtained from boreholes and belong to oil companies.

In the remainder of the extra-andean portion of Argentina, those marine sections which have been studied micropaleontologically are Maastrichtian and younger. It is from this moment of time that we are able to detect certain Atlantic influences, especially in the basins called Paraná, Salado, Neuquén, Colorado, Valdés, San Jorge, and Austral Basins by Criado Roque and others (1960) (Text-fig. 1).

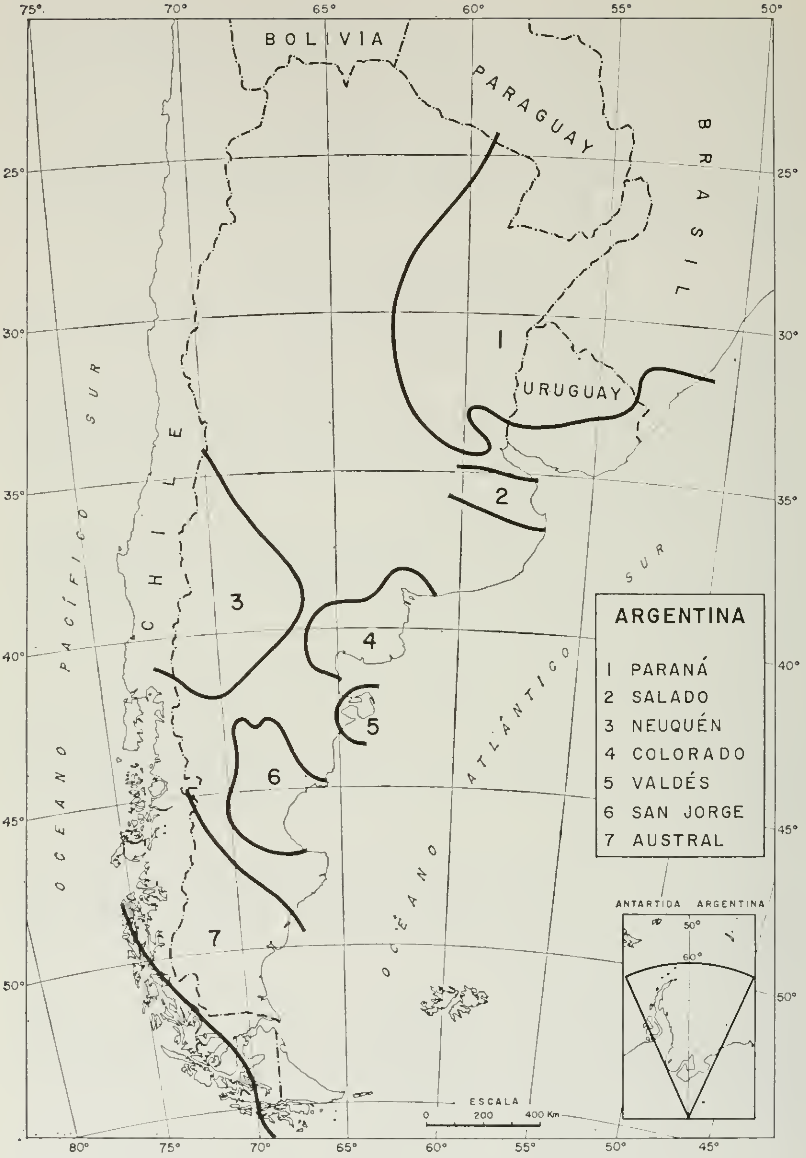
Jagüelian Stage (Lower and Middle Maastrichtian) (Text-fig. 2)

This stage is particularly well represented in the Neuquén and Colorado Basins (Text-fig. 1). The author, on the basis of the similarity of their contained microfaunas has joined these two basins, during the Maastrichtian and Danian, into a large basin which she refers to as the North Patagonian Basin (Bertels, 1969a, 1970a).

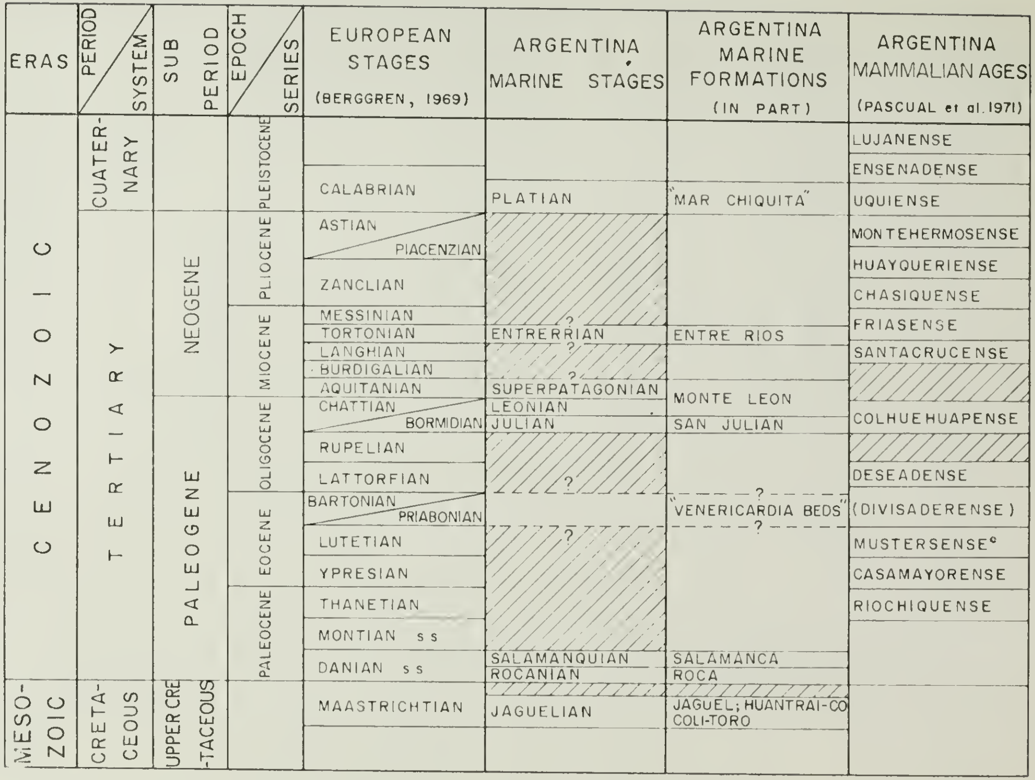
In this basin and after the deposition of continental strata, the Neuquén Group (Groeber, 1946, emended category Herrero Ducloux, 1946), began the gentle subsidence which gave rise to the origin of deposits of great regional extent, predominantly of lacustrine type, known in the literature as "Lacustrine Senonian" (Wichmann, 1924).

After the subsidence which produced these deposits, others of greater magnitude followed which were responsible for the later marine transgressions. The southern region of the country however, did not subside completely and continuously as is evidenced by the frequent alternation of marine and continental deposits throughout the Tertiary.

The transgressive deposits of the Upper Cretaceous occupied a great part of northern Patagonia and are represented by the Malargüe (Gerth, in Mühlmann, 1937, em. cat. Bertels, 1969a), Jagüel (Windhausen, 1914, em. cat. Bertels, *op cit.*), Aguada Cecilio, Huantrai-co, and Coli Toro (Bertels, *op. cit.*) Formations.



Text-figure 1. Principal Argentina marine Upper Cretaceous and Tertiary sedimentary basins.



Text-figure 2. Correlation chart between Upper Cretaceous and Cenozoic Argentina marine stages.

The corresponding stage was called the Jagüelian Stage (Windhausen, 1914, em. cat. Bertels, 1969a), which is equivalent to the Lower and Middle Maastrichtian. Included in this stage are the beds of lacustrine origin and the overlying brackish water and marine deposits. These together represent a continuous sedimentary cycle, within which can be distinguished three microfaunal assemblages:

a) Fresh water, with *Ilyocypris, Candona,* and *Wolburgia.*
b) Polyhaline (classification of Välikangas, 1933) composed mostly of ostracodes to the exclusion of other microfossils excepting in the Huantrai-co area.
c) Marine, with a typical marine microfauna, composed predominantly of foraminifers and ostracodes.

The fresh and brackish water assemblages correspond to the Lower Jagüelian Stage (Lower Maastrichtian) whereas the marine associations belong to the Upper Jagüelian Stage (Middle Maastrichtian).

1) The Lower Jagüelian Stage (Lower Maastrichtian) is composed of beds of lacustrine and brackish water origin.

The fresh water beds, known as "Lacustrine Senonian" (Wichmann, 1924) are well represented in the Huantrai-co area (Neuquén Basin, text fig. 1) by the lower member of the Huantrai-co Formation (Bertels, 1968) and contain an ostracode microfauna composed principally of *Ilyocypris triebeli* Bertels, 1972, *Candona? huantraicoensis* Bertels, 1972, and *Wolburgia? neocretacea* Bertels, 1972 (Bertels, 1972).

The brackish water assemblage was found in the Neuquén and Colorado basins and is well represented in the lower beds of the Jagüel, Huantrai-co, Malargüe, Coli Toro, and Aguada Cecilio Formations.

The brackish water ostracode assemblage (Plate I) is very probable mostly polyhaline (classification of Välikangas, 1933). Ostracodes are the only microfossils found, except in the Huantrai-co area where Foraminifera also occur.

The ostracode assemblage is principally composed of:

Trachyleberis princeps Bertels, 1969
Alatacythere? rocana Bertels, 1969
Wichmannella araucana Bertels, 1969
Platycythereis? n. sp.
Wolburgia? n. sp.

Amongst these forms, only *Wichmannella araucana* passes up into the upper beds of purely marine character, of the Jagüelian Stage.

This assemblage is amply distributed throughout the whole north Patagonian area, from the most western outcrops almost to the Atlantic coast. In many cases they are the only microfossils encountered, all other groups, including Foraminifera being absent, whereas in other cases they are encountered associated with other microorganisms which are known to be marine as in the case of the assemblages found in the Huantrai-co Formation (Bertels, 1968, 1969c).

From these observations I was able to infer the following possibilities for the assemblage concerned:

That they were:

a) Euryhaline. They were able to withstand salinities ranging from those of the open sea to those of brackish water (polyhaline).
b) Shallow water species.
c) Adapted to withstand a certain degree of turbidity (since in some cases the clayey and silty sediments contain some pyroclastics).
d) Not restricted to any particular substrate.
e) Were very probably adapted to tolerate some pH changes because from the microfauna it is possible to suggest that the coastlines in the Lower Jagüelian were indented with bays, peninsulas, and tidal lagoons within which, given the sediment types (pelites), the pH could probably have reached values greater than 8.1. This is thought to have been most probable along the coast bordering the ancient North Patagonian Shield (southern coast line of the Neuquén and Colorado Basins).

2) The Upper Jagüelian Stage (Middle Maastrichtian) is also particularly well developed in the Neuquén and Colorado Basins (Text-fig. 1) and is represented by the upper beds of the Jagüel, Huantrai-co, Malargüe, and Coli-Toro Formations (Bertels, 1969a).

During this time began in some parts a marked deepening, especially of the Neuqüen Basin, which was accompanied by the appearance of a great quantity of ostracode and foraminiferal species which were the most abundant microfossils.

Concomitantly with the deepening of the North Patagonian basin several species, different from those that prevailed in the Lower Jagüelian, first appeared.

These include among others (Bertels, 1968, 1969c, 1973c) (Plate II):

Veenia (Nigeria) punctata Bertels, 1968
Cythereis? excellens Bertels, 1969
Protocosta n. sp.
Togoina n. sp.
Actinocythereis n. sp.
Cythereis n. sp.
Trachyleberis n. sp.
Bradleya? n. sp.
Cytheromorpha? n. sp.
Anticythereis n. sp.

Other species persist from the Lower Jagüelian Stage until the present such as:

Wichmannella araucana Bertels, 1969

In some cases the species are very probably phylogenetically related, for example: *Trachyleberis princeps* and *Trachyleberis* n. sp. from the Lower and Upper Jagüelian stages respectively.

The Upper Cretaceous ostracode species are found associated with abundant planktonic Foraminifera — some of them carinate but the majority heterohelicids — and also benthonic arenaceous and calcareous genera (*Bolivina, Bulimina, Neobulimina),* typical of outer shelf to bathyal environments.

According to Bandy (1967), Recent planktonic carinate Foraminifera are limited in the Northern Hemisphere and Southern Hemisphere by the isotherm of 17° C which is located between latitudes of 20 and 40 degrees in both hemispheres depending upon local oceanographic conditions.

Within the context of local conditions of the Atlantic Coast of Argentina, Boltovskoy (1968) assigned great importance to the cold Antarctic and Malvinas currents and the warm Brazil current, which are responsible for restricting the planktonic Foraminifera to latitudes between 30-36° S.

Consequently it is possible to deduce from the occurrence of carinate planktonic Foraminifera in strata of the Jagüel Formation, located at 39° S, two important conclusions:

1) Warm waters;
2) Absence or lack of influence of cold currents.

From this basis it is possible to deduce that the ecologic conditions pertaining at the time of the deposition of the Upper Jagüelian Stage, and the contained ostracodes were preferentially adapted to:

a) Normal salinity of the waters (stenohaline ostracodes);
b) Warm water temperature;
c) Water rather deep, estimated between 150-300 meters in the deepest part of the basin;
d) Limpid waters;
e) Clayey substrates;
f) Normal pH (7-8 - 8.1).

However, whereas in the marine environment the above ecologic conditions prevailed, on the adjacent continent the flora, markedly related with that of Australia and New Zealand, indicates tropical and subtropical climatic conditions (Menendez, 1969).

Microfaunal affinities

From the contributions of Apostolescu (1961, 1963), Reyment (1960, 1963), and later Dingle (1969), it is possible to observe certain similarities between the ostracode faunas mentioned above from Argentina and those of the same age from the western and southern parts of the African continent.

Given the limitations of the present work it is not possible to discuss this matter at greater length, but a common origin is inferred for both assemblages, each developing later along parallel lines.

At the end of the Cretaceous all the ostracode species, generally if not entirely, became extinct, and were replaced by new forms.

II. TERTIARY

1) Rocanian Stage (Lower Danian)

The Rocanian Stage is well represented in the Neuquén and Colorado Basins, where it is represented by the Roca Formation (von Ihering, 1903, em. cat. Bertels, 1969a) with a wide regional extent; it was mostly deposited paraconcordantly with the Upper Cretaceous strata belonging to the above mentioned Jaqüelian Stage.

At the beginning of the Tertiary, with the deposition of the Roca Formation, the Cretaceous microfaunas of ostracodes and Foraminifera are totally replaced.

Between the Jagüelian (Upper Cretaceous) and Rocanian (Lower Tertiary) stages, a paleontological hiatus has been recorded based on the assemblages of planktonic Foraminifera (Bertels, 1970a) ; this break is equivalent to the uppermost Maastrichtian.

Between all the sections studied in the Roca Formation — which encompass a wide areal extent within the basin — it is observable that the strata correspond to a clearly regressive facies, comprising at their base clays, above which, in various parts of the basin are to be found fossiliferous calcareous marls, calcareous sands, and limestones.

Without doubt the most interesting sequence for the gathering of paleoecologic conclusions is that of the stratotype of the Roca Formation located north of the city of that name (Provincia de Rio Negro) (Bertels, 1964, 1969a, 1970a, 1973a).

The preponderant ostracode species are the following (Bertels, 1973a (Plate III) :

Cytherella sp. aff. *C. utilis* Bertels, 1968
Cyamocytheridea felix Bertels, 1973
Paracypris? sp.
Krithe rocana Bertels, 1973
Togoina australis Bertels, 1968
Huantraiconella prima Bertels, 1968
Actinocythereis indigena Bertels, 1969
Actinocythereis biposterospinata Bertels, 1973
Trachyleberis weiperti Bertels, 1969
Anticythereis schilleri Bertels, 1973
Rocaleberis nascens Bertels, 1969
Wichmannella meridionalis Bertels, 1969
Loxoconcha similis Bertels, 1973
Cytheropteron rocanum Bertels, 1973

associated with the following most abundant foraminiferal species:

Globoconusa daubjergensis (Brönnimann, 1953)
Subbotina triloculinoides (Plummer, 1926)
Globorotalia pseudobulloides (Plummer, 1926)

Cibicides vulgaris (Plummer, 1926)
Alabamina midwayensis Brotzen, 1948
Pulsiphonina prima (Plummer, 1926)

and others previously described by the author (Bertels, 1964).

This ostracode assemblage is, at the species level, completely different from those indicated for the Upper Cretaceous, although some phylogenetic trends can be inferred, such as:

Wichmannella araucana — *Wichmannella meridionalis*
Togoina n. sp. — *Togoina australis*
Anticythereis n. sp. — *Anticythereis schilleri*

Some ostracodes, associated with abundant Foraminifera — either planktonic or benthonic — are found only in the lower part of the sequence. For example:

Rocaleberis nascens Bertels, 1969
Trachyleberis weiperti Bertels, 1969
Anticythereis schilleri Bertels, 1973

This lower part of the sequence — basically clayey — corresponds, on the basis of its contained Foraminifera to:

a) Water rather deep (80-150 m);
b) Warm-temperate waters, although somewhat lower than in the Upper Cretaceous, inferred from the small size of planktonic Foraminifera;
c) Normal salinity;
d) Limpid waters;
e) Clayey substrates;
f) Normal pH.

The majority of the ostracode species mentioned and illustrated correspond to these physical parameters, with the exception of:

Wichmannella meridionalis
Togoina australis
Actinocythereis indigena
Cytheropteron rocanum
Loxoconcha similis

all of which persist throughout the section in all facies being consequently:

a) Euryhaline;
b) Adapted to live at different depths;
c) Eurythermal (in respect of the fact that superficial waters mostly have higher temperature than deeper ones).

However, it is notable that all these species show some morphologic changes throughout the section in concomitance with the ecological changes, such as smaller size and reduction of the strength of the ornamentation.

Parallel to these marine conditions, in the Argentine continent including the Antarctic sector, warm climatic conditions prevailed (Menendez, 1969) based upon floral evidence.

MICROFAUNAL AFFINITIES

The microfaunal affinities, as outlined for the Upper Cretaceous, continued to demonstrate similarities to the African ostracode faunas of approximately the same age. These similarities with Africa, and at the same time the probable lack of connection with other assemblages is evidenced by a comparison of the present assemblages with those of North America and Europe.

2) Salamanquian Stage (Upper Danian)

In the Argentine Republic the Salamanquian Stage is particularly well developed in the San Jorge basin (fig. 1) with outcrops of these strata being found near the Atlantic Coast, represented by the Salamanca Formation and extending to the northern part of this basin in different facies, *i.e.,* the Bororó Formation (Andreis, *et. al.,* in press).

Although some foraminiferal associations were studied by Mendez (1966) and Masiuk (1967) the ostracode microfauna is not well known which is principally a consequence of the poor representation of these organisms in these strata. However, *Wichmannella meridionalis* and *Actinocythereis indigena* have a wide areal distribution and are practically the only abundant species of the few ostracodes which otherwise range up from the Rocanian Stage.

Based on Foraminifera the ecologic conditions were those of a normal marine environment, warm-temperate and rather limpid waters. The assemblages indicate mostly the inner shelf environment, water depth being not greater than 100-150 meters.

The abundance of Foraminifera and relatively small numbers of ostracodes, with the exception of a few species, is a notable characteristic of the deposits.

Vertebrate paleontologists (Pascual and Odreman Rivas, 1971) reported, from the Salamanquian Stage of Patagonia, reptiles of the order Chelonia and Crocodilia, amongst other organisms, similar to forms of the Upper Cretaceous of North America. They conclude that the climate in the Patagonian region — at least in what is now the central part — was sufficiently warm to maintain such a specialized fauna.

3) "Venericardia Beds" (Eocene?)

Deposits attributed to the Eocene, based on the presence of *Venericardia* belonging to the *planicosta* group, mentioned by Camacho (1956), and also found in many places by the author, are widely represented in the San Jorge and Austral basins (Camacho, 1956, 1967).

Despite innumerable attempts, until now no microfossils have been found.

They are deposits of marked littoral characteristics, composed in the great part of fine sediments with a large pyroclastic content.

These two important characteristics — littoral waters and sediment with a large pyroclastic content — can be interpreted as a consequence of:

Environment with high energy and very probable high turbidity of the waters originating principally from the pyroclastic contribution and fine sediments (clay) in suspension. Besides this primary factor other secondary factors were produced which, in their totality, certainly inhibited the productivity of the waters breaking the biologic chain, elemental for survival in this Eocene sea. However, this could be the product of diagenetic causes or weathering.

4) Julian, Leonian, and "Superpatagonian" Stages = "Patagonian Stage s.l." (*Oligocene-Miocene?*)

The deposits of the "Patagonian Stage s.l." have a wide areal distribution in the eastern region of the Argentina Republic. They crop out in the Austral Basin, where are located the stratotypes of this stage, and in the San Jorge and Valdés Basins (Text-fig. 1). Also there have been mentioned equivalent subsurface sections belonging to this stage (Kaasschieter, 1963; Malumian, 1968, 1969) in the Colorado and Austral Basins.

The sections of the "Patagonian Stage s.l." in the Austral Basin have been subdivided by Ameghino (1898) into Julian, Leonian, and Superpatagonian Stages and were almost always correlated with European lower Miocene stages (Ameghino 1898, 1906; Camacho, 1967) and latterly on the basis of planktonic Foraminifera with the Oligocene (Bertels, 1970b).

The "Patagonian Stage s.l." is only represented up to now by the San Julián and Monte León Formations (Ameghino, 1898, em. cat. Bertels, 1970b) which at the same time are the statotypes of the Julian and Leonian Stages respectively.

Becker (1964) first studied the microfauna of the "Superpatagonian Stage" and this work is used here to arrive at the conclusions considered important to my interpretation.

The most prominent lithologic features of the San Julián Formation are clays at the base followed by sandstones with coquinas at the top. The overlying Monte León Formation is predominantly pelitic sediments with a marked pyroclastic contribution and with sedimentary structures such as cross and current bedding. The sediments assigned to the "Superpatagonian Stage" by Ameghino (1898, 1906) possess approximately the same sedimentological features as those of the Monte León Formation and some transitional with the overlying Santa Cruz Formation.

The sediments of the San Julian and Monte León Formations and those assigned to the "Superpatagonian Stage" conform to a transgressive-regressive sequence, resting on the Mesozoic "Porphiritic Serie" and underlying the continental Santa Cruz Formation (Ameghino, 1898, 1906).

The ostracode assemblage of the Superpatagonian Stage described by Becker (1964) is composed of (Plate IV): (Generic names in parentheses are revised assignments by the present author).

Cytherelloidea sp. 1
Mutilus (Aurila) cf. convexa (Baird, 1850)
Urocythereis sp. 1
Echinocythereis sp. 1
Leguminocythereis sp. 1 *(=Bensonia)*
Leguminocythereis sp. 2 *(=Soudanella)*

Trachyleberis sp. 1
Trachyleberis sp. 2
Hermanites sp. 1
Hermanites sp. 2
Brachycythere sp. 1 *(=Aurila* group*)*
Krithe sp. 1
Cytherois sp. 1
Xestoleberis ? sp. 1
Henryhowella ? sp.

Amongst the species of Foraminifera described by Becker (1964) are some which today inhabit the South American shelf, limited in depth to littoral and shallow waters (up to 15 m). These forms have been taken into account by Boltovskoy (1970) to establish the distribution of littoral marine benthonic Foraminifera in Argentina, Uruguay, and southern Brazilian waters between the latitudes of 30°S and 57°S approximately. In his research he arrived at interesting results concerning the species distribution which are influenced by the warm Brazil current and by the cold Antarctic and Malvinas currents.

In this work he found some cosmopolitan species — although with preference to determined latitudes — and others with restricted habitats between certain parallels. Amongst the latter are *Pyrgo nasuta* and *Elphidium discoidale* which in the Recent are limited in their occurrence between 44°S and 28°S or lower latitudes; both these species were found by Becker in her Las Cuevas locality *(op. cit.)*, in the present day latitude of 52°S approximately. On the other hand Becker (1964) mentioned *Miliolinella subrotunda* from Las Cuevas, a form which today is cosmopolitan extending from Tierra del Fuego (55°S) to Porto Alegre (30°S) or farther north, although it is more abundant north of the latitude of Bahia Blanca.

Taking into account the Recent distribution of the Foraminifera mentioned above, and with the assumption that the assemblage found by Becker *(op. cit.)* is of shallow waters, confirmed also by the presence of typical epineritic genera of ostracodes such as *Hermanites, Urocythereis,* and those of *Aurila* group, because the facies of the "Superpatagonian Stage" in the Las Cuevas locality (50-51°S) is regressive and of littoral environment — I arrive at the conclusion that the temperature conditions of the waters, during the deposition of the "Superpatagonian Stage" were warmer than at present. This can be the result of various causes:

a) Changes of the position of terrestrial poles;
b) Greater influence of the warm Brazil current;
c) Lesser influence of the Antarctic and Malvinas currents;
d) Different course of the cold currents;
e) Absence of the Antarctic and Malvinas currents.

The sedimentological features mentioned for the San Julian and Monte León Formations and those which compose the "Superpatagonian Stage", together with their Foraminifera indicate:

a) Temperate climate (similar to recent latitudes 30-40°S);
b) Normal salinity of open sea conditions;
c) Rather agitated waters (cross bedding) and with some turbidity (fine sediments and volcanic contribution);
d) Shallow waters, no deeper than the inner shelf;
e) Normal pH, at least in the samples which contain microfossils.

Consequently the ostracodes described by Becker (1964) respond to the environmental features mentioned above.

In this manner it can be concluded that the ostracodes belonging to the genera described by Becker, or related forms could inhabit today lower latitudes and that consequently they are forms of shallow and warm-temperate or temperate waters.

The study made by Benson (1964) on Antarctic ostracodes shows that the species diversity found in this region is less than in that of warm waters; otherwise the populations are numerous and the size large. These species range between 55°S and 75°S and related forms to 50°S, which is the approximate latitude of the outcrops of the "Superpatagonian Stage" studied by Becker (1964).

From the ostracodes mentioned by Becker it is evident that there does not exist a relation between her fauna and that of the Antarctic Recent with the exception of *Xestoleberis, Krithe,* and *Echinocythereis,* which are widespread forms, being the last of cold and rather deep waters.

Also it is not possible to find any relation with those Recent species described from the equatorial Pacific by Allison and Holden (1971), excepting for the genera *Mutilus, Xestoleberis,* and *Cytherelloidea.*

On the other hand there are some similarities with regard to the ostracode assemblage between the Recent forms recorded by Puri, *et al.* (1964) from the Gulf of Naples, essentially by the genera *Aurila, Mutilus, Urocythereis, Buntonia,* and *Krithe,* with the exception of the genus *Cytherelloidea* which is present in our microfauna.

Although Puri, *et al.* (1964) concluded that the waters are not warm and that the microfauna is similar to that described from Norway by Sars, the genus *Cytherelloidea* is as far as I know exclusive to warm waters and supports my thesis of at least temperate waters for Patagonia at this time.

Vertebrate paleontologists and paleobotanists arrived at their own conclusions about climatic conditions pertaining on the continent, which in some manner must be related to the littoral marine waters.

Pascual and Odreman Rivas (1971), on the basis of vertebrates found in the continental Colhue Huapi Formation established their conclusions. The Colhue Huapi Formation, after these authors, passes very gradually to marine sediments of the "Patagonian Stage" which themselves pass gradually to sediments of a Santacrucense Age.

Amongst the most conspicuous vertebrate faunas, in the sense of environmental indicators, there are the primates of the Colhue Huapi Formation; these would represent for the continental region at last, a warm-temperate climate.

In the marine sediments attributed to the "Patagonian Stage s.l.", Pascual and Odreman Rivas *(op. cit.)* mentioned tetrapods, like the turtle *Testudo gringorum,* and varied remains of penguins; these authors indicated that the Testudinidae (turtles) as well as the penguins are good paleotemperature indicators. The presence of these two groups of fossils is contradictory: the first being distributed today throughout tropical and warm-temperate regions, whereas the penguins are birds without question adapted to cold waters. This fact would indicate that, whereas on the Patagonian continent the climate was warm, the waters which bathed its coasts were cold, surely because at that time the cold marine Malvinas current was already operative. This would perhaps have had little or no influence on the continental climatic conditions.

In the overlying Santa Cruz Formation (of the "Patagonian Stage s.l.") Pascual and Odreman Rivas (1971) concluded that for the first time the climate could be benign to very warm, as is indicated by the presence of primates and marsupial cenolestids and also like the extraordinary variety and quantity of edentates, especially Megalonychidae.

Menendez (1969) believed however, from the fossil plants, that toward the end of the Eocene and the beginning of the Oligocene began the retraction northwards of the warm and humid floral elements. These earlier had extended to higher latitudes in Patagonia and Antarctica. At the same time he noted the advance in the same direction of cold-temperate elements, registered in the Oligocene and Miocene of Rio Negro (lat. 40°S) as the remains of widespread forest, and which today extend to Tierra del Fuego (lat. 55°S) in the eastern side of the Andean ranges.

The results of these two studies appear to be contradictory.

The Foraminifera and ostracodes reveal temperate to warm-temperate water conditions, at least higher than those at the same latitude today, whilst the presence of penguins in sediments of the "Patagonian Stage s.l." farther north than the area from which the microfaunas were obtained, reveals cold waters.

In the continental region called Patagonia, the cold temperate floral elements and vertebrates of warm climates, constitute a second contradiction at this time in its geologic history.

The penguins are found in the basal beds of the "Patagonian Stage s.l." and the described ostracodes from near the top of this stage and near the base of the Santa Cruz Formation in which warm climate primates and cenolestid marsupials occur. This could indicate a lowering of the temperature of the waters during the early Patagonian Stage which gradually increased to a temperature sufficiently warm to allow the presence of such genera as *Cytherelloidea.*

MICROFAUNAL AFFINITIES

In the microfauna it is possible to observe on the one hand some elements still related to older elements from Africa and South America, for example in Argentina (cf. Upper Cretaceous and Paleocene) there are such forms as

Echinocythereis (Wichmannella) and *Soudanella*. On the other hand, it is evident that at this time the arrival of other elements from the Northern Hemisphere is revealed by the appearance of *Aurila* and *Urocythereis* or related genera which had been present in the Northern Hemisphere. For this reason it is supposed that the existing intraoceanic barriers of the Upper Cretaceous and Lower Tertiary disappeared, allowing the incursion of elements from other faunal provinces.

It is interesting to note the near absence from Argentina of affinities with the New Zealand Upper Cretaceous and Tertiary marine ostracode assemblages with the exception of cosmopolitan genera such as *Trachyleberis, Actinocythereis, Cytheropteron,* and *Hemicytherura* (cf. Hornibrook, 1953a,b).

The abundance in the Superpatagonian Stage of the genus *Bensonia* is also notable because it seems to have reached a wide distribution throughout the American Tertiary as is shown by the work of Ulrich and Bassler (1904). These authors illustrate many species resembling *Bensonia, Cytheretta,* and *Leguminocythereis* which appear to be closely related forms to those under consideration.

5) Entrerrian Stage (Tortonian?)

The Entrerrian Stage was originally distinguished by Ameghino (1894) although its outcrops were considered originally by d'Orbigny (1842) and Darwin (1844) as integral parts of the "Patagonian Stage".

It is best exposed in the Paraná and Valdés basins (Text-fig. 1) and has been found in subsurface explorations in the Salado and Colorado river basins (Malumian, 1969).

This stage is at the present well represented by the Entre Rios Formation with an apparently wide areal distribution.

The age of these deposits is difficult to determine and has been variously assigned to the upper Miocene (Rossi de García, 1966,69; Camacho, 1967) and lower Pliocene (Pascual and Odreman Rivas, 1971).

In the associations present in many facies of the Entre Rios Formation it is possible to observe, generally speaking, a diminution in the number of species, and also in many cases in the number of individuals in comparison with the faunal communities of older stages, this being well marked among the Foraminifera.

With regard to the ostracodes described by Rossi de García (1966, 1969) from an approximate latitude of 32°S there are relatively few forms, which are dominated by:

Cytherella (Cytherelloidea) damottae Rossi de García, 1966
Henryhowella aff. *H. evax* (Ulrich and Bassler), 1904
Cyprideis camachoi Rossi de García, 1966
Buntonia entrerriensis Rossi de García, 1966
Echinocythereis boltovskoyi Rossi de García, 1966
Cytheropteron victoriensis Rossi de García, 1966
Perissocytheridea litoralensis Rossi de García, 1966 (= *Callistocythere*)

Cytheretta argentinensis Rossi de García, 1966 (= *Bensonia*)
Paracytheridea ? laudata Rossi de García, 1966
Caudites kennedyi Rossi de García, 1966
Trachyleberis nova Rossi de García, 1966
Cyamocytheridea ovalis Rossi de García, 1966
Loxoconcha paranensis Rossi de García, 1966
Cytheropteron aff. *C. newportensis* Crouch
Cytheropteron benedictus Rossi de García, 1966
Sclerochilus sp.

These ostracodes are associated with Foraminifera described by Pisetta (1968) who found in the Entre Rios Formation of the Paraná Basin the following foraminiferal species:

Rotalia beccarii parkinsoniana
Protelphidium cf. *P. tuberculatum*
Buccella peruviana campsi
Pyrgo ringens
Quinqueloculina seminulum

which are the same species, with the exception of *Protelphidium* cf. *tuberculatum* — extinguished in the Pliocene — as those living today along the Argentine coast.

Boltovskoy (1970) in a detailed appraisal, delimited areally the distribution of living species and found that *Rotalia beccarii parkinsoniana* is restricted to the littoral zone between Bahia Blanca (lat. 39°S) and Porto Alegre (lat. 30°S) and perhaps even farther north, whereas *Buccella peruviana campsi, Pyrgo ringens,* and *Quinqueloculina seminula* range between Tierra del Fuego (55°S) and Porto Alegre (30°S) each being more abundant between certain particular latitudes.

It is possible to conclude that the ecological conditions towards the end of the Miocene were, with regard to the temperature, practically similar or somewhat higher than those of today at the same latitude, *i.e.* subtropical-temperate, being in all cases of very shallow water origin, with salinity somewhat lower than normal at least insofar as we can deduce from the microfaunal evidence which we have to date.

Consequently the ostracodes studied by Rossi de García (1966, 69) correspond to these features. This is confirmed by the presence of *Cytherelloidea,* which supports our inferences concerning temperature, by *Cyprideis,* a typical brackish water genus and others, like *Callistocythere, Cyamocytheridea, Loxoconcha,* and *Paracytheridea* which generally inhabit shallow waters.

Summarizing, therefore, we have that the Entrerrian ostracodes:

a) Preferred temperate warm waters;
b) Were adapted to some changes from the normal salinity;
c) Inhabit very shallow waters (not deeper than 50 m);
d) Were adapted to sandy and clayey substrates;

e) Could withstand a pH possibly lower than normal resulting from the changes of salinity and by the outline of the basin, which in the case of the Paraná Basin could not have reached the conditions of an open sea.

On the other hand vertebrate researchers (Pascual and Odreman Rivas, 1971) on the basis of turtles and crocodiles present in outcrops of the Entre Rios Formation, in the province of the same name, infer subtropical conditions reigning in the Mesopotamian, Santa Fe and Chaco pampa regions (Paraná Basin) corresponding approximately to the latitude of 30-34°S.

MICROFAUNAL AFFINITIES

From the ostracode assemblages present in the Entre Rios Formation it is possible to observe faunistic similarities with those of the "Superpatagonian Stage," for example the genera *Cytherelloidea, Henryhowella, Buntonia, Echinocythereis, Trachyleberis,* and *Bensonia,* represented by species which seem to be closely related.

This would mean that the genera which lived during the upper Miocene at latitude 30-34°S were related to those of the upper Oligocene-lower Miocene at latitude 50-51°S.

This confirms once more my conclusion that the waters were warmer than those of the present day, during the Oligo-Miocene, at the same latitudes of approximately 50°S. It is feasible also, that a migration took place toward the north during the late Miocene, which may have continued later.

6) Pliocene

In the Argentine Republic marine outcrops with microfaunas attributed to the marine Pliocene are virtually absent.

III. QUATERNARY

1) Pleistocene

In the Argentine Republic the marine transgressions attributed to the Pleistocene were limited to the coastal region; the outcrops extend only a little way inland and, therefore, left their seal in the greater part as subparallel littoral belts around the coast, such as those described by Rossi de García (1967) and Suarez Soruco (1968), and are located bordering the continent from Buenos Aires to the south of the Republic.

The lithology of the sequences, in particular those assigned to the Platian Stage studied by Suarez Soruco (1968) is that of clays at the base followed toward the top by sands and coquina sands indicating a regressive facies.

The ostracodes found by Suarez Soruco (unpublished thesis, 1968) in the Buenos Aires Province (lat. 38°S) are (Plate V):

Cypridopsis, n. sp.
Protocytheretta, n. sp.
Cyprideis, n. sp.
Krithe, n. sp. (resembles *Parakrithella hanai* Hartmann, 1962)

Callistocythere, n. sp. (resembles *C.* n. sp. A Whatley and Moguilevsky, in this volume)
Cushmanidea, n. sp.
Cytherura, n. sp.
Cytherura, n. sp. (resembles *Hemicytherura* sp. aff. *Cytherura obliqua* Brady, 1880)
Cytherura, n. sp.
Hemicytherura, n. sp. (resembles *H.* sp. aff. *C. lilljeborgii* Brady, 1880)
Hemicytherura, n. sp.
Hemicythere, n. sp.
Caudites, n. sp.
Patagonacythere, n. sp. 1
Patagonacythere, n. sp. 2
Loxoconcha, n. sp. (resembles *L. paranensis* Rossi de García, 1966)
Urocythereis, n. sp.
Munseyella, n. sp. (*Mesocythere?*)
Munseyella, n. sp.

Rossi de García (1967) mentioned from the littoral belts of Chubut Province (approx. 45°S):

Cytherura tajamarensis Rossi de García, 1967
Cythere americana Rossi de García, 1967
Quadracythere? litoralis Rossi de García, 1967
Caudites? chubutensis Rossi de García, 1967
Hemicythere patagonica Rossi de García, 1967

It can be concluded that these species are of one particular environment and the ostracodes different from those described by Suarez Soruco (1968) from Buenos Aires Province (38°S), and those described by Hartmann (1962) from the marine littoral of southern Argentina (55°S up to Golfo Nuevo at 42°S). A fauna intermediate between those two is indicated by the Chubut assemblage.

The most abundant Foraminifera species found by Suarez Soruco (1968) are: *Rotalia* ex gr. *parkinsoniana* and *Elphidium discoidale,* followed in order of abundance by *Pyrgo nasuta, Bulimina patagonica, Bolivina striatula, Quinqueloculina lamarckiana* and *Bucella frigida.* The two first mentioned have today a restricted distribution: *Rotalia* ex gr. *parkinsoniana* from Bahia Blanca (39°S) to Porto Alegre (30°S) whereas *Elphidium discoidale* extends its habitat from the Pininsula Valdés (42° 5′S) to Porto Alegre (30°S) becoming really abundant from Bahia Blanca (39°S) to the north.

From the rest of the Foraminifera species *Bulimina patagonica* extends from Rio Gallegos (52°S) to Porto Alegre (30°S) without any particular abundance; *Pyrgo nasuta* from Peninsula Valdés (42°30′S) to Porto Alegre, being abundant only off and north of Buenos Aires Province (40°S) to the north; *Bolivina striatula* from Puerto Deseado (47°S) to Porto Alegre (30°S) without any particular abundance and *Quinqueloculina lamarckiana* from 45°S to Porto Alegre (30°S).

The distribution and abundance of the species in the Recent sea seems to be very coincidental with those living in the Pleistocene.

The considered assemblages, taking also into account the lithology, shows that the habitat of the Ostracoda was littoral. On the other hand, *Buccella frigida* is a very widespread species in austral Patagonia, whereas *Rotalia beccarii parkinsoniana* inhabits preferably warm waters. From this can be deduced that the water temperature was temperate, a product of the conjunction of the Antarctic and Malvinas cold currents and the Brazilian warm current, such as exists today (Boltovskoy, 1970).

Consequently the existence of the cold and warm currents — Antarctica-Malvinas, and Brazil respectively — is inferred in the Platian Stage.

The paleoecology can be summarized:

a) temperate waters due to zones of current convergence at latitudes of 35°S and 40°S;

b) in general normal salinity, with many hypohaline micro-environments, although a great part of the Foraminifera and ostracodes are euryhaline;

c) quiet waters (mollusks preserved as entire shells).

GENERAL CONCLUSIONS

Ecological conclusions

1) Depth

The seas since the Upper Cretaceous were progressively shallower with respect to the outcrops in the present continent, fundamentally the product of isostatic equilibrating factors which were the consequence on one hand of the paulatine deepening of the Atlantic Ocean and on the other the rise of the Andean ranges.

During the Upper Cretaceous (Maastrichtian) and Lower Tertiary (Lower Danian) the deepest (150-300 m) sea conditions occurred.

2) Temperature

During the late Cretaceous through the Paleogene the water temperatures were markedly higher than in the Recent at the same latitudes. They reached nearly the present day temperatures in the upper Miocene and the present day regime was firmly established in the Pleistocene.

Some rapid lowering of the sea temperature could be inferred at the beginning of the Lower Tertiary (Lower Danian) during the deposition of the Rocanian Stage and also at the end (lower Oligocene) during the deposition of the basal "Patagonian Stage s.l.", but at other times reaching higher temperatures until the middle Miocene.

The cold Antarctica and Malvinas currents probably were of importance in the microfaunal distribution from the upper Miocene onward, and were definitely established in the Pleistocene in the form which still exists today.

3) Salinity

The salinity remained normal between the Upper Cretaceous and the lower Miocene, with features of an open sea, except those littoral regions developed along the borders of ancient massifs.

During the upper Miocene the sea exhibited features of nearly enclosed nature, revealed by the particular assemblages, whereas during the Pleistocene the sea, although open, was very shallow and had fresh and brackish water contributions.

TAXONOMIC AND PHYLETIC CONCLUSIONS

1) The absence (cf. Brady, Benson, Hartmann) in the Recent of genera related with *Togoina* and *Bensonia* is remarkable. These *probably* became extinct at the end of the Miocene. *Togoina* from the Upper Cretaceous and Lower Tertiary could be phylogenetically related to *Bensonia* from the Oligocene and Miocene.

2) The abundance and persistence from the Upper Cretaceous to the Recent of species of the genus *Wichmannella* and strongly related forms assigned mostly to *Echinocythereis* Puri, 1953 is remarkable. To the genus *Wichmannella* could belong, or be related, some species like those described by Brady (1880):

Cythere cribriformis
C. viminea
C. melobesioides
C. dasyderma
C. ericea
C. irpex

3) Argentina ostracode assemblages seem to be related to the western and southern African communities for which it is supposed an ancestral common origin. These affinities are strong in the late Cretaceous and early Tertiary.

During the late Oligocene and early Miocene genera from the Northern Hemisphere appeared; for that reason it can be suspected that intraoceanic barriers disappeared at this time to allow free migration.

STRATIGRAPHIC CONCLUSIONS

Ostracodes can be used in Argentina as time markers, because the assemblages as now found in the various marine stages, at both the assemblage and the generic level, show marked differences.

REFERENCES

Allison E. C., and Holden, J. C.
1971. *Recent Ostracodes from Clipperton Island eastern tropical Pacific.* San Diego Soc. Nat. Hist., Trans., vol. 16, No. 7, pp. 165-214, 1 table, 31 text figs.

Ameghino, F.
1894. *Enumération synoptique des espèces de mamifères fossiles des formations éocènes de Patagonie.* 80, Buenos Aires, pp. 1-196.
1898. *Sinopsis geológico-paleontológica. Segundo Censo de la República Argentina,* T. I, Buenos Aires, pp. 116-121.
1906. *Les formations sedimentaires du Crétacé Supérieur et du Tertiaire de Patagonia.* Anales Museo Nacional Buenos Aires, serie III, T. VIII, 3 plates, 358 text figs.

Andreis, R., Spaletti, M., and Mazzoni, A.
Geología y sedimentología del cerro Bororó, Provincia del Chubut, República Argentina. (In press.)

Apostolescu, V.
1961. *Contribution a l'étude Paléontologique (Ostracodes) et Strati-*

graphique des Bassins Crétacés et Tertiaires de l'Afrique occidentale. Revue de l'Institut Français du Pétrole, vol. XVI, Nos. 7-8, pp. 779-830, 18 pls.

1963. *Essai de Zonation par les Ostracodes dans le Crétacé du Bassin du Sénégal.* Revue de l'Institut Français du Pétrole, vol. XVIII, No. 12, pp. 1675-1694, 6 pls., 2 tables.

Bandy, Orville L.

1967. *Cretaceous planktonic foraminiferal zonation.* Micropaleontology, vol. 13, No. 1, pp. 1-31.

Becker, D.

1964. *Micropaleontología del Superpatagoniense de las localidades Las Cuevas y Monte Entrance (Provincia de Santa Cruz).* Ameghiniana, T. III, No. 10, pp. 319-351, 6 pls., 1 text fig., 4 tables.

Benson, R. H.

1964. *Recent Cytheracean Ostracodes from McMurdo Sound and the Ross Sea, Antarctica.* Univ. of Kansas Paleont. Contrib., Arthropoda, Art. 6, pp. 1-36, 4 pls., 25 text figs.

Bertels, A.

1964. *Micropaleontología del Paleoceno de General Roca (Prov. de Rio Negro).* Rev. Museo La Plata, Nueva Serie, T. IV, No. 23, Paleont. pp. 125-184, 7 pls., 3 text figs., 3 tables.

1968. *Estratigrafía y micropaleontolgía del límite Cretácico-Terciario en Huantrai-co (Provincia de Neuquén). Parte I.* Ameghiniana, T. V, No. 8, pp. 279-295, 3 pls.

1969a. *Estratigrafía del límite Cretácico-Terciario en Patagonia Septentrional.* Rev. Asoc. Geol. Argentina, T. 24, No. 1, pp. 21-54, 2 text figs.

1969b. *"Rocaleberidinae", nueva subfamilia (Ostracoda, Crustacea") del límite Cretácico-Terciario de Patagonia Septentrional (Argentina).* Ameghiniana, T. VI, No. 2, pp. 116-171, 5 pls.

1969c. *Micropaleontología y Estratigrafía del límite Cretácico-Terciario en Huantrai-co (Provincia del Neuquén). Ostracoda. Parte II.* Ameghiniana, T. VI, No. 4, pp. 253-289, 9 pls., 2 tables.

1970a. *Los foraminíferos planctónicos de la cuenca cretácico-terciaria en Patagonia septentrional (Argentina), con consideraciones sobre la estratigrafía de Fortín General Roca (Provincia de Rio Negro).* Ameghiniana, T. VII, No. 1, pp. 1-56, 9 plates, 10 text figs., 2 tables.

1970b. *Sobre el "Piso Patagoniano" y la representación de la época del Oligoceno en Patagonia austral, República Argentina.* Rev. Asoc. Geol. Argentina, T. XXV, No. 4, pp. 495-501.

1972. *Ostrácodos de agua dulce del miembro inferior de la Formación Huantrai-co (Maastrichtiano Inferior), Provincia del Neuquén, República Argentina.* Ameghiniana, T. IX, No. 2, pp. 173-182, 1 plate, 2 text-figs.

1973a. *Ostracods of the type locality of the Lower Tertiary (Lower Danian) Rocanian Stage and Roca Formation (Argentina).* Micropaleontology, vol. 19, No. 3, pp. 308-340, 6 plates, 5 text-figs.

1973b. *Upper Cretaceous (Lower Maastrichtian) Ostracodes of Argentina* (in press).

1973c. *Upper Cretaceous (Middle Maastrichtian) Ostracodes of Argentina* (in press).

Boltovskoy, E.

1968. *Hidrología de las aguas superficiales en la parte occidental del Atlántico Sur.* Rev. Museo Argentino Ciencias Naturales. "B. Rivadavia". Hidrobiología, T. II, No. 6, pp. 199-224, 2 text figs., 2 tables.

1970. *Distribution of the marine littoral Foraminifera in Argentina, Uruguay and Brazil.* Marine Biology, vol. 6, No. 4, pp. 335-344, 2 text figs.

Brady, G. S.

1880. *Report on the Ostracoda dredged by H. M. S. Challenger during the years 1873-1876. Report on the Scientific Results of the Voyage of H. M. S. Challenger.* Zoology, vol. I, pp. 1-184, 44 pls.

Camacho, H. H.

1956. *La transgresión patagoniense en la costa atlántica entre Comodoro Rivadavia y el curso inferior del Rio Chubut.* Rev. Asoc. Geol. Argentina, T. XI, No. 1, pp. 23-45, 6 pls., 6 text figs., 1 map.

1967. *Las transgresiones del Cretácico superior y Terciario de la Argentina.* Rev. Asoc. Geol. Argentina, T. XXII, No. 4, pp. 253-280, 6 text-figs.

Criado Roque, P., de Ferraris, C., Mingramm, A., Rolleri, E., Simonato, I. B., and Suero, T.

1960. *Cuencas sedimentarias de la Argentina.* Boletín de Informaciones Petroleras, No. 320. Buenos Aires, pp. 1-21, 11 text- figs.

Darwin, Charles

1844. *Geological observations on the volcanic islands and parts of South America, visited during the Voyage of H. M. S. Beagle. . . .* London.

Dingle, R. V.

1969. *Upper Senonian ostracods from the coast of Pondoland, South Africa.* Roy. Soc. S. Africa, Trans., 38, Part 4, pp. 347-385, 20 text figs.

d'Orbigny, Alcide

1842. *Voyage dans l'Amérique Méridionale,* T. 3, part 3. *Geologie,* pp. 1-140, 15 pls.

Groeber, P.

1946. *Observaciones Geológicas a lo largo del meridiano 70. 1. Hoja Chos Malal.* Rev. Soc. Geol. Argentina, T. I, No. 3, Buenos Aires, pp. 177-208, 1 map, 4 text figs.

Hartmann, G.

1962. *Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens under besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil III. Ostracoden des Eulitorals.* Mitteil. Hamburgischen Zool. Mus. Institut. Ergänzungsband zu Bd. 60, pp. 169-270, 223 text figs., 1 table.

Herrero Ducloux, A.

1946. *Contribución al conocimiento geológico del Neuquén extraandino.* Bol. Informaciones Petroleras. Reimpresión No. 266. Buenos Aires, pp. 1-39, 8 text figs.

Hornibrook, N. de B.

1953a. *Tertiary and Recent marine Ostracoda of New Zealand. Their origin, affinities and distribution:* New Zealand Geol. Sur., Palaeont. Bull. 18, pp. 1-82, 18 pls. 4 text figs., 3 tables.

1953b. *Some New Zealand Tertiary marine Ostracoda useful in stratigraphy.* Roy. Soc. New Zealand Trans., 81, Part 2, pp. 303-311, 2 pls.

Kaasschieter, J. P. H.

1963. *Geologia de la Cuenca del Colorado.* Actas Segundas Jornadas Geológicas Argentinas, pp. 251-269, 5 text figs.

Malumian, N.

1968. *Foraminíferos del Cretácico Superior y Terciario del subsuelo de la Provincia de Santa Cruz, Argentina.* Ameghiniana, T. V, No. 6, pp. 191-227, 8 pls.

1969. *Micropaleontología y Bioestratigrafía del Terciario marino del subsuelo de la Prov. de Buenos Aires.* Tesis de doctorado Facultad Ciencias Exactas y Naturales, Univ. Buenos Aires (inedit).

Masiuk, V.

1967. *Estratigrafía del Rocanense del Puesto P. Alvarez. Curso inferior del Rio Chico, Provincia del Chubut.* Rev. Museo La Plata, Nueva Serie, Sección Paleont., T. V, pp. 197-258, 8 pls.

Mendez, I.

1966. *Foraminíferos, edad y correlación estratigráfica del Salamanquense de Punta Peligro (45° 30′ S; 67° 11′ W) Provincia del Chubut.* Asoc. Geol. Argentina, T. XXI, No. 2, pp. 127-157, 4 pls.

Menendez, C. A.

1969. *Die fossilen Floren Südamerikas. Biogeography and ecology in South America.* Ed. Fittkau, Illies, Klinge, Schwabe and Sioli, Dr. W. Junk, N. V. Pub., The Hague, pp. 519-561, 10 pls.

Mühlmann, P.

1937. *Algunas observaciones preliminares sobre los "Estratos de Malargüe".* Boletín Informaciones Petroleras, XIV, No. 153, pp. 44-54.

Pascual, R., and Odreman Rivas, O. E.

1971. *Evolución de las comunidades de los Vertebrados del Terciario argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados.* Ameghiniana, T. VIII, Nos. 3-4, pp. 372-412, 1 table.

Pisetta, J. L.

1968. *Descripción de una faúnula de Foraminíferos de la Provincia de Entre Rios.* Thesis Facultad Ciencias Exactas y Naturales, Universidad Buenos Aires (unpublished).

Puri, H. S., Bonaduce, G., and Malloy, J.

1964. *Ecology of the Gulf of Naples.* Pubbl. staz. zool. Napoli, 33 suppl., pp. 87-199, 67 text figs., 1 table.

Reyment, R. A.

1960. *Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 1: Senonian and Maestrichtian Ostracoda.* Stockholm Contr. Geology, vol. VII, pp. 1-238, 23 pls.

1963. *Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 2: Danian, Paleocene and Eocene Ostracoda.* Stockholm Contr. Geology, vol. X, pp. 1-286, 23 pls., 81 text figs.

Rossi de Garcia, E.

1966. *Contribución al conocimiento de los ostrácodos de la Argentina. 1. Formación Entre Rios, de Victoria, Provincia de Entre Rios.* Rev. Asoc. Geol. Argentina, T. XXI, No. 3, pp. 194-208, 4 pls.

1967. *Contribución al conocimiento de los ostrácodos cenozoicos de la Argentina. Parte II. Ostrácodos del cordón litoral Loma de Tajamar.* Rev. Asoc. Geol. Argentina, T. XXII, No. 3, pp. 203-208, 1 pl.

1969. *Algunos ostrácodos del Entrerriense de Paraná, Provincia de Entre Rios, República Argentina.* Rev. Asoc. Geol. Argentina, T. XXIV, No. 3, pp. 276-280, 1 plate, 1 table.

Stipanicic, P. N., Rodrigo, F., Baulies, O. F., and Martinez, C. G.

1968. *Las formaciones presenonianas en el denominado Macizo Nordpatagónico y regiones adyacentes.* Rev. Asoc. Geol. Argentina, T. XXIII, No. 2, pp. 67-98, 4 pls., 1 text fig., 3 tables.

Suarez Soruco, J. R.

1968. *Estudio micropaleontológico del Cordón litoral de la localidad de Mar Chiquita, Provincia de Buenos Aires.* Thesis Facultad Ciencias Exactas y Naturales, Univ. Buenos Aires. (unpublished).

Ulrich, E. O., and Bassler, R. S.

1904. *Systematic paleontology of the Miocene deposits of Maryland.* Maryland Geol. Sur., Miocene, pp 98-130, pls. XXXV-XXXVIII.

Välikangas, I.

1933. *Über die Biologie der Ostsee als Brackwassergebiet.* Verhandl. Intern. Vereining. theoret. angewandte Limnol., 6, pp. 63-112.

von Ihering, H.
1903. *Les Mollusques des térrains crétaciques supérieurs de l'Argentine orientale.* Anales Museo Nacional Buenos Aires, serie 3, T. II, 205 pp.
Wichmann, R.
1924. *Nuevas observaciones Geológicas en la parte oriental del Neuquén y en el Territorio del Rio Negro.* Dirección General de Minas, Geología Hidrol. (Geolog.), Publ. No. 2, pp. 1-22, 8 pls.
Windhausen, A.
1914. *Contribución al conocimiento geológico de los territorios del Rio Negro y Neuquén.* Anales Ministerio Agricultura. Secc. Geología, Mineralogía Minería, T. X, No. 1, pp. 1-60, 8 pls.

Alwine Bertels,
Facultad de Ciencias Exactas y Naturales,
Universidad Buenos Aires,
Argentina

DISCUSSION

Dr. R. H. Benson: I think this paper represents an important contribution. We have had a considerable lack of information from this part of the world of the ages reported here. I'm also impressed with the age of the genus she calls *Wichmannella.* You probably know more about it in Argentina than I, but it is living today in the Straits of Magellan, and it has large eye tubercles. Its eyes are particularly significant I think because this genus, described not as a genus but as a species, *Cythere circumdentata* by Brady, occurs in deep water throughout the Southern Ocean at the present day. However, it is almost always blind. It's a very curious thing that it should occur living and cited in this region. I think it also has eye tubercles in Bertel's pictures.

Liebau: The first-mentioned fauna from the Lower Maastrichtian is considered to be polyhaline, but the figured genera seem to represent an euhaline biofacies. If this were really a brackish water fauna, there must have been some other genera. Especially some typically euryhaline Cytherideidae.

Bertels: (written answer to Liebau)

The first Upper Cretaceous ingression of the sea produced in some regions brackish water environments, most probably polyhaline, allowing the development of a microfauna of this nature: that is to say, communities which under certain conditions could withstand some variations of the normal marine salinity.

This assemblage is amply distributed in the North Patagonian area, and in general they are the only represented microfaunal groups; although in a few cases the ostracodes are associated with Foraminifera, the first always predominate percentagewise.

Given the distribution of the outcrops in this basin, which borders to the north the Pampean Massif and to the south the North Patagonian Massif, the lithology and the contained microfauna composed mostly of ostracodes, we can infer that the salinity could have reached levels somewhat below the normal of an open sea, at least in those places where the ostracodes are the only represented group. In the sense of Välikangas (1933) the environment is classified as polyhaline, that is to say, that the salinity could have reached levels somewhat below the normal.

EXPLANATION OF PLATE 1

Lower Jagüelian Stage assemblage (Lower Maastrichtian).

Figure

1. **Wichmannella araucana** Bertels, 1969
   1a. Female left valve (LM-No. 588); × 50.
   1b. Female dorsal view (LM-No. 589).

2. **Wichmannella araucana** Bertels, 1969
   Male left valve (LM-No. 590); × 50.

3. **Alatacythere**? **rocana** Bertels, 1969
   Female right valve (LM-No. 591); × 60.

4. **Alatacythere**? **rocana** Bertels, 1969
   Male right valve (LM-No. 592); × 60.

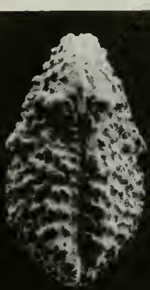
5. **Platycythereis**? n. sp.
   × 60.
   5a. Female left valve (LM-No. 593).
   5b. Female dorsal view (LM-No. 594).

6. **Platycythereis**? n. sp.
   × 60.
   6a. Male left valve (LM-No. 595).
   6b. Male dorsal view (LM-No. 596).

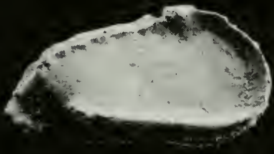
7. **Trachyleberis princeps** Bertels, 1969
   Female left valve (LM-No. 597); × 50.

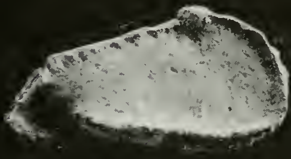
8. **Wolburgia**? n. sp.
   Left valve (LM-No. 598); × 80.


1a


1b

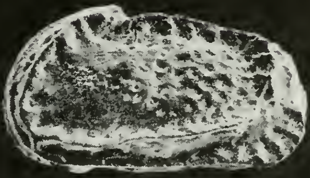

2


3


4

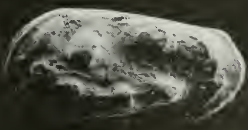

5a


5b


6a


6b

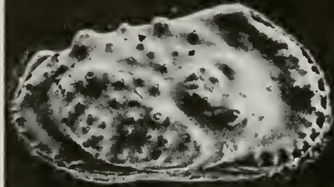

7


8

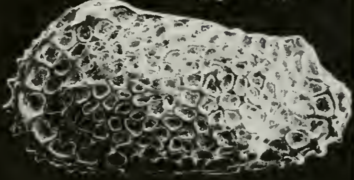

1

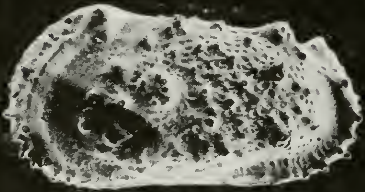

2a

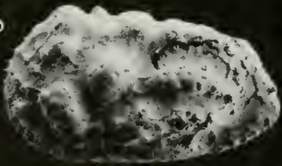

2b


3a


3b


4

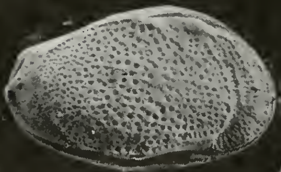

5


6a


6b


7


8


9


10


11

EXPLANATION OF PLATE 2

Upper Jagüelian Stage assemblage (Middle Maastrichtian).

Figure

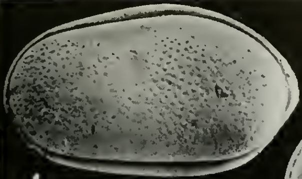
1. **Cythereis**? sp.
   Female right valve (LM-No. 599); × 60.
2. **Cythereis**? **excellens** Bertels, 1969
   × 60.
   2a. Female left valve (LM-No. 600).
   2b. Female dorsal view (LM-No 601).
3. **Cythereis**? n. sp.
   × 50.
   3a. Female right valve (LM-No. 602).
   3b. Female dorsal view (LM-No. 603).
4. **Protocosta** n. sp.
   Female left valve (LM-No. 604); × 60.
5. **Trachyleberis** n. sp.
   Female left valve (LM-No. 605); × 50.
6. **Actinocythereis** n. sp.
   × 60.
   6a. Female left valve (LM-No. 606).
   6b. Female dorsal view (LM-No. 607).
7. **Anticythereis** n. sp.
   Female right valve (LM-No. 608); × 60.
8. **Veenia (Nigeria) punctata** Bertels, 1968
   Female right valve (LM-No. 609); × 50.
9. **Togoina** n. sp.
   Female right valve (LM-No. 610); × 50.
10. **Bradleya**? n. sp.
    Female right valve (LM-No. 611); × 60.
11. **Cytheromorpha**? n. sp.
    Left valve (LM-No. 612); × 70.

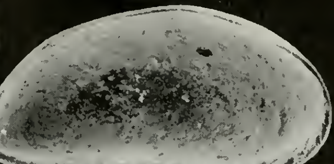
EXPLANATION OF PLATE 3

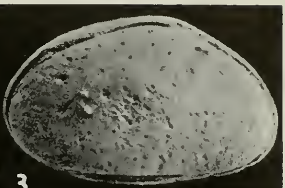
Rocanian Stage assemblage (Lower Danian).

Figure

1. **Cytherella** sp. aff. **C. utilis** Bertels, 1968
   Female left valve (LM-No. 613); × 50.
2. **Paracypris**? sp.
   Right valve (LM-No. 614); × 50.
3. **Cyamocytheridea felix** Bertels, 1973
   Female right valve (LM-No. 615); × 70.
4. **Togoina australis** Bertels, 1968
   Female right valve (LM-No. 616); × 50.
5. **Huantraiconella prima** Bertels, 1968
   Female left valve (LM-No. 617); × 40.
6. **Actinocythereis indigena** Bertels, 1969
   Female right valve (LM-No. 618); × 50.
7. **Actinocythereis biposterospinata** Bertels, 1973
   Female left valve (LM-No. 619); × 50.
8. **Trachyleberis weiperti** Bertels, 1969
   Female left valve (LM-No. 620); × 40.
9. **Rocaleberis nascens** Bertels, 1969
   × 50.
   9a. Female left valve (LM-No. 621).
   9b. Female dorsal view (LM-No. 622).
10. **Wichmannella meridionalis** Bertels, 1969
    Female left valve (LM-No. 623); × 50.
11. **Wichmannella meridionalis** Bertels, 1969
    Male left valve (LM-No. 624); × 50.
12. **Anticythereis schilleri** Bertels, 1973
    × 55.
    12a. Female right valve (LM-No. 625).
    12b. Female left valve (LM-No. 626).
13. **Loxoconcha similis** Bertels, 1973
    Female left valve (LM-No. 627); × 80.
14. **Cytheropteron rocanum** Bertels, 1973
    Right valve (LM-No. 628); × 70.
15. **Krithe rocana** Bertels, 1973
    Left valve (LM-No. 629); × 50.

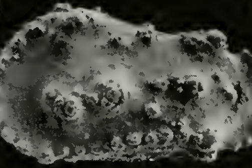

1


2

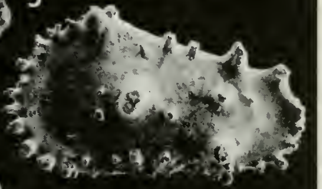

3


4


5


7


6

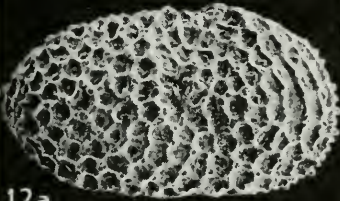

8


9a

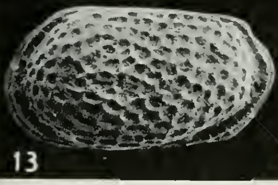

10


11


9b


12a


12b


13


14

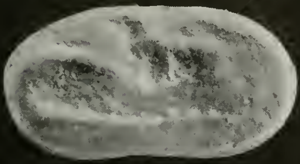

15

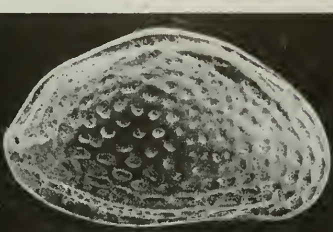
EXPLANATION OF PLATE 4

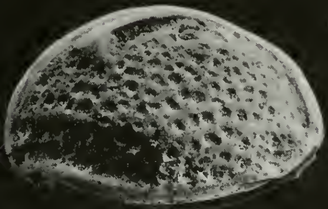
"Patagonian Stage *s.l.*" assemblage (Upper Oligocene-Lower Miocene?) (after Becker, 1964) Nomenclature modified in part in the present work.

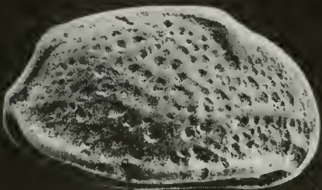
Figure

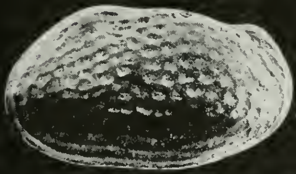
1. **Cytherelloidea** sp. 1
   Left valve (LM-No. 114); × 50.
2. **Mutilus (Aurila)** cf. **convexa** (Baird)
   Female right valve (LM-No. 630); × 60.
3. **Aurila** sp.
   × 60.
   3a. Female left valve (LM-No. 631).
   3b. Female right valve (LM-No. 632).
4. **Bensonia** sp.
   Female left valve (LM-No. 633); × 60.
5. **Soudanella** sp.
   Right valve (LM-No. 634); × 50.
6. **Henryhowella** ? sp.
   Left valve (LM-No. 635); × 50.
7. **Urocythereis**
   Female left valve (LM-No. 636); × 50.
8. **Urocythereis**
   Male left valve (LM-No. 637); × 50.
9. **Hermanites** sp. 1
   × 50.
   9a. Female left valve (LM-No. 638).
   9b. Female dorsal view (LM-No. 639).
   9c. Female right valve (LM-No. 640).


1

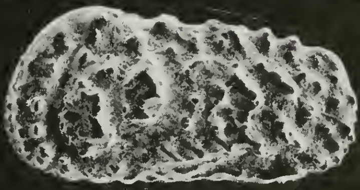

2

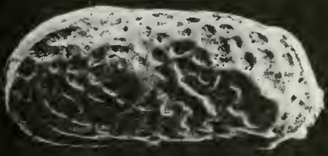

3a

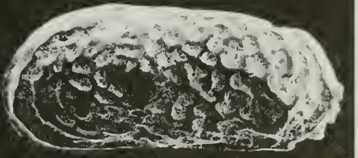

3b


4


5


6


7


8


9a


9b


9c

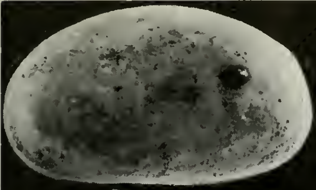
EXPLANATION OF PLATE 5

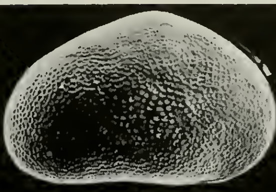
Platian Stage assemblage (Pleistocene) (Nomenclature after Suarez Soruco, 1968)

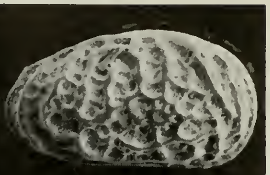
Nomenclature modified in part in the present work.

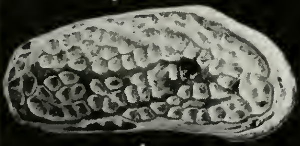
Figure

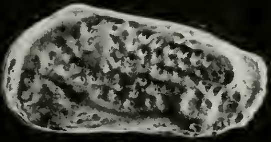
1. **Cyprideis,** n. sp.
   Left valve (LM-No. 641); × 50.
2. **Cypridopsis,** n. sp
   Right valve (LM-No. 642); × 60.
3. **Callistocythere,** n. sp. resembles **C.,** n. sp. A of Whatley and Moguilevsky, this volume
   Right valve (LM-No. 643); × 90.
4. **Mesocythere,** ?
   Right valve (LM-No. 644); × 80.
5. **Munseyella,** n. sp.
   × 80.
   5a. Left valve (LM-No. 645).
   5b. Right valve (LM-No. 646).
6. **Caudites,** n. sp.
   Female left valve (LM-No. 647); × 70.
7. **Patagonacythere,** n. sp. 1
   Female left valve (LM-No. 648); × 60.
8. **Urocythereis,** n. sp..
   Male right valve (LM-No. 649); × 50.
9. **Quadracythere,** n. sp.
   Right valve (LM-No. 650); × 60.
10. **Patagonacythere,** n. sp. 2
    Right valve (LM-No. 651); × 80.
11. **Protocytheretta,** n. sp.
    Left valve (LM-No. 652); × 70.
12. **Loxoconcha paranensis** Rossi de Garcia, 1966
    Left valve (LM-No. 653); × 60.
13. **Cushmanidea,** n. sp.
    Right valve (LM-No. 654); × 80.
14. **Pellucistoma,** n. sp.
    Right valve (LM-No. 655); × 60.
15. **Hemicytherura** sp. aff. **Cytherura obliqua** Brady, 1880
    Right valve (LM-No. 656); × 80.
16. **Hemicytherura** aff. **Cytherura lilljeborgii** Brady, 1880
    Left valve (LM-No. 657); × 80.


1

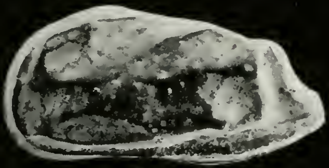

2

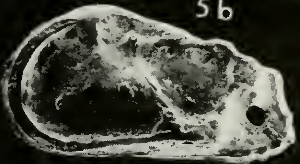

3

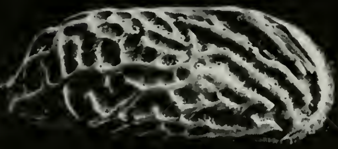

4


5 a


5 b


6

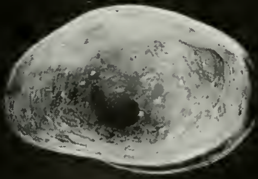

7

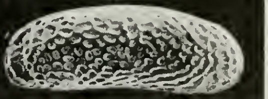

8


9

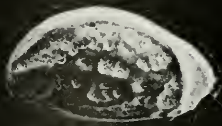

10


11


12


13


14


15


16

ZOOGEOGRAPHY AND BIOLOGY OF LITTORAL OSTRACODA FROM SOUTH AFRICA, ANGOLA, AND MOZAMBIQUE

GERD HARTMANN AND G. HARTMANN SCHRÖDER
Zoologisches Institut und Museum

ABSTRACT

During the year 1967 the authors undertook an extended expedition to Africa. The expedition started at Luanda in Angola, followed the West Coast of Africa southward to the Cape of Good Hope, and turned then northward to Beira in Mozambique. Purpose of this expedition was to collect littoral ostracodes along the visited coasts to solve the following problems:

1. Comparison of the ostracode fauna of the Humboldt-Current along the West Coast of South America and the Benguela Current at the West Coast of Africa. Both cold currents show numerous similarities and agreements in their pelagic faunas;
2. To find out the influence of Antarctic faunistic elements in South Africa;
3. To compare the zoogeographic connections between the Indopacifican fauna of the East Coast of Africa and the faunas of the Red Sea and the Indopacific Region; and
4. To make biological and ecological studies of the ostracodes of the mentioned regions.

Former studies were made by Klie (1940) in Lüderitzbucht, by Benson and Maddocks (1964) in the Knysna Estuary, by Omatsola (1970/71) in Nigeria, and by Hartmann (1964) in the Red Sea.

The results:

The Benguela and Humboldt Currents do not have strong affinities in their littoral faunas. The Antarctic influence is very much stronger in South America than in South Africa. The East Coast of Africa has an ostracode fauna of its own, influenced markedly by indomalayan elements. The brackish-water fauna of South Africa is an endemic fauna. *Cyprideis,* for example, is substituted by *Sulcostocythere.* Ecological and biological studies show differences in the behaviour of ostracodes from Humboldt and Benguela Current and limiting effects of different factors in littoral habitats. The distribution of the ostracodes found by Klie and Benson and Maddocks was made more precise. The question of comparability of ecological and paleoecological studies is briefly discussed.

ZUSAMMENFASSUNG

Die Arbeit gibt eine Übersicht über die im Oberen Litoral des Humboldt-Stromes und im Oberen Litoral des Benguela-Stromes gefundenen Ostracodenarten. Auch die Ostracodenfauna der angrenzenden subtropisch-tropischen Gebiete wird berücksichtigt. Nach Ostracoden wird eine zoogeographisch-klimatologische Einteilung der Litoralbezirke versucht. Beide Stromgebiete weisen weitgehend übereinstimmende klimatische Bedingungen auf, sind aber hinsichtlich ihrer Ostracodenfauna sehr verschieden. Lediglich einige antarktische Faunenelemente sorgen für geringe Übereinstimmung. Zur Ökologie und Biologie der Ostracoden beider Stromgebiete werden einige Anmerkungen gemacht.

INTRODUCTION

If we exclude the Antarctic coasts from our discussion, coastlines which are in any case not very interesting for a biologist who works on intertidal communities of animals, we find intertidal zones influenced by cold water in the Southern Hemisphere only in South America, Africa, and Australia. In South America these are mainly the coasts of the Humboldt Current, in

Africa those of the Benguela Current, and in Australia the coasts exist along the West Australia Current. These three currents are arms of the large anticyclones of the southern oceans. In contrast to the Northern Hemisphere where all the cold water coasts are in contact which each other at least by means of the continental shelf, the cold water regions of the southern continents are separated from each other by deep water and great distances. This large separation, and the fact that many species of littoral animals do not possess larval planktonic stages (as for example the ostracodes) and, therefore, cannot cross the separating oceans, presents interesting questions to the biologists:

1. Is the oceanographic and zoogeographic zonation of the cold water regions on all southern continents the same;
2. Are the littoral communities of animals formed by the same systematic units; and
3. How strong is the influence of the neighboring tropical-subtropical regions on the composition of the cold water communities?

For nearly 20 years my wife and I have studied these problems. We have published several papers on cold water coasts of South America and adjacent warmer areas (1953-1965). Our main subjects are Polychaeta and Ostracoda. We undertook our last expedition in the year 1967 to the coasts of southern Africa and consequently we missed the ostracode symposium at Hull. The results of this expedition are now available, and it is for the first time that we are able to compare the ostracode fauna of the Humboldt Current coasts with those of the Benguela Current (including the neighboring areas), and the Indopacific coast of Africa with that of South America.

The oceanographic zonation of both currents shown in the illustration is only a little different. The southern tip of South America reaches a little farther into the water of the Westwind Drift. The Humboldt Current becomes thus stronger and influences to a higher degree the warmer regions north of it. But in the contrast to the Benguela Current the Humboldt Current warms up quicker to boreal cool temperate conditions, perhaps because the upwelling of the cool water is stronger at the African coast. Further differences between the areas of both currents are the existence of a subantarctic zone in South America, which is not present in Africa, and the greater extension of the tropical-subtropical transition zone in South America. Because the results of our South American investigations are already published, I will treat here mainly our African material.

LITTORAL OSTRACODA OF SOUTHERN AFRICA

More comprehensive papers on ostracodes of southern Africa are scarce. Only two intensive studies exist: the paper of Klie (1940) on ostracodes of Lüderitz Bay in southwest Africa, and the paper of Benson & Maddocks on ostracodes of the Knysna Estuary. These authors, however, collected samples from a single locality. Beyond these we have certain information from Brady (1880), G. W. Müller (1908), and Poulsen (1962, 1965), primarily concerning single findings of species. Omatsola (1970, 1971) worked in tropical West

Africa, and papers on fossil African species were presented by Grekoff (1958), Krömmelbein (1965, 1966), Reyment (1959, 1960), and van den Bold (1966). The publications on fossils are not considered in this paper.

At the beginning of our studies, 111 species of ostracodes were known from the coasts considered in this discussion. Most of them were very superficially described, especially those from Brady (1880). During our studies, we could find only 61 of the species, and we redescribed some of them. Two of the species found were known hitherto only from the Red Sea, we found them on the east coast, and finally we discovered and described 84 new species, several of them belong to new genera. All our samples came from the higher littoral and from the intertidal zone of the African west and east coasts. The maximum depth sampled was two meters.

The following tables show all the ostracodes found by us, all of them previously known species, and their zoogeographic distribution. It is at first glance, clearly visible that the distribution of the ostracodes fits exactly into the climatic zonation of the African coasts (Hartmann-Schröder and Hartmann, 1962, 1965). Each climatic region has its own ostracode population and most frequently has some species in common with the neighboring region. Although we do not have very much information from the tropical West Africa, it seems probable that the ostracode fauna of the tropical terminal part of the Benguela Current is different from that of West Africa. The coast section between Moçamedes in South Angola and Swakopmund in southwest Africa is clearly tropically influenced but also possess its endemic subtropical elements. Very interesting are disjunctions between the warmer Atlantic and warmer Indopacific zone of both coasts. We will discuss them later on. The antiboreal (cool temperate) part of the West Coast has a very typical character and limits itself sharply against the tropical-subtropical coast to the north and against the east coast on the other side of the Cape of Good Hope. There are no connections with the cold water fauna of the Northern Hemisphere, in contrast to the West Coast of South America where such relations do exist. It is very probable that historical events are responsible for such an occurrence. Some of the antiboreal ostracodes of the West Coast penetrate into the waters of the Knysna Estuary. A subantarctic influence is (very much less than in South America) visible: species of *Procythereis, Conchoecia skogsbergi* and *Cytherois minor* belong to it. The east coast of Africa is characterized by a quick diminution of cold water species from the south towards the north, and by the appearance of an ostracode fauna which is completely different from that of the west coast of Africa, and has a strong Indopacific impression: *Perissocytheridea, Tanella,* and other species and genera belong to it. We had hoped to get contact with the Red Sea ostracode fauna described by the author (1964) and with that of the Persian Gulf described by Bate (1971). Only a few species are present (*Neonesidea schulzi, Xestoleberis rotunda,* and *Paradoxostoma breve*). Thus we can assume that a special Red Sea-Persian Gulf faunal province of ostracodes exists. As in other animal groups, the ostracodes have their own Cape Province fauna including species which possess the same ecological niches, as other species in other zoogeographical provinces. *Sulcostocythere* Benson and Maddocks is an example of this (see later). In the tropical part of the east coast of Africa we finally discovered an endemic ostracode fauna in coral reefs, unknown until this time.

Table 1. Ostracoda from tropical West Africa (Gulf of Guinea to Nigeria).

LAGOS
Cytherella olosa Omatsola, 1970
Carinocythereis asterospinosus Omatsola, 1970
Ruggieria nigeriana Omatsola, 1970
Paijenborchella kuznetsovae Omatsola, 1970
Neomonoceratina ikoroduensis Omatsola, 1970
Neomonoceratina iddoensis Omatsolo, 1970
Cyprideis nigeriensis Omatsola, 1970
Reymentia ijebuorum Omatsola, 1970
Reymentia microdictyota Omatsola, 1970
Loxoconcha lacunensis Omatsola, 1970
Phlyctocythere hartmanni Omatsola, 1970
Cytheropteron ebutemettaensis Omatsola, 1970

TENERIFFE
Polycope teneriffae Hartmann, 1959
Loxoconcha dimorpha Hartmann, 1959
Paradoxostoma curtum Hartmann, 1959
Paradoxostoma insigne Hartmann, 1959

It is interesting that connections between the Humboldt coast fauna and the Benguela coast fauna are nearly absent. If we exclude the subantarctic elements from our discussion (see above), both coasts have a completely different fauna at the species level. We believe the east African coast has clearly an Indopacific character, and it is apparent that the occurrence of *Perissocytheridea* in the Knysna Estuary (Benson & Maddocks, 1964) is the end point of the distribution of this genus all over the warmer part of the Indopacific-West atlantic. *Tanella,* found up to this time only in the Indonesian seas, is another proof for this theory.

A strange distribution is shown by a small group of ostracodes which occurs as disjunct populations in the warmer parts of the East coast and West coast. *Aurila dayii* Benson and Maddocks, 1964, *Sclerochilus disjunctus* (Hartmann, 1972), and perhaps *Asteropteron nodulosum* Poulsen we assign to it. These species do not occur in antiboreal waters. It seems evident that the area of these species was in contact around the southern tip of the continent in warmer times (perhaps interglacial or late Tertiary times), and that the advance of cooler water and antiboreal faunas divided it into two separated areas. This finding is even more interesting when we remember that the same conditions exist at the southern tip of South America. *Callistocythere dispersocostata* Hartmann, 1962, and *Parakrithella hanaii* Hartmann, 1962, occur as disjunct populations on the west and east coasts of South America. Evidently the climatic influence was the same on both ostracode faunas in the Recent past.

Table 2. Ostracoda from the tropical part of the Benguela Current
(Cacuaco to Benguela-Baia Farta)

× = found by us + = previously reported	Cacuaco	Luanda	Novo Redondo	Lobito	Benguela	Mozamedes	Swakopmund	False Bay	Knysna
Philomedes, n. sp.	×								
Cyprideis, n. sp.	×	×	×	×	+	+	×		
Aurila dayii Benson & Maddocks, 1964	×	×	+	×	×	×		?	×
Aglaiella, n. sp.	×	×	+	×	×	×			
Synasterope, n. sp.		×							
Cylindroleberis sp. 11		×							
Asteropteron aff. A. nodulosum Poulsen, 1965		×						×	×
Cytherella, n. sp.		×	+	+	+	+	×		
Bairdoppilata, n. sp.		×	+	×					
n. gen. problematica, n. sp.		×	+	+	+	×			
N. gen., n. sp. 1		×	+	×	+	×			
Costa, n. sp.		×	+	×	+	×			
Loxoconcha, n. sp.		×	+	×	+	×			
Paracytheridea, n. sp.		×							
Semicytherura, n. sp.	×	×							
Xestoleberis, n. sp. 1		×							
Xestoleberis, n. sp. 2		×	+	+	×	×			
Xestoleberis, n. sp. 3		×	+	×					
Xestoleberis, n. sp. 4		×	+	+	×	×			
Paradoxostoma, n. sp. 1		×	+	+	+	×			
Paradoxostoma, n. sp. 2		×							
Cytherelloidea, n. sp.				×	×				
Bairdoppilata, n. sp.				×	+	×			
N. gen., n. sp. 2				×					
Cobanocythere, n. sp.				×	+	+	+	×	
N. gen., n. sp. 3				×					
Cytherella, n. sp.					×				
Cytherura, n. sp.					×	×			
Cytherois, n. sp.					×				

DISCUSSION

So much for our zoogeographical overview. It is not possible, to discuss now all the biological and ecological results inferred from the zoogeographical discussion. These results will be discussed in a separate paper. Only some interesting aspects may be presented:

1. Fauna of the open beaches where the action of the waves can operate without hindrance. As on all open beaches of the world, the surface of the beaches in Africa is not populated by ostracodes. The population, on the contrary, is in the interstitial water and in the moist sand just above it in a depth, where the action of the waves cannot affect the population, and the

Table 3. Ostracoda from the subtropical part of the Benguela Current (Moçamedes to Swakopmund)

	Mozamedes	Swakopmund	Luderitzbucht	Langebaan	Knsyna
Bairdoppilata, n. sp.	×				
Bairdia sp. 32	×				
Costa sp. 36	×				
Chrysocythere, n. sp.	×				
Hemicytherura, n. sp.	×				
Xestoleberis humilis Klie, 1940	×	+	×		
Xestoleberis, n. sp.	×				
Sclerochilus, n. sp.	×				×
aff. Aglaiocypris, n. sp.	×				
Paradoxostoma, n. sp.		×			
Loxoconcha, n. sp.		×			
Cypridopsis glabrata Sars, 1924		×	×	×	

× = found by us
+ = reported previously

substrate remains undisturbed. Population is moreover only possible, if the sand grains are large enough to produce a wide interstitial system. *Polycope,* and also *Cobanocythere* and *Parvocythere* were present here. *Cobanocythere* and *Parvocythere* were described by the author from the Pacific Coast of Central America (Hartmann, 1964). Later on they were found by Reys (1961), and Marinov (1962) in the Mediterranean Sarmatian region. We found them in a higher number of species than known until now, and it is probable that they are distributed worldwide in temperate and warm waters. The Polycopidae found by us belong to two different groups *sensu* Bonaduce (1964), to the *clathrata*-group and the *loscobanosi*-group. All species found at the West Coast belong to the *clathrata*-group, most species of the East Coast to the *loscobanosi*-group. Species of the *clathrata*-group are known, until now, mainly from North Europe and the Mediterranean. Species of the *loscobanosi*-group are known, until now, only from the warm and temperate Americas. This group seems to be an Indopacific-West Atlantic element.

2. When we compare the protected beaches of the Humboldt Current and the Benguela Current, we find that many ecological niches are occupied by species of worldwide distributed genera. Only these species form the similarity in the biota of these beaches. But there are differences too: *Paracytheroma* f. ex., frequent in America, is not present in Africa. Species of *Loxoconcha* and *Cytherura* replace it. Species of the Bairdiidae play an important role on beaches of the warmer parts of the Benguela Current. They are scarce in the comparable biotypes of the Humboldt Current. Only *Cytherois* and *Procythereis* exist in both antiboreal regions.

3. Most interesting are the phytal communities of ostracodes. It is also here that the Bairdiidae are characteristic for the Benguela Current, very much less frequent in America. *Hemicytheria* of South America is replaced by *Semicytherura*. Thus the similar composition of ostracode populations of both currents is much less than in other animal groups, *i.e.,* Polychaeta and fishes. A difficult problem is the distribution of plant-sucking ostracodes of the genus *Paradoxostoma*. The phytal communities of the Benguela Current have a very high percentage of species of *Paradoxostoma*. In earlier papers (Hartmann-Schröder and Hartmann, 1962, 1965) we pointed out that *Paradoxostoma* is very scarce in the phytal zone of the Humboldt Current. We do not know whether differences in the chemical composition of the algae-liquors cause this phenomenon. A similar discordance is true for species of *Xestoleberis* which are very frequent in the algae of the Benguela Current.

4. The composition of the brackish-water communities of ostracodes of both continents is also very different. These biotopes are systematically, by far, richer in America. *Perissocytheridea, Paracytheroma,* and species of the Thalassocypridini are not present in Africa, when we compare only the West Coast. *Cyprideis,* a classical element of brackish water, is present at both coasts, but more diverse in America. The *Cyprideis* species of the African west coast all belong to one closely related group, those from America are not so uniform. *Cyprideis* is not present in the brackish water of the Cape Province. It is completely replaced there by the endemic *Sulcostocythere*. *Cyprideis* is also missing along the east coast of Africa, as far as our studies indicate.

5. At least we should have a look at the specific ostracode fauna of the coral reefs. Until now all papers on the meiofauna of coral reefs negate the existence of a specifically adapted meiofauna. The opinion prevails that it is the phytal fauna which also populates the coral reefs (v. Gerlach, 1959). Our studies in the coral reef of Tanga lead to another conclusion: other than typical species of the phytal and typical species of the interstitial communities, such as *Polycope, Cobanocythere, Microcytherura* and some species of *Xestoleberis,* we found a series of new genera, that we have regarded as representatives of ostracodes which to high degree are adapted to the life in coral reefs. Their shell morphology resembles that of the interstitial ostracodes (f. ex. *Mesocorallicythere,* Hartmann, 1973) or possesses special morphological characters (f. ex. *Corallicythere* Hartmann, 1973). Typical is the structure of the limbs; we observe the following features:

1. Reduction of bristles and claws,
2. Reinforcement of the remaining claws and bristles,
3. Enlargement of one walking leg (maxilla or one of the two thoracic limbs),
4. Transformation of one or more extremities to a specialized form.

Considering these findings, we can be almost sure that the coral reefs harbour not only phytal and interstitial ostracodes, but also a specific coral ostracode fauna.

Table 4. Ostracoda from the antiboreal part of the Benguela Current (Luderitzbucht to Kommetje/Simmonstown)

	Luderitzbucht	Langebaan	Velddrift	Kometje	False Bay	Knysna	Tongaat	St. Lucia	Tropisch
Paradoloria dorsoserrata (G. W. Müller, 1908)	×	+	+	×					
Euphilomedes africana (Klie, 1940)	×								
Cylindroleberis grimaldi (Skogsberg, 1920) sensu Klie, 1940	×	+	+	×	+	×			
Cylindroleberis muelleri (Skogsberg, 1920)	×								
Rutiderma cf. compressa Brady & Norman, 1898	×	+	+	+	+	+	×		×
Polycope, n. sp. 1	×								
Polycope, n. sp. 2	×								
Bairdia, sp. 44	×	+	+	+	+	×			
Cyprideis remanei Klie, 1940	×								
Aurila, n. sp. 1	×	+	+	×					
Aurila, n. sp. 2	×	+	+	×					
Hemicythere mirabilis (Klie, 1940)	×								
Aurila levetzovi (Klie, 1940)	×								
Mutilus, n. sp.	×	+	+	+	+	×			
Procythereis major Klie, 1940	×								
Procythereis minor Klie, 1940	×	+	+	×					
Procythereis serrata Klie, 1940	×								
Loxoconcha megapora Benson & Maddocks, 1964, n. subspec.	×	+	+	×	+	×			
Semicytherura, n. sp.	×								
Xestoleberis baja Klie, 1940	×								
Xestoleberis crenulata Klie, 1940	×								
Xestoleberis ferax Klie, 1940	×	+	+	×					
Xestoleberis ramosa G. W. Müller, 1908	×	+	+	×	+	×			
Sclerochilus incurvatus Klie, 1940	×								
Cytherois minor G. W. Müller, 1908	×					to Antarctica			
Paradoxostoma auritum Klie, 1940	×	+	+	+	+	×			
Paradoxostoma angustissimum Klie, 1940	×								
Paradoxostoma caeruleum Klie, 1940	×								
Paradoxostoma griseum Klie, 1940	×	×	+	×					
Paradoxostoma reflexum Klie, 1940	×								
Paradoxostoma semilunare Klie, 1940	×								
Paradoxostoma, n. sp. 1	×	+	+	×					
Paradoxostoma, n. sp. 2	×	+	+	×					
Paradoxostoma, n. sp. 3	×								
Parvocythere, n. sp. 4	×								
Propontocypris flava G. W. Müller, 1908	×	+	+	×					
Sulcostocythere knysnaensis Benson & Maddocks, 1964			×	+	+	×	+	×	
Xestoleberis capensis G. W. Müller, 1908				×					
Macrocypris africana G. W. Müller, 1908				×					
Macrocypris dispar G. W. Müller, 1908				×					
Propontocypris gaussi G. W. Müller, 1908				×					

× = found by us
\+ = reported previously

Table 5. Ostracoda from the antisubtropical Indic Coast of South Africa (Kap to St. Lucia-Astuar)

	False Bay	Knysna	Tongaat	St. Lucia	bis tropisch
Parvocythere, n. sp. 1	×				
Parvocythere, n. sp. 2	×				
Cytherella cf. punctata Benson & Maddocks, 1964		?×			
?Bairdoppilata villosa (Brady, 1880)		?×			
Perissocytheridea aestuaria Benson & Maddocks, 1964		×	+	×	×—?
Caudites, n. sp. 1		×			
Procythereis, n. sp.		×			
Cytheretta knysnaensis Benson & Maddocks, 1964		×			
Loxoconcha parameridionalis Benson & Maddocks, 1964		×			
N. gen., n. sp. 1		×	+	×	×—?
N. gen., n. sp. 2		×			
Semicytherura, n. sp.		×			
Aglaiella railbridgensis Benson & Maddocks, 1964		×			
Ghardaglaia, n. sp.		×	+	+	×—?
Polycope, n. sp.			×	+	×—?
Caudites, n. sp. 2			×	+	×—?
Tanella, n. sp.				×	×—?

× = found by us
+ = reported previously

SUMMARY

Summing up, we can give the following statements:

1. The Humboldt Current and Benguela Current have a slightly different oceanographical zonation. The zonation of faunas is nearly the same in the upper littoral of both currents.
2. The ostracode fauna of both regions is completely different in species, but are similar at the generic level as evidenced by worldwide-distributed genera and some Antarctic elements.
3. The interstitial communities of the sandy beaches are similar in both regions. Their genera seem to be distributed worldwide. The communities of other biotopes show more differences than similarities: many genera are replaced in their ecological niches by other genera. Plant-sucking ostracodes such as *Paradoxostoma* are scarce in the Humboldt littoral but frequent in the Benguela littoral. Bairdiidae play an important role in the Benguela littoral, at least in the warmer parts of the current; they are not nearly so important in the Humboldt littoral.

4. The Cape of Good Hope is a border between the Atlantic and Indopacific communities of ostracodes as in other groups of animals.

5. There exists a typical coral reef ostracode community.

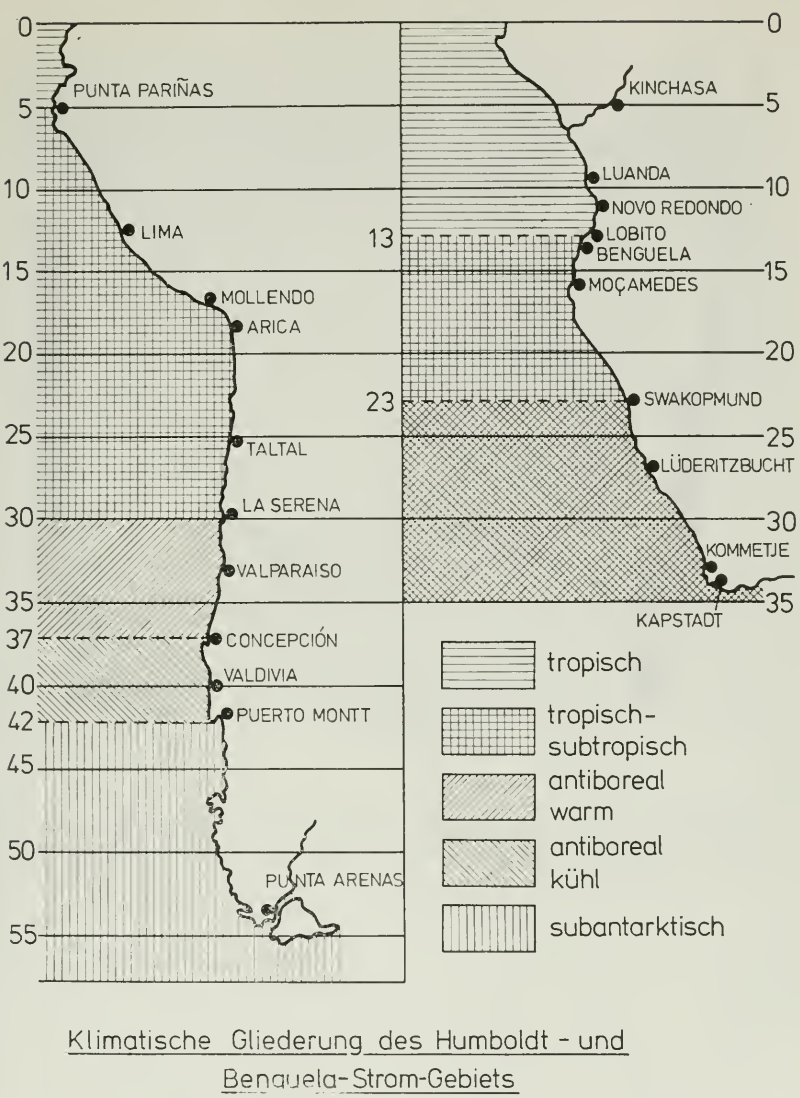
Table 6. Ostracode from the tropical coast of Mozambique and Tanzania (from Lourenco Marques to Mtwara)

	Lourenco Marques	Xai-Xai	Inhambane	Mtwara	Weiternordlich	Rotes Meer
Callistocythere, n. sp.	×					
Caudites, n. sp.	×					
N. gen., n. sp.	×					
Thalassocypria, n. sp.	×					
Polycope, n. sp.		×				
Neonesidea, n. sp.		×	+	+	×	
Mutilus, n. sp.		×				
Loxoconcha algicola		×	×			
Xestoleberis, n. sp. 1		×	×			
Xestoleberis, n. sp. 2		×				
Sclerochilus, n. sp.		×	×			
Paradoxostoma breve G. W. Müller, 1894		×	×	+	×—	×
Paradoxostoma, n. sp. 1		×	×			
Paradoxostoma, n. sp. 2		×				
Parvocythere, n. sp.		×				
Loxoconcha, n. sp.			×			
Asteropteron cf. spinosum Poulsen, 1965				×		
Paranesidea aff. algicola Maddocks, 1969				×		
Xestoleberis aff. rotunda Hartmann, 1964				×	——	×

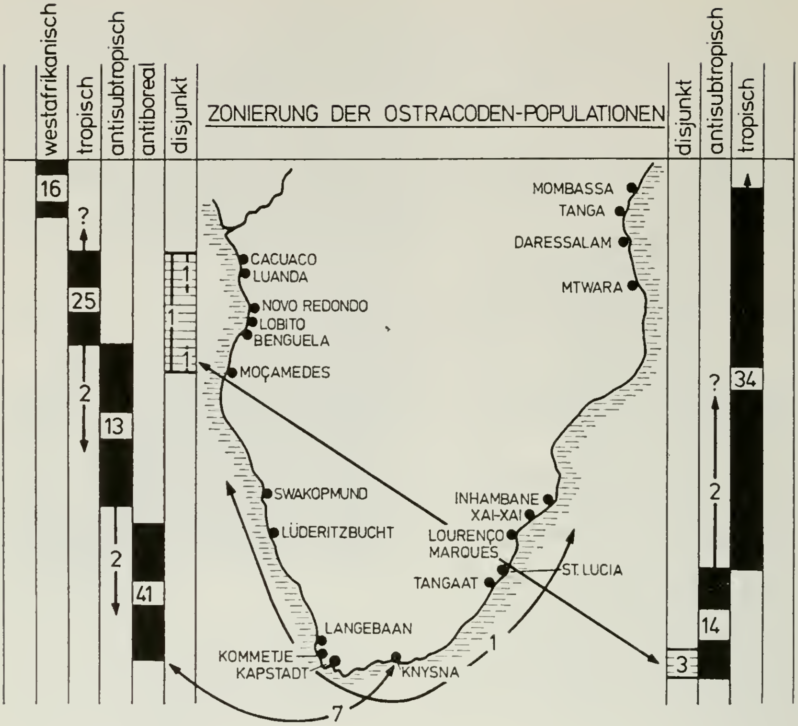
× = found by us
+ = reported previously

Table 7. Ostracoda from the coral reef of Tanga (a sample of broken coral)

Polycope, n. sp.
Polycope, sp.
Neonesidea schulzi (Hartmann, 1964)
N. gen. n. sp.
Cobanocythere, n. sp.
Microcytherura, n. sp.
Microloxoconcha, n. sp.
Xestoleberis, n. sp.
N. gen., n. sp. 2
N. gen., n. sp. 3
Cobanocythere sp. 168
?Eusarsiella, n. sp.



Text-figure 1. Climatic zonation of the waters of the Humboldt and Benguela Currents, as proposed in this paper.



Text-figure 2.
Zonation of ostracode populations along the coasts of the southern Africa (Angola, SW-Africa, South Africa, Moçambique, and Tanzania). Numbers refer to degrees of latitude.

Text-figure 3.
Section of a tropical beach (Sandstrand = sandy beach, Feuchtsandzone = zone of moist sand, Grundwasserloch = hole to take interstitial water, Prallhang = surf beach, MTHW = Middle high water line, Meer = sea, marines, brackiges Küstengrundwasser = marine, brackish interstitial coastal water, Süβwassereinfluβ = fresh water influence.

REFERENCES

Bate, R. H.

1971. *The distribution of Recent Ostracoda in the Dhabi Lagoon, Persian Gulf.* Paléoécologie des Ostracodes, Colloque Pau (1970). Bull. Centre Rech. Pau SNPA 5: 239-256, 3 figs., 3 pls. Editor: H. Oertli.

Benson, R. H., and Maddocks, R. F.

1964. *Recent Ostracodes of Knysna Estuary, Cape Province, Union of South Africa.* Univ. Kansas Paleont. Contr., Arthropoda Art. 5, pp. 1-39, pls. 1-6, figs. 1-22.

Bold, W. A., van den

1966. *Les Ostracodes du Néogène du Gabon.* Revue Inst. Franç. Pétrole XXI, 2, pp. 155-188, 6 planches, 1 map.

Bonaduce, Gioacchino

1964. *Contributo alla conoscenza e correlazione sistematica nell ambito della Famiglia Polycopidae (Ostracoda, Cladocopa) con particolare riferimento alle relazioni tra parte molle e carapace.* Pubbl. staz. zool. Napoli, 34, pp. 137-159.

Brady, G. S.

1880. *Challenger Report. Ostracoda.* Zoology, 1, 3, pp. 1-184, pls. 1-44.

Gerlach, S. A.

1959. *Über das tropische Korallenriff als Lebensraum.* Verhandl. Deutsche Zool. Gesellschaft, 1959, 4 Abbild., pp. 356-363.

Grekoff, N.

1958. *Ostracodes du Bassin du Congo, III. Tertiaire.* Mus. Roy. Congo Belge, Ann. Sci. geol., ser 8, vol. 22, pp. 1-36, pls. 1-3.

Hartmann, G.

1953. *Iliocythere meyer-abichi n. sp., ein neuer Ostracode des Schlickwattes von San Salvador.* Zool. Anz., 151, 11-12, pp. 310-316, Textfigs. 1-17.

1956. *Zur Kenntnis des Mangrove-Estero-Gebiets von El Salvador und seiner Ostracodenfauna I.* Kieler Meeresforschungen, 12, 2, pp. 219-248, Tafel 30-32.

1957. *Idem.,* Teil II. *Ibid,* 13, 1, pp. 134-159, Tafel 39-50.

1959. *Zur Kenntnis der lotischen Lebensbereiche der pazifischen Küste von El Salvador unter besonderer Berücksichtigung seiner Ostracodenfauna.* Kieler Meeresforschungen, 15, 2, pp. 187-241, Tafel 27-48.

1964. *Zur Kenntnis der Ostracoden des Roten Meeres. Ibid.* Sonderheft 20, pp. 35-127, 62 Tafeln.

Hartmann-Schröder, G., and Hartmann, G.

1962. *Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der Küste Südpatagoniens — unter besonderer Berücksichtigung der Polychaeten und Ostracoden.* Mitt. Hamburg Mus. Inst., Ergänzungsband 60, pp. 1-270, Textfiguren, Tabellen, Karten.

1965. *Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden (mit Bemerkungen über den Einfluß sauerstoffarmer Strömungen auf die Besiedlung von marinen Sedimenten. Ibid.,* Ergänzungsband 62, pp 1-384, Textfiguren, Tabellen, Karten.

Klie, W.

1940. *Beiträge zur Fauna des Eulitorals von Deutsch-Südwest-Afrika II. Ostracoden von der Küste Deutsch-Südwest-Afrikas.* Kieler Meeresforschungen, III, 2, pp. 404-448, 91 Abb., Tabellen.

Krömmelbein, K.
1965. *Ostracoden aus der nicht-marinen Unterkreide ("Westafrikanischer Wealden") des Kongo-Küstenbereichs.* Meyniana, 15, pp. 59-74, 4 Tafeln, 1 Abb.
1966. *On "Gondwana Wealden". Ostracoda from NE Brazil and West Africa.* Proc. 2nd W. African Micropal. Coll. (Ibadan, 1965), pp. 119-123, figs. 1a-3c.

Marinov, T.
1962. *Über die Muschelkrebs-Fauna des westlichen Schwarzmeerstrandes.* Bull Inst. Central de Recherche scientifique des pisciculture et de pêcheries, Varna, Acad. Bulgarie Sciences, II, pp. 81-108, 10 Tafeln.

Müller, G. W.
1908. *Die Ostracoden der Deutschen Südpolar-Expedition 1901-1903, im Auftrag des Reichsamtes des Inneren herausgegeben von E. v. Drygalski.* X, Zoologie, Heft II, pp. 51-181, Tafel 4-19, Textfiguren.

Omatsola, M. E.
1970. *On occurence of cytherellids (Ostr. Crust.) in a brackish-water environment.* Bull. Geol. Inst. Univ. Uppsala, n.s. II, 10, pp. 91-96, pl. III, fig. 3 (Publ. No. 99).
1970. *Notes on three new species of Ostracoda from the Niger Delta. Ibid.* II, 11, pp. 97-102 (Publ. No. 98).
1971. *Podocopid Ostracoda from the Lagos Lagoon, Nigeria.* Micropaleontology, 16, 4, pp. 407-445, pls. 1-13.

Poulsen, E. M.
1962. *Ostracoda-Myodocopida, part I (Cypridiniformes-Cypridinidae).* Dana-Report, 57, pp. 5-413, 181 figs., 26 tables.
1965. *Pt. II: Rutidermatidae, Sarsiellidae, Cylindroleberididae. Ibid.,* 65, pp. 1-483, 156 figs.
1969. *Pt. IIIA: Halocypriformes-Thaumatocyprididae and Halocyprididae. Ibid.,* 75, pp. 5-100, 40 figs., 19 tables.

Reyment, R. A.
1959. *Die Gattung Paijenborchellina im Unter-Eozän Nigeriens.* Contr. Geol. Stockholm Univ., 3, 7, pp. 139-143, pls. 1-2.
1960. *Studies on Upper Cretaceous and Lower Tertiary Ostracoda. Pt. 1: Senonian and Maestrichtian Ostracoda. Ibid.,* 7, pp. 1-238, 23 pls., 71 figs.
1960. *Pt. 2: Danian, Paleocene, and Eocene Ostracoda. Ibid.,* 10, pp. 1-286, 23 pls., 81 figs., 1 Tab.
1960. *Pt. 3: Stratigraphical, paleoecological and biometrical conclusions. Ibid.,* 14, pp. 2-143.

Reyment, R. A., and Reyment, E.
1959. *Bairdia ilaroensis n. sp. aus dem Paleozän Nigeriens und die Gültigkeit der Gattung Bairdoppilata (Ostr. Crust.) Ibid.,* 3, 2, pp. 59-67, pl. 1, text-figs. 1-5.

Reys, S.
1961. *Recherches sur la systematique et la distribution des ostracodes de la region de Marseille.* Rec. Trav. St. Mar. Endoume, Bull. 22, 36, pp. 53-109, 10 Tafeln, Tabellen.

Gerd Hartmann
and
G. Hartmann-Schröder,
Zoologisches Institut and Museum,
2 Hamburg,
Germany.

DISCUSSION

Dr. I. G. Sohn: I would like to compliment Dr. Hartmann for his meticulous bookkeeping. More than once I have needled many of my colleagues to cite the author and date of each species. Otherwise, it is sometimes impossible to know which taxon is discussed. Dr. Hartmann's slides are excellent examples of identifying each species by author and date, and that, I think, is the proper way of doing it.

Dr. R. C. Whatley: I would like to congratulate Dr. Hartmann on a really fundamental and beautifully presented paper. I think he's given us all a very clear idea on what's going on. I'd just like to make one small point. I think you probably knew I was going to make it. As a result of more detailed sampling, I demonstrated, for example, at least *Callistocythere dispersocostata* is not disjunct and it goes right the way round, I got it living going right down at almost all my little stations. And also I found it in Puerto Montt. I don't really know how far it goes up. In my paper with Moguilevsky we cite its occurrence living as far south as the Beagle Channel and I have recently recorded it, also living, at Puerto Natales in Southern Chile. In addition, it occurs not uncommonly in the Southern Patagonian and Fuegian littoral.

Dr. Hartmann: That's very interesting.

Dr. Hazel: I missed what you said. At what depth did sampling stop on the West African Coast.

Dr. Hartmann: Upper littoral, to a depth of 2 meters I'd say. We sampled from the shore outward.

Dr. Hazel: Did you have relatively consistent diversity or was it very erratic?

Dr. Hartman: Oh no. We could find the different species always along the coast, the climatic zones had their special ostracode fauna. It is possible that some of the northern forms occur in deeper water in the south, but we sampled from shore because most of the work was done up to now from ships.

Dr. Hazel: Were you able to determine that distributional limits in some species were being controlled by winter temperatures and others by summer temperatures?

Dr. Hartmann: We did only one sampling. We have to go on to sample in other seasons at our stations. We tried only to find the boundaries more or less. We have to make more exact studies of the life cycles.

Dr. Kornicker: I'd like to know if you found any species present both along the South American coast, either side, and also the African coast? Were there any similar species?

Dr. Hartmann: Oh yes. *Cytherois minor*. This occurs also in Africa. That's the only one.

Dr. Löffler: Are there any relationships of your assemblages to those of the Antarctic?

Dr. Hartmann: I would say that between South America and the Antarctic there would exist a close relationship but less between Africa and the Antarctic.

Dr. Benson: What do you think are the affinities of *Sulcostocythere*?

Dr. Hartmann: The soft parts are very close to what you called Cytheridae. *Sulcostocythere* belongs to the Cytheridae. I place it in a tribe: Schistocytherini. The soft parts are close to *Cythere s.s.* The same is true for *Schizocythere* as Hanai showed.

A PRELIMINARY SURVEY OF THE OSTRACODES OF HALIFAX INLET

Q. A. Siddiqui and U. M. Grigg
Saint Mary's University

ABSTRACT

The marine and brackish-water ostracode fauna of Nova Scotia, hitherto little known, is now being investigated. The area is described, with special reference to Halifax Inlet on the Atlantic Coast, where the investigation was begun.

Two ostracode assemblages are recognized: (1) Littoral assemblage typified by *Cytherura elongata* Edwards, 1944, and (2) Sublittoral assemblage in which *Xestoleberis* sp., *Baffinicythere emarginata* (Sars, 1865), *Paradoxostoma variabile* (Baird, 1835), *Sclerochilus contortus* (Norman, 1861), *Muellerina canadensis* (Brady, 1870), *Cythere lutea* Müller, 1785, and *Hemicythere villosa* (Sars, 1865) occur most commonly.

DES OSTRACODES RECENTS DE LA CRIQUE DE HALIFAX NOVA SCOTIA, CANADA

RÉSUMÉ

Des Ostracodes sont en train d'être receuillis des eaus près du bord de la mer et du plateau continental de Nova Scotia, avec une concentration actuellement sur la faune de la Crique de Halifax. Des informations sur la taxonomie, la distribution locale, et l'écologie des espèce receuillies, et des illustrations sont aussi en train d'être compilées.

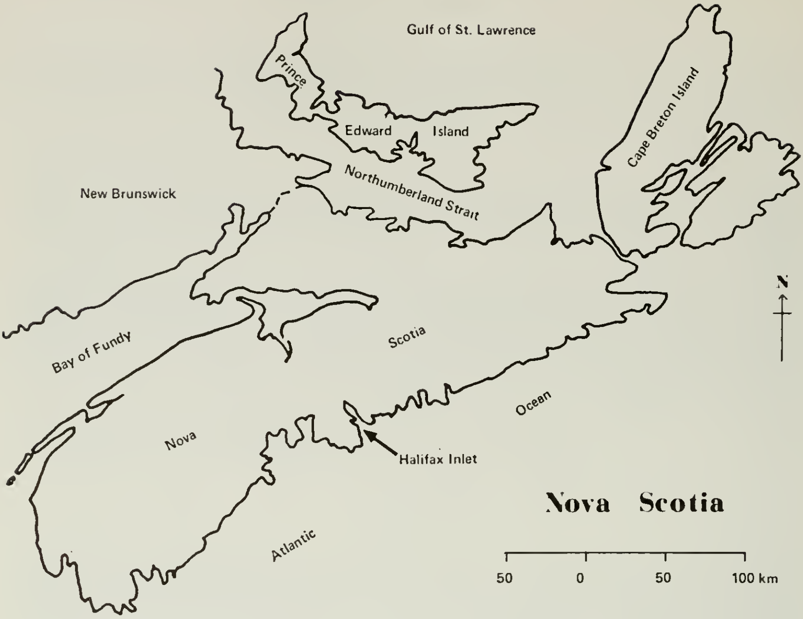
Le travail actuel exposera les résultats de ces investigations jusqu'ici.

INTRODUCTION

This investigation was planned as a pilot study for a survey of the marine and brackish-water ostracodes of the Nova Scotia coast. Little work has been done in the region; the nearest and latest was published by Hazel (1970), on samples collected by United States vessels from off the coast of eastern North America. Hazel summarised previous research and also discussed the question of faunal provinces. The present authors have adopted his delimitation of the Nova Scotian faunal province as extending roughly from Cape Cod, Mass., U.S.A., to Cape Race, Newfoundland, Canada. Nova Scotia is a focal point for research in oceanography and oil prospecting, centered upon the cities of Halifax and Dartmouth, so that access to certain facilities is assured.

The province of Nova Scotia is a peninsula joined to the Canadian mainland by the low and marshy Isthmus of Chignecto. Its long axis lies roughly northeast to southwest, parallel to the mainland coast. It slopes down towards the Atlantic Ocean and also dips to the southwest, the highest hills being in the Cape Breton Highlands and the lowest land mainly around Shelburne.

The sea coast of Nova Scotia can be divided into three regions. The first is the northwest coast, along the Nova Scotia shores of the Bay of Fundy, from Brier Island to the New Brunswick border. This coast is subject to a very large tidal range, a heavy load of suspended sediment and extensive mudflats at low tide; there is relatively little exchange of water with the seas outside. The second is the Gulf Shore, along the margin of the Gulf of St.



Text-figure 1. Map of Nova Scotia coast, showing position of Halifax Inlet.

Lawrence; much of this is sheltered from the main circulation of the Gulf by Prince Edward Island which forms the other boundary of Northumberland Strait. It is thought by some workers that there was a strait through the present Isthmus of Chignecto, and an isthmus between Caribou, Nova Scotia, and Wood Island, P.E.I., during at least one interglacial period. During this time elements of the Virginian Fauna may have reached the Gulf of St. Lawrence through the sheltered Bay of Fundy, accounting for certain species found today in some areas with high summer temperatures, for example, *Crassostrea virginica* (Gmelin) in P.E.I.

Finally, there is the Atlantic Coast including the northeast and southwest shores. This coast is subject to extensive wave action, and exposed to oceanic currents. The Atlantic Coast is much incut, and scoured by ice, forming long inlets, many of them protected from the ocean by the local topography and by barrier beaches. Thus they provide sheltered habitats with varying salinity, and extensive marshes which, like the shores on the other coasts, are frequented by water birds, especially during migration. The deepest inlet is Halifax Inlet, which has been used as a harbour for trade and defense for over two hundred years.

HALIFAX INLET

Halifax Inlet is about 25 km long and trends from northwest to southeast, following the preglacial course of the Sackville River, now deepened by ice. The innermost part, Bedford Basin, is practically landlocked, and has a central deep which descends to 75 metres, the deepest part of the Inlet. Bedford Basin is connected to Halifax Harbour by the Narrows, a channel constricted by Halifax Peninsula jutting out into the inlet and which has a rock sill at 20 m depth. Halifax Harbour is the longest part of the inlet and is navigable over most of its area, with the main channel on the west side and always at least 23 m deep. An arm of the sea, the Northwest Arm, runs up from the seaward end of Halifax Harbour dividing the Halifax Peninsula from the mainland to the west: this also is navigable for some distance.

Last comes the Seaward Approaches, opening to the ocean between Hartlen Point and Chebucto Head. Cow Bay, a marshy inlet east of Hartlen Point, was included in the study area when the extent of the pollution of Halifax Inlet became apparent.

The district has a temperate and foggy climate with a mean annual temperature of 44°F: most of Halifax Inlet remains ice-free all winter. Precipitation averages 50" a year, about 5" of it in the form of snow. The largest fresh-water inflow is from the Sackville River which empties into the head of Bedford Basin, and discharges as little as 0.25m^3/sec. in the dry season and as much as 86m^3/sec. after Hurricane Beth in 1970. There is a certain amount of land drainage and runoff from inland lakes, some of it controlled by weirs.

It is estimated that the volume of fresh-water inflow into Halifax Inlet may be equalled during most of the year by domestic and industrial waste waters. There is settlement round most of the margin, heavily concentrated in Halifax on the west, with most of the docks, and Dartmouth on the east with less. More than 50 industrial sewers are reported to open into Halifax Harbour in the 5 km occupied by Halifax docks. The main sewer from residential Halifax opens into the Northwest Arm at its seaward end, whence its effluent is swept out to sea along the bottom quite effectively (Stanley 1968).

Hydrographic conditions are fairly stable; salinities are not much less than that of seawater, and freshwater is not found near the bottom except at the mouths of streams. Surface waters are seldom less saline than 29 o/oo, and bottom waters in the deepest parts have salinities of 31-32 o/oo. Stratification occurs in summer; inversion is unusual but has been known to occur. Oxygen concentrations are reported to be almost always high.

Considering this harbour's long history it is surprising to find that its current system is not well understood. The Bedford Institute has recently completed a survey of salinity, temperature, and density of the water along eight survey lines traversing the inlet from Bedford Basin to the outer approaches. Thirty-one stations were visited monthly for over a year. The data were published without comment in July, 1972 and have not yet been assimilated (Jordan, 1972). Bottom water enters Halifax Inlet along its eastern side, and flows out on the west; the offshore current sets southwestward parallel to the

Text-figure 2. Map of Halifax Inlet. Collecting stations are indicated by large black dots: those in lines A-H are Bedford Institute hydrographic stations. Areas with small dots appear to be devoid of ostracodes.

coast. Flushing out must be fairly effective since little garbage is thrown up on shore, but there are places where few organisms can live, and the state of Bedford Basin is causing concern.

Bottom deposits vary from muds at the landward end of the Inlet to boulders, sands and gravels at the mouth, with scoured rock in some places such as the Narrows. The muds are often sticky and foetid, supporting a limited fauna, all of it at the mud/water interface.

Exploratory collections were made in 1970-72 around the shores of Bedford Basin, the Northwest Arm, and Cow Bay, and from a launch in various parts of the Inlet. In June 1971 collections were made on several of Bedford Institute's hydrographic stations. All the hydrographic stations were run again in the spring of 1972, except for some on the A and B lines, which could not be worked because of rough weather. It was thought that the correlation of the STD data with the results of sample analysis for ostracodes would be useful although the STD apparatus stopped 3 m short of the bottom. Some of the material collected by Murray Gregory for his thesis on the Foraminifera of Halifax Harbour has also been examined for ostracodes.

Collecting methods at sea involved use of an Eckman grab with a 36 sq. in. sampling area and a modified Forster anchor dredge with an adjustable bite. Material was sieved through a series of steel sieves: mesh sizes used were 0.25 mm and 0.125 mm. A 1/4" mesh garden sieve was sometimes used to screen out coarse material, and the finest sieve was omitted for samples of sticky mud. Sieving was carried out on the spot, and material was sorted fresh if possible and stored in 70% isopropyl alcohol. Shore collections were treated the same way at first, samples of the substratum being sieved and sorted; recently methods have been changed to the sorting of material skimmed in small quantities from the substratum with dipnets lined with nylon hoisery mesh; weed washings are also examined. Ostracodes collected this way survive the journey back to the laboratory well and can be cultured or dissected.

Two species from brackish water have been cultured successfully so far. *Cytherura elongata* has gone through two generations in six weeks, the whole adult population breeding together and then dying, while an unidentified species is breeding in the laboratory, but not synchronously, and the adults have survived reproduction. *Cytherura elongata* feeds on algae, while the other species is thriving on a suspension of baking yeast.

Current preoccupation is with the collation of data giving the geographical distribution of local species, with reference also to the physical environment, and association with other organisms. A start has been made on investigating and illustrating some common species. There are a few collections on hand from other parts of the province, and the investigation will be extended as soon as possible.

OSTRACODE FAUNA

The ostracode fauna in Halifax Inlet can conveniently be divided into two assemblages, namely littoral and sublittoral.

LITTORAL ASSEMBLAGE

These species occur in Mill Cove and some areas of Bedford Basin, Wrights Cove, and Cow Bay. The water is usually brackish in these localities with measured salinities ranging from 28°/oo to less than 1°/oo in spring.

PODOCOPA

Campylocythere? sp.
Cytherois fischeri (Sars, 1866)
Cytheromorpha curta Edwards, 1944
Cytherura elongata Edwards, 1944
Hirschmannia viridis (Müller, 1785)
Leptocythere sp.
Semicytherura nigrescens (Baird, 1838)

MYODOCOPA

Parasterope pollex Kornicker, 1967
Sarsiella cf. *S. zostericola* Cushman, 1906

The most common ostracode in the assemblage is *Cytherura elongata* followed by *Leptocythere* sp., *Cytherois fischeri* and *Cytheromorpha curta*. The occurrence of the genus *Hirschmannia* is of particular interest because this genus so far has not been reported from North America (Van Morkhoven, vol. II, p. 401).

The myodocopid ostracodes *Parasterope pollex* and *Sarsiella* cf. *S. zostericola* have been found in eelgrass beds in lagoons at Hartlen Point and Cow Bay, extending the range of these genera northwards. (Kornicker, pers. comm.)

SUBLITTORAL ASSEMBLAGE

This is a truly marine assemblage occurring in water of salinity greater than 29°/oo (Jordan, 1972). These species are found mainly in the Harbour and towards the seaward side of the Inlet. We have not found any ostracodes in the deeper part of the Basin.

This assemblage includes:

Actinocythereis dawsoni (Brady, 1870)
Baffinicythere emarginata (Sars, 1865)
Baffinicythere howei Hazel, 1967
Bensonocythere americana Hazel, 1967
Bensonocythere sp.
Cythere lutea Müller, 1785
Cytheretta edwardsi (Cushman, 1906)
Cytheropteron sp.
Cytherura? mainensis Hazel and Valentine, 1969
Cytherura? undata Sars, 1866
Elofsonella concinna (Jones, 1857)

Eucythere declivis (Norman, 1865)
Eucytheridea bradii (Norman, 1864)
Finmarchinella finmarchica (Sars, 1865)
Hemicythere villosa (Sars, 1865)
Hemicytherura clathrata (Sars, 1866)
Loxoconcha sp.
Microcytherura sp.
Muellerina canadensis (Brady, 1870)
Munseyella mananensis Hazel and Valentine, 1969
Normanicythere leioderma (Norman, 1869)
Palmenella limicola (Norman, 1863)
Paradoxostoma variabile (Baird, 1835)
Robertsonites tuberculata (Sars, 1865)
Sahnia faveolata (Brady, 1880)
Sclerochilus contortus (Norman, 1861)
Xestoleberis sp.

The species which occur most commonly are *Xestoleberis* sp., *Baffincythere emarginata, Paradoxostoma variabile, Sclerochilus contortus, Muellerina canadensis, Cythere lutea,* and *Hemicythere villosa.*

ACKNOWLEDGMENTS

The research is financed by grants from the National Research Council of Canada and St. Mary's University.

The authors wish to thank their assistants, Valerie Scholey, Bob Grantham, and Jon Walker, and to acknowledge the help of many colleagues, especially Dr. Francis Jordan of Bedford Institute, Dr. Franco Medioli of Dalhousie University, and Dr. Murray Gregory, now at the University of Auckland.

REFERENCES

Gregory, M. R.
1971. *Distribution of benthonic Foraminifera in Halifax Harbour, Nova Scotia.* Ph.D. thesis, Dalhousie University.

Hazel, J. E.
1970. *Ostracode zoogeography in the southern Nova Scotian and northern Virginian Faunal Provinces.* U.S. Geol. Sur., Prof. Paper 529-E, pp. V, E 21, 69 pls.

Jordan, F.
1972. *Oceanographic data of Halifax Inlet.* Unpublished manuscript.

Stanley, D. J.
1968. *Reworking of glacial sediments in the North West Arm, a fjord-like inlet on the southeast coast of Nova Scotia.* Jour. Sed. Petrol., 38, pp. 1224-1241.

Q. A. Siddiqui
and
U. M. Grigg,
Saint Mary's University,
Halifax,
Nova Scotia, Canada.

DISCUSSION

Hartmann: What is the percentage of American and European species in the samples?

Siddiqui and Grigg: Of the 36 species definitely identified, 19, or 52.8 percent, are also found in Europe.

Explanation of Plate 1

All figures except 8 and 11 are scanning electron micrographs.

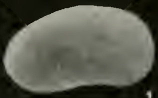
Littoral Assemblage

Figure

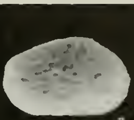
1. *Campylocythere* ? sp. External view, right valve; × 38.
2. *Cytherois fischeri* (Sars 1866). Right view, carapace; × 46.
3. *Cytheromorpha curta* Edwards 1944. Right view, carapace, female; × 43.
4. *Cytherura elongata* Edwards 1944. Right valve, male; × 41.
5. *Hirschmannia viridis* (Müller 1785). Right view, carapace, male; × 46.
6. *Leptocythere* sp. Right view, carapace; × 48.
7. *Semicytherura nigrescens* (Baird 1838). Right view, carapace, female; × 43.
8. *Sarsiella* cf. *S. zostericola* Cushman 1906. Carapace open with animal, subadult male; × 18.

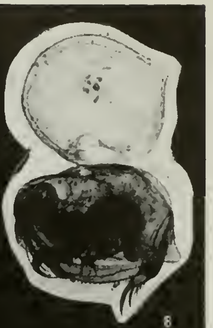
Sublittoral Assemblage

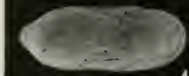
9. *Actinocythereis dawsoni* (Brady 1870). Left view, carapace, male; × 37.
10. *Baffinicythere emarginata* (Sars 1865). Left view, carapace, female; × 44.
11. *Baffinicythere howei* Hazel 1967. Right view, carapace, male; × 49.
12. *Bensonocythere americana* Hazel 1967. Right view, carapace, male; × 37.
13. *Bensonocythere* sp. External view, right valve, male; × 36.
14. *Cytheretta edwardsi* (Cushman 1906). External view, right valve, male; × 44.
15. *Cythere lutea* Müller 1785. External view, left valve; × 40.
16. *Cytheropteron* sp. External view, left valve; × 40.

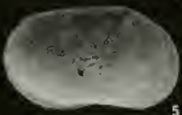

1


2

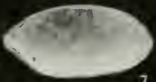

3

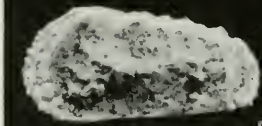

8

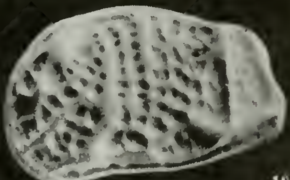

4

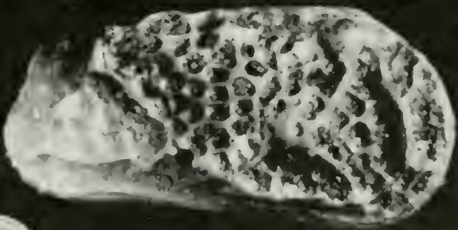

5

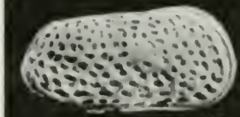

6


7


9

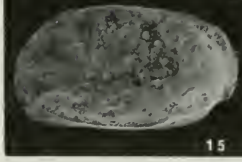

10


11


12


13


14


15


16

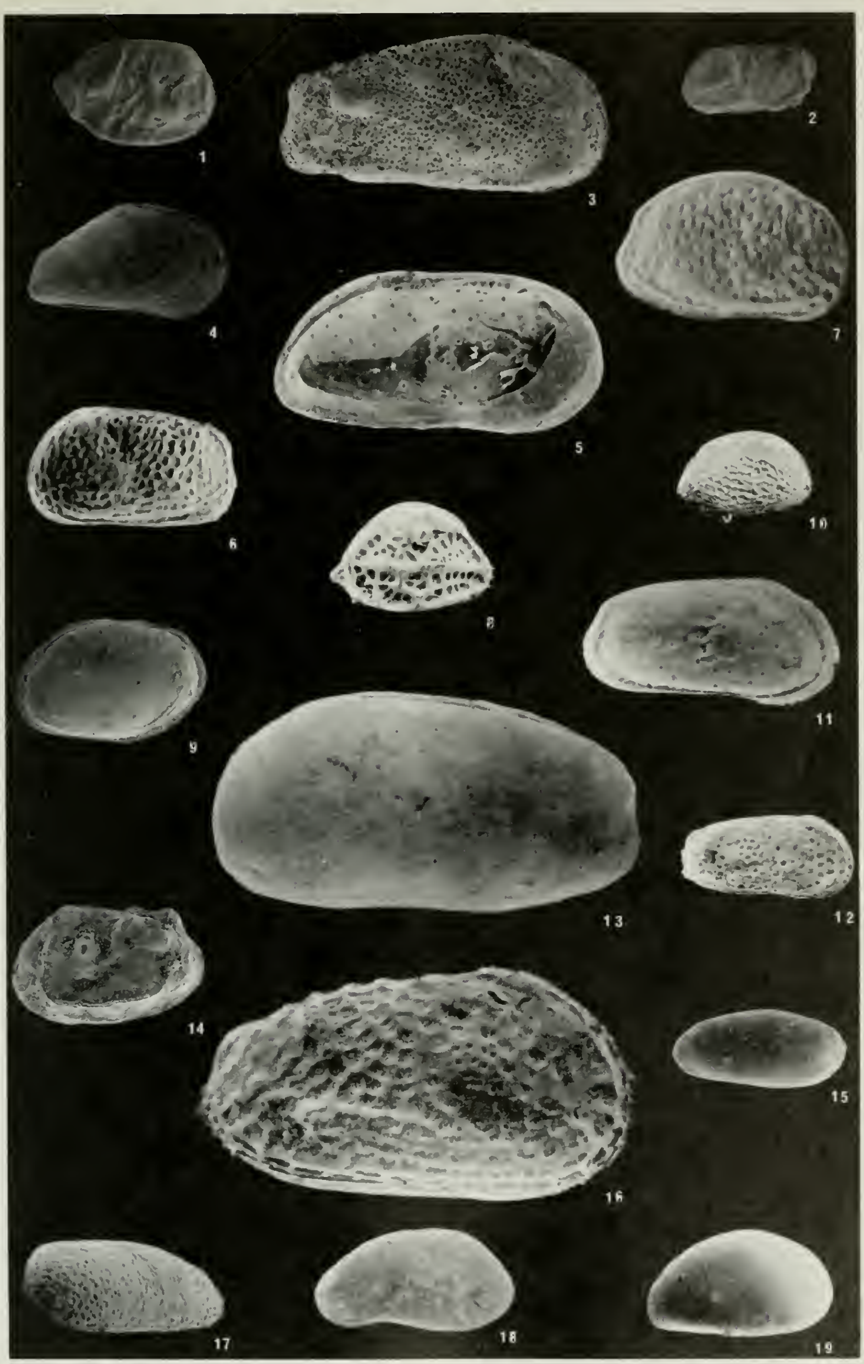
EXPLANATION OF PLATE 2

All figures are scanning electron micrographs.

Sublittoral Assemblage (continued)

Figure

1. *Cytherura? mainensis* Hazel and Valentine 1969. Right view, carapace; × 39.
2. *Cytherura? undata* Sars 1866. External view, left valve, male; × 36.
3. *Elofsonella concinna* (Jones 1857). External view, right valve, male; × 40.
4. *Eucythere declivis* (Norman 1865). Right view, carapace; × 39.
5. *Eucytheridea bradii* (Norman 1864). Internal view, left valve; × 39.
6. *Finmarchinella finmarchica* (Sars 1865). Left view, carapace, female; × 36.
7. *Hemicythere villosa* (Sars 1865). External view, right valve, female; × 42.
8. *Hemicytherura clathrata* (Sars 1866). External view, right valve, female; × 37.
9. *Loxoconcha* sp. Left view, carapace; × 38.
10. *Microcytherura* sp. Right view, carapace; × 36.
11. *Muellerina canadensis* (Brady 1870). External view, right valve; × 38.
12. *Munseyella mananensis* Hazel and Valentine 1969. Right view, carapace, male; × 39.
13. *Normanicythere leioderma* (Norman 1869). Left view, carapace, female; × 49.
14. *Palmenella limicola* (Norman 1863). Left view, carapace; × 40.
15. *Paradoxostoma variabile* (Baird 1835). External view, left valve; × 37.
16. *Robertsonites tuberculata* (Sars 1865). Right view, carapace; × 49.
17. *Sahnia faveolata* (Brady 1880). External view, right valve; × 32.
18. *Sclerochilus contortus* (Norman 1861). External view, left valve; × 38.
19. *Xestoleberis* sp. External view, left valve; × 41.


1
3
2
4
7
5
6
10
8
11
9
13
12
14
15
16
17
18
19

THE MARINE OSTRACODA OF RUSSIAN HARBOUR, NOVAYA ZEMLYA AND OTHER HIGH LATITUDE FAUNAS

JOHN W. NEALE
University of Hull
and
HENRY V. HOWE*
Louisiana State University

> "We have had a mere glimpse of that 'wonderland' which underlies the vast ocean; and our curiosity is very far from being satisfied, especially as regards the arctic seas. It is a new world, full of interest not only to naturalists but to every man of science". — Dr. J. Gwynn Jeffreys in Preliminary Report of the Biological Results of a cruise in H.M.S. *Valorous* to Davis Strait in 1875 (Proc. Royal Soc. London, 1876, p. 186).

ABSTRACT

A sample of silty-sand taken at Russian Harbour (Russkaya Gavan) at 76°13'N, 62°40'E in 8 fathoms of water in 1937 yielded 4,004 ostracodes. This sample is the richest ostracode sample ever recovered from the Arctic and comes from the eastern margin of the Barents Sea which is an area of high productivity. The large number of specimens allows the relative proportions of the various species present to be assessed with considerable accuracy for the first time in an Arctic fauna which is dominated by the Hemicytheridae and Trachyleberididae. Four families, Hemicytheridae 33.4%, Trachyleberididae 20.1%, Cytheruridae 20.1% and Cytherideidae 17.7% account for 91.3% of the ostracode fauna. Four species, *Robertsonites tuberculata* 16.98%, *Baffinicythere howei* 12.34%, *Baffinicythere emarginata* 11.49% and *Eucytheridea punctillata* 10.27% make up over half the specimens obtained. Comparisons are made with other Arctic faunas and an Arctic sublittoral ostracode province is defined and divided into an Eastern and Western Sub-Province. The Norwegian and Celtic Provinces to the South are defined and the latter is divided into a northern Britannic Sub-Province and a southern Gascoynian Sub-Province. Increasing differences from the poles southwards between the ostracod sublittoral faunas on the western and eastern sides of the Atlantic are ascribed to sea floor spreading and the increasing separation and isolation between the two sides in a southerly direction due to the intervention of the bathyal and abyssal environments with their own fauna.

RÉSUMÉ

Un échantillon du sable vaseux obtenu en 1937 au Port Russe, Novaya Zemlya (Russkaya Gavan) à 76°13'N, 62°40'E à la profondeur de 8 brasses d'eau fournit 4,004 ostracodes. Cet èchantillon est le plus riche en ostracodes qu'on ait jamais obtenu dans l'Arctique et il provient du bord oriental de la Mer Barents, zone de haute producticité. Grâce au grand nombre d'exemplaires nous pouvons établir les proportions relatives des espèces différentes, et c'est pour la première fois dans une faune arctique dominé par les Hemicytheridae et Trachyleberididae. Quatre familles, les Hemicytheridae 33.4%, Trachyleberididae 20.1%, Cytheruridae 20.1% et Cytherideidae 17.7% constituent 91.3% de la faune d'ostracodes. Quatre espèces, *Robertsonites tuberculata* 16.98%, *Baffinicythere howei* 12.34%, *Baffinicythere emarginata* 11.49%, et *Eucytheridea punctillata* 10.27% constituent plus de 50 p.c. des spécimens obtenus.

Nous établissons des comparaisons avec d'autres faunes arctiques, et nous définisons une Province arctique sous-littorale d'ostracodes: celle-ci se divise en sous-Province occidentale et orientale. Au sud, les Provinces norvègenne et celtique sont définies; celle-ci se divise en une sous-Province britannique nord, et une sous-Province gasconne sud. Les différences entres les faunes d'ostra-

---

*Deceased September 27, 1973.

codes sous-littorales des côtés occidentales et orientales de l'Atlantique, qui accroissent vers le sud sont attribués à la dispersion du fond de la mer et la séparation et l'isolement croissant qui a lieu entre les deux côtés vers le sud et l'intervention des milieux bathyal et abyssal avec leur propre faune.

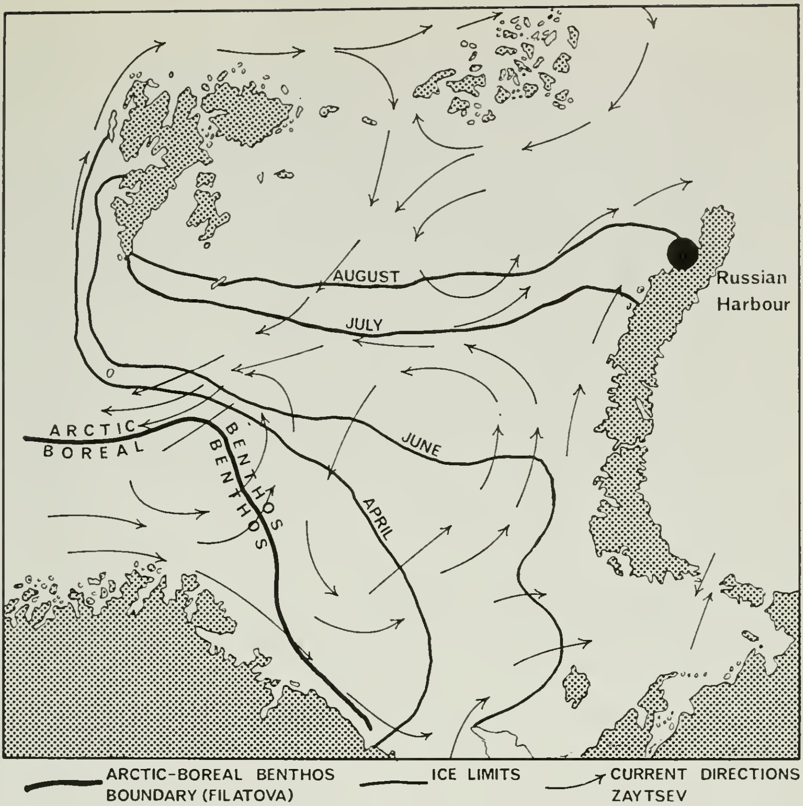
INTRODUCTION

As the ship approached Russian Harbour (Russkaya Gavan 76°13'N, 62°40'E) on 13th August, 1937, from 8 fathoms of water the lead brought up a sample of silty sand which was collected by one of the authors (H.V.H.). This sample yielded over 4,000 specimens of ostracode and provides the richest fauna yet recovered from high latitudes thus enabling us for the first time to get a valid quantitative evaluation of the faunal composition of Arctic shallow water ostracodes.

Russian Harbour lies on the western side of Novaya Zemlya which forms the boundary between the Barents Sea to the west and the Kara Sea to the East. Both seas are Arctic Shelf seas with the deeper Arctic Basin to the north, but while the Barents Sea shows some influence of the North Atlantic Drift, the Kara Sea does not and forms the 'ice-cellar' of Colonel Feilden. The difference is also reflected in the terminology of some authors who regard the Barents Sea as a Low Arctic shallow subregion and the Siberian and North Greenland areas as a High Arctic shallow sub-region with the abyssal Arctic sub-region lying centrally. To the south the Norwegian Sea is sometimes called sub-arctic and we shall return to the faunas of these seas later.

As the Atlantic waters flow into the Barents Sea from the west between North Cape and Bear Island they are cooled from 8°C to -1.8°C setting up a complex vertical circulation as they meet the colder local waters of the shelf, thus ensuring good oxygenation of the bottom waters and a large biomass which may be 150-600 g/m^2 or more. Where the circulation is not so marked as in the more northern parts the biomass may fall to 20-50 g/m^2 or less, and brown mud is the characteristic bottom. In the northern and eastern regions of the middle part of the sea, only the surface layer is heated in summer, and in the northern, eastern, and southeastern parts of the sea the whole column of water is below zero all the year round. The salinity is fully marine and varies between 32‰ and 37‰ depending on area and season. Pack ice forms on the sea each winter, retreating northwards during the summer and data over the years suggest a long term general warming up of the sea, the ice cover for 1901-6 averaging 57% and for 1921-31 –44%. On the basis of the benthos the Russians have divided the Barents Sea into six principal biocoenoses. On their classification the Russian Harbour fauna belongs to the Eastern shallows.

The literature covering Arctic ostracode faunas is rather limited and widely scattered. In the east Akatova (1946) has described limited faunas from the Novosiberian shelf and there are records of a few species from the Kara Sea and Matochkin Shar based on the material from the Nordenskjold Expedition and noted by Elofson (1941). On the northern margins of the Barents Sea itself, Scott (1899) covered the fauna from Franz Joseph Land



Text-figure 1. The Barents Sea. Current directions, mean ice margins from April to August and Arctic/Boreal benthos boundary of Filatova (1957). (After Zenkevitch.)

and Brady and Norman (1889) gave records for Spitzbergen. The latter faunas have also been detailed by Müller (1931) and Klie (1942). To the South, Akatova (1957) has noted a number of White Sea species and Norman (1891, 1902) dealt with the northern Norway faunas in more detail. Elofson (1941) adds some new records for the area generally, especially for Bear Island and Jan Mayen. In the west, material from Greenland and the Baffin Island area was examined in the last century by Brady (1868, 1878) and Norman (1877) and in this century Stephensen (1913, 1936) has published compilations for the Greenland region. More recently Hazel (1970) has examined faunas from eight samples from Greenland Seas and nine from the Canadian area north of 60°N. There are no estimates or details of abundance in the literature except for Klie's work (1942) in Spitzbergen and Hazel's work (1970) which gives an indication of the abundance of species in generalised terms. In this lies the significance of the principal fauna covered here.

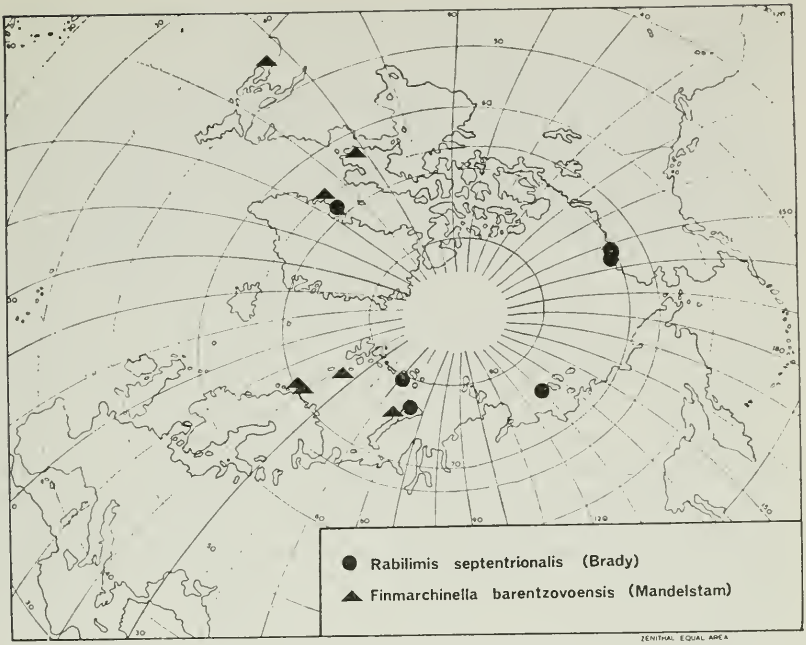
The present sample contained 4004 ostracodes none of which showed soft parts. It is, strictly speaking, a thanatocoenose, but its dissimilarity to the known Pleistocene faunas of the region, and its similarity to the biocoenoses of Greenland and Spitzbergen give no reason for supposing that it is not typical of the biocoenose.

One of the principal problems which cannot be stressed too often is the importance of accurate taxonomy. At the 1963 Naples Symposium one of the authors (Neale, 1965, p. 258) stated "In studies of ecology and distribution accurate synonymy is a *sine qua non,* and in this respect the species is the most significant and important unit". These sentiments were reiterated by the other author (Howe, 1969, p. 3) at the 1967 Hull Symposium. Both authors would once again stress this aspect of ecological studies.

In the present study considerable taxonomic problems have arisen. Formal taxonomic descriptions have, quite rightly, no place in this Symposium and so the new taxa are not dealt with here but are covered elsewhere. Publications dealing with these are listed in the references at the back. Nevertheless, it is necessary to draw attention to a number of taxonomic aspects in passing, particularly to the two principal problems which concern the genera *Finmarchinella* and *Cytheropteron.* The problem of *Eucytheridea* has already been dealt with by van den Bold (1961).

In the case of *Finmarchinella, F. finmarchica* (Sars) appears to have been correctly interpreted in the literature, the species being clear cut and raising no problems. It is widely distributed in northern seas extending as far south as Brittany. Occurrences in the Bay of Biscay are now thought to belong to the palaeothanatocoenese. (Moyes and Peypouquet, 1971; Peypouquet, 1971). On the other hand, *Finmarchinella angulata* (Sars) has suffered from confusion, even in Recent times, being confused with two other species, *Finmarchinella barentzovoensis* (Mandelstam) and *F. curvicosta* Neale. Material supplied by the Zoologisk Museum in Oslo and labelled by Sars has established the correct interpretation of *F. angulata,* and the new species *F. curvicosta* has been based on the excellent material collected by H.M.S. *Valorous* at Holsteinsborg Harbour, Greenland, in 1875 (Neale, 1974). This latter species is very characteristic of Arctic waters. The same is true of Mandelstam's species *Finmarchinella barentzovoensis* for which Russian Harbour is the type locality, and which is also found in west and northwest Greenland (Text-fig. 2).

The genus *Cytheropteron* is in an even more confused state and is difficult to deal with. Abundant material, however, has made the task much easier and Neale and Howe (1973) have established three new species namely *C. arcticum, C. nodosoalatum,* and *C. dimlingtonensis.* The first two are characteristically developed at Russian Harbour. The last occurs in the Pleistocene at Dimlington, East Yorkshire, and in englacial material at Spitzbergen. Comparison with material from Norman's type locality — probably the type material itself — shows that *C. dimlingtonensis* is related to, but distinct from, *C. latissimum* (Norman) with which it has hitherto been confused, and the same is true of *C. paralatissimum* Swain which is also found at Russian Harbour and widely in Arctic seas. One small *Cytheropteron* has been left under open nomenclature. It is difficult to interpret with confidence but seems related to *C. nodosum* Brady on the one hand and an undescribed species from the Pleistocene of Alaska on the other. One species each of *Cytherois* and *Semicytherura* believed



Text-figure 2. Distribution of *Rabilimis septentrionalis* (Brady) and *Finmarchinella barentzovoensis* (Mandelstam).

to be new have been left under open nomenclature for the present, as have three single valves, two of them very small, belonging to three distinct species.

The material used in this study has been named at the specific level and counted so as to give some information on abundance which may be used in comparison. However, before considering the fauna in more detail a number of remarks must be made about the techniques used and some of their relative advantages and disadvantages. After completing the taxonomic determinations two approaches are possible in determining the affinity of any particular fauna with others, namely the qualitative presence/absence method and the quantitative composition of the fauna method. Both have certain advantages and disadvantages and both have been used in this study. From our previous remarks it is clear that for any meaningful results both depend on accurate taxonomy.

The qualitative method depends simply on comparison of species present or absent in individual localities. It has the advantage that it is fairly quick and that use can often be made of previous work although in the latter case the taxonomy must usually be taken on trust. It suffers from the fact that rare species are given as much weight as common species and may thus unbalance any comparisons made unless some form of weighting or arbitrary restriction is introduced. Further refinements may be made, and by the use of computers vast amounts of data can be processed quickly and comparison charts printed out, always with the proviso about the effect of rare species and the taxonomic determinations mentioned above.

Using quantitative methods gives information on the abundance of various species, rare species are not overstressed and to this extent the results are more meaningful than simple presence/absence data. It means, however, that the method is time consuming, data from other workers are rarely in usable form and the work needs to be rigidly controlled and self-consistent. The results may be expressed by a number of methods such as histograms, fence diagrams, pie diagrams etc., but the value of easy comparison by these methods falls off after the number of localities or samples compared reaches a certain size after which other techniques are better employed. Ideally the data should be self consistent and uniform as regards collection, processing and taxonomy and below we examine how far the present study is satisfactory in this respect.

1. Collection

As this was not a specially funded research programme, the study was dependent on the material readily available. This consisted of material brought up at Russian Harbour by the sounding lead, material from the stations occupied by H.M.S. *Vidal* and the *Ernest Holt* and brought up by conical dredge, and Museum material. Because the work was not based on uniform weights or volumes, the samples present no problems except for the Museum material about which there are reservations as given below.

2. Processing

In the case of most of the samples this was under the direct control of the authors and all material held on a B.S.S. 100 sieve was picked and counted. The choice of sieve represented a compromise between obtaining a representative fauna in a reasonable time on the one hand, and losing the early instars on the other. Because this was consistent for all the samples except those detailed below this raises no problem. It is a problem, however, in the case of the three Museum samples from Greenland and Franz Joseph Land and the Spitzbergen sample taken from the literature. There is no certainty that this was processed on a sieve of similar size, but the value of at least some roughly comparable data from Greenland and Spitzbergen was thought to outweigh any possible lack of consistency. Again, whilst the whole of the available Museum material was examined and counted, there is no guarantee that this was the full fauna recovered, but again provided that this is borne in mind, some comparison seemed better than none.

3. Taxonomy

With the single exception of the Spitzbergen Station 6 of Römer and Schaudinn, data for which were taken from Klie (1942), all the specimens used in the quantitative work were examined by the authors personally.

4. Size of sample

Being dependent on what material happened to be available, all specimens were counted and no restriction imposed on size because in this sort of work the more specimens available the more accurately the resulting percentages reflect the actual occurrence of the species. It is generally held that 300 specimens form an acceptable minimum for this type of work. In the present case the Spitzbergen Shelf Sample 46 (176 specimens), Dimlington (251), the Museum Greenland samples (127, 233) and Römer and Schaudinn's Spitzbergen Station 6 (74) fall short of this but interest was thought to justify their inclusion.

From this one may conclude that with the exception of the Museum samples and the Spitzbergen data from Klie (1942) which should be treated with circumspection, the other data which were under the direct control of the authors are reasonably self-consistent.

THE RUSSIAN HARBOUR FAUNA

The fauna is dominated by trachyleberids, hemicytherids, and the genus *Eucytheridea* and the details are given in Table 1. Altogether 45 species are present of which *Robertsonites tuberculata* (Sars), *Baffinicythere howei* Hazel, *B. emarginata* (Sars), *Eucytheridea punctillata* (Brady), and *E. macrolaminata* (Elofson) make up more than half the total population. With the addition of *Finmarchinella barentzovoensis* (Mandelstam), *Cytheropteron paralatissimum* Swain, *Semicytherura undata* (Sars), *Normanicythere leioderma* (Norman), *Cytheropteron nodosoalatum* Neale and Howe, and *Acanthocythereis dunelmensis* (Norman) these 11 species account for over three-quarters of the total population.

Robertsonites tuberculata (Sars), the commonest form, is a well-known trachyleberidinid component of shallow water boreal and Arctic faunas and prefers the sublittoral, reaching its maximum abundance at depths of less than 50 fathoms. It is found round the British Isles and has been found by one of the authors in a Recent study of the Celtic Sea where it occurs in 44% of the samples from the Cockburn Bank (ca. 49°45′N, 9°20′W) where it may make up to 6% of the fauna. Here it has been interpreted as being at about the southern limit of its range. It occurs farther to the south in the Bay of Biscay where it has been interpreted by Peypouquet (1971) as part of a palaeothanatocoenose indicative of a colder environment. It is of considerable interest that all five species characteristic of Peypouquet's V2 thanatocoenose I, namely *Robertsonites tuberculata* (Sars), *Finmarchinella finmarchica* (Sars), *Eucytheridea punctillata* (Brady), *E. bradii* (Norman) [as *E. bairdii* (Sars)], and *Acanthocythereis dunelmensis* (Norman), are well represented in the Russian Harbour fauna.

Eucytheridea punctillata shows a similar distribution to *Robertsonites tuberculata*. In the past *Eucytheridea macrolaminata* (Elofson) has been confused with *E. bradii*. Elofson (1939) found it from King Charles Land, between Bear Island and Hope Island, from Clavering Island and Cape Steward. Van den Bold (1961) described material from Russian Harbour and Hazel (1970) has found it off North Wolstenholme Island in West Greenland and off Clavering Island and Cape Stosch in East Greenland. The present authors have found it in Colonel Feilden's material from Matochkin Shar, Novaya Zemlya. Its known distribution is exclusively Arctic and is shown in Text-figure

Table 1. Marine Podocopida from Russian Harbour, Novaya Zemlya

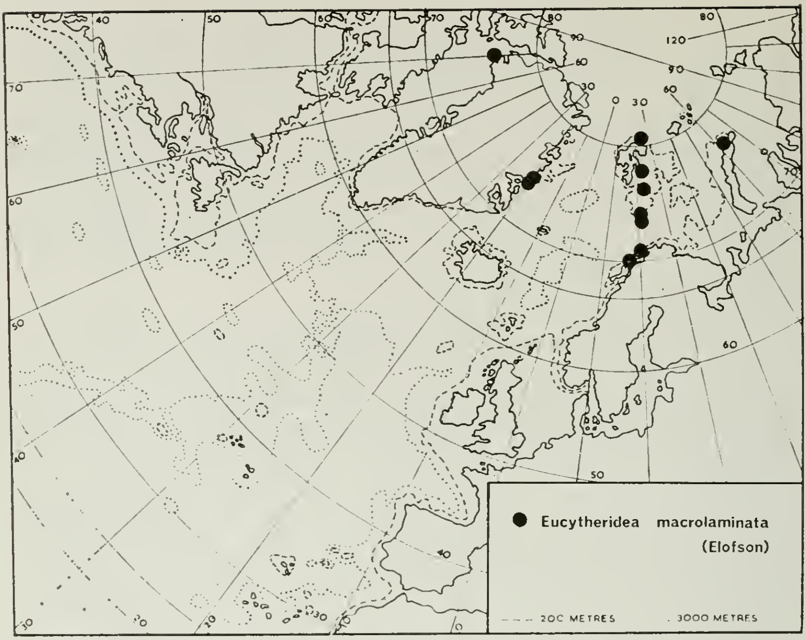
		No.	Total Fauna %	No. Adults	Adult Fauna %	No. Juveniles	♂	♀	% ♂	Adults % age cf. Juveniles
1	*Robertsonites tuberculata* (Sars)	680	16·93	134	9·35	548	42	92	31·34	19·76
2	*Baffinicythere howei* Hazel	494	12·34	145	10·12	349	45	100	30·33	29·12
3	*Baffinicythere emarginata* (Sars)	460	11·49	180	12·56	280	69	111	38·32	39·11
4	*Eucytheridea punctillata* (Brady)	411	10·27	110	7·68	301	46	64	41·82	26·77
5	*Eucytheridea macrolaminata* (Elofson)	241	6·02	95	6·63	146	32	63	33·68	39·09
6	*Finmarchinella barentzavoensis* (Mandelstam)	146	3·65	64	4·47	82	26	38	40·62	43·83
7	*Cytheropteron paralotissimum* Swain	148	3·65	68	4·75	78				46·57
8	*Semicytherura undata* (Sars)	143	3·57	132	9·21	10	41	92	28·69	98·46
9	*Normanicythere leioderma* (Norman)	138	3·45	24	1·68	114	8	16	33·33	17·39
10	*Cytheropteran nodosoalatum* Neale & Howe	137	3·42	44	3·07	93				32·12
11	*Acanthocythereis dunelmensis* (Norman)	126	3·15	29	2·02	97	10	19	34·48	23·01
12	*Cytheropteron pyramidale* Brady	91	2·28	54	3·77	37				59·34
13	*Semicytherura concentrica* (Brady, Crosskey, Robertson)	83	2·07	54	3·77	29	19	35	35·19	65·06
14	*Xestoleberis depressa* Sars	76	1·90	38	2·65	38				50·00
15	*Cythere lutea* O. F. Müller	62	1·55	8	0·56	54				12·90
16	*Semicytherura affinis* (Sars)	54	1·35	34	2·37	20	11	23	32·35	62·96
17	*Cytheropteron arcticum* Neale & Howe	53	1·32	25	1·74	28				47·17
18	*Finmarchinella curvicosta* Neale	52	1·30	14	0·98	38	5	9	35·72	26·93
19	*Hemicytherura clathrata* (Sars)	51	1·27	27	1·89	24	12	15	44·44	52·94
20	*Finmarchinella angulata* (Sars)	48	1·20	11	0·77	37	2	9	18·18	22·92
21	*Finmarchinella finmarchica* (Sars)	39	0·97	12	0·84	27	5	7	41·68	30·77
22	*Palmenella limicola* (Norman)	38	0·95	13	0·91	25				34·21
23	*Sclerochilus contortus* (Norman)	31	0·77	13	0·91	18				41·93
24	*Paradoxostoma arctica* Elofson	30	0·75	20	1·40	10				66·66
25	*Heterocyprideis sorbyana* (Jones)	30	0·75	7	0·49	23				23·33
26	*Eucytheridea bradii* (Norman)	26	0·65	10	0·70	16				38·46
27	*Cytheropteron* cf. *C. nodosoalatum* Neale & Howe	26	0·65	9	0·63	17				34·61
28	*Argilloecia conoidea* Sars	24	0·60	22	1·54	2				91·68
29	*Cytherois* sp. nov.	15	0·37	6	0·42	9				40·00
30	*Cytheropteron* sp. nov.	10	0·25	1	0·07	9				10·00
31	*Bythocythere constricta* Sars	9	0·23	4	0·28	5				44·44
32	*Rabilimis septentrionalis* (Brady)	7	0·18	2	0·14	5				28·57
33	*Paracytherois tenera* (Brady, Crosskey, Robertson)	6	0·15	6	0·42	0				100·00
34	*Semicytherura similis* (Sars)	4	0·10	3	0·21	1	0	3	0	75·00
35	*Semicytherura* sp. nov. 1	4	0·10	4	0·28	0	1	3	25·00	100·00
36	*Cytheromorpha macchesneyi* (Brady & Crosskey)	3	0·08	3	0·21	0				100·00
37	*Paradoxostoma* aff. *P. pulchellum* Sars	2	0·05	1	0·07	1				50·00
38	*Paradoxostoma ensiforme* Brady	1	0·03	1	0·07	0				100·00
39	*Paracytherois* aff. *P. vitrea* (Sars)	1	0·03	1	0·07	0				100·00
40	*Paracytherois* cf. *P. arcuata* (Brady)	1	0·03	0	0	1				0
41	*Paracypris* cf. *P. polita* Sars	1	0·03	0	0	1				0
42	*Roundstonia globulifera* (Brady)	1	0·03	1	0·07	0	1	0		100·00
43	*Bensonocythere* ? sp.	1	0·03	0	0	1				0
44	*Tetracytherura* ? sp.	1	0·03	0	0	1				0
45	*Semicytherura* sp. nov. 2	1	0·03	1	0·07	0				100·00

3. The hemicytherinid species *Baffinicythere emarginata* and *B. howei* are both characteristic Arctic forms although not confined to that region. *B. emarginata* is fairly widely distributed as far south as northern Britain in the eastern Atlantic and as far South as 41°N in the western Atlantic. It is most abundant in Arctic seas at depths of less than 25 fathoms and becomes rare and sporadic towards its southern limits, a feature clearly appreciated by Brady and Norman (1889). *B. howei* is similarly distributed but not so well known on the eastern side of the Atlantic. It, too, is confined to the Norwegian and Arctic Provinces not venturing south of the Shetland-Faroes ridge, a fact which may be linked with a change of the order of 6° to 8°C in bottom temperatures across the ridge.

The next six species in order of abundance contain some typically Arctic forms. *Finmarchinella barentzovoensis* (Text-fig. 2) was first described from Russian Harbour by Mandelstam (1957) and has since been found at a number of other localities in the Arctic in both the H.M.S. *Vidal* and *Ernest Holt* material and in Museum material from the Hunde Islands and Holsteinsborg Harbour in West Greenland. It has not so far been found below 66°N in the Eastern Atlantic although it is found in Frobisher Bay and Kneeland Bay in the Western Atlantic at 63°10′N, 67°45′W and 62°59′N, 67°28′W respectively and also appears to be present in the Gulf of Maine at 44°08′N, 68°13′W. *Cytheropteron paralatissimum* originally described by Swain (1963) from the Pleistocene Gubik Formation in Alaska has been found in the Hunde Islands, Greenland and Franz Joseph Land material (where it was placed in *C. latissimum*), and at Novaya Zemlya and has so far not been found outside the Arctic. *Semicytherura undata* (Sars), eighth in order of abundance between *Cytheropteron paralatissimum* and *Normanicythere leioderma,* has a distribution reminiscent of *Robertsonites tuberculata,* and the same is true of *Acanthocythereis dunelmensis* (Norman) which is eleventh in order of abundance. *Normanicythere leioderma* (Norman) a characteristic Arctic species which is also found in the Norwegian Province has been described and its distribution and affinities covered in a series of papers (Neale, 1959, 1961, Neale and Schmidt, 1967) and needs no further discussion here. The allied *N. concinella* Swain does not occur at Russian Harbour although it occurs fossil in the Pleistocene of mainland Russia (v. Lev, 1969). *Cytheropteron nodosoalatum* Neale and Howe has so far only been found in the Arctic eastern Atlantic.

The less abundant species show a similar general division into two types-characteristic Arctic species such as *Rabilimis septentrionalis* (Brady) *Finmarchinella curvicosta* Neale, *Cytheropteron arcticum* Neale and Howe and *C.* cf. *C. nodosoalatum* Neale and Howe, and those which have a more ubiquitous distribution such as *Cythere lutea* O. F. Müller, *Finmarchinella finmarchica* (Sars), *Heterocyprideis sorbyana* (Jones), *Semicytherura concentrica* (Brady, Crosskey and Robertson), and others.

In summary one can say that the fauna is characterized, firstly by a number of typical Arctic species, secondly by a number of species whose range is wide but which are much more abundant in Arctic waters, and thirdly a



Text-figure 3. Distribution of *Eucytheridea macrolaminata* (Elofson).

group of wide ranging species which show no change in abundance or an abundance which increases southwards, this third category forming a minor element in the fauna. Here we may remark on the absence of typical Loxoconchidae and Leptocytheridae so characteristic of shelf areas farther south. These are represented in the Barents Sea and other Arctic Seas by rare examples of the two small, tuberculate genera *Roundstonia* (loxoconchid) and *Cluthia* (leptocytherid) which are fully adult at only about two-thirds the length of typical members of these families and show marked sexual dimorphism. It is uncertain whether *Roundstonia globulifera* (Brady), which is represented by a single valve at Russian Harbour, is still living. *Cluthia cluthae* (Brady, Crosskey, and Robertson) is found at Matochkin Shar and is regarded as a living species.

As well as plotting the total population, the adults were plotted separately in the same manner to gauge the effect of juveniles on the abundances. This had two main effects. Firstly, it modified the order of abundance in the case of some of the larger forms, particularly noticeable in the case of *Robertsonites tuberculata* which had a large number of juveniles present at the time the sample was taken. Secondly it increased the relative proportions of the smaller species such as *Semicytherura undata* (Sars), *S. concentrica* (Brady, Crosskey and Robertson), *Xestoleberis depressa* Sars, and others.

The same exercise was carried out for two other samples. In the case of *Ernest Holt* Station 6 (Text-fig. 9) the differences between the total population and adult only plots were slight. In H.M.S. *Vidal* Station 6 the results were somewhat intermediate between the other two. The results reflect two main factors. Firstly, the size of sieve used which controls the minimum size retained and thus means that specimens which only attain a small adult size are under-represented in the total population, although, it must be added, that provided each sample is accorded the same treatment the samples are strictly comparable. Secondly the number of juveniles in any one species is a reflection of the particular breeding season together with a random factor in the sample itself and this may well explain any apparent discrepancies between the two sets of data. Provided enough specimens are available it is preferable to consider only adults, always providing that a check is made on juveniles to ascertain that sorting and transport is not affecting a particular fauna. On the other hand, with total populations, if all samples are treated in the same manner, they will be comparable between themselves although perhaps not such a true reflection of the actual faunal composition. In this latter respect one must also bear in mind that the fragile, thin-shelled forms may be under-represented. In the Novaya Zemlya, *Ernest Holt* 6 and H.M.S. *Vidal* 6 faunas the adults represented respectively 35.96%, 35.22%, and 30.21% of the total population which shows remarkable agreement from three widely scattered areas. These populations are considered to be indigenous breeding populations and there is nothing to suggest sorting. Only in the relatively rare cases of single specimens of rather small size may derivation be suspected. This is possibly the case with the single valve of *Roundstonia globulifera* at Russian Harbour mentioned above and in the case of one or two other specimens.

Another aspect which was noted was the proportion of males to females in those species where the sex was determinable, and the data are given in Table 1. The results were much as expected. *Finmarchinella angulata* (Sars) with 18.18% males showed the lowest ratio. The other 15 species all showed proportions lying between 25% (*Semicytherura,* sp. nov. 1) and 44.44% (*Hemicytherura clathrata*) with a clustering round about the 32-35% level for the majority. In most cases a good working rule would seem to be about one-third males and two-thirds females and as far as it is possible to tell there is no tendency to increasing parthenogenesis among these marine forms in colder waters.

Some comparisons with other faunas can now be made.

COMPARISONS WITH OTHER AREAS

1. Novaya Zemlya, Matochkin Shar

One of the most interesting discoveries made during the course of the present work was two slides brought to light during work on the Brady Collection in the Hancock Museum, Newcastle-upon-Tyne. These were labelled respectively "Sounding 10 fathoms Matyushin Shar June 24. Capt. Feilden" and "Sounding 15 fathoms N. side Matyushin Shar (Capt. Feilden)". These are obviously from what is referred to on current maps as the Strait Matochkin Shar which provides a sea passage from west to east through the middle of the island, the settlement of that name lying at the eastern end. As far as the authors know these slides have never been described or mentioned in the literature. Research has revealed a little about the circumstances surrounding their collection. In 1897, following an unsuccessful attempt two years previously to penetrate ice in this area, Mr. H. J. Pearson with three companions (one of whom was Colonel Feilden who acted as naturalist), chartered the Norwegian steam yacht 'Laura' which sailed from Bergen on June 4th, arriving back at Trömso on August 20th. An illuminating and entertaining account of this voyage is given by Feilden (1898). The expedition sailed right through the Strait into the Kara Sea and northwards for some distance along the eastern side of northern Novaya Zemlya. Unfortunately the position of the dredgings is not given. Statements that "At mid-day Nameless bay opened up; we stopped and sounded 3 miles from shore, and got 20 fathoms" (Nameless Bay is about 20 miles south of the western entrance of the Strait) and that on the way back "Before quitting the strait, the ship was stopped for a few hours, and Mr. Pearson ascended a mountain" suggest that the soundings may have been taken on the western side, and this is indicated on figure 2. There is no reason, however, why the soundings might not equally well be from the Strait itself or from the eastern side and this should be kept in mind. The date 'June 24th' which appears on one slide is quite unhelpful and is unconnected with the collection of the sample. As might be expected, both soundings show a closer relationship to the Russian Harbour fauna than to any other fauna.

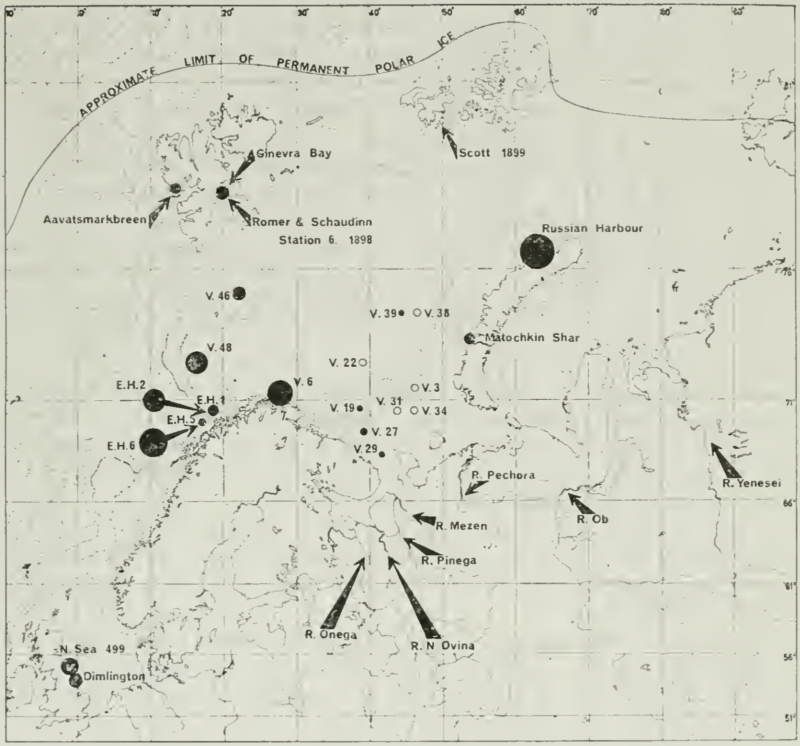
A. The ten fathom sounding yielded altogether 17 specimens belonging to seven species:

3 *Acanthocythereis dunelmensis* (Norman)	1 male carapace, 1 juvenile left and right valve
1 *Rabilimis septentrionalis* (Brady)	1 juvenile carapace
3 *Eucytheridea macrolaminata* (Elofson)	2 carapaces & 1 juvenile left valve
2 *Eucytheridea bradii* (Norman)	2 carapaces
2 *Eucytheridea punctillata* (Brady)	1 female and 1 male carapace
5 *Palmenella limicola* (Norman)	3 carapaces, 1 right and 1 left valve
1 *Cluthia cluthae* (Brady, Crosskey, and Robertson)	1 carapace

The *P. limicola* correspond with the subspecies *denticulata* described by Akatova (1946) from the Novosiberian Shelf with the small spine terminating the principal ventral rib postero-ventrally. All these species except for *Cluthia cluthae* represented by one small carapace (l. = 0.338 mm) occur in the Russian Harbour fauna.

B. The 15 fathom sounding consisted of seven specimens belonging to four species:

1 *Eucytheridea macrolaminata* (Elofson)	1 carapace
2 *Eucytheridea punctillata* (Brady)	1 carapace, 1 juvenile carapace
2 *Robertsonites tuberculata* (Sars)	1 juvenile left and 1 juvenile right valve
2 *Argilloecia conoidea* Sars	2 left valves



Text-figure 4. Location of sample stations and some places mentioned in the text.

All these species occur at Russian Harbour. The juvenile carapace (l = 0.305 mm) almost certainly belongs to *E. punctillata* but at this size a certain amount of doubt must attach to the identification.

The Nordenskjold Expedition also collected material at Matochkin Shar and Elofson (1941) recorded two marine podocopids *Heterocyprideis sorbyana* (Jones) and *Eucytheridea bradii* (Norman) [as *Cytheridea papillosa* Bosquet] both of which occur at Russian Harbour.

2. The Novosiberian Shelf

Akatova (1946) described a limited fauna of ostracodes from a number of stations on the Novosiberian Shelf. It is difficult to assess the relationship of the fauna to that of Russian Harbour. *Paracyprideis fennica* Hirschmann and *Eucythere undulata* Klie which are found in the northern parts of the Laptev Sea do not occur at Russian Harbour nor does *Krithe glacialis* (Brady, Crosskey, and Robertson). *Rabilimis mirabilis* does not occur at Russian Harbour but at least some of this material is in fact *R. septentrionalis* (Text-fig. 2 and Akatova 1957 p. 432 where it is recorded from a depth of 19 m — presumably indicating Station 81 at 75°37′N, 131°36′E). *Palmenella limicola* occurs in both areas as does *Bythocythere constricta* Sars which she records as *B. montrosiensis*. In *B. constricta* (Pl. 4, fig. 4), the surface ornamentation is very well developed in these northern communities. The form which she figured as *Hemicythere angulata* G. O. Sars, is in fact *Finmarchinella barentzovoensis* (Mandelstam) the type area for which is Russian Harbour, and *Eucytheridea bradii* also occurs in both areas. Unfortunately Akatova did not deal with the *Cytheropteron* species which she found, because of "the intricate characteristics of this genus" and so no comparison of these is possible. There are obvious similarities between the two areas, the characteristically cold water *R. septentrionalis* (Text-fig. 2) being a case in point. Until more detailed work is done on the Novosiberian Shelf it is not possible to say whether there is in fact an "ice cellar" effect (Feilden, 1898) in the Laptev and Kara Seas which is discernible in the faunas, unless the presence of *K. glacialis* in the area and not on the western side of Novaya Zemlya can be taken as significant in reflecting the warming influence of the Gulf Stream.

In the Kara Sea there are also isolated records of *Eucytheridea punctillata* at 73°38′N, 63°45′E in 77 fathoms and *Heterocyprideis sorbyana* at 71°6′N ca. 63°E in 16 fathoms collected by the Vega Expedition (Elofson 1941).

3. Franz Joseph Land

One of the nearest areas to Russian Harbour where comparative sublittoral faunas might be expected is Franz Joseph Land. Scott (1899) described the fauna brought back by the Jackson-Harmsworth Expedition of 1896-7 and through the kindness of Dr. A. Rodger Waterston it has been possible to borrow the material from the Royal Scottish Museum, Edinburgh for re-examination. The 13 slides of marine Ostracoda confirm most of Scott's findings but some of his records need modification.

They confirm the presence of *Pontocypris (?) hyperborea* Scott, *Sclerochilus contortus* (Norman), *Pseudocythere caudata* Sars, *Xestoleberis depressa* Sars, *Eucythere declivis* (Norman), *Semicytherura undata* (Sars), *Hemicytherura clathrata* (Sars), *Cytheropteron angulatum* Brady, *Heterocyprideis sorbyana* (Jones), *Palmenella limicola* (Norman), *Cluthia cluthae* (Brady, Crosskey, and Robertson), *Acanthocythereis dunelmensis* (Norman), *Baffinicythere emarginata* (Sars), *B. howei* Hazel, *Rabilimis septentrionalis* (Brady), *Robertsonites tuberculata* (Sars), and *Polycope orbicularis* Sars.

The excellently preserved paradoxostomatids prove to be Elofson's species *Paradoxostoma arcticum,* not *P. variabile* (Baird) as thought by Scott. The two specimens from 30 fathoms off East Glacier are not *Roundstonia globulifera* (Brady) but the young of *Robertsonites tuberculata* (Sars), and the former can be removed from the species list. The same is true of *Rabilimis mirabilis* (Brady). The authors were fortunate in having Brady's material of *R. septentrionalis* (Brady) from the Hunde Islands, Greenland, in front of them when examining this fauna and the three specimens Scott regarded as *R. mirabilis* are in fact pre-adult forms of *R. septentrionalis.* Much of Scott's *R. septentrionalis* material is excellent but under this heading he has included a large number of specimens of another form. The Franz Joseph Land Fauna only became available at a late stage in this work and this form, which is represented by well-preserved closed carapaces, is still awaiting detailed examination. On general shape and ornamentation it has been placed in *Cytheretta* and this will form the subject of a separate study at a later date. The cytheropterons required some revision. The four specimens from 15 fathoms off Cape Flora labelled *C. pyramidale* Brady are *C. paralatissimum* Swain although the true *C. pyramidale* does occur as a single specimen from 30 fathoms off Cape Gertrude. The three specimens from 2 to 4 fathoms off Cape Flora placed as *C. latissimum* (Norman) consist of one specimen of *C. nodosoalatum* Neale and Howe, and two of *C. punctatum* Brady. The two specimens labelled *C. pyramidale* and *C. pyramidale* ? in slide No. 2 from the same locality also appear to belong in *C. punctatum.* The largest group of Cytheropterinae agrees better with *C. inflatum sensu* Sars than with *C. subcircinatum* Sars. The material agrees very well with Sars figure but differs from actual material we have in front of us from Dryleys, Montrose which Brady, Crosskey, and Robertson placed in this species. Brady, Crosskey and Robertson (1874) are regarded as the arbiters of this species, because although figured by Brady six years earlier in the Annals and Magazine of Natural History the species was first described by the authors of the former work. There has been insufficient time to make a detailed analysis of the material placed in *Semicytherura* by Scott but it seems that at least three species are included in material assigned to *S. fulva* (Brady and Robertson). Part of the material agrees with the single specimen from Novaya Zemlya tentatively assigned to *Tetracytherura* sp. and is so shown here. Part of the material belongs to *S. similis* (Sars) which can be added to the species list and the other species has for the present been left as *Semicytherura* sp. The *Paracytherois* is for the time being placed as *P.* cf. *flexuosa* (Brady).

The '*Cythere marginata* Norman' of Scott's paper, taken in 15 fathoms off Cape Flora appears to be recorded on the two slides from this locality as '*Cythere laticarina*'. In neither case do the specimens belong to these species. The four specimens in Slide No. 1 belong to *Finmarchinella finmarchica* (Sars) which may now be added to the species list, and the one specimen in Slide No. 2 belongs to *Baffinicythere emarginata* (Sars). Thus out of the 30 species of marine Podocopida from Franz Joseph Land, 19 or 63.3% are also found in the Russian Harbour fauna, which emphasizes the great similarity between the two faunas.

Scott's slides cover the Cape Gertrude and East Glacier localities and three stations between 2 and 5 fathoms off Cape Flora, with an additional five slides of duplicate material labelled 'Vicinity of Cape Flora'. The latter, together with the three Cape Flora stations have been combined to give the composite data plotted on Text-figure 9. Details of the individual faunas are given in Table 2.

The only addition to Scott's list given by Müller (1931) is *Cytheridea dentata* Sars, now regarded as a synonym of *Heterocyprideis sorbyana* (Jones).

4. Spitzbergen

Details of ostracode faunas from Spitzbergen are very limited. A paper by Klie (1942) dealing with the material collected by Römer and Schaudinn in 1898 gives some of the best information on Spitzbergen and his updated taxonomy is given below.

In his Fauna Arctica (1931) Müller augments the Spitzbergen fauna considerably adding *Bythocythere constricta* Sars, *Bythocythere turgida* Sars, *Paradoxostoma variable* Baird, (probably = *P. arcticum* Elofson), *Xestoleberis depressa* Sars, *Semicytherura rudis* (Brady), *Cytheropteron hamatum* Sars, *Cytheropteron latissimum* (Norman) (probably = either *C. paralatissimum* Swain or *C. dimlingtonensis* Neale and Howe), *Eucytheridea bradii* (Norman), *E. punctillata* (Brady), *Acanthocythereis dunelmensis* (Norman), *Elofsonella concinna* (Jones), *Muellerina abyssicola* (Sars), *Pterygocythereis jonesii* (Baird), *Robertsonites tuberculata* (Sars), and *Cluthia cluthae* (Brady, Cross-

Station 6.	Stor Fjord at the entrance to Ginevra Bay, 105-110 m, blue, sticky with some small stones set in loam.
Station 15.	S. entry to Hinlop Strait at Behm Island, 80 m a little mud with stones up to fist size.
Station 20.	Advent-Bucht in Eis Fjord, 40 m, blue mud with small stones.
Station 24.	Ca. 12 sea miles W. of South Cape, 135 m, fine blue mud mixed with sand in many sizes part-rolled, part sharp-edged stones.
Station 25.	S.E. coast of Edge Land, 20 nautical miles N.E. of Halbmond Island, grey-blue mud with mollusc shells and worm casts and many, head sized, part-rolled, part-slaty stones.
Station 31.	In front of a large glacier on N.E. Cape of Konig Karl's Land called Jena Island, 36 m, Coarse-grained blue mud with a few small stones.
Station 41.	Ice sea N. of Spitzbergen 81°20'N, 20°30'E at land ice edge, 1000 m blue mud with a few small to nut-sized stones.

Table
Land

1
2
3
4
5

6
7
8
9
10

11
12
13
14
15

16
17
18
19
20

21
22
23
24
25

26
27
28
29
30

31

Table 2 Details of the Franz Joseph Land Ostracod Faunas

Cape Flora 79° 57'N 50° 01'E

		Off Cape Flora One Mile 15 fathoms	West Bay Cape Flora 2-10 fms.	Off West Point Cape Flora 2-4 fms.	Cape Flora Vicinity of, Duplicate Ostracoda	Composite Cape Flora 2-15 fms No	Composite Cape Flora 2-15 fms %	Off Cape Gertrude 30 fathoms	Off East Glacier Cape Flora No	Off East Glacier Cape Flora %
1	*Heterocyprideis sorbyana* (Jones)	7			18	25	7·79			
2	*Robertsonites tuberculata* (Sars)	5			9	14	4 36	1	5	7·14
3	*Eucytheridea bradii* (Norman)	5	4		20	29	9·03	1	4	5·71
4	*Eucytheridea punctillata* (Brady)	5			10	15	4·67	1		
5	*Finmarchinella finmarchica* (Sars)	4				4	1·25			
6	*Cytheropteron paralatissimum* (Swain)	4				4	1·25			
7	*Baffinicythere emarginata* (Sars)	3	1	6	28	38	11·84	1	6	8 57
8	*Cytheretta* sp	3	4		16	23	7 17			
9	*Acanthocythereis dunelmensis* (Norman)	2				2	0·62			
10	*Rabilimis septentrionalis* (Brady)	2			2	4	1·25		7	10·00
11	*Polycope orbicularis* Sars	2			7	9	2·80	1		
12	*Sclerochilus contortus* (Norman)	1	2		12	15	4 67	3		
13	*Xestoleberis depressa* Sars	1	1	1	4	7	2·18		3	4 29
14	*Pararadoxostom arcticum* Elofson		1	7	21	29	9·03			
15	*Semicytherura* sp		1	2	5	8	2·49		5	7·14
16	*Pontocypris* (?) *hyperborea* Scott		1			1	0·31			
17	*Cytheropteron punctata* Brady			3		3	0·93		4	5·71
18	*Cytheropteron nodosoalatum* Neale & Howe			1		1	0·31			
19	*Cytheropteron inflatum sensu* Sars			1	39	40	12·46	1		
20	*Semicytherura undata* (Sars)			1		1	0·31		4	5·71
21	*Paracytherois* cf *P flexuosa* (Brady)				8	8	2·49			
22	*Tetracytherura* sp ?				6	6	1·86		7	10·00
23	*Pseudocythere caudata* Sars				4	4	1·25			
24	*Hemicytherura clathrata* (Sars)				4	4	1·25		5	7 14
25	*Semicytherura similis* (Sars)				4	4	1·25			
26	*Cytheropteron angulatum* Brady & Robertson				3	3	0·93		3	4 29
27	*Cytheropteron pyramidale* Brady							1		
28	*Palmenella limicola* (Norman)								4	5 71
29	*Eucythere declivis* (Norman)								3	4 29
30	*Cluthia cluthae* (Brady, Crosskey, Robertson)								1	1 43
31	*Baffinicythere howei* Hazel				20	20	6·23		9	12·85
		44	15	22	240	321		10	70	
		13 sp	8 sp.	8 sp.	19 sp.	27 sp.		8 sp.	15 sp	

key, and Robertson). His records of *Cytheridea dentata* Sars and *C. inermis* Sars are now regarded as synonyms of *Heterocyprideis sorbyana* (Jones). He also adds as species dubiae *Cytheropteron montrosiense* (Brady, Crosskey, and Robertson), *Rabilimis mirabilis* (Brady), *Roundstonia globulifera* (Brady), and *Semicytherura concentrica* (Norman).

Leaving aside the planktonic species it will be seen that there is a good correspondence between the faunas found by Klie and those from Russian Harbour, there being positive correspondence in the case of eight species (66%) of the fauna. There are, nevertheless, elements characteristic of the more westerly areas such as *Krithe producta* and *Thaerocythere crenulata.* This point is taken up at a later stage. Similarly eight (42%) of the additional forms noted by Müller are common to the two areas and if one accepts that his *P. variabile* and *C. latissimum* need reinterpretation this probably adds two more.

An interesting fauna actually examined by the authors which has affinities with the Novaya Zemlya fauna in the abundance of *Robertsonites tuberculata* came from a sample kindly obtained by the University of East Anglia Expedition to Spitzbergen and collected from the terminal ice cliff of Aavatsmarkbreen, Oscar II Land, Vestspitzbergen. This sample came from within the glacier with about 200 feet of ice above and below but the sediment was lithologically identical with material dredged from the fjord floor. The fauna consisted of 22 specimens of *Robertsonites tuberculata* and one adult valve of *Cytheropteron dimlingtonensis.* The fauna is too small to do more than draw attention to the commonest species and is certainly sub-Recent or even earlier from its location, as is also suggested by the presence of *C. dimlingtonensis.*

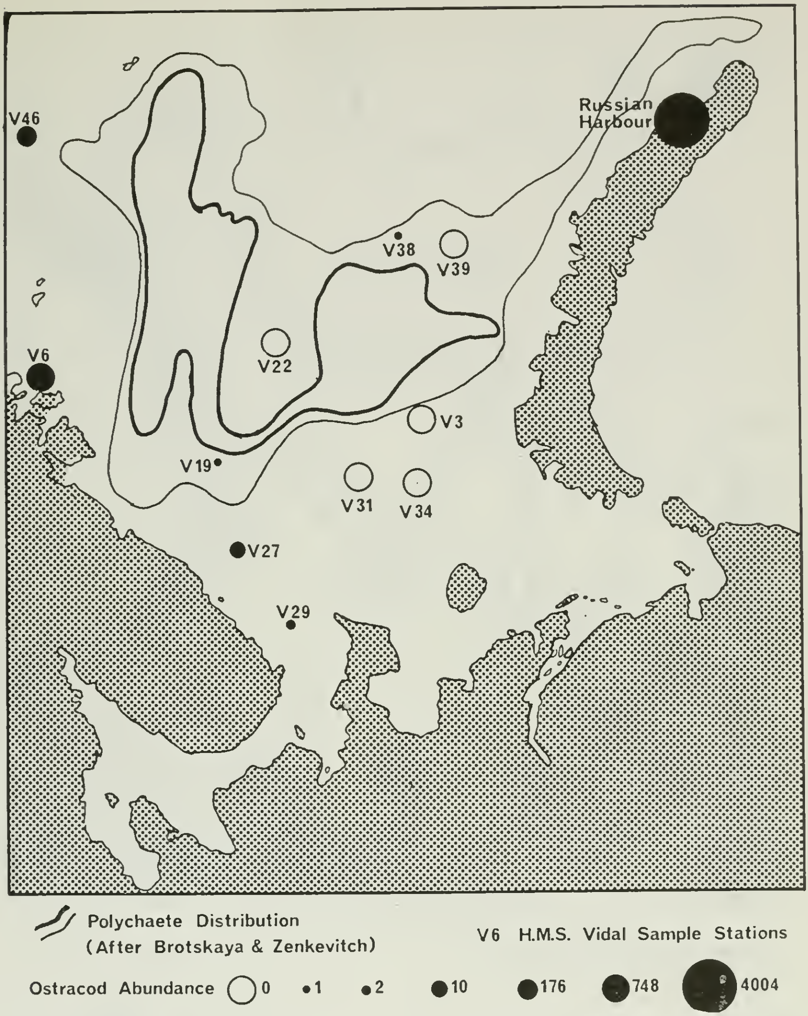
5. The Barents Sea

Thanks to the kindness of Dr. D. R. C. Kempe and Dr. J. D. H. Wiseman of the British Museum (Nat. Hist.) it was possible to work on a series of samples collected from the Barents Sea by H. M. S. *Vidal* in 1955, and on samples collected from the margins of this sea and the Norwegian Sea by this ship at the same time and the *Ernest Holt* in 1962 (Text-fig. 4). In the eastern and central part of the Barents Sea nine samples were examined (Text-figs. 5, 6). Five of the samples were barren and the other four together yielded only fourteen ostracodes. Compared with the rich faunas at the margins of the Barents Sea these impoverished faunas are difficult to explain. There is no reason to suppose that the explanation lies in the sampling and the area is one of generally high biomass ranging from about 50 g/m^2 to 300 g/m^2 in the vicinity of the sampling stations. It is possible that predation is the answer. Polychaetes *(Nereis)* have been shown to have an adverse effect on the abundance of ostracodes (Rees, 1940) and represent one possibility. On the other hand the distribution of polychaetes given by Brotskaya and Zenkovitch (1939) shows little correlation although the samples with abundant ostracodes lie outside the principal area of polychaete distribution. (Text-fig. 5). The

Table 3. Spitzbergen faunas determined by Klie (1942)

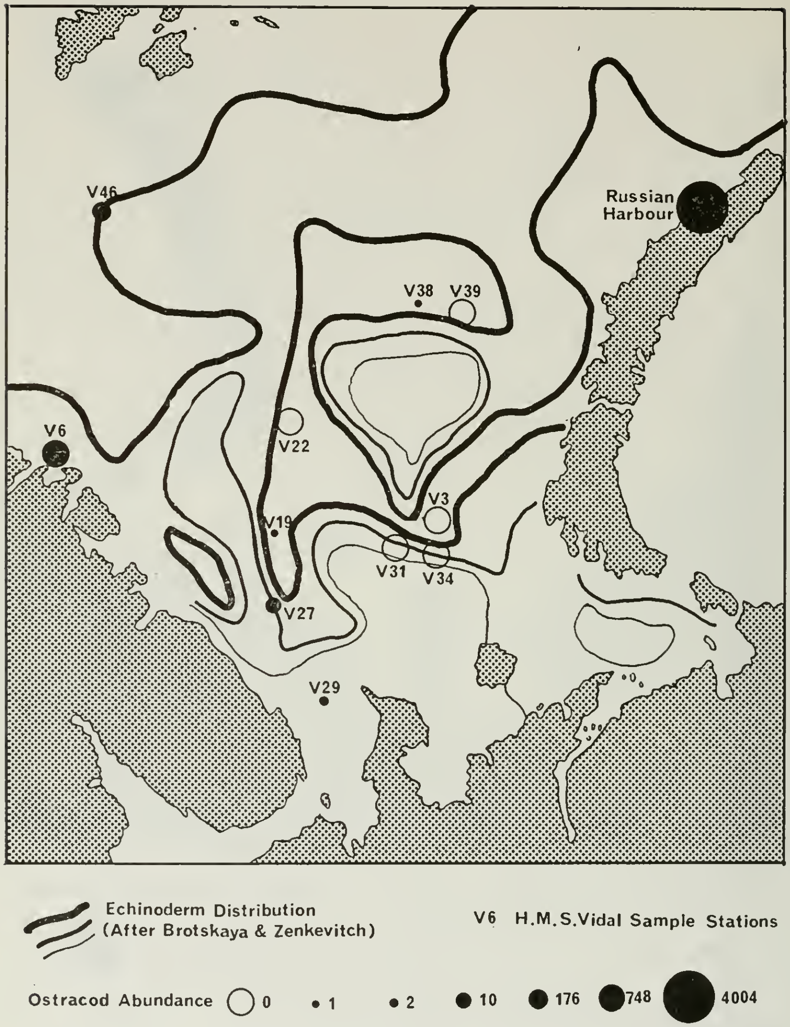
		Station 6	Station 6 % Adults	Station 15	Station 20	Station 24	Station 31	Station 41
1	*Baffinicythere emarginata* (Sars)	8♀6♂11j	19·45					
2	*Baffinicythere howei* Hazel			?1	5			15♀c 10♂c
3	*Thaerocythere crenulata* (Sars)	3♀2♂	6·95					20♀v 14♂v
4	*Heterocyprideis sorbyana* (Jones)	1L	1·39		3L4R	1L		4cj 21vj
5	*Cytheropteron angulatum* Brady & Robertson	1♀1♂	2·78					
6	*Cytheropteron nodosum* Brady	1♀ many j	1·39					
7	*Cytheropteron pyramidale* Brady	5♀2♂	9·72					
8	*Semicytherura affinis* (Sars)	1♀	1·39					
9	*Hemicytherura clathrata* (Sars)	6♀	8·34	?1				
10	*Semicytherura undata* (Sars)	15♀4♂	26·39					
11	*Krithe producta* Brady			?1				
12	*Sclerochilus contortus* (Norman)	12♀6♂	22·22	1♂			1♀	
13	*Philomedes globosus* (Lilljeborg)			7♀2j	3♀			

In addition Klie notes a *Pseudocythere*, two *Paracytherois* and two *Paradoxostoma*



Text-figure 5. Ostracode abundance in Barents Sea samples compared with Polychaete distribution.

distribution of echinoderms (Text-fig. 6) accords better with the observed sample distribution although echinoderms have not so far been shown to feed on ostracodes; in fact commensalism has been demonstrated in the case of at least one ostracode species and a starfish (Maddocks, 1968). Nevertheless, in lieu of a better explanation predation by some organism seems the most probable cause of paucity. The six species represented in these stations are all known from Russian Harbour and are *Eucytheridea punctillata* (Brady),



Text-figure 6. Ostracode abundance in Barents Sea samples compared with echinoderm distribution.

E. macrolaminata (Elofson), *E. bradii* (Norman), *Robertsonites tuberculata* (Sars), *Finmarchinella finmarchica* (Sars), and *Baffinicythere emarginata* (Sars).

Table 4 Marine Ostracoda
— Barent

1. *Thaerocythere crenulat*
2 *Muellerina abyssicola* (
3 *Bairdia inflata* (Norman
4 *Pseudocythere caudata*
5. *Pterygocythereis mucr*

6. *Finmarchinella finmarc*
7. *Cytheropteron* cf. *C. rho*
8 *Xestoleberis depressa* S
9 *Kangarina septentriona*
10. *Argilloecia conoidea* Sar

11 *Bythocypris obtusata* (
12. *Eucytheridea macrolam*
13 *Cytheropteron latissim*
14 *Hemicytherura clathrat*
15. *Cytheropteron* sp

16. *Pontocypris hispida* Sa
17 *Baffinicythere howei* H
18 *Eucythere* sp.
19 *Cytherella abyssorum* S
20 *Semicytherura affinis* (

21 *Paracytheridea norvegi*
22. *Eucytheridea punctillat*
23 *Semicytherura lineata* (
24 *Cytheropteron nodosoal*
25. *Pontocypris trigonella*

26 *Sclerochilus contortus* (
27 *Krithe producta* Brady
28. *Semicytherura undata*
29 *Cytheropteron alatum*
30. *Cytheropteron hamatun*

31. *Cytheropteron dromed*
32. *Elofsonella concinna* (
33 *Bythocythere constrict*
34 *Semicytherura acutico*
35. *Paracytherois product*

36. *Heterocyprideis sorbyc*
37. *Bythocypris bosquetia*
38. *Baffinicythere emargi*
39 *Hemicytherura cellulos*
40. *Semicytherura nigresc*

41. *Finmarchinella barentz*
42. *Loxoconcha* sp
43 *Bensonocythere ?*
44 *Finmarchinella angulat*
45. *Cytheropteron pyramid*

46 *Cytheropteron nodosum*
47 *Eucytheridea bradii* (N
48. *Krithe* cf *K. glacialis* (B
49 *Semicytherura* cf *S str*
50 *Semicytherura similis* (

51. *Hirschmannia viridis* (M
52 *Hirschmannia tamarind*
53 *Rabilimis mirabilis* (Bra
54 *Normanicythere leioder*
55 *Paracypris* sp

56. *Cytheropteron testudo*
57. *Cytheropteron arcticum*
58. *Cytheropteron angulatu*
59. *Heterocyprideis fascis*
60. *Undetermined*

Total Number of specin

Number of species

Table 4 Marine Ostracoda from the Norwegian Sea – Barents Sea Area

		Ernest Holt Station 1		Ernest Holt Station 2		Ernest Holt Station 5		Ernest Holt Station 6				H M S Vidal Station 6				H M S Vidal Station 48	
		70° 32' N 18° 23' E Depth 105f		70° 29' N 17° 27' E Depth 105f		69° 58' N 17° 00' E Depth 65f		69° 54' N, 17° 00' E Depth 143 fathoms				71° 15 0' N, 27° 54 0' E Depth 142 fathoms				72° 20 7' N 16° 38' E Depth 204f	
		Total		Total		Total		Total		Adults		Total		Adults		Total	
		No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%
1	Thaerocythere crenulata (Sars)	5	14 71	201	39 80	1	11 11	60	3 74	7	1 24	261	34 89	41	18 14	3	0. 66
2	Muellerina abyssicola (Sars)	13	38 23	145	28 72	5	55 55	932	57 99	325	57 42	161	21 52	57	25 23	6	1 32
3	Bairdia inflata (Norman)	5	14 71	25	4 95	1	11 11										
4	Pseudocythere caudata Sars	1	2 94	20	3 96			1	0 06	1	0 18						
5	Pterygocythereis mucronata (Sars)	1	2 94	13	2 57	1	11 11	228	14 19	95	16 78	2	0 27			3	0 66
6	Finmarchinella finmarchica (Sars)			11	2 18			26	1 62	4	0 71						
7	Cytheropteron cf C rhomboidea (Brady)			10	1 98							73	9 76	35	15 49	97	21 32
8	Xestoleberis depressa Sars			9	1 78			59	3 67	20	3 53						
9	Kangarina septentrionalis Neale			7	1 39			8	0 50	5	0 88						
10	Argilloecia conoidea Sars			5	0 99			6	0 37	4	0 71	8	1 07	5	2 21	6	1 32
11	Bythocypris obtusata (Sars)			5	0 99												
12	Eucytheridea macrolaminata (Elofson)			4	0 79												
13	Cytheropteron latissimum (Norman)			4	0 79			16	1 00	2	0 35						
14	Hemicytherura clathrata (Sars)			4	0 79			14	0 87	10	1 77	3	0 40	1	0. 44		
15	Cytheropteron sp			4	0 79			3	0 19								
16	Pontocypris hispida Sars			3	0 59												
17	Baffinicythere howei Hazel			3	0 59												
18	Eucythere sp			3	0 59			2	0 12	2	0 35	2	0 27	1	0 44		
19	Cytherella abyssorum Sars			2	0 40			77	4 79	20	3 53	12	1 60	6	2 66		
20	Semicytherura affinis (Sars)	1	2 94	2	0 40			5	0 31	1	0. 18	4	0 53	3	1 33		
21	Paracytheridea norvegica Neale			2	0 40			1	0 06	1	0 18	5	0 67	4	1 77		
22	Eucytheridea punctillata (Brady)	2	5 88	2	0 40			4	0 25								
23	Semicytherura lineata (Brady)			2	0 40												
24	Cytheropteron nodosoalatum Neale & Howe			2	0 40												
25	Pontocypris trigonella Sars			2	0 40												
26	Sclerochilus contortus (Norman)	1	2 94	2	0 40			6	0 37	4	0 71						
27	Krithe producta Brady			1	0 20			42	2 61	19	3 36	24	3 21	15	6 64	155	34 06
28	Semicytherura undata (Sars)			1	0 20			16	1 00	15	2 65	1	0 11				
29	Cytheropteron alatum Sars			1	0 20												
30	Cytheropteron hamatum Sars			1	0 20			35	2 18	16	2 83	20	2 67	13	5 75	41	9 01
31	Cytheropteron dromedaria (Sars)			1	0 20			3	0 19			136	18 18	28	12 39	137	30 11
32	Elofsonella concinna (Jones)			1	0 20			2	0 12								
33	Bythocythere constricta Sars			1	0 20												
34	Semicytherura acuticostata (Sars)			1	0 20			3	0 19	3	0 53					1	0 22
35	Paracytherois producta (Brady & Norman)			1	0 20			1	0 06	1	0 17						
36	Heterocyprideis sorbyana (Jones)	1	2 94	1	0 20			1	0 06	1	0 17						
37	Bythocypris bosquetiana (Brady)					1	11 11										
38	Baffinicythere emarginata (Sars)							12	0 75			3	0 40			1	0 22
39	Hemicytherura cellulosa (Norman)							4	0 25	4	0 71						
40	Semicytherura nigrescens (Baird)							4	0 25	1	0 18						
41	Finmarchinella barentzovoensis (Mandelstam)	2	5 88					1	0 06	1	0 18						
42	Loxoconcha sp	1	2 94														
43	Bensonocythere ?	1	2 94														
44	Finmarchinella angulata (Sars)							3	0 19								
45	Cytheropteron pyramidale Brady							1	0 06								
46	Cytheropteron nodosum Brady							3	0 19								
47	Eucytheridea bradii (Norman)							2	0 12								
48	Krithe cf K glacialis (Brady Crosskey & Robertson)							3	0 19								
49	Semicytherura cf S striata (Sars)							1	0 06	1	0 18						
50	Semicytherura similis (Sars)							1	0 06	1	0 18						
51	Hirschmannia viridis (Muller)							5	0 31								
52	Hirschmannia tamarindus (Jones)							2	0 12								
53	Rabilimis mirabilis (Brady)							1	0 06								
54	Normanicythere leioderma (Norman)							1	0 06								
55	Paracypris sp							2	0 12	1	0 18						
56	Cytheropteron testudo Sars							3	0 19	1	0 18						
57	Cytheropteron arcticum Neale & Howe											3	0 40	3	1 33		
58	Cytheropteron angulatum Brady & Robertson											24	3 21	11	4 87		
59	Heterocyprideis fascis (Brady)											3	0 40				
60	Undetermined	0		3	0 59	0		7	0 44			3	0 40			5	1 10
	Total Number of specimens	34		505		9		1607		566		748		228		455	
	Number of species	12		38		5		43		28		18		15		12	

Neale and Howe – Table 4

6. The margins of the Barents Sea

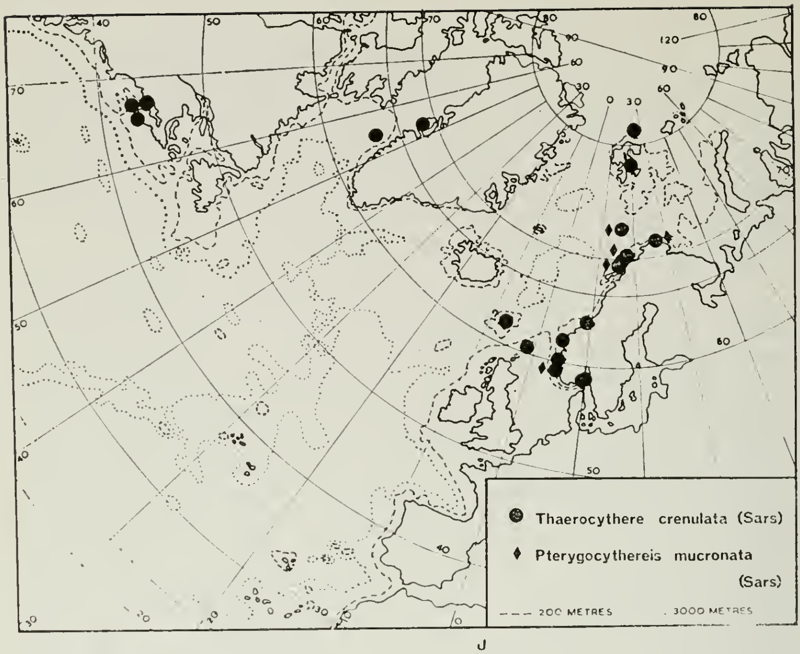
Seven samples were examined from the margins of the Barents Sea. Details of six of these are given in Table 4, the seventh (H. M. S. *Vidal* 46) from the Spitzbergen Shelf is given in Table 6 with the Greenland material. The Spitzbergen sample from 35 fathoms agrees closely with the Russian Harbour fauna although lacking *Robertsonites tuberculata,* the five most abundant species being in order *Finmarchinella finmarchica* (Sars), *Baffinicythere howei* Hazel, *Hemicytherura clathrata* (Sars), *Cytheropteron pyramidale* Brady, and *Sclerochilus contortus* (Norman).

The four *Ernest Holt* samples on the western margin and H. M. S. *Vidal* Station 6 on the southern margin come from somewhat deeper water (65-143 fathoms) and show a marked change in fauna. This is partly, but not entirely, due to changing depth, being also connected with the increased influence of the North Atlantic Drift. In consequence, *Thaerocythere crenulata* (Sars), *Muellerina abyssicola* (Sars), and *Pterygocythereis mucronata* (Sars) are the most important species in the fauna with *Cytheropteron dromedaria* (Sars) and *C.* cf. *C. rhomboidea* Brady making an important contribution in the most westerly sample. *Thaerocythere crenulata* is much more widespread than suspected by Hazel (1970) and occurs North of Spitzbergen at the margin of the permanent ice. Its known distribution is given in Text-figure 7. Typical Arctic elements found in the Novaya Zemlya fauna are rare or absent, for example single specimens of *Cytheropteron pyramidale* Brady, *Normanicythere leioderma* (Norman), and *Finmarchinella barentzovoensis* (Mandelstam) are present in *Ernest Holt 6,* and the principal forms are characteristic of the Norwegian Province. The boreal influence appears to extend along the North Norwegian coast to take in H. M. S. *Vidal* Station 6 and the boundary between the Norwegian and Arctic Provinces appears to agree well with that of Filatova (1957) and Brotskaya and Zenkovitch (1939) based on other invertebrates. The Norwegian Province can be extended down to the Shetland — Faroes — Iceland ridge and is typified by *Thaerocythere crenulata, Muellerina abyssicola* and *Pterygocythereis mucronata,* with typical loxoconchids and leptocytherids appearing in the shallower waters.

H. M. S. *Vidal* 48 differs from the other samples in being from deeper water (204 fathoms) and in being taken from the top of a core. It shows dominant *Krithe producta* Brady (34.06%), *Cytheropteron dromedaria* (Sars), and *C.* cf. *C. rhomboidea* Brady and shows affinities with many of the more deeper water faunas described for example from the North Atlantic by Tressler (1942).

7. The White Sea

Akatova (1957) described a small but interesting fauna from the White Sea and as might be expected this is close to the Novaya Zemlya one. With the exception of *Philomedes globosus,* all the forms she records — *Heterocyprideis sorbyana, Eucytheridea bradii, Rabilimis septentrionalis,* and *Acanthocythereis dunelmensis* occur in the present fauna.

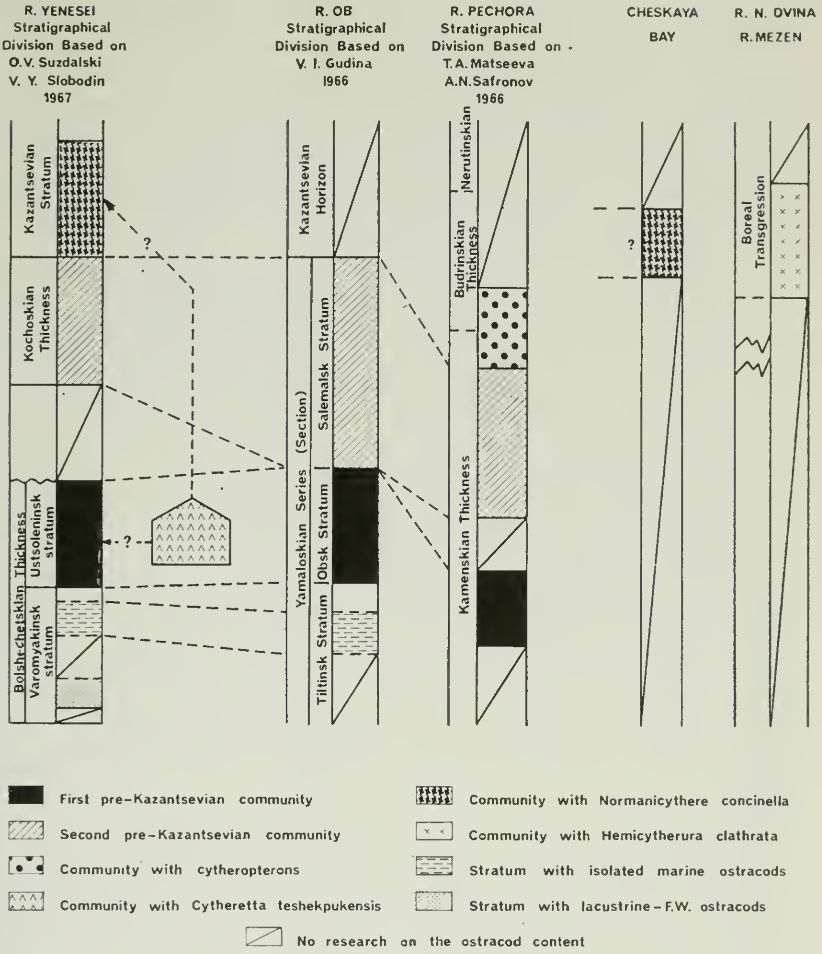


Text-figure 7. Known distribution of *Thaerocythere crenulata* (Sars) and *Pterygocythereis mucronata* (Sars).

8. The Russian mainland

On the Russian mainland a number of authors have dealt with the ostracodes from deposits in northern Russia. Zagorskaya, *et al,* (1969) deal with the stratigraphy and palaeogeography of the Pechora lowlands and cover various faunal elements including the ostracodes. The fauna from the Keinmusyursk (Kazantsevian) horizon corresponding to their latest transgression (Deposit III) contains *Normanicythere leioderma, Finmarchinella finmarchica,* and *Cythere lutea* all of which occur in the Russian Harbour fauna. As might be expected this fauna is closer to the Novaya Zemlya fauna than the earlier ones.

Lev (1969) covers a wider field and deals with the late Cainozoic ostracode faunas from the Yenesei lowlands to the Kola Peninsula. Following Milyakov (1969) we may look on these as Quaternary rather than Neogene. Lev recognises six communities with ostracodes (Text-fig. 8). The earliest communities, his first and second pre-Kazantsevian communities which are fairly widely developed and found in the basins of the Yenesei, Ob, and Pechora, show a marked affinity with the Hoxnian Dimlington fauna (Text-figures 8, 9) with their *Rabilimis mirabilis, Cytheropteron montrosiense, Elofsonella concinna,* and *Krithe glacialis* none of which occur at Russian Har-



After Lev 1969

Text-figure 8. Development of late Tertiary/Quaternary ostracode faunas in northern Russia. (After Lev, 1969).

bour, Novaya Zemlya. The Dimlington fauna is somewhat intermediate between pre-Kazantsevian I and pre-Kazantsevian II for it contains *Heterocyprideis sorbyana* found in the former, and *Eucytheridea punctillata* and *Cluthia cluthae* which are found in the latter. *H. sorbyana* and *E. punctillata* are also found at Russian Harbour. Common to all four faunas are *N. leioderma*, *Acanthocythereis dunelmensis*, and *Eucytheridea bradii*. The most obvious difference between the English Hoxnian fauna and the Russian pre-Kazantsevian fauna lies in the presence of *Robertsonites tuberculata* in the former and its absence in the latter. This was one of the reasons for selecting the Hoxnian fauna for comparison. The presence of this species appears to indicate an inshore environment which can be deduced in the case of the Pleistocene fauna by the associated buried cliff line and is self evident in the case of the Russian Harbour community.

The third fauna of Lev, the *Cytheropteron* community and similarly the fourth *Cytheretta teshekpukensis* community are both somewhat restricted as regards development of species and have less in common with the English Hoxnian or the Russian Harbour Recent fauna.

The fifth and sixth communities show the closest relationship to the Novaya Zemlya fauna. Both agree in the absence of *Elofsonella concinna, Cytheropteron montrosiene* and *Rabilimis mirabilis.* The fifth Kazantsevian or *Normanicythere concinella* community contains a well-developed hemicytherid fauna including *N. leioderma, Finmarchinella finmarchica,* and *Baffinicythere emarginata.* Also present are *Hemicytherura clathrata, Palmenella limicola,* and *Eucytheridea bradii* all of which occur at Russian Harbour. The fifth community differs however, in the presence of *Normanicythere concinella, Cytheretta teshekpukensis, Cytheropteron nodosum,* and *C. latissimum.* The fifth community is recorded from deposits of the north Russian lowlands in the area of the R. Yenesei and the Cheskaya Bay.

The sixth, *H. clathrata* fauna, represents the Boreal Transgression in the region of the River North Dvina, the R. Mezen, the R. Telz (a tributary of the R. Onega), and the R. Chapan in the Kola Peninsula. The fauna is closely related to the previous Kazantsevian fauna but is more varied and is of the same general age or slightly younger. Notable are the presence of *Semicytherura undata, Cythere lutea,* and *Finmarchinella angulata,* also important in the Novaya Zemlya fauna. *Patagonacythere dubia, Semicytherura nigrescens,* and *Cytheropteron nodosum* are also present which differentiates it from the Recent fauna.

9. The Hoxnian, Pleistocene fauna of Dimlington, East Yorkshire

The Bridlington Crag of Dimlington, whose age and geographical setting have been studied in detail by Catt and Penny (1966) yields a fine fauna of Ostracoda and, as noted above, has an important component of *Robertsonites tuberculata* (Sars). One of the authors noted this fauna in connection with his work on *Normanicythere leioderma* (Neale 1959) and a new sample was specially collected to incorporate in Text-figure 9. The results are incorporated in the updated taxonomic list given in Table 5. It will be clear that it agrees in many aspects with the Russian Harbour fauna, particularly in the presence of a fauna characteristic of waters colder than those found in the area at the present day. In particular one may mention *Krithe glacialis, Cytheropteron arcticum, Normanicythere leioderma,* and *Baffinicythere emarginata,* the latter three occurring in the Russian Harbour fauna and the first in the Laptev Sea. It differs in the presence of a number of species not found in the fauna under review, notably *Cytheropteron dimlingtonensis* Neale and Howe, *C. nodosum*

Dimlington, East Yorks.
Bridlington Crag, Hoxnian
Species recorded by
Catt & Penny 1966, p.409

1. *Elofsonella concinna*
2. *Trachyleberis dunelmensis*
3. *Aurila mirabilis*
4. *Normanicythere leioderm*
5. *Cythere tuberculata*

6. *Krithe glacialis*
7. *Cyamocytheridea punctill*
8. *Heterocyprideis sorbyana*
9. *Cytheropteron montrosien*
10. *Cytheropteron latissimum*

11. *Cytheropteron nodosum*
12.
13.
14.
15.

16.
17.
18.
19.
20.

21.
22.
23.
24.
25.

26.
27.
28.
29.
30.

31.
32.
33.
34.
35.

36.
37.
38.
39.
40.

41.

Table 5 Ostracods from Hoxnian (Pleistocene) of England compared with two recent collections

	Dimlington, East Yorks Bridlington Crag, Hoxnian Species recorded by Catt & Penny 1966, p 409	Updated taxonomy	Dimlington Hoxnian Present Work %	Bridlington Hoxnian B,C & R 1874 p 103	Russian Harbour Novaya Zemlya 76°13′N 62°40′E Recent 8 fathoms	North Sea Sample 499 55°1′55″N, 1°14′05″W Recent 27 fathoms
1	*Elofsonella concinna*	*Elofsonella concinna* (Jones)	27·09	*		
2	*Trachyleberis dunelmensis*	*Acanthocythereis dunelmensis* (Norman)	10·36	*	3·15	0·60
3	*Auria mirabilis*	*Rabilimis mirabilis* (Brady)	2·79	*		
4	*Normanicythere leioderma*	*Normanicythere leioderma* (Norman)	7·17	*	3·45	
5	*Cythere tuberculata*	*Robertsonites tuberculata* (Sars)	15·14	*	16·98	15·37
6	*Krithe glacialis*	*Krithe glacialis* Brady, Crosskey & Robertson	1·59			
7	*Cyamocytheridea punctillata*	*Eucytheridea punctillata* (Brady)	11·95	*	10·27	
8	*Heterocyprideis sorbyana*	*Heterocyprideis sorbyana* (Jones)	7·57	*	0·75	
9	*Cytheropteron montrosiense*	*'Cytheropteron' montrosiense* Brady, Crosskey & Robertson	3·59			
10	*Cytheropteron latissimum*	*Cytheropteron dimlingtonensis* Neale & Howe	2·79			
11	*Cytheropteron nodosum*	*Cytheropteron nodosum* Brady	3·19	*		0·90
12		*Baffinicythere emarginata* (Sars)	0·40	*	11·49	
13		*Finmarchinella finmarchica* (Sars)	0·80		0·97	0·30
14		*Hemicytherura clathrata* (Sars)	0·40	*	1·27	
15		*Eucytheridea bradii* (Norman)	3·19	*	0·65	19·58
16		*Cytheropteron arcticum* Neale & Howe	0·40		1·32	
17		*Cytheropteron arcuatum* Brady, Crosskey & Robertson	0·80			
18		*Cytheropteron* cf *C inflatum* Brady, Crosskey & Robertson	0·40			
19		*Cytheropteron* cf *C pipistrella* Brady	0·40			
20		*Cluthia cluthae* (Brady, Crosskey & Robertson)	0·80			
21		*Roundstonia globulifera* (Brady)	0·80	*	0·03	
22		*Hemicythere villosa* (Sars)	0·40	*		
23		*Finmarchinella angulata* (Sars)		*	1·20	
24		*Baffinicythere howei* Hazel		*	12·34	
25		*Cytheropteron angulatum* Brady & Robertson		*		
26		*Cushmanidea elongata* (Brady)		*		
27		*Paradoxostoma ensiforme* Brady		*	0·03	
28		*Paradoxostoma pyriforme* Brady, Crosskey & Robertson		*		
29		*Sclerochilus contortus* (Norman)		*	0·77	
30		*'Cythere' cribrosa* Brady, Crosskey & Robertson		*		
31		*Pterygocythereis jonesii* (Baird)				33·44
32		*Celtia quadridentata* (Baird)				6·02
33		*Palmenella limicola* (Norman)			0·95	4·52
34		*Loxoconcha guttata* (Norman)				2·41
35		*Cytheropteron latissimum* (Norman)				12·65
36		*Eucythere declivis* (Norman)				0·90
37		*Costa emaciata* (Brady)				0·30
38		*Hirschmannia elliptica* (Brady)				0·30
39		*Semicytherura* cf *S granulosa*				0·30
40		*Eucythere* sp				1·81
41		*Krithe* sp				0·60

* indicates species is present

Brady, *C. montrosiense* (Brady, Crosskey, and Robertson), *Cluthia cluthae* (Brady, Crosskey, and Robertson), and *Rabilimis mirabilis* (Brady) amongst others. It is thought that *C. dimlingtonensis* and *C. montrosiense* are probably exclusively fossil. A single male valve of *Roundstonia globulifera* (Brady) occurs in the Russian Harbour material. It is doubtful if this species is alive today (Neale, 1973b) and here it is thought that the occurrence represents derivation from an earlier fauna. At Dimlington it is considered indigenous.

10. The North Sea

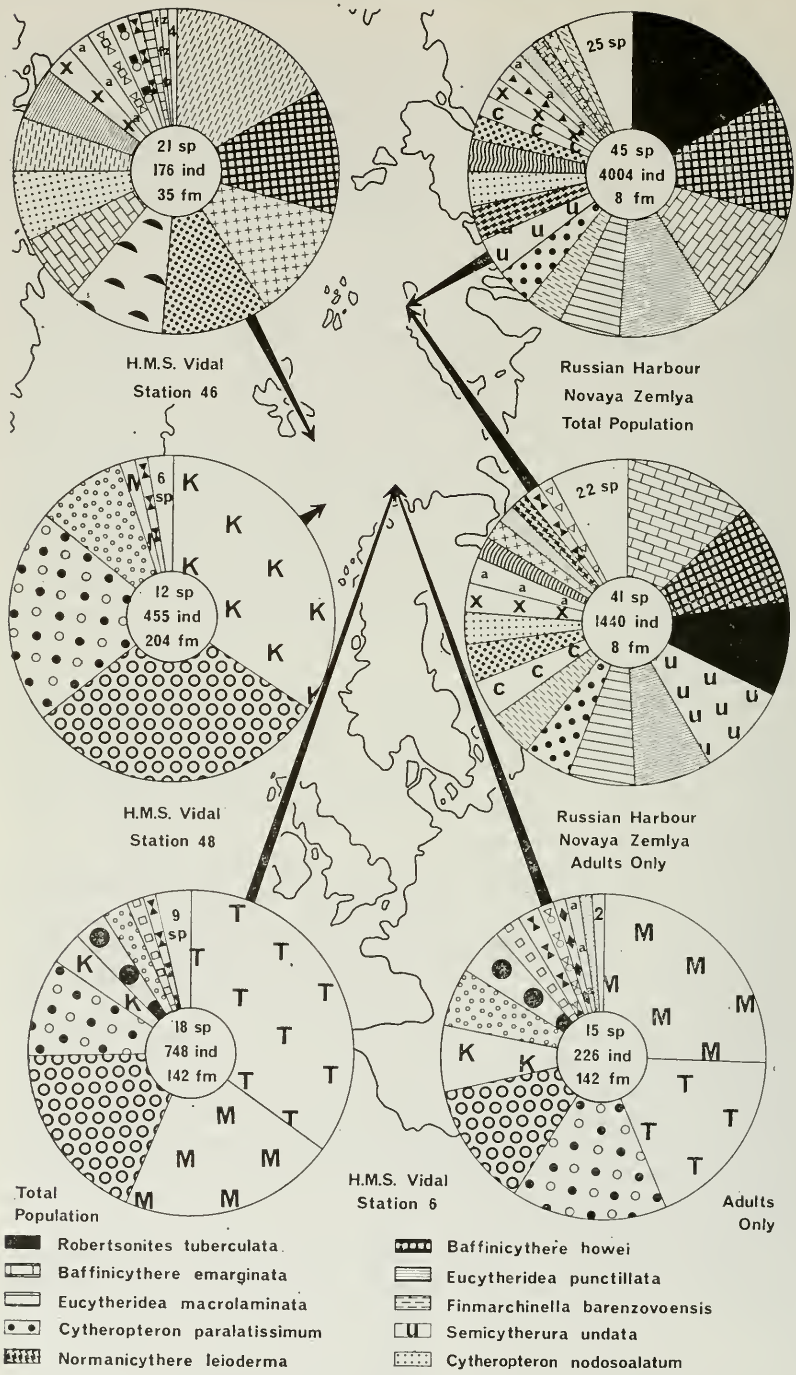
From a series of samples collected during a North Sea Survey project 1963-66 by the University of Hull, one sample considered typical and containing a substantial proportion of *Robertsonites tuberculata* was taken (Table 5, and Text-figure 9). This sample from a depth of 27 fathoms at 55°1′55″N, 1°14′05″W (approximately 7 miles E.N.E. of the entrance to the River Tyne) showed almost exactly the same proportion of this species as the Russian Harbour fauna but scarcely any other correspondence. The only other species common to the two faunas are *Eucytheridea bradii*, here 19.58% against 0.65% at Novaya Zemlya, *Palmenella limicola* 4.52% against 0.95%, *Acanthocythereis dunelmensis* 0.60% against 3.15%, and *Finmarchinella finmarchica* 0.30% against 0.97%. There is a notable lack of the typical cold water trachyleberids and hemicytherids. Any similarity is based entirely on the abundance of *Robertsonites tuberculata* a wide ranging species which appears to be confined to the inner shelf, shallow water areas where it is possibly controlled by type of food supply.

The principal species in this typical temperate or Celtic assemblage is *Pterygocythereis jonesii* (33.44%) allied with *Eucytheridea bradii* (19.58%). In more northerly areas as in the Norwegian Sea (Table IV) *Pterygocythereis mucronata* replaces *P. jonesii*, and *Thaerocythere crenulata* and *Muellerina abyssicola* are the most important species although at somewhat greater depths.

11. Greenland and the North-west

Material from various localities in this area, particularly that collected by H.M.S. *Alert* and H.M.S. *Discovery* and H.M.S. *Valorous* in the 1870's was examined in the British Museum and the Hancock Museum. The two most abundant faunas, together with data from the same area from Hazel (1967, 1970) are given in Table 6. There is a very close similarity between these faunas and those of the eastern Arctic sublittoral. In the 19 samples species which occur most commonly are *Eucytheridea bradii* (12 samples), *Finmarchinella angulata* (12), *Baffinicythere howei* (11), *Robertsonites tuberculata* (10), *Hemicytherura clathrata* (7), *Normanicythere leioderma* (6), and *Semicytherura undata* (6) all of which are found at Russian Harbour, Novaya Zemlya (Table 1) and in the eastern Arctic generally. The records of *Finmarchinella angulata* in material other than that examined by the authors must be treated with caution because this taxon generally includes *Finmarchinella barentzovoenis* and *F. curvicosta* as well.

Species which are not found round Novaya Zemlya but which occur commonly in the Western Arctic include *Elofsonella concinna* (9 samples)



Text-figure 9 i. Composition of ostracode faunas at various localities.

Table 6 Hol

1 *Cythere lute*
2 *Hemicythere*
3 *Semicytheru*
4 *Finmarchine*
5. *Finmarchine*

6 *Finmarchine*
7 *Robertsonite*
8 *Xestoleberis*
9 *Baffinicyth*
10 *Sclerochilus*

11 *Semicytheru*
12 *Eucytheride*
13 *Baffinicythe*
14 *Paradoxosto*
15 *Rabilimis se*

16 *Cytheropter*
17 *Finmarchine*
18. *Jonesia sim*
19 *Eucytheride*
20 *Palmenella*

21 *Hemicytheru*
22 *Elofsonella*
23 *Heterocypri*
24 *Argilloecia*
25 *Cytheropter*

26 *Muellerina*
27 *Normanicyth*
28 *Xestoleberis*
29 *Cluthia clut*
30 *Cytheromorp*

31 *Eucytheride*
32 *Paradoxosto*
33 *Pseudocythe*
34 *Sclerochilus*
35. *Hemicythere*

36. *Cytherura* s
37 *Eucythere* s
38 *Cytheroptero*
39 *Patagonacyt*
40 *Cytheroptero*

41 *Acanthocyth*
42. *Bythoceratin*
43 *Krithe* spp
44 *Rabilimis mi*
45 *Cytheroptero*

46 *Cytheroptero*

Total number

Number of sp

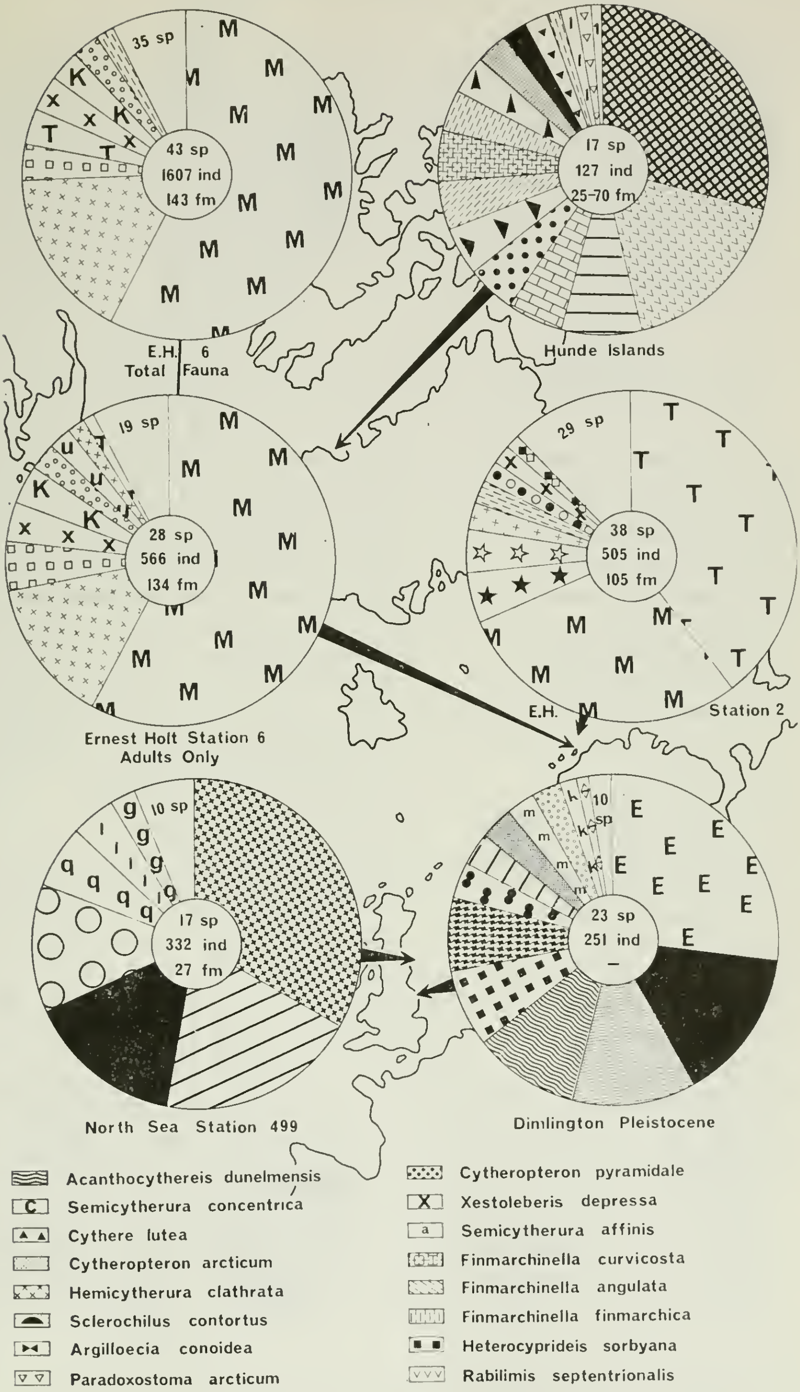
Table 6 Holocene Ostracoda from Greenland and nearby areas

	Holsteinborg Harbour		Hunde Islands		Western Greenland *					Foxe * Basin Canada	Frobisher Bay		Baffin Island *			Ungava Bay, Labrador *			Eastern Greenland *		Shannon Island	H M S Vidal Station 46	
					Humboldt Glacier	North Star Bay	N Wolstenholme Is	Parker Snow Bay	Vaigat Strait										Cape Stosch	Clavering Island			
	66° 55′ N 53° 25′ W		68° 52′ N 53° 07′ W		79° 30′ N 66° 30′ W	76° 33′ N 68° 52′ W	76° 27′ N 70° 00′ W	76° 06′ N 68° 25′ W	70° 00′ N 52° 30′ W	66° 43′ N 80° 07′ W	63° 25′ N 68° 19′ W	63° 11′ N 67° 50′ W	63° 10′ N 67° 45′ W	63° 00′ N 67° 00′ W	62° 59′ N 67° 28′ W	60° 08′ N 67° 47′ W	60° 00′ N 68° 00′ W	60° 00′ N 68° 00′ W	74° 04′ N 21° 45′ W	74° 15′ N 21° 00′ W	75° 20′ N 19° 00′ W	75° 11 2′ N 22° 14′ E	
	10 fathoms		25-70f		110f	17f	13-21f	21-45f	?	110f	55f	80f	30f	13f	17f	40f	36f	26f	7f	50-57f	110f	35f	
	No	%	No	%																		No	%
1 *Cythere lutea* O F Muller	50	21 46	3	2 36																			
2 *Hemicythere borealis* (Brody)	34	14 59	6	4 73					r						r								
3 *Semicytherura undata* (Sars)	27	11 59				r	c	r								r	r						
4 *Finmarchinella angulata* (Sars)	22	9 44	6	4 73		r	c	r	c			r	r		r	c	r				r		
5 *Finmarchinella curvicosta* Neale	19	8 16	6	4 73																			
6 *Finmarchinella finmarchica* (Sars)	18	7 73	2	1 58												r						29	16 47
7 *Robertsonites tuberculata* (Sars)	17	7 30	3	2 36		c	c	r	c				c	r	c		r				r		
8 *Xestoleberis depressa* Sars	14	5 95																				5	2 84
9 *Baffinicythere emarginata* (Sars)	11	4 72	7	5 51		r	c	r	r					r	c	c	r	r			r	12	6 82
10 *Sclerochilus contortus* (Norman)	7	3 00																				17	9 66
11 *Semicytherura rudis* (Brady)	6	2 58				r	c		c			r	r		r	c	r				r		
12 *Eucytheridea bradii* (Norman)	5	2 15	10	7 87		c			r	r	r			r	c	a	r		r		c		
13 *Baffinicythere howei* Hazel	2	0 86	37	29 14			r		r	r		c		r		c	r	r			r	22	12 50
14 *Paradoxostoma arcticum* Elofson	1	0 43	2	1 58																			
15 *Robilimis septentrionalis* (Brady)			22	17 32																			
16 *Cytheropteron paralatissimum* Swain			6	4 73																		9	5 11
17 *Finmarchinella barentzovoensis* (Mandelstam)			5	3 94																			
18 *Jonesia simplex* (Norman)			5	3 94																			
19 *Eucytheridea punctillata* (Brady)			4	3 15						r					r	r	r		r		a	9	5 11
20 *Palmenella limicola* (Norman)			2	1 58										r									
21 *Hemicytherura clathrata* (Sars)			1	0 79			r	r				r		r		c	r					20	11 36
22 *Elofsonella concinna* (Jones)						r	r			r	r		r	r	r	c	r						
23 *Heterocyprideis sorbyana* (Jones)					r											r				r	a		
24 *Argilloecia* spp						c															r		
25 *Cytheropteron* spp						c		r	r	c	r	r	r		c	a			r		r		
26 *Muellerina mananensis* Hazel & Valentine						r	r		c				r		r	r	r						
27 *Normanicythere leioderma* (Norman)						r						r		r	r	c	r						
28 *Xestoleberis* spp						r	r	r					r			a	r						
29 *Cluthia cluthae* (Brady, Crosskey & Robertson)							r												r	r	c	1	0 57
30 *Cytheramorpha* spp							c																
31 *Eucytheridea macrolaminata* (Elofson)							r												r	r		2	1 14
32 *Paradoxostoma* spp							c		r	r								r					
33 *Pseudocythere caudata* Sars							r						r								r		
34 *Sclerochilus* spp							c	c	r							r					r		
35 *Hemicythere pulchella* (Brady)									r														
36 *Cytherura* spp									r		r		r	r	r	r	r				r		
37 *Eucythere* spp									r							r	r				r		
38 *Cytheropteron inflatum* Brady, Crosskey & Robertson										r													
39 *Patagonacythere dubia* (Brady)										c	r	r	r			c	r						
40 *Cytheropteron angulatum* Brady & Robertson																c							
41 *Acanthocythereis dunelmensis* (Norman)																					r		
42 *Bythoceratina* spp																					r		
43 *Krithe* spp																					r		
44 *Robilimis mirabilis* (Brady)																					r		
45 *Cytheropteron alatum* Sars																					r		
46 *Cytheropteron arcuatum* Brady, Crosskey & Robertson																					r		
Total number of specimens	233		127																			176	
Number of species	14		17		1	12	16	8	14	8	5	7	10	9	12	20	16	3	5	3	21	21	

No	%	
19	10 80	*Cytheropteron pyramidale* Brady
12	6 82	*Cytheropteron nodosoalatum* Neale & Howe
4	2 27	*Semicytherura affinis* (Sars)
3	1 70	*Cytherois* sp nov
2	1 14	*Argilloecia canadea* Sars
2	1 14	*Paracytherois* cf *P flexuosa* (Brady)
1	0 57	*Paradoxostoma normani* Brady
3	1 70	Species a
2	1 14	Species b
2	1 14	Undetermined (2 species)

* Data taken from Hazel (1967, 1970). Note that in these samples *Finmarchinella barentzovoensis* and *F curvicosta* are included with *F angulata*

Neale & Howe - Table 6



Text-figure 9 ii. Composition of ostracode faunas at various localities.

Text-figure 9 iii. Composition of ostracode faunas at various localities.

which is known on the eastern side of the Atlantic, but not from the Arctic except for an isolated record from Spitzbergen. The authors have not found it in any of their material. *Semicytherura rudis* (10 samples) and *Muellerina mananensis* (7) also have not been found so far in the eastern Arctic.

Other species found by the authors in Greenland material that they have examined and also found in the eastern Arctic include *Finmarchinella barentzovoensis, F. curvicosta, Cythere lutea, Xestoleberis depressa, Sclerochilus contortus, Rabilimis septentrionalis, Eucytheridea punctillata,* and *Palmenella limicola.*

12 The Colville Delta, Alaska

Two samples collected by Dr. J. Walker from the Colville Delta, northern Alaska were examined and confirm the general circumpolar nature of the sublittoral faunas. The samples, Nos. 583 and 791, yielding 75 and 83 specimens respectively, had as dominant species *Eucytheridea macrolaminata* (Elofson) (26.66% and 56.63%), *Rabilimis septentrionalis* (Brady) (30.66% and 3.61%), *Heterocyprideis sorbyana* (Jones) (8.00% and 18.07%), and *Cytheromorpha macchesneyi* (Brady and Crosskey) (28.00% and 3.61%). Also present were *Cytheropteron paralatissimum* Swain, *C. montrosiense* Brady, Crosskey and Robertson, *Palmenella limicola* (Norman), *Eucytheridea bradii* (Norman), *Roundstonia globulifera* (Brady), two semicytherurids, a *Cytherura,* a hemicytherid, and a broken specimen of *Limnocythere.* Comparison with the post-Tertiary of Canada material of Brady and Crosskey (1871) confirms the presence of *Cytheromorpha macchesneyi* (Brady & Crosskey) off both northern Alaska and Novaya Zemlya and provides yet another species common to both the eastern and western Arctic sublittoral.

SUBLITTORAL FAUNAS AND PROVINCES

It is becoming increasingly clear that a number of geographical divisions based on the Ostracoda may be recognised in the eastern Atlantic and some of these may now be outlined.

From comparisons and distributions given above it is obvious that throughout sublittoral Arctic seas there is a community of fauna that merits the designation of Arctic Province. Characteristic species include *Finmarchinella barentzovoensis* (Mandelstam) (Text-fig. 2), *F. curvicosta* Neale, *Rabilimis septentrionalis* (Brady) (Text-fig. 2), *Eucytheridea macrolaminata* (Elofson) (Text-fig. 3), *Paradoxostoma arcticum* Elofson, *Cytheropteron paralatissimum* Swain, *C. arcticum* Neale and Howe, *C.* cf. *C. nodosoalatum* Neale and Howe, and *C. nodosoalatum* Neale and Howe which are confined to the Arctic. Other species which occur further south but reach their maximum abundance in the Arctic are *Robertsonites tuberculata* (Sars), *Baffinicythere emarginata* (Sars), *B. howei* (Sars), *Normanicythere leioderma* (Norman), and *Cytheropteron pyramidale* Brady. Loxoconchidae and Leptocytheridae are represented only by the small tuberculate genera *Roundstonia* and *Cluthia.* The fauna is circumpolar and found at lower latitudes in the western Atlantic than in the east. Some differences occur between west and east — notably in the presence of *Hemicythere borealis* (Brady) and *Muellerina mananensis* Hazel and Valentine in the west. The differences are minor, however, compared with the similarities and the authors regard these as only sub-Provincial in status in recognising an eastern Arctic and western Arctic fauna. The faunas of the deeper water Arctic Basin to the North are unknown but in the Eastern Atlantic, with increasing depth, there is an approach in the southwest to the more uniformly distributed bathyal fauna characterised by abundant *Krithe,* thin-shelled *Cytheropteron* species, *Pseudocythere caudata,* and *Cytherella.*

To the south the boundary with what the authors here call the Norwegian Province agrees well with that drawn by Filatova (1957) and Brotskaya and Zenkevitch (1939) for other benthos. Southwards the Norwegian Province which extends as far as the Shetland — Faroes — Iceland Rise is typified by the absence of the forms restricted to the Arctic noted above, and by the presence of *Pterygocythereis mucronata* (Sars) (Text-fig. 7), *Muellerina abyssicola* (Sars), and *Thaerocythere crenulata* (Sars) (Text-fig. 7). Although the latter has been recorded farther north it reaches its maximum development in this Province. Loxoconchidae and Leptocytheridae other than the two genera mentioned above make their appearance and the ameliorating influence of the North Atlantic Drift is seen in the appearance of *Loxoconcha fragilis* (Sars), *Leptocythere pellucida* (Baird), *Semicytherura nigrescens* (Baird), *S. sella* (Sars), and other species in East Finmark.

The Baltic Province in the east is characterised by reduced salinity with a combination of euryhaline and brackish-water species such as *Paradoxostoma variabile* (Baird), *Palmenella limicola* (Norman), *Heterocyprideis sorbyana* (Jones), *Paracyprideis fennica* (Hirschmann), *Eucytheridea punctillata* (Brady), and others.

South of the Shetland — Faroes — Iceland Rise the sublittoral is characterised by *Pterygocythereis jonesii* (Baird) instead of *P. mucronata* (Sars), and by *Celtia quadridentata* (Baird), *Aurila convexa* (Baird), *Loxoconcha guttata* (Norman), *L. impressa* (Baird), *L. multifora* (Norman), *Cuneocythere semipunctata* (Brady), and others. For this Province we have adopted Forbes term 'Celtic' and since it extends at least as far south as Cape Finisterre we have provisionally drawn the southern boundary at this point which was the boundary taken by Forbes. Within this Province a northern and southern Sub-Province may be recognised. The boundary between the two sub-provinces occurs in the region of Lands End and the English Channel and Dana's term 'Caledonian' is obviously inappropriate for the northern one. The term 'Anglian' is also open to the same objection and the authors here suggest the term 'Britannic'. It is characterised by the occurrence of forms such as *Carinocythereis antiquata* (Baird) without *C. carinata* (Roemer), *Costa emaciata* (Brady) without *C. edwardsii* (Roemer) and the development of species such as *Robertsonites tuberculata* (Sars) and *Eucytheridea bradii* (Norman) which are here at the southern limits of their range. The southern Sub-Province, which we here designate 'Gascoynian' is typified by the development of *Carino-*

cythereis carinata (Roemer), *Costa edwardsii* (Roemer), *Costa runcinata* (Baird), *Hemicytherura videns* (Müller), *Semicytherura arcachonensis* (Yassini), *Eucytherura alata* (Müller) and a number of other species. Details may be found in Caralp, *et al* (1968, 1969), Yassini (1969), and Peypouquet (1971). To the south lies the poorly known Moroccan Province. The Mediterranean Province has been adequately covered in a series of papers by Rome (1965, *et ante*), and Puri, *et al* (1965, 1969).

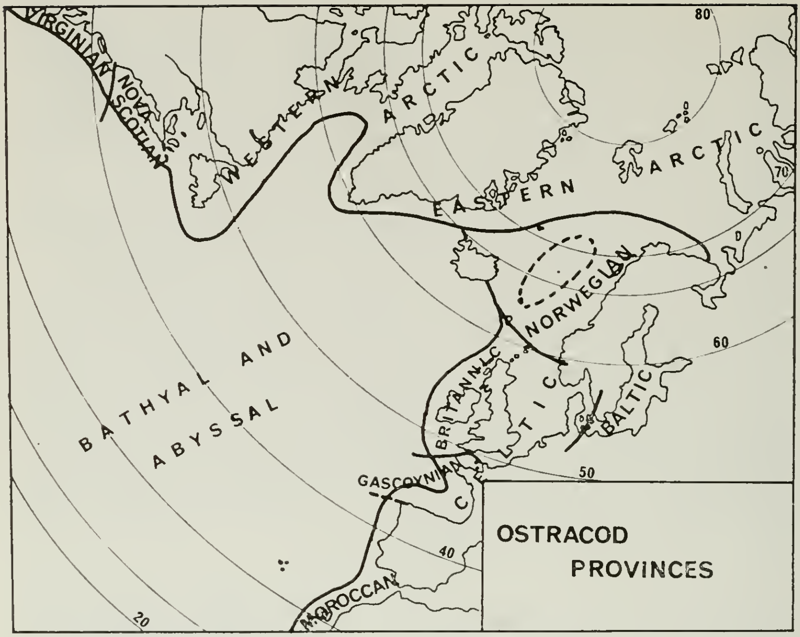
These units which we have here outlined seem to provide a useful subdivision of the eastern Atlantic coast from the Mediterranean to the Pole which reflects the broad distribution patterns of the podocopid Ostracoda. Obviously they can be considerably subdivided on a local scale, principally on an ecological basis, as reference to the detailed literature will show. To the west lie the deeper bathyal and abyssal faunas which separate these provinces from their counterparts on the other side of the Atlantic. To compare the Nova Scotian and Virginian Provinces of Hazel (1970) and the more southerly Carolinian and Caribbean Provinces of others with the Eastern Atlantic is outside the scope of this contribution, but it is obvious that as one moves southwards, so the similarity in faunas decreases, a feature which can be linked with the increasing separation and isolation due to sea floor spreading.

CONCLUSIONS

Detailed examination of this and other faunas leads us to believe that we are here dealing with a fauna typical of the present biocoenose of the Russian Harbour area where the proportion of adults above the 100 BSS sieve size is approximately 36% of the total fauna. There is no evidence of sorting and where it is possible to differentiate the sexes, the males form approximately one-third of the adult population. The fauna is that characteristic of the Arctic sublittoral and has affinities with other Arctic areas and particularly with Franz Joseph Land, Spitzbergen, and Greenland. This fauna is generally circumpolar although it is possible to recognise minor differences between East and West which may be regarded as of sub-provincial status. The fauna is clearly differentiated from that of the Norwegian Province by the absence of *Thaerocythere crenulata* (Sars), *Muellerina abyssicola* (Sars) and *Pterygocythereis mucronata* (Sars), and the absence of 'normal' Loxoconchidae and Leptocytheridae, here represented by *Roundstonia* and *Cluthia* respectively.

South of the Shetland — Faroes — Iceland rise a Celtic Province may be defined, divided into a northern Britannic Province and a southern Gascoynian Province. The southern boundary which separates it from the poorly known Moroccan Province needs further detailed examination.

From the Pleistocene faunas in the area the Novaya Zemlya fauna differs in the abundance of hemicytherids and trachyleberids, and the absence of species such as *Cytheretta teshekpukensis* Swain, *Normanicythere concinella* Swain, *Elofsonella concinna* (Jones), *Cytheropteron montrosiense* Brady, Crosskey, and Robertson, and others.



Text-figure 10. Ostracode Provinces of the North Atlantic.

There remain a considerable number of interesting problems connected with such aspects as the deep water Arctic Basin faunas, the poorly known Moroccan Province, and taxonomic problems concerning the genera *Cytheretta, Cytheromorpha,* and *Semicytherura* which will provide a fertile field for investigation and which the authors hope to return to at a later date.

ACKNOWLEDGMENTS

A great many people have aided us in this work, patiently answering our enquiries and enabling us to consult and borrow material, and we would particularly like to thank Dr. D. R. C. Kempe and Dr. J. D. H. Wiseman of the Mineralogy Department and Dr. G. Bennell of the Zoology Department, British Museum of Natural History, Mr. A. M. Tynan and Mrs. O. Marshall of the Hancock Museum, Newcastle-upon-Tyne; Dr. M. Christiansen of the Zoologisk Museum, Oslo; and Dr. A. R. Waterston of the Royal Scottish Museum, Edinburgh; Dr. E. Oele and Mr. A. du Saar of the Rijks Geologische Dienst, Haarlem, Netherlands; Mrs. Ann Shirley, Department of Manuscripts, National Maritime Museum, Greenwich; the Librarian, the

Royal Geographical Society, London. Professor C. E. Pickford kindly helped with the preparation of the French Résumé. To Miss K. Clarkson, and Messrs. T. Choung, J. Garner, J. Jendrzejewaki, P. McSherry and A. R. Tute we are indebted for technical assistance at various times.

REFERENCES

Akatova, N. A.

1946. *K faune Ostracoda Novosibirskogo Melkovdya In: Toma III "Tyaudov Dripfuyushchei Expeditsii Glavsevmorputi na Ledokolnov Parokhoe., G. Sedov 1937-1940 gg.* Iz Datelstvo Glavsevmorputi Moskva, Leningrad, pp. 224-230, 8 figs.

1957. *Ostracody onczhskogo zaliva Belogo Morya Materialy po Komplexnomu izucheniyu.* Vyp. 1., pp. 428-433, 5 text-figs.

Bold, W. A. van den

1961. *The genus Eucytheridea Bronstein (Crustacea: Ostracoda) with a redescription of the type species.* Ann. Mag. Nat. Hist., ser. 13, 4, pp. 283-303, pls. VIII, IX, 25 text-figs.

Brady, G. S.

1868. *Contributions to the Study of the Entomostraca. No. I. Ostracoda from the Arctic and Scandinavian Seas.* Ann. Mag. Nat. Hist., ser. 4, 2, pp. 30-35, pls. IV, V.

1878. *Notes on the Ostracoda. In: Narrative of a voyage to the Polar Sea during the years 1875-1876 in H.M.Ships "Alert" and "Discovery" by Capt. Sir G. S. Nares R.N., K.C.B., F.R.S.,* II, pp. 253-256.

Brady, G. S., Crosskey, H. W.

1871. *Notes on fossil Ostracoda from the Post-Tertiary deposits of Canada and New England.* Geol. Mag. 8, pp. 60-65, pl. II.

Brady, G. S., Crosskey, H. W., and Robertson, D.

1874. *A monograph of the Post-Tertiary Entomostraca of Scotland including species from England and Ireland.* Palaeontogr. Soc., pp. 1-232, 16 pls.

Brady, G. S. and Norman, A. M.

1889. *A monograph of the marine and freshwater Ostracoda of the North Atlantic and of North-Western Europe. Section 1. Podocopa.* Sci. Trans. Royal Dublin Soc., ser. 2, 4, pp. 63-270, pls. 8-23.

Brotskaya, V. and Zenkevitch, L.

1939. *Kolichestvennyi uchet donnoi fauny Barentseva Morya.* Trudy vses. nauchno-issled. Inst. morsk. ryb. Khoz. Okeanogr., 4.

Caralp, M., Klingebiel, A., Lamy, A., Latouche, C., Moyes, J., and Vigneaux, M.

1968. *Étude micropaléontologique, sédimentologique et géochimique de quelques carottes de sédiments récents du Golfe de Gascogne.* Bull. Inst. Géol. Bassin d'Aquitaine, No. 5., 73 pp., 17 pls.

Caralp, M., Dumon, J. C., Klingebiel, A., Latouche, C., and Moyes, J.

1969. *Contribution à la connaissance géologique du Golfe de Gascogne Chapter VII,* pp. 125-272 in Vigneaux, M., *et al. Bilan des études géologiques effectuées au titre de la Convention de Recherche No. 66.00,451 "Océanographie" dans le Golfe de Gascogne.* Bull. Inst. Géol. Bassin d'Aquitaine, No. 6, 370 pp.

Catt, J. A. and Penny, L. F.

1966. *The Pleistocene deposits of Holderness, East Yorkshire.* Proc. Yorks. Geol. Soc., 35, pp. 375-420, pl. 24.

Elofson, O.
1939. *Cytheridea macrolaminata, n. sp. eine neue arktische Ostracoda.* Arkiv Zoologi, 31, pp. 1-7, 10 figs.
1941. *Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks.* Zool. Bidr. Uppsala, 19, pp. 215-534, 52 text-figs., 42 maps.

Feilden, H. W.
1898. *Visits to Barents and Kara Seas with rambles in Novaya Zemlya, 1895 and 1897.* Geog. Jour., 11, pp. 334-365, 1 map.

Filatova, Z. A.
1957. *Zoogeograficheskoe raionirovanie Cevernykh Morei po rasprostraneniyu dvustvoriatykh Mollyuskov.* Trudy Inst. Okeanol., 23, pp. 195-215, 1 text-fig.

Hazel, J. E.
1967. *Classification and distribution of the Recent Hemicytheridae and Trachyleberididae (Ostracoda) off northeastern North America.* U.S. Geol. Sur., Prof. Paper, 564, pp. 1-45, 11 pls., 2 text-figs.
1970. *Atlantic Continental Shelf and Slope of the United States. Ostracode Zoogeography in the southern Nova Scotian and northern Virginian Faunal Provinces.* U.S. Geol. Sur., Prof. Paper. 529-E, pp. i-v, E1-E20, 69 maps, 11 text-figs., 3 tables.

Howe, H. V.
1969. *Homonymy and other man-created taxonomic afflictions of Recent Ostracoda* in *J. W. Neale, Ed., The Taxonomy, Morphology and Ecology of Recent Ostracoda (Hull Symposium),* Oliver & Boyd, Edinburgh & London, pp. 3-13.

Klie, W.
1942. *Die von Römer und Schaudinn 1898 bei Spitzbergen gesammelten Ostracoden.* Zool. Anz., 137, pp. 1-10, 7 figs.

Lev, O. M.
1969. *Analiz i Sopostavlenie Komplexov Ostrakod iz Pozdnekainozoiskikh Otlozhenii Nizovev Rek Eniseya, Obi, Pechory, Mezeni i Severnoi Dviny.* Uchen. Zap. Paleont. Biostrat., nauch-issled. Inst. geol. Arktiki, Vyp., 28, pp. 25-34, 5 pls.

Maddocks, R. F.
1968. *Commensal and free-living species of Pontocypria Müller 1894 (Ostracoda, Pontocyprididae) from the Indian and southern Oceans.* Crustaceana, 15 (2), pp. 121-136, 7 figs., 2 pls.

Mandelstam, M. I., Schneider, G. F., Kuznetsova, Z. V., and Kats, F. I.
1957. *Novye Rody v Semeistvakh Cypridae i Cytheridae.* Ezheg. vses. paleont. Obshch., 14, pp. 166-193, pls. I-IV.

Milyukova, N. N.
1969. *K Stratigrafii Pliotsenovykh i Chetvertichnykh Otlozhenii, razvitykh v Basseine Reki Kamy i na Srednei Volge. Materialy k Problemam Geologii Pozdnego Kainozoya (Sbornik Statei).* Nauchno-issled. Inst. Geol. Arktiki. Leningrad, pp. 30-36, 1 table.

Moyes, J., and Peypouquet, J. P.
1971. *Les Ostracodes indicateurs d'un paléorivage pléistocène en bordure du plateau continental du Golfe de Gascogne.* C. R. Somm. Séances Soc. Géol. France, fasc. 44, pp. 219-220.

Müller, G. W.
1931. *Die Ostracoden des arktischen Gebietes.* Fauna Arctica, VI, pp. 23-32.

Neale, J. W.
1959. *Normanicythere gen. nov. (Pleistocene and Recent) and the division of the ostracod family Trachyleberididae.* Palaeontology, 2, (1), pp. 72-93, pls. 13, 14, 5 text-figs.

1961. *Normanicythere leioderma (Norman) in North America.* Palaeontology, 4 (3), p. 424.

1965. *Some factors influencing the distribution of Recent British Ostracoda.* Pubbl. staz. zool. Napoli, 33 suppl., pp. 243-307, pl. 1, 11 text-figs., 1 table.

1972. *Kangarina septentrionalis and Paracytheridea norvegica n. spp. from offshore north Norway.* Astarte, Tromsö, Jour. Arctic Biology. 5 (½), pp. 33-37, pl. 1.

1973a. *Cluthia (Crustacea, Ostracoda) a new Pleistocene and Recent leptocytherid genus.* Jour. Paleont. 47 (4), pp. 683-688, 1 pl., 2 figs.

1973b. *Roundstonia globulifera (Brady 1868), gen. nov. (Crustacea, Ostracoda), une espèce caractéristique du Pleistocene et (?) de l'actuel.* Revue Micropaléontologie. 16, pp. 125-131, 1 pl., 1 fig.

1973c. *Celtia gen. nov., a new genus of marine Ostracoda from the Celtic Province and Neogene deposits.* Revista Espanola de Micropaleontologia. 5, pp. 435-445, 1 pl., 3 figs.

1974. *Species of the boreal and arctic genus Finmarchinella Swain 1963, (Crustacea, Ostracoda).* Bull. Brit. Mus. (Nat. Hist.). 27, pp. 183-93, 2 pls.

Neale, J. W., and Howe, H. V.

1973. *New cold water Recent and Pleistocene species of the ostracod genus Cytheropteron (Crustacea, Ostracoda)* Crustaceana. 25, pp. 237-244, 1 pl.

Neale, J. W., and Schmidt, R. A. M.

1967. *On Normanicythere leioderma (Norman) and Normanicythere concinella Swain.* Micropaleontology, 13 (3), pp. 345-350, 6 figs.

Norman, A. M.

1877. *Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Foraminifera, Polycystina, and Spongida.* In Jeffreys, J. G. *Preliminary report of the biological results of a cruise in H.M.S. 'Valorous' to Davis Strait in 1875.* Royal Soc., Proc., 25, pp. 202-215.

1891. *Notes on the marine Crustacea Ostracoda of Norway.* Ann. Mag. Nat. Hist., ser. 6, 7, pp. 108-121.

1902. *Notes on the Natural History of East Finmark.* Ann. Mag. Nat. Hist., ser. 7, 10, pp. 341-361, 472-486.

Peypouquet, J. P.

1971. *La distinction des biocenoses, thanatocenoses, paleothanatocenoses: problème fondamental sur une plateforme continentale.* Bull. Inst. Géol. Aquitaine, 11 (1), pp. 191-208, 1 map.

Puri, H. S., Bonaduce, G., and Malloy, J.

1965. *Ecology of the Gulf of Naples.* Pubbl. staz. zool. Napoli, 33 suppl., pp. 87-199, 67 figs.

Puri, H. S., Bonaduce, G., and Gervasio, A. M.

1969. *Distribution of Ostracoda in the Mediterranean.* In J. W. Neale, Ed., *The taxonomy, morphology and ecology of Recent Ostracoda (Hull Symposium),* Oliver & Boyd, Edinburgh & London, pp. 356-411, 2 pls., 17 figs., 2 tables.

Rees, C. B.

1940. *A preliminary study of the ecology of a mud flat.* Jour. Marine Biol. Assoc. Plymouth, 24 n.s., pp. 185-199, 4 text-figs., 6 tables.

Rome, D. R.

1965. *Ostracodes des environs de Monaco, leur distribution en profundeur, nature des fonds marins explorés.* Pubbl. Staz. zool. Napoli, 33 suppl., pp. 200-212, 1 map, 1 table.

Scott, T.
1899. *Report on the marine and freshwater Crustacea from Franz Joseph Land, collected by Mr. William S. Bruce, of the Jackson-Harmsworth Expedition.* Jour. Linn. Soc. London, 27, pp. 60-126, pls. 3-9.

Stephensen, K.
1913. *Grønlands Krebsdyr og Pycnogonider (Conspectus Crustaceorum et Pycnogonidorum Groenlandiae).* Meddel. om Grønland, 22, pp. 1-479.
1936. *The Godthaab Expendition 1928. Crustacea Varia.* Meddel. om Grønland, 80, (2), pp. 1-38.

Swain, F. M.
1963. *Pleistocene Ostracoda from the Gubik Formation, Arctic Coastal Plain, Alaska.* Jour. Paleont., 37 (4), pp. 798-834, pls. 95-99, 13 text-figs.

Tressler, W. L.
1942. *Geology and Biology of North Atlantic Deep-Sea Cores between Newfoundland and Ireland. Pt. 4. Ostracoda.* U.S. Geol. Sur., Prof. Paper 196, pp. 95-106, pl. 19.

Yassini, I.
1969 *Écologie des Associations d'Ostracodes du Bassin d'Arcachon et du littoral Atlantique. Application à l'interpretation de quelques populations du Tertiare Aquitain.* Bull. Inst. Géol. Bassin d'Aquitaine, pp. 228 + XXIV, 39 pls.

Zagorskaya, N. G., Baranovskaya, O. F., Berdovskaya, N., Gladkova, I. G., Lev, O. M., and Ryumina, I. I.
1969. *Kratkii Ocherk Stratigrafii i Paleogeografii Pozdnego Kainozoya Pechorskoi Nizmennosti. Materialy k Problemam Geologii Pozdnego Kainozoya (Sbornik Statei).* Nauchno-issled. Inst. Geol. Arktiki. Leningrad, pp. 6-29, 22 text-figs.

Zenkevitch, L. A.
1963. *Biology of the seas of the U.S.S.R.* George Allen and Unwin, London, 955 pp., 427 figs., 328 tables.

John W. Neale,
University of Hull,
England

Henry V. Howe, late of the
School of Geology,
Louisiana State University,
Baton Rouge,
Louisiana 70803

DISCUSSION

Dr. R. C. Whatley: Why do you consider it necessary to erect these new names for faunal provinces and subprovinces already in existence and based upon the nature of the distribution of species belonging to various groups of animals. How do you define and delimit a faunal province based upon one group of animals, in this case Ostracoda, and do you in fact really consider that they have: (a) reality, (b) value.

What for example are the criteria, in terms presumably of fidelity of species to subprovinces, which you have used to separate the Brittanic and Gasconian subprovinces.

Dr. Neale: We would take issue with the speaker on his implicit assumption that faunal provinces based on 'various groups of animals' necessarily apply to *all* groups of animals. Testing this is a legitimate part of our science and in this respect faunas of ostracodes have as much claim to attention as faunas of any other group or groups. In fact, we have introduced only two new terms —

those for the subdivision of the Celtic Province (see Neale, Naples Symposium for preliminary assessment of this province). Reference to the text will clarify the reasons and basis for this and go much of the way towards answering the questioners others points. 'Reality' has been argued by philosophers for centuries and would require considerable space to argue even in outline. We would say, however, that we consider that these provinces and subprovinces are a reasonable reflection of the state of our knowledge at this time and that their value as a succinct means of communication increases as the individual worker's familiarity with the faunas increases.

Dr. R. H. Benson: Did you find *Pterygocythereis mucronata* in your study region? I wonder if you noticed any gradation in the distinctive spines that separate it as a species from *P. jonesii*?

Dr. Neale: No, we did not as far as I recall.

Dr. Benson: The last instar of *P. mucronata* of course looks like the penultimate instar of *P. jonesi*. The gaining of the large conelike spines could possibly be an adaptation related to the cooling of the water. I think that this might be a very interesting form to trace.

Dr. Neale: You are asking, in fact, "Is there any gradation between adult *jonesii* and adult *mucronata*?"

Dr. Benson: Yes, they're obviously extremely, closely related. It is the only *Pterygocythereis* we have with the extreme development of this one taxonomic feature, the large complex spines.

Dr. Neale: We agree that *P. jonesii* and *P. mucronata* are closely related and the suggestion that the relative development of spination could be related to cooling of the water is an interesting one. Nevertheless, we were fortunate in being able to work with excellent adult material and the differences between the two species were distinct and clear cut.

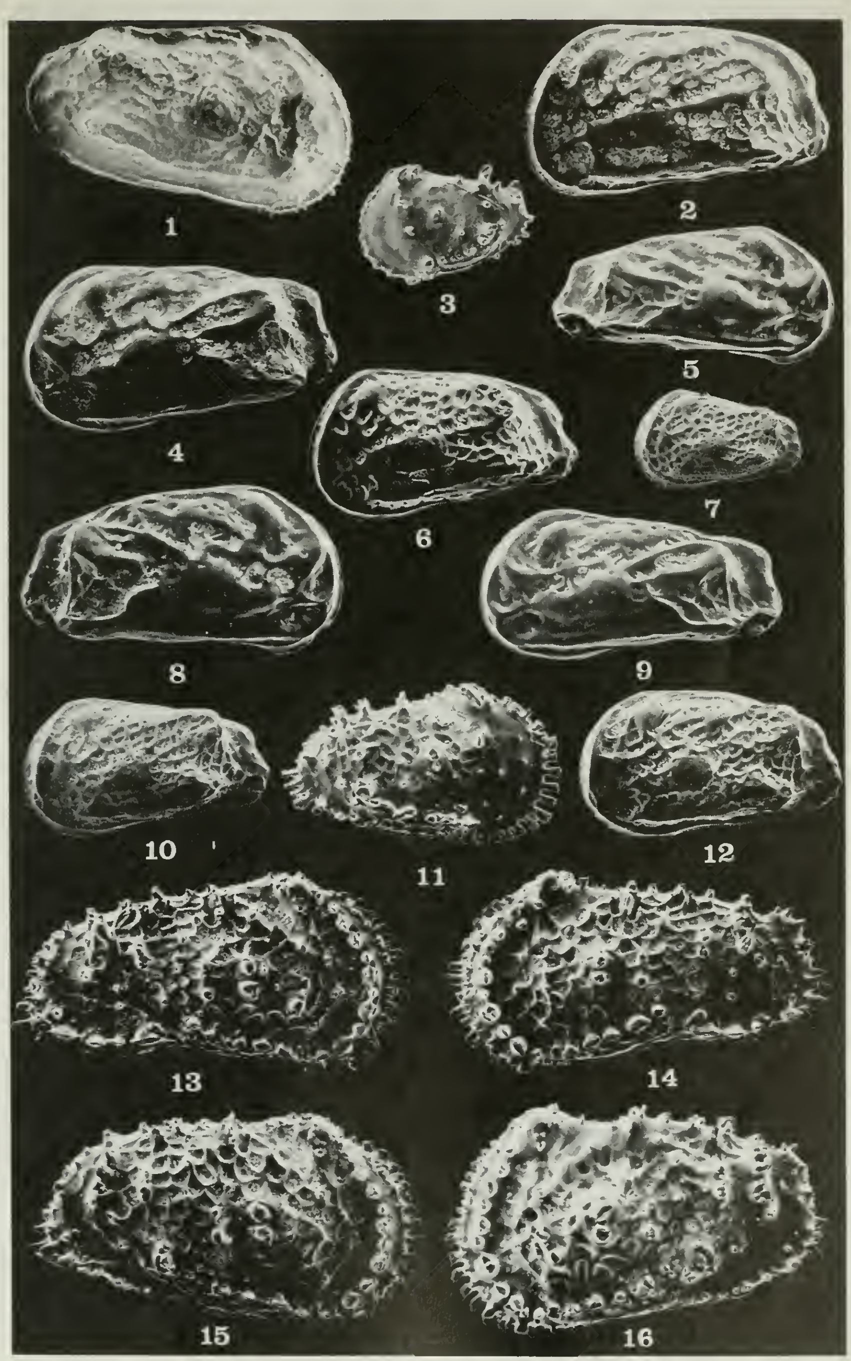
EXPLANATION OF PLATE 1

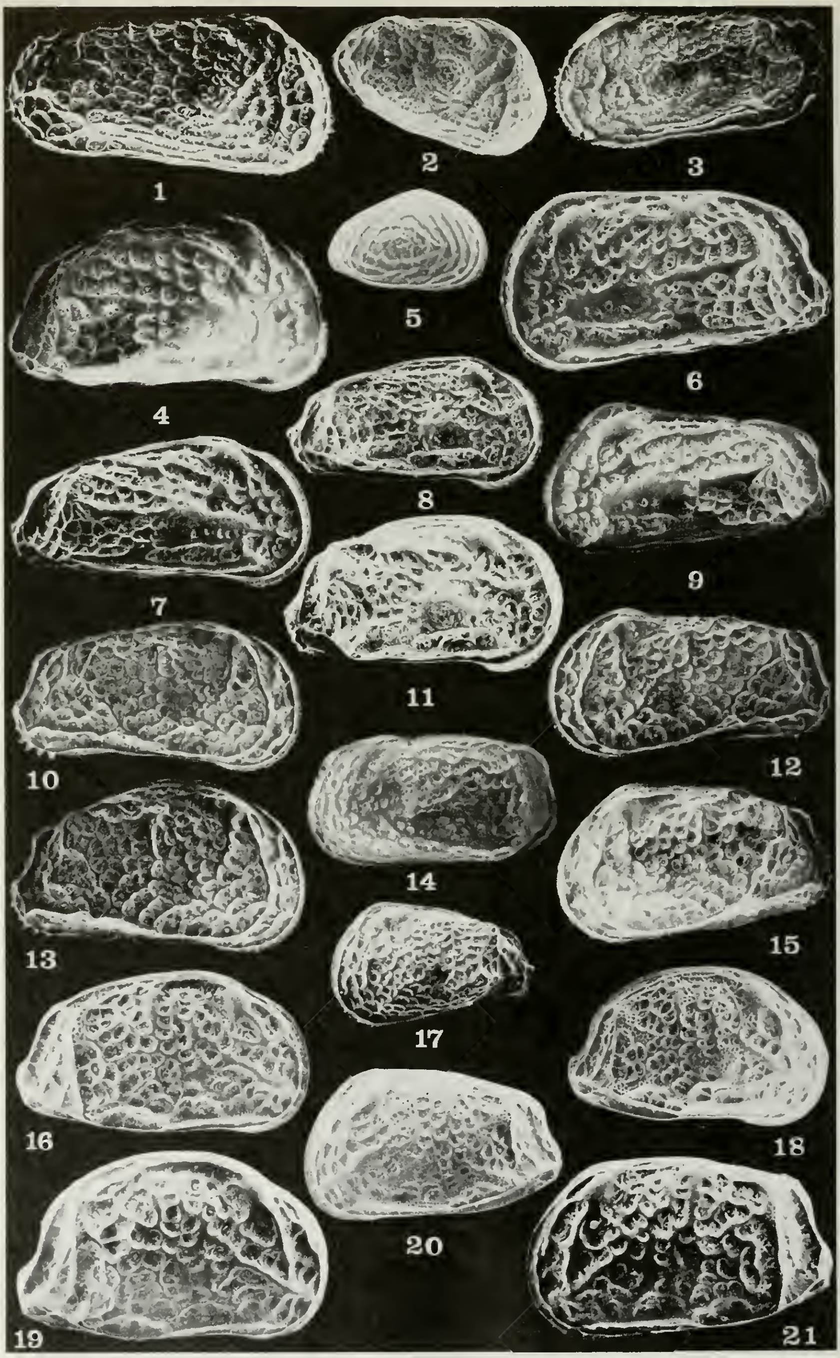
All material from Russian Harbour, Novaya Zemlya, seen in external lateral view.

Magnification × 51 ± 2, except where stated

Figure

1. *Robertsonites tuberculata* (Sars). Female right valve. HVH. 9599 × 38
2. *Finmarchinella curvicosta* Neale. Female left valve. HVH. 9600
3. *Acanthocythereis dunelmensis* (Norman). Juvenile left valve. HVH. 9601
4. *Finmarchinella barentzovoensis* (Mandelstam). Female left valve. HVH. 9602
5. *Finmarchinella barentzovoensis* (Mandelstam). Male right valve. HVH. 9603
6. *Finmarchinella curvicosta* Neale. Juvenile left valve. HVH. 9604
7. *Finmarchinella angulata* (Sars). Juvenile left valve. HVH. 9605 × 46
8. *Finmarchinella barentzovoensis* (Mandelstam). Female right valve. HVH. 9606
9. *Finmarchinella barentzovoensis* (Mandelstam). Male left valve. HVH. 9607
10. *Finmarchinella angulata* (Sars). Male left valve. HVH. 9608
11. *Acanthocythereis dunelmensis* (Norman). Juvenile right valve. HVH. 9609
12. *Finmarchinella angulata* (Sars). Female left valve. HVH. 9610 × 46
13. *Acanthocythereis dunelmensis* (Norman). Male right valve. HVH. 9611 × 45
14. *Acanthocythereis dunelmensis* (Norman). Male left valve. HVH. 9612 × 45
15. *Acanthocythereis dunelmensis* (Norman). Female right valve. HVH. 9613 × 45
16. *Acanthocythereis dunelmensis* (Norman). Female left valve. HVH. 9614 × 48


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

EXPLANATION OF PLATE 2

All material from Russian Harbour, Novaya Zemlya, seen in external lateral view.

Magnification × 50 ± 2 except where stated

Figure

1. *Robertsonites tuberculata* (Sars). Male right valve. HVH. 9615 × 40
2. *Robertsonites tuberculata* (Sars). Juvenile right valve. HVH. 9616
3. *Robertsonites tuberculata* (Sars). Male left valve. HVH. 9617 × 33
4. *Finmarchinella curvicosta* Neale. Female right valve. HVH. 9618
5. *Rabilimis septentrionalis* (Brady). Juvenile right valve. HVH. 9619
6. *Finmarchinella curvicosta* Neale. Female left valve. HVH. 9620
7. *Finmarchinella curvicosta* Neale. Male right valve. HVH. 9621
8. *Finmarchinella angulata* (Sars). Male right valve. HVH. 9622
9. *Finmarchinella curvicosta* Neale. Male left valve. HVH. 9623
10. *Baffinicythere howei* Hazel. Male right valve. HVH. 9624 × 32
11. *Finmarchinella angulata* (Sars). Female right valve. HVH. 9625
12. *Baffinicythere howei* Hazel. Male left valve. HVH. 9626 × 33
13. *Baffinicythere howei* Hazel. Female right valve. HVH. 9627 × 33
14. *Finmarchinella finmarchica* (Sars). Female left valve. HVH. 9628 × 47
15. *Baffinicythere howei* Hazel. Female left valve. HVH. 9629 × 32
16. *Baffinicythere emarginata* (Sars). Male right valve. HVH. 9630
17. *Baffinicythere howei* Hazel. Juvenile left valve. HVH. 9631
18. *Baffinicythere emarginata* (Sars). Juvenile right valve. HVH. 9632
19. *Baffinicythere emarginata* (Sars). Female right valve. HVH. 9633
20. *Baffinicythere emarginata* (Sars). Juvenile left valve. HVH. 9634
21. *Baffinicythere emarginata* (Sars). Female left valve. HVH. 9635

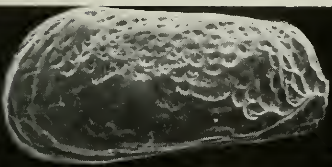
EXPLANATION OF PLATE 3

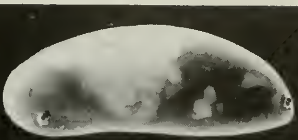
All material from Russian Harbour, Novaya Zemlya seen in external lateral view.

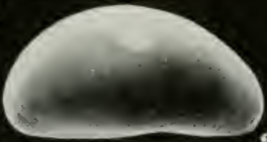
Magnification × 63 ± 3 except where stated.

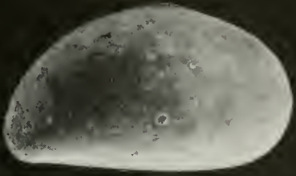
Figure

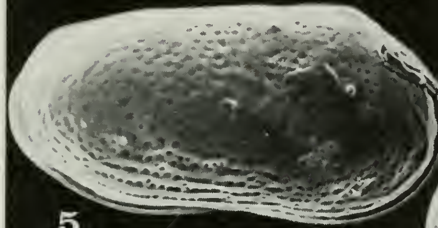
1. *Finmarchinella finmarchica* (Sars). Male left valve. HVH. 9636
2. *Argilloecia conoidea* Sars. Left valve. HVH. 9637
3. *Xestoleberis depressa* Sars. Right valve. HVH. 9638
4. *Eucytheridea macrolaminata* (Elofson). Right valve. HVH. 9639
5. *Cytheromorpha macchesneyi* (Brady and Crosskey). Right valve. HVH. 9640 × 87
6. *Cytheromorpha macchesneyi* (Brady and Crosskey). Left valve. HVH. 9641 × 85
7. *Sclerochilus contortus* (Norman). Right valve. HVH. 9642
8. *Sclerochilus contortus* (Norman). Left valve. HVH. 9643
9. *Normanicythere leioderma* (Norman). Female left valve. HVH. 9644
10. *Normanicythere leioderma* (Norman). Male left valve. HVH. 9645
11. *Bensonocythere* ? sp. Left valve. HVH 9646 × 94
12. *Tetracytherura* ? sp. Left valve. HVH. 9647 × 96

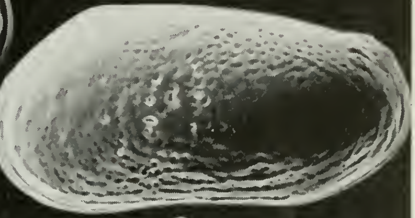

1

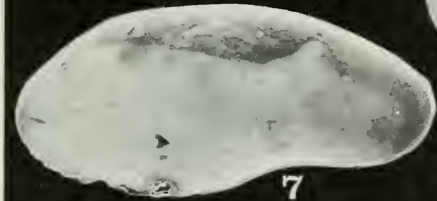

2

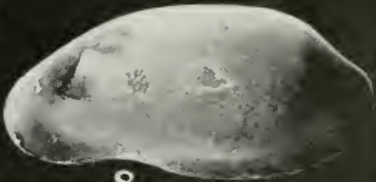

3

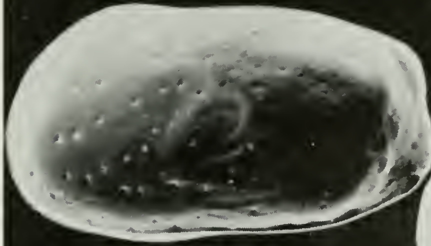

4

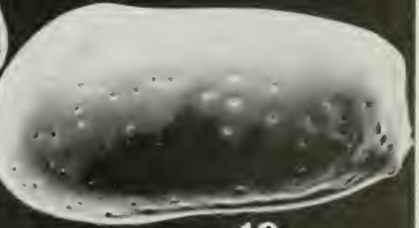

5

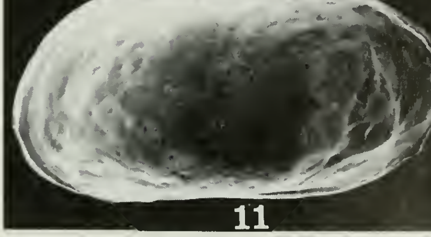

6

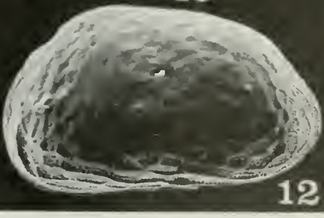

7

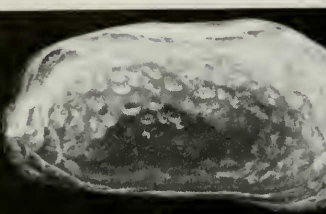

8


9

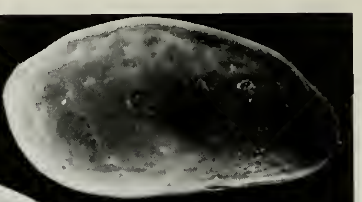

10


11

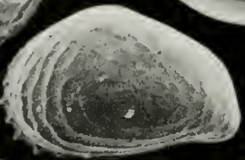

12



1



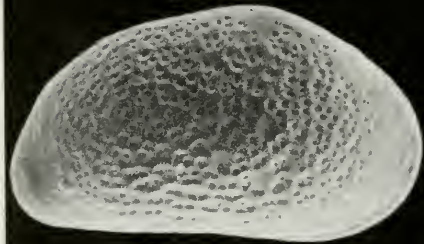
2



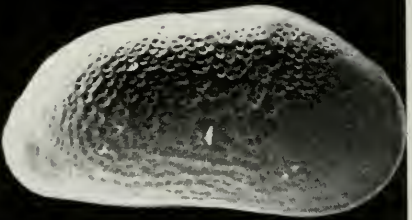
3

4

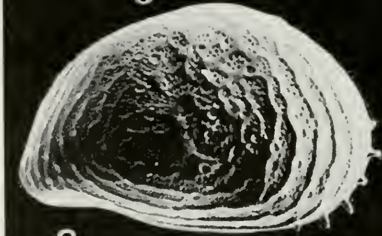
5



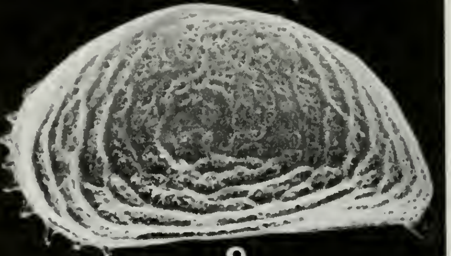
6



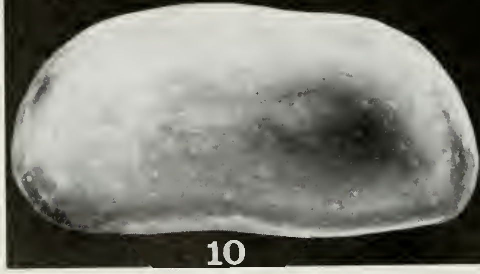
7



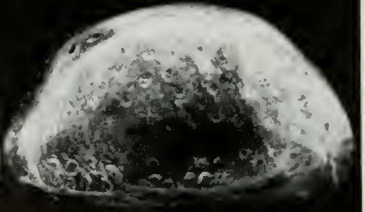
8



9



10



11

EXPLANATION OF PLATE 4

All material from Russian Harbour, Novaya Zemlya, seen in external lateral view.

Magnification × 63 ± 3

Figure

1. *Finmarchinella finmarchica* (Sars). Female right valve. HVH. 9648
2. *Paradoxostoma arctica* Elofson. Right valve. HVH. 9649
3. *Heterocyprideis sorbyana* (Jones). Juvenile left valve. HVH. 9650
4. *Bythocythere constricta* Sars. Right valve. HVH. 9651
5. *Paradoxostoma arctica* Elofson. Left valve. HVH. 9652
6. *Eucytheridea punctillata* (Brady). Female right valve. HVH. 9653
7. *Eucytheridea punctillata* (Brady). Male right valve. HVH. 9654
8. *Heterocyprideis sorbyana* (Jones). Juvenile right valve. HVH. 9655
9. *Heterocyprideis sorbyana* (Jones). Left valve. HVH. 9656
10. *Eucytheridea bradii* (Norman). Male left valve. HVH. 9657
11. *Cythere lutea* O. F. Müller. Right valve. HVH. 9658

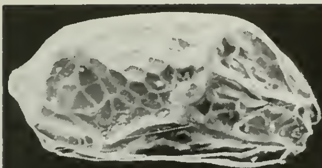
EXPLANATION OF PLATE 5

All material from Russian Harbour, Novaya Zemlya, seen in external lateral view, except where stated.

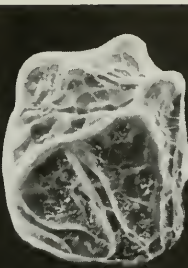
Magnification × 93 ± 5 except where stated

Figure

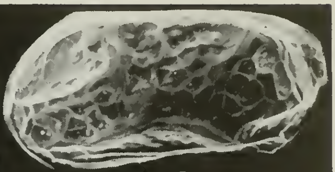
1. *Semicytherura undata* (Sars). Male right valve. HVH. 9659
2. *Semicytherura undata* (Sars). Male left valve. HVH. 9660
3. *Semicytherura undata* (Sars). Female right valve. HVH. 9661
4. *Semicytherura undata* (Sars). Female left valve. External anterior oblique view. HVH. 9662 × 87
5. *Semicytherura undata* (Sars). Female left valve. HVH. 9662
6. *Semicytherura* sp. nov? Right valve. HVH. 9663
7. *Palmenella limicola* (Norman). Right valve. Oblique postero-ventral view. HVH. 9664 × 63
8. *Palmenella limicola* (Norman). Left valve. HVH. 9665 × 67
9. *Hemicytherura clathrata* (Sars). Male left valve. HVH. 9666
10. *Semicytherura affinis* (Sars). Female right valve. HVH. 9667
11. *Hemicytherura clathrata* (Sars). Female left valve. HVH. 9668
12. *Semicytherura concentrica* (Brady, Crosskey, and Robertson). Female left valve. HVH. 9669
13. *Roundstonia globulifera* (Brady). Male left valve. HVH. 9670
14. *Semicytherura affinis* (Sars). Female left valve. HVH. 9671



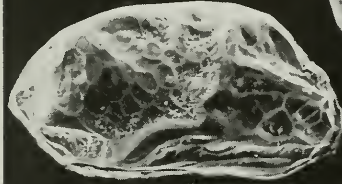
1



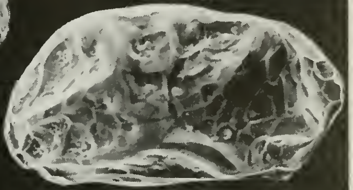
4



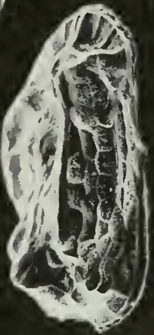
2



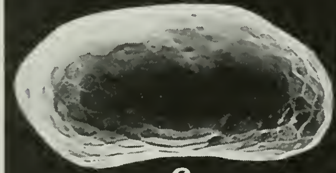
3



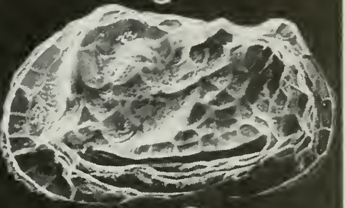
5



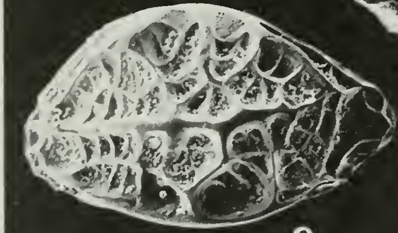
7



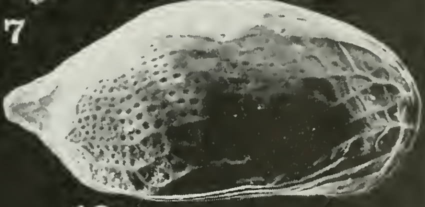
6



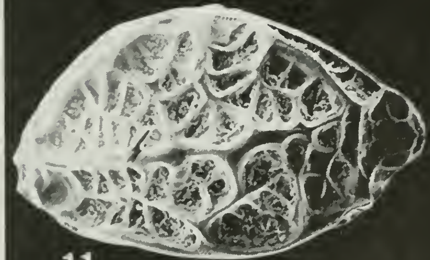
8



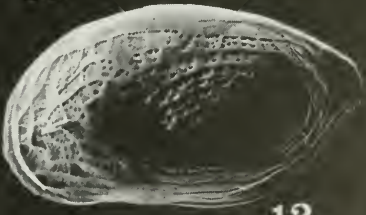
9



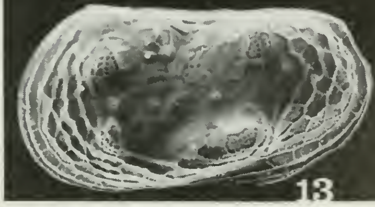
10



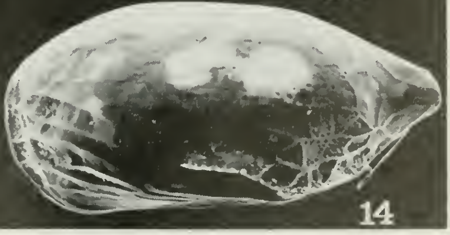
11



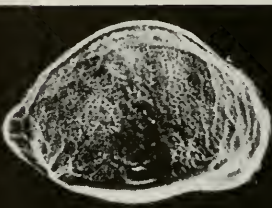
12

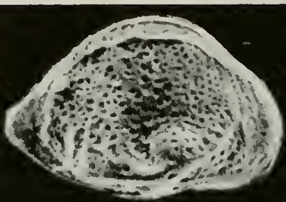


13

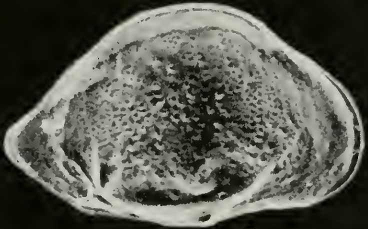


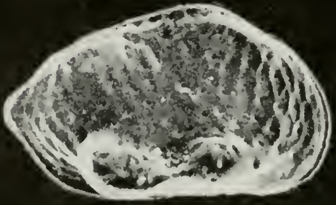
14

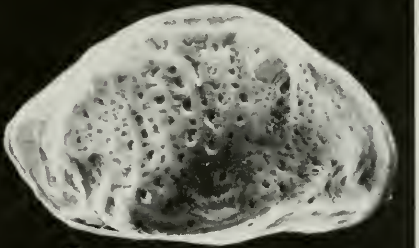

1

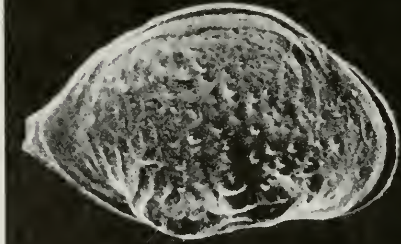

2


3


4

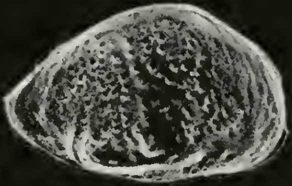

5


6


7


8


9


10

EXPLANATION OF PLATE 6

All specimens from Russian Harbour, Novaya Zemlya except where stated, and seen in external lateral view.

Magnification × 94 ± 2 except where stated

Figure

1. *Cytheropteron arcticum* Neale and Howe. Paratype, juvenile right valve. HVH. 9672
2. *Cytheropteron pyramidale* Brady. Juvenile right valve. HVH. 9673
3. *Cytheropteron arcticum* Neale and Howe. Paratype, juvenile right valve. HVH. 9674
4. *Cytheropteron pyramidale* Brady. Juvenile right valve. HVH. 9675
5. *Cytheropteron,* sp. nov.? right valve. HVH. 9676
6. *Cytheropteron nodosum* Brady. Right valve. Hoxnian, Pleistocene, Dimlington, East Yorkshire. HU. 166. R. 35
7. *Cytheropteron paralatissimum* Swain. Juvenile right valve. HVH. 9677
8. *Cytheropteron nodosoalatum* Neale and Howe. Paratype, juvenile right valve. HVH. 9678
9. *Cytheropteron paralatissimum* Swain. Juvenile right valve. HVH. 9679
10. *Cytheropteron nodosoalatum* Neale and Howe. Paratype, juvenile right valve. HVH. 9680

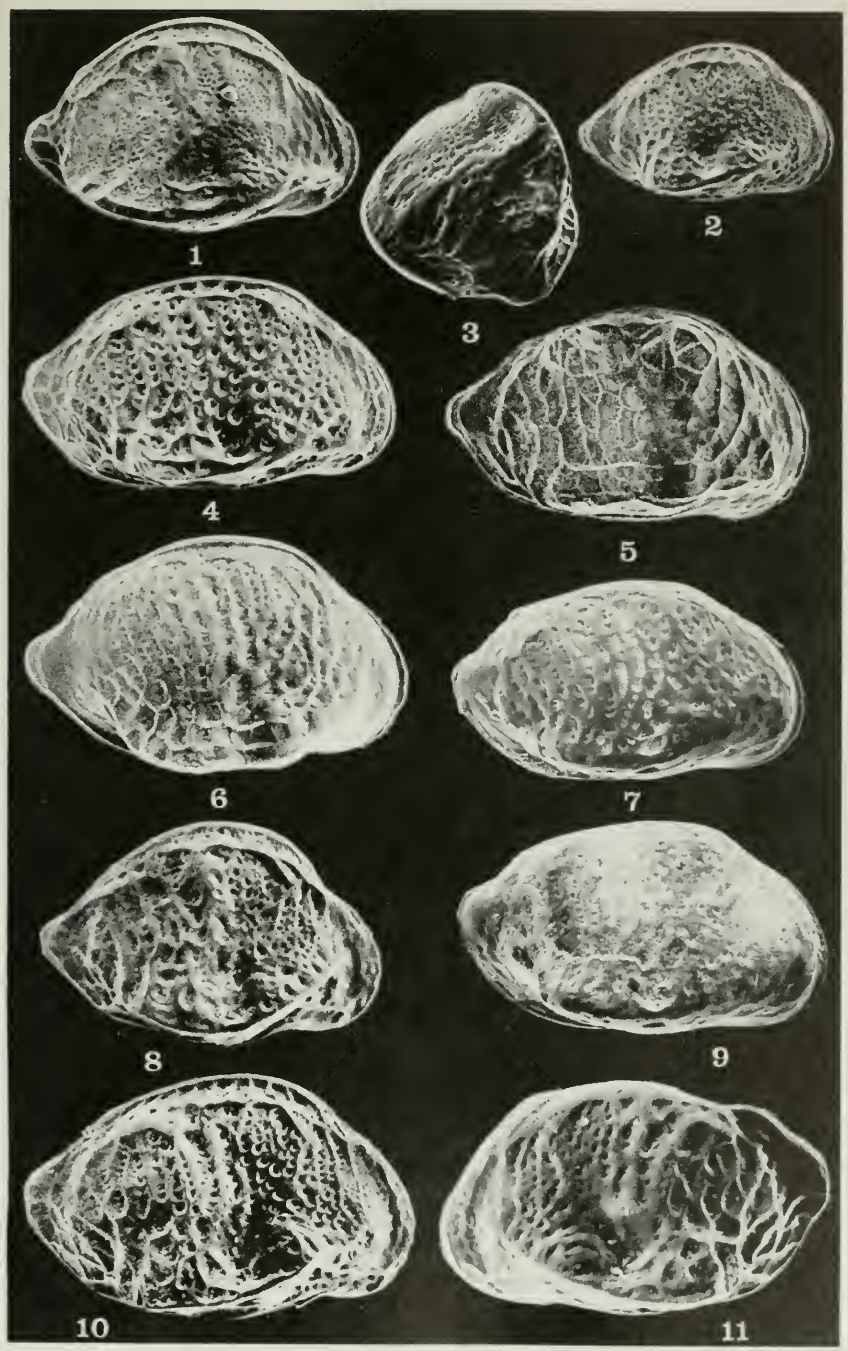
EXPLANATION OF PLATE 7

All material in external lateral view and from Russian Harbour, Novaya Zemlya, except where stated.

Magnification × 76 ± 4

Figure

1. *Cytheropteron arcticum* Neale and Howe. Paratype, right valve. HVH. 9681
2. *Cytheropteron nodosoalatum* Neale and Howe. Paratype, juvenile right valve. HVH. 9682
3. *Cytheropteron arcticum* Neale and Howe. Left valve. External oblique anterior view. Hoxnian, Pleistocene, Dimlington, E. Yorks. HU. 166. R. 32
4. *Cytheropteron nodosoalatum* Neale and Howe. Paratype, right valve. HVH. 9683
5. *Cytheropteron cf. C. nodosoalatum* Neale and Howe. Right valve. HVH. 9684
6. *Cytheropteron paralatissimum* Swain. Right valve. HVH. 9685
7. *Cytheropteron latissimum* (Norman). Right valve. HU. 166. R. 14. North Sea, Sample 497
8. *Cytheropteron pyramidale* Brady. Right valve. HVH. 9686
9. *Cytheropteron latissimum* (Norman). Right valve. HU. 166. R. 15. North Sea, Sample 497
10. *Cytheropteron nodosoalatum* Neale and Howe. Paratype, right valve. HVH. 9687
11. *Cytheropteron nodosoalatum* Neale and Howe. Left valve. Specimen lost.


1
2
3
4
5
6
7
8
9
10
11

THE EVOLUTION OF OSTRACODE FAUNAS IN ALPINE AND PREALPINE LAKES AND THEIR VALUE AS INDICATORS

H. Löffler
University of Vienna

ABSTRACT

Cores taken in Lake Constance (1), in Lunzer Untersee (2), in Lunzer Obersee (3), in Rehbergmoor near Lunzer Untersee (4), in Längsee, Klopeiner See (5) and Kleinsee (5a), and in Neusiedlersee and its adjacent areas (6) have been analyzed for pollen (2, 5), diatoms (1, 2, 5) and ostracodes (1-6). It appears that lakes of the oligotrophic type (2, 4) and lakes in the upper forest zone of the alps (3) have an unbroken ostracode tradition restricted to a few species, whereas meromictic lakes (5) exhibit very distinct successions due to dramatic changes in their physiographic properties. Species such as *Ilyocypris* cf. *lacustris* and *Cytherissa lacustris* have totally or partly disappeared from these lakes. The latter species has also disappeared very recently from the deeper parts and eutrophicated bays of Lake Constance (1). The history of Neusiedlersee (6) might be elucidated to some extent by means of ostracodes, the combination of certain cytherids indicating the extent of a cold precursor of the present shallow lake.

DIE EVOLUTION DER OSTRAKODEN-FAUNA IN ALPINEN UND PRAEALPINEN SEEN UND DER INDIKATORISCHE WERT DER OSTRAKODEN

ZUSAMMENFASSUNG

Sedimentprofile aus dem Bodensee (1), Lunzer Untersee (2), Lunzer Obersee (3), Rehbergmoor nahe dem Lunzer Untersee (4), Längsee, Klopeiner See (5) und Kleinsee (5a) sowie dem Neusiedlersee und dessen benachbartem Gebiet (6) wurden hinsichtlich des Pollens (2, 5), der Diatomeen (1, 2, 5) und Ostrakoden (1-6) untersucht. Es hat den Anschein, als ob oligotrophe Seen (2, 4) und Seen der oberen Waldstufe in den Alpen (3) eine ununterbrochene Tradition ihrer artenarmen Ostrakodenfauna besitzen, während sich in meromiktischen Seen (5) deutliche Sukzessionen ablesen lassen, die auf dramatische Änderungen der physiographischen Eigenschaften dieser Seen zurückzuführen sind. So sind Arten wie *Ilyocypris* cf. *lacustris* und *Cytherissa lacustris* völlig oder wenigestens teilweise in diesen Seen ausgefallen. Letztere Art ist auch in allerjüngster Zeit aus den den tiefsten Teilen und eutrophierten Buchten des Bodensees verschwunden (1). Mit Hilfe der Ostrakoden wird schliesslich versucht, die Geschichte des Neusiedler Sees (6) aufzuklären, wobei die Kombination bestimmter Cytheriden auf den Umfang eines Kaltwasser-Vorläufers des rezenten seichten Sees schliessen lässt.

INTRODUCTION

There exists a striking paradox in paleolimnology: ostracodes, though one of the most important groups to the paleontologist have been used to a very limited extent in interpreting the history of Recent lakes. Undoubtedly shells of ostracodes are not always preserved, especially if dylike or peatlike sediments are present. Under such circumstances, however, mandibulas, parts of the ductus ejaculatorius, or the copulatory organ are likely to exist; albeit up-to-date no study in this respect has been undertaken. Most lakes, at least within sedimentary rock areas will nonetheless offer optimum conditions for the preservation of ostracode shells. The main reason for their neglect originates in the palynological tradition of small samples (0.1 cc) which rarely provide ostracodes (Frey, 1955). Therefore, all the results presented here are based on 5-10 cc for each core section investigated (cores taken with the Kullenberg piston sampler modified by Livingstone (1955). Within the last eight years workers have shown the enormous indicatory value of ostracodes for the interpretation of the development of modern lakes (Benson and MacDonald, 1963; Swain and Gilby, 1964; Delorme, 1969, 1970; Löffler, 1969, 1971). This is partly due to the fact that ostracodes, in contrast to Cladocera, include long-living species [such as *Cytherissa lacustris* (Sars, 1863)] as well as species dwelling within the deep profundal zone, whereas most of the chydorids and also the benthic diatoms are restricted to the littoral belt of any lake.

OSTRACODES OF ALPINE AND PREALPINE LAKES

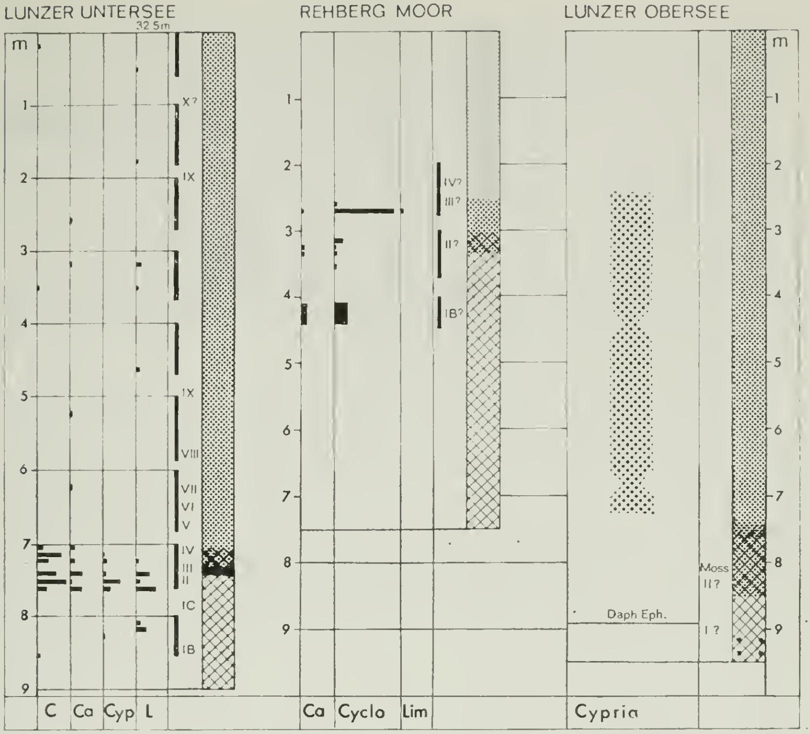
In alpine and subalpine lakes the main events resulting in dramatic quantitative or even qualitive changes in ostracode faunas of a lake are threefold:

1. The onset of the warmer climate during the late Pleistocene and during the beginning of the Preboreal (IV). In some of the Carinthian lakes this seems to have resulted in meromictic conditions with the transition from a cold polymictic towards a dimictic circulation regime thus providing for a marked faunal change.

2. The collapse of great lakes caused by outbreak and resulting in small successors, and

3. Human influence with respect to increasing eutrophication resulting in low profundal oxygen content and (or) change in the quality and structure of the sediment.

In oligotrophic alpine and prealpine lakes the composition of ostracode faunas from the time of their formation (late Pleistocene) up to most Recent times will most probably not have changed (unless influenced by eutrophication). However, with the beginning of the Holocene or during the Preboreal a change in quantity or abundance may be observed. A good example for this is Lunzer Untersee which has been investigated, with respect to its palynology, by Gams (1927) and Burger (1964). Gams, although he very carefully mentions most of the subfossil organisms he found, gave no information on ostracodes. Both authors took their cores from littoral zones whereas the one referred to here has been taken close to the maximum depth of the lake. In contrast to the cores taken so far the rate of sedimentation during the Subatlanticum is considerable (4 m or more) which is in good agreement with the most recent findings for fluviatile sedimentation rates. It is also with the beginning of the Subatlanticum that vivianite becomes abundant in the sediment. More information about this and the pollen analysis will be given elsewhere (Klaus and Löffler in prep.). The first species which occurs (Text-fig. 1) most likely



Text-fig. 1. — Distribution of ostracodes in cores from Lunzer Untersee, left, columns representing (left to right) *Cytherissa, Candona candida, Cypria,* and *Limnocythere sanctipatricii.* Breadth of each column: 20 shells. Black bars: actual cores taken. Symbols of sediments, presented right of the former, see Text-fig. 2. Rehberg Moor: Columns representing (left to right) *Candona candida, Cyclocypris, Limnocythere sanctipatricii.* Lunzer Obersee: schematic presentation of the distribution of *Cypria,* from 0-2.5 m not investigated but present.

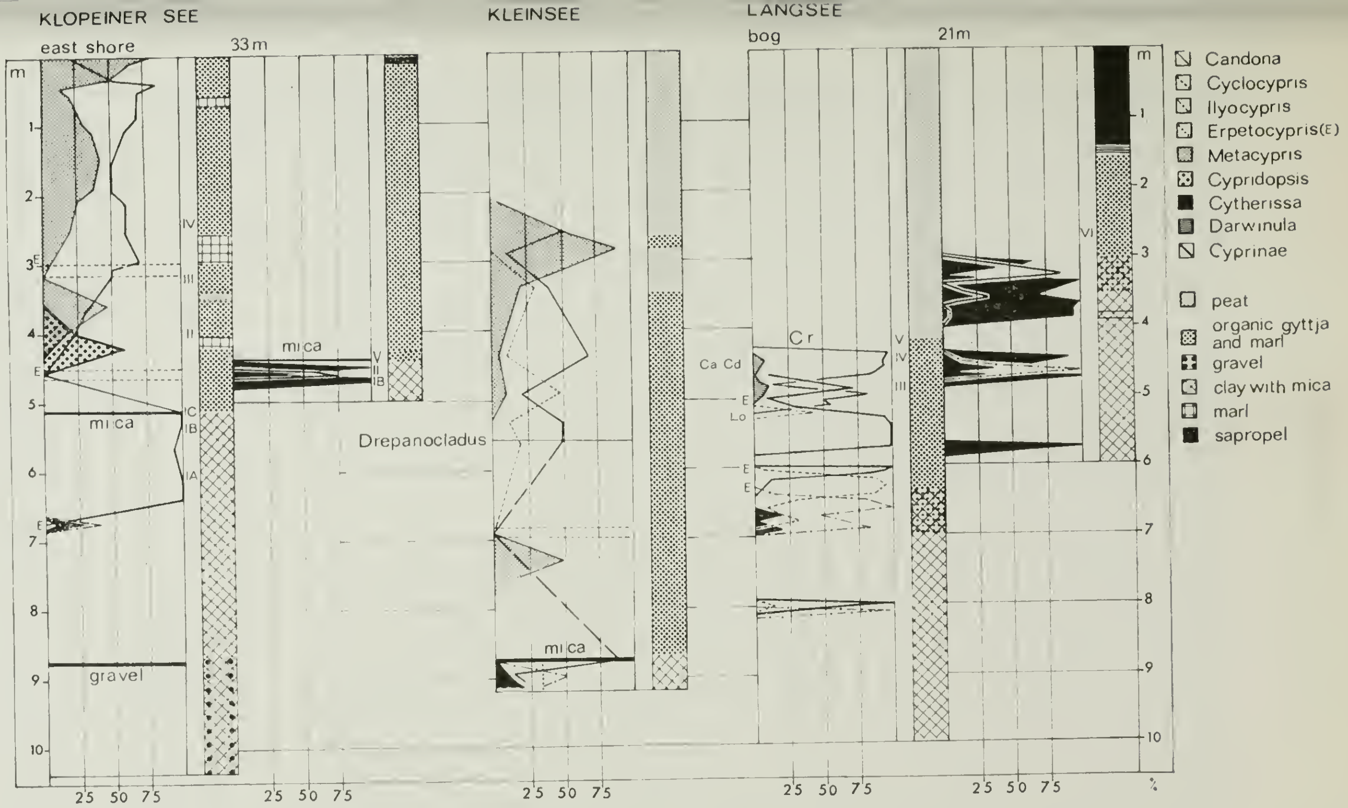
during the Bölling is *Cytherissa lacustris* followed by *Cypria ophthalmica* (Jurine, 1820), and *Limnocythere sanctipatricii* (Brady and Robertson, 1869). During the older Subarctic time (I C) they all disappear but recur together with *Candona candida* (O. F. Müller, 1776) during the Alleröd (II). After this period and during the "Schlussvereisung" (III) they again disappear and finally after a short time of relative abundance their number drops to present frequencies during the Preboreal. During this time the sediment also changes from a mainly inorganic gyttja towards a brownish organic one caused mainly by detritus brought in by the Seebach.

Similarly the short-lived Rehberg-moss lake which disappeared during the early Holocene shows fluctuations only in species abundance. It is noteworthy that *Cytherissa lacustris* either never reached this shallow lake (close to Lunzer Untersee and only some hundred meters above it) or that for some reason were not appropriate for it. In Lunzer Obersee only one species *(Cypria ophthalmica)* (Sars, 1891) has been found throughout the core and from late Pleistocene onward. None of the other Untersee species occur in Obersee which is well known for its floating vegetation and for its occasional meromictic behaviour.

The combination of ostracodes mentioned for Lunzer Untersee is quite typical for most of the profundal of prealpine and alpine lakes. There may be one or two species of *Candona* more and in great lakes *Ilyocypris* cf. *lacustris* Kaufmann, 1900, is often present in addition. It is most likely that in such great lakes, if remaining unspoiled, this profundal ostracode fauna once it had developed was not subsequently subjected to major changes. However, very little information exists about such lake types.

In some of the great lakes eutrophication during the last decades has resulted in either the disappearance of *Cytherissa lacustris* or in an overall deficiency of profundal species. The latter situation can certainly be correlated with the absence of oxygen and the formation of sapropelic sediments (Löffler, 1969), as has been shown for some of the bays of Lake Constance. *Cytherissa lacustris,* however, in numerous lakes of relictary distribution (Löffler, 1972), starts to disappear long before the occurrence of a dramatic decrease in oxygen. The deep basin of Lake Constance provides an example of such a situation. The present interpretation makes the increase of fine organic sediment with increasing eutrophication the main cause of this. Available evidence suggests that *Cytherissa* has relatively high specific weight (1.2 and more) and may also be distinguished by its stilting movement from, for example, the more pincerlike movement in *Candona* species. However, as yet no experimental proof has been advanced for a species-sediment relationship.

The collapse of a great lake by outbreak resulting in the formation of small descendants and its consequences on ostracode faunas is nicely demonstrated by Kühnsdorf Lake. This lake was formed during the retreat of the Drau-glacier and most likely persisted only until the Alleröd or for an even shorter period (until I C). A strong indication of this is the abrupt termination of mica in littoral cores of Klopeiner See and Kleinsee (Text-fig. 2) which were parts of the Kühnsdorf See whose level according to Stiny (1934) was approximately 15-20 m above those of the modern lakes. The mica itself was brought by the Drau River to Kühnsdorf See but not to its descendants which lie well above the modern river bed. As has been previously explained in detail (Löffler, 1972) the littoral cores of Klopeiner- and Kleinsee within the mica level are characterized by an association of *Cytherissa lacustris, Ilyocypris* cf. *lacustris, Candona candida,* and *Erpetocypris* sp. This composition is typical of the sublittoral in great lakes. Above the sediments containing mica the present-day littoral fauna with *Metacypris, Cyclocypris, Cypridopsis vidua* (O. F. Müller, 1776), and *Candona rostrata* Brady and Norman, 1889, starts in both lakes and shows a striking similarity in the proportions of the species mentioned (in Kleinsee because of more organic sedimentation the time-scale is considerably expanded).



Text-fig. 2. — Distribution of ostracodes in cores from Klopeiner See, Kleinsee and Längsee. Left diagram: ostracodes, given in percentage. Right diagram: type of sediment. Ca: *Cypria ophthalmica*, Cd: *Cypridopsis vidua*, Lo: *Limnocythere inopinata*, C.r.: *Candona rostrata*. In Klopeiner See, 33m the bathymetric scale 0.5, 1, 2, 3, 4m.

In order to learn about the onset of meromixis in Klopeiner See a core well below the lowest level of the mixolimnion at 33 m was taken (maximum depth 46 m). Ostracodes in the lowest part obtained *(Cytherissa lacustris* and *Candona candida)* occur between Bölling and Preboreal according to pollen analysis and then cease abruptly, although the sediment then differs but little from that of the holomictic Lunzer Untersee. Along with the ostracodes, head capsules of chironomids also decrease dramatically and only very few individuals can be found throughout the core even in the most modern strata. These, as with the few ostracodes from the littoral, most likely spread to the profundal by drifting. It should be mentioned that the sedimentation rate in Klopeiner See it extremely low (from Alleröd until now ca 3.5 m, compared with Lunzer Untersee: about 8 m!) because of the lack of any important inflow (fed mainly by submerged springs). Therefore, the exact identification of the time of onset of ostracode disappearance is somewhat vague but is certainly not earlier than Alleröd and not later than Preboreal. Mica is abundant in the sediment only until 345 cm which corresponds, as in the core from the eastern shore, to I C. Particles of mica can be, however, found at 340 cm though they are rare and may have drifted from the littoral when, during the initial period of the existence of the modern lake, mica-containing sediment still was exposed to wave action. As mentioned, Klopeiner See in contrast to its shallow and holomictic twin Kleinsee has been meromictic at least since the first observations in 1931 and because of climatic features of the area. Findenegg (see 1965) has verified its meromictic conditions several times in detail. The onset of meromixis in this lake, however, was not known. From the profundal core it seems most likely that at least a severe decrease in oxygen if not meromictic conditions did occur at the time of the disappearance of the profundal fauna both of ostracodes and chironomids. This then would have happened during the first holocenic warming most likely during Preboreal and according to the available information well after the collapse of Kühnsdorf See. The explanation for the beginning of meromixis could be the changeover of the lake from a cold polymictic stage in the late Pleistocene into a dimictic one during the holocenic warming which does not, according to Findenegg, provide for regular full circulations in this area and in deeper lakes lacking any big inflow. To verify this hypothesis investigations of many more of the meromictic lakes in the same area are, of course, necessary. Thus far only Längsee has been studied in this respect. The results obtained not only strongly support the interpretation of the beginning of meromixis outlined above but are also of interest since a detailed paleolimnological study of this lake had been carried out previously (Frey, 1955).

Längsee another small and shallow lake (maximum depth 22 m) in southern Carinthia belonged to the same Drau glacier system as Klopeiner and Kleinsee. Its elevation is approximately two hundred meters above that of the latter. The most obvious feature in contrast to the Klopeiner See core is the extent of sapropel in the uppermost section. Below and after a transition zone almost purely organic and brownish material starts which may be compared with the situation in Klopeiner See where from three meters downward this brownish organic material is replaced by finally almost purely inorganic gyttja containing mica. As Frey (1955) has carefully described, the lower onset of the sapropelic transition zone (with alternating brown and black layers) is also marked by the appearance of pollen of various agricultural weeds indicating the presence of man several hundred years B.C. Frey then identifies the sapropelic part of the core with the time Längsee has been meromictic (about 2000 years) and he thinks that early agricultural activities resulting in the clearing of the forest around the lake finally led to increasing runoff of morainic clay into the lake and a triptogenic factor initiated biogenic meromixis. As indicated above the author was at that time using counting samples of 0.1 cc which is normally adequate for the study of groups such as chydorids or protozoans. Frey thus was able to give a very careful account of the chydorids which, however, mainly reflect littoral conditions and hardly any profundal events. On the other hand his samples were obviously too small for the detection of any ostracodes apart from a single shell of *Candona* (at a core depth little less than 4 m) which at the same time was the first organism he found in his core. Text-figure 2 presents the ostracode development found in the present core and close to the area of maximum depth. It starts with a *Cytherissa* maximum in late Pleistocene which on current evidence probably indicates a warmer period before Bölling. A second period of ostracodes (Bölling) which ceases probably during I C is composed of *Cytherissa lacustris* and *Ilyocypris* cf. *lacustris*. During the last ostracode period (Alleröd?) which in its general shape resembles that of the profundal core of Klopeiner See, though there it is much more compressed, *Ilyocypris* being present only at the beginning followed by *Candona candida*. *Cytherissa lacustris* is present throughout the entire period which in contrast to Klopeiner See (where it has at present a very restricted area of distribution in a littoral section) in modern Längsee is lacking. This third ostracode period ends (as abruptly as its starts) approximately during Preboreal and there are no ostracodes found in the rest of the core apart from a few shells of the littoral *Cyclocypris*. Again, as in Klopeiner See, chironomid head capsules decrease together with ostracodes and drop from about 100/5 cc at 340 cm to virtually none above three meters, although an isolated individual may be present in a sample of the size mentioned which, however, is also true for the sapropelic section. As Frey has also observed *Chaoborus* starts to become abundant above 280 cm and thus well below the sapropelic part of the core. (*Chaoborus* has not until now been detected in the Klopeiner See core though a small population of it lives in the lake at present.) *Chaoborus* is not necessarily indicative of hypolimnic water lacking oxygen though in the Carinthian meromictic lakes it is one of the common organisms.

Längsee, thus according to the evidence afforded by the ostracodes, almost certainly became meromictic in early Holocene and a more detailed study of chironomids would probably verify this statement. It is therefore only the onset of the sapropelic section which may be related with the early agricultural activities in the area. Such a sapropelisation (excepting a few black layers within the top centimeters) never occurred in Klopeiner See and preliminary heavy weight coring in Wörthersee further indicate its absence though parts of this lake have become sapropelic through sewage.

Thus Längsee and Klopeiner See have about the same time of onset of meromixis. In Längsee, however, climatic factors may have played only partly a rôle in the onset of meromixis insofar as the early lake's extent was considerably greater and subsequently became reduced during the late holomictic stage. The lake at that time not only lost its southern portion which gradually altered into the present-day bog but according to preliminary investigations must also have, at some time, incurred a lowering of water level to the extent of at least one meter. The time of that event, however, is not yet known. Therefore, in Längsee both the climatic change in the early Holocene as well as a decrease in lake area may have resulted in meromixis. Text-fig. 2 also presents the development of the ostracode fauna in the southern basin of the early lake. The core was taken about 600 m south of the actual shore and collected from 10 m upward through boring even down to 17 m did not reach morainic gravel. Three periods of ostracodes may once more be distinguished. The first, below 7 m, consists of *Candona candida, Ilyocypris lacustris,* and *Cyclocypris* cf. *ovum* (Jurine, 1820). Strangely enough *Cytherissa* was not present at this time. There is some evidence that this period is not identical in time with the first one described from the profundal core. The second one, however, may correspond to it. Situated between 6 and 7 meters it shows a distinct succession of *Cytherissa lacustris* and *Ilyocypris* cf. *lacustris* followed firstly by a *Cyclocypris* and then by a *Candona candida* maximum. During the late stage of this period *Erpetocypris* is also present. The third period starts only 20 cm higher and consists almost exclusively of *Candona candida* followed initially by *Candona rostrata* which finally totally replaces the former. The other species occurring during this final period before bog formation are mainly *Cyclocypris* cf. *ovum* and *Darwinula stevensoni* Brady and Robertson, 1870, and to a lesser extent *Erpetocypris* sp., *Cypria ophthalmica, Cypridopsis vidua* and *Limnocythere inopinata* Baird, 1843. Most likely this last period of ostracodes corresponds to the late Pleistocene (Bölling onward?) and early Holocene whilst it vanishes during the Preboreal.

SUMMARY

If one summarizes the data so far obtained for the evolution of ostracode faunas in alpine and prealpine lakes it appears that in the profundal of medium- to large-sized lakes *Cytherissa lacustris* is the first species to occur in late Pleistocene followed by the few other forms which still belong to the profundal fauna. In the sublittoral and perhaps also deeper *Ilyocypris* cf. *lacustris* and *Candona candida* may be among these pioneer species. In all of the lakes observed a striking change in species or their abundance occurred during the early Holocene. In addition to changes in thermal and nutrient conditions the onset of more organic sedimentation must have played a fundamental rôle.

Even before the onset of the Holocene remarkable periods of ostracodes may be observed in Längsee and most probably reflect warmer periods such as Alleröd, Bölling. All of the lakes belonging to the Drau glacier system are lacking in *Limnocythere sanctipatricii,* a species otherwise most typical of alpine lakes and cold water both littoral and profundal.

All the lakes mentioned so far are subjected to a more or less normal seston and fluviatile (especially Lunzer Untersee) sedimentation. In the shallow (maximum depth at present 2 m) and large (at present some 300 km^2)

Text-fig. 3. — Localities of subfossil *Cytherissa lacustris, Limnocythere sanctipatricii, Limnocythere inopinata,* and *Metacypris cordata* east and west of Neusiedlersee (its configuration presented together with the extent of the *Phragmites* belt). Numbers indicate the drilling profiles carried out by ÖMV in 1971. Dotted area: extent of Pleistocene gravel. Broken lines: Depth of rock. From Löffler (1972).

Neusiedlersee most recent sediment (Löffler, 1971) is deposited on top of Tertiary (Pannonian) material and is thus lacking in any older Holocenic or even Pleistocenic deposits. This is due partly to the fact that irregular periods of drought and flooding are experienced as well as a shifting of the sediments from this shallow lake into reed belts resulting in a frequent renewal of the sediments present at any time. It also reflects the origin of the lake which represents a subsidence of late Pleistocene (and early Holocene) origin. Ostracodes in this case have been used not only to describe the extent of the former lake but also to learn from their associations something of the climatic conditions present at various stages. More than a thousand drill samples (mainly taken by an oil firm) have, therefore, been collected around the lake as has been described elsewhere in greater detail. Text-figure 3 illustrates only those localities where species of interest have so far been found (mainly *Cytherissa lacustris,* an indicatory species for non-periodic bodies of water, *Limnocythere sanctipatricii,* an indicatory species for cold water and *Limnocythere inopinata* which is most typical of the present lake (besides *Ilyocypris gibba* and several species of *Candona* in the reed belt) and which tolerates wide ranges of salinity and thermal conditions though it never occurs in permanent cold water lakes). From this distribution it appears that a precurser of the present lake existed during a cold period, the maximum temperature of which was unlikely to have exceeded 15°C, southeast of the modern lake and characterized by *Limnocythere sanctipatricii* in combination with *Cytherissa lacustris.* At a later stage the lake probably underwent displacement to the west as a result of continued weak subsidence mainly in the area of the actual lake. The recovery of *Cytherissa lacustris* together with *Limnocythere inopinata* but not *L. sanctipatricii* would indicate warmer conditions during this later stage. It is quite likely that the downward movement may have continued after this period especially in the southwestern portion of the recent lake. So far neither *Cytherissa* nor *Limnocythere sanctipatricii* has been found along the lakes southwestern shore. There are some indications that ostracode material of a lacustrine period of the last interglacial time may be present east of Neusiedlersee. However, this remains to be substantiated.

BIBLIOGRAPHY

Benson, R. H. and MacDonald, H. C.

1963. *Postglacial (Holocene) ostracodes from Lake Erie.* Univ. Kansas Pal. Contrib., Arthropoda, Art. 4, pp. 1-26.

Burger, B.

1964. *Results of a pollenanalytic investigation in the Untersee near Lunz in Austria.* Geol. Mijnbouw, 43, pp. 94-102.

Delorme, L. D.

1969. *Ostracodes as Quaternary paleoecological indicators.* Canadian J. Earth Sci., 6, pp. 1471-1476.

1971. *Paleoecological determinations using Pleistocene freshwater ostracodes.* Bull. Centre Rech. Pau-SNPA, 5 suppl., pp. 341-347.

Frey, D. G.
1955. *Längsee: A history of meromixis.* Mem. Ist. Ital. Idrobiol., suppl. 8, pp. 141-146.
1964. *Remains of animals in Quaternary lake and bog sediments and their interpretation.* Ergeb. Limnol., Beih. 2, Arch. Hydrobiol., pp. 1-114.

Findenegg, I.
1965. *Die Eutrophierung des Klopeiner Sees. Österr. Wasserwirtschaft,* 17, pp. 175-181.

Gams, H.
1927. *Die Geschichte der Lunzer Seen, Moore and Wälder.* Int. Rev. Hydrobiol., 18, pp. 305-336.

Löffler, H.
1969. *Recent and subfossil distribution of Cytherissa lacustris.* Comm. Int. Ass. Limnol., 17, pp. 240-251.
1971. *Daten zur subfossilen und lebenden Ostrakodenfauna in Wörthersee und Klopeinersee.* Carinthia, Sonderh. 31, pp. 79-89.
1972. *The distribution of subfossil ostracods and diatoms in pre-alpine lakes.* Int. Ass. Limnol. Trans. 78, pp. 7039-7050.

Stiny, J.
1934. *Zur Kenntnis der Hochfläche von Rückersdorf (Kärnten).* Jahrb. Geol. Bundesanst., Wien, 84, pp. 1-12.

Swain, F. M., and Gilby, J. M.
1964. *Ecology and taxonomy of Ostracoda and an alga from Lake Nicaragua.* Publ. staz. zool. Napoli, 43. pp. 361-381.

H. Löffler,
University of Vienna,
Vienna,
Austria 1099

DISCUSSION

Dr. L. D. Delorme: Where do you find *Cytherissa lacustris* living today?

Dr. Löffler: You find it everywhere except in organic ooze. That means, for example, if you think in terms of fecal pellets or if you think in terms of algae which are decomposed and formed of a very fine matter the animals could not walk on it. We have done experiments on this, partly with plastic beads of different grain size as well as with natural substrates.

Dr. Delorme: Do you find that *Cytherissa lacustris* occurs more abundantly or more commonly in lakes that are thermally stratified vs. lakes that are not? What about its occurrence in deep stratified lakes?

Dr. Löffler: Oh yes, but it is not such an expressed cold water form like *Limnocythere sanctipatricii.* It is more sensitive because of the span of its lifetime which is certainly 2 years but may be even more than that, but *Limnocythere* are much shorter lived species.

UTILISATION DES OSTRACODES POUR LA MISE EN EVIDENCE ET L'EVOLUTION D'UNE LAGUNE HOLOCENE A L'OUEST DE LA GIRONDE, GOLFE DE BISCAY

Pierre Carbonel, Jean Moyes, et Jean-Pierre Peypouquet
Université de Bordeaux

ABSTRACT

In a zone of the Bay of Biscay, located west of the Gironde estuary (45°40′N., 1°30′W.) on and about the 50 m depth line, the ostracode faunal associations found in the surficial sediments sometimes show an incompatibility with the present depth of the deposits. Thus are found areas rich in "phytal" and euryhaline species, as well as zones with no ostracodes.

The study of cored sediments permitted us to tie in these surface anomalies with the presence of a lagoon which, from C^{14} dates, was formed approximately 10,000 years B. P. when the strand line was located at 50 m below present sea level.

At this time, to the east of an azoic zone, an euryhaline ostracode association developed (*Cyprideis torosa* Jones, *Cushmanidea elongata* Brady) followed by a "phytal" association (*Paradoxostoma* spp. *Schlerochilus* spp., *Hirschmannia* spp.).

Farther east, the amount of euryhaline species increased, and, in certain limited zones to the northeast and to the south, oligohaline forms (*Ilyocypris, Cypridopsis, Candona*) increased. The ostracode associations thus permit the reconstitution of different environments in which the salinity varied from west to east with two zones of minimum values, suggesting fluvial deposits.

One can thus imagine at 10,000 B. P. the formation of a lagoon behind a dune complex, which was influenced by marine water as well as fresh water brought in by two outlets from the Gironde estuary. Then, during the Holocene transgression, the lagoon was submerged and the ostracode associations acquired the characteristics of the present water depth (*Loxoconcha guttata* (Norman), *Carinocythereis* sp., *Costa edwardsii* (Roemer).

INTRODUCTION

Dans la zone située à l'Ouest de l'estuaire de la Gironde (entre 45°20′ et 46° de latitude Nord et 1° et 2° de longitude Ouest), par des fonds de 20 à 60 m, des campagnes en mer ont permis de recueillir des sédiments à la fois par bennes et carottages (Text-fig. 1) qui se sont révélés généralement riches en ostracodes. Les associations fauniques ont été étudiées dans un premier temps dans les matériaux recueillis au niveau du fond et leur répartition a été cartographiée. Puis, l'évolution de ces ensembles a été examinée dans les sédiments carottés, de manière à déceler les modifications éventuelles dans le temps. Les résultats acquis ont autorisé une utilisation de ces associations dans la reconstitution des environnements successifs de ce domaine durant l'Holocène.

I. OSTRACODES RECUEILLIS DANS LES SEDIMENTS DE SURFACE

Parmi les 120 échantillons examinés, les uns sont totalement dépourvus d'Ostracodes, les autres renferment une population riche. Ces microorganismes constituent soit un ensemble homogène, soit des associations hétérogènes au sein desquelles se trouvent juxtaposés certains groupes dont les caractères écologiques sont difficilement compatibles.

Ainsi, nous avons reconnu:

1. Une association "A", typique de la zone infralittorale interne (M. Vigneaux, *et al.*, 1972), comprenant:

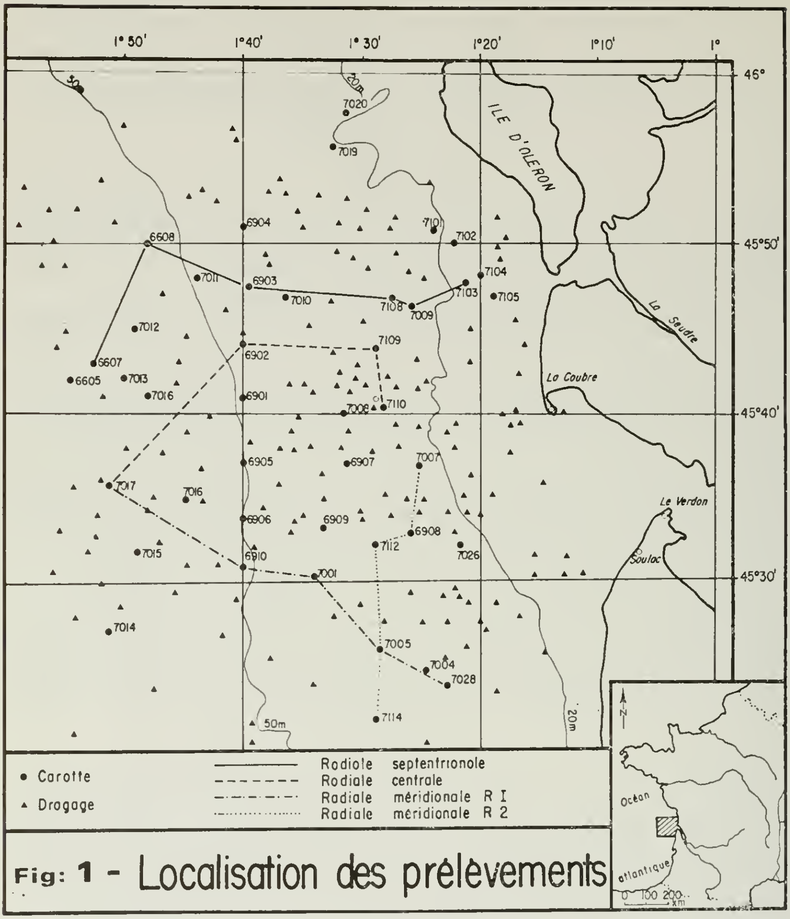


Fig: 1 - Localisation des prélèvements

des espèces caractéristiques: *Loxoconcha guttata* (Norman, 1865), *Carinocythereis carinata* (Roemer, 1838), *Costa edwardsii edwardsii* (Roemer, 1838), *Eucythere declivis* (Norman, 1865), *Bythocythere constricta* Sars, 1866.

des espèces accessoires: *Loxoconcha multiflora* (Norman, 1865), *Leptocythere pellucida* (Baird, 1850), *Leptocythere tenera* (Brady, 1867), *Carinocythereis emaciata* (Brady, 1867), *Cytheropteron crassipinnatum* Brady & Norman, 1889.

2. Une association "B", plus complexe groupant d'une part les formes typiques de l'association "A", d'autre part les espèces suivantes, qui habitent les algueraies dans les zones à salinité normale (I. Yassini, 1969), avec:

   des espèces caractéristiques: *Semicytherura arcachonensis,* Yassini, 1969, *S. acuticostata* (Sars, 1866), *Hemicytherura videns* (G. W. Müller, 1894), *Microcytherura fulva* (Brady and Robertson, 1874), *Paradoxostoma sarniense* Brady, 1867, *Aurila convexa* (Baird, 1850), petite forme, *Heterocythereis albomaculata* (Baird, 1838), petite forme, *Pontocypris mytiloides* (Norman, 1862).

   des espèces accessoires: *Semicytherura producta* (Brady, 1867), *S. striata* (Sars, 1865), *S. angulata* (Brady, 1867), *Loxoconcha rhomboidea* (Fischer, 1855), *Propontocypris pirifera* (G. W. Müller, 1894) *Sahnia subulata* (Brady, 1867), *Neocytherideis fasciata* (Brady and Robertson, 1874), *Hirschmannia tamarindus* (Jones, 1856), *Paracytherois flexuosa* (Brady, 1867), *P. producta* (Brady and Norman, 1889), *P. arcuata* (Brady, 1867), *Xiphichilus* sp. I, *Microcythere* sp. I.

3. Une association "C", très hétérogène comprenant 4 types:

   un groupement de type "A",

   un ensemble de formes connues sur les algues dans les zones euryhalines en aval de l'estuaire de la Gironde (P. Carbonel, J. Moyes, J. P. Peypouquet, 1972), comprenant:

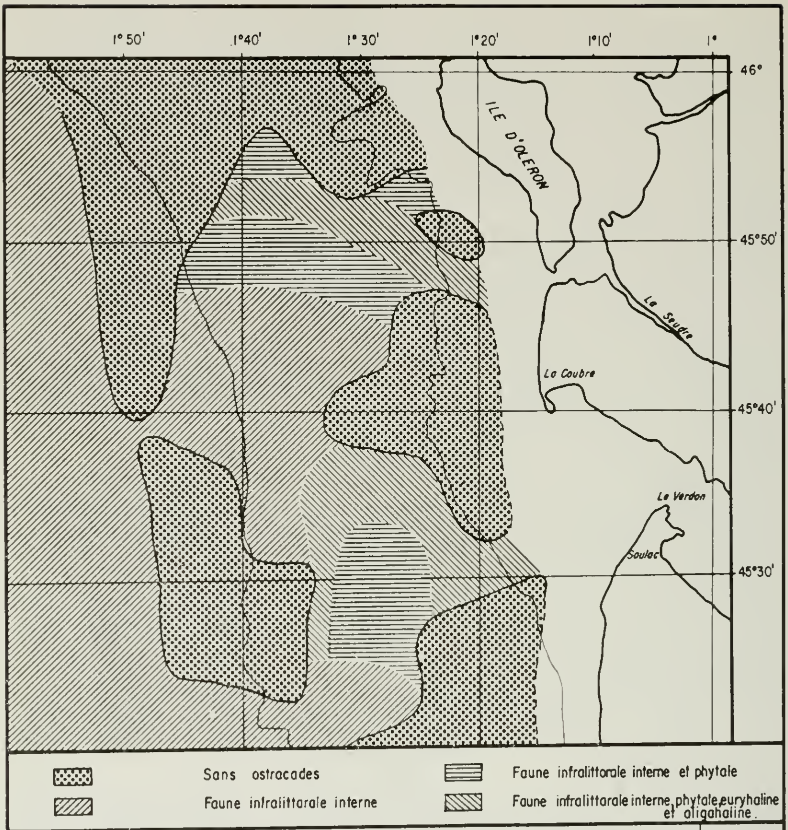
   > des espèces caractéristiques: *Paradoxostoma ensiforme* Brady, 1867, *P. normani* Brady, 1867, *Sclerochilus contortus* (Norman, 1861), *Loxoconcha rhomboidea* (Fischer, 1855), *Cytherois fischeri* (Sars, 1866).
   >
   > des espèces accessoires: *Semicytherura nigrescens* (Baird, 1838), *S. sella* (Sars, 1866), *Callistocythere pallida* (G. W. Müller, 1894), *Hirschmannia viridis* (O. F. Müller, 1785), *Paradoxostoma bradyi,* Sars, 1928.

   un autre ensemble caractéristique du domaine euryhalin, représenté par: *Leptocythere castanea* (Sars, 1866), *Loxoconcha elliptica* (Brady, 1868), *Cyprideis torosa* (Jones, 1850), *Aurila convexa* (Baird, 1850), grande forme, *Heterocythereis albomaculata* (Baird, 1838), grande forme, *Cushmanidea elongata* (Brady, 1868), *Urocythereis oblonga* (Brady, 1866).

   Enfin, quelques espèces typiques d'eaux oligohalines: *Candona sp. div., Ilyocypris gibba* (Ramdohr, 1808), *Limnocythere inopinata* (Baird, 1843), *Cypridopsis vidua* (O. F. Müller, 1776).

La répartition des divers ensembles fauniques que nous venons de définir (Text-fig. 2), ne se fait pas au hasard, mais suivant des lois particulières. Ainsi, les sédiments dépourvus d'Ostracodes constituent-ils deux domaines alignés parallèlement à la côte actuelle et situés vers les isobathes — 50 m et — 20 m.

La faune de type infralittoral interne, qui constitue la totalité de la population dans deux aires limitées (Text-fig. 2), caractérise bien du point de



Associations fauniques des sédiments superficiels. **Fig: 2**

vue bathymétrique la zone considérée. Ailleurs, elle est associée à des groupements soit d'espèces "phytales" sténohalines, soit euryhalines et oligohalines qui sont toutes incompatibles avec la profondeur actuelle du dépôt.

Dans le matériel examiné, les carapaces et les valves présentent un excellent état de conservation, mais en général, les valves translucides ne contiennent pas de restes de l'animal. Si les associations homogènes, de type infralittoral interne, en harmonie avec la profondeur actuelle des dépôts, peuvent être considérées comme représentatives d'une biocénose, en revanche les ensembles "phytaux", euryhalins et oligohalins sont soit des formes apportées en suspension par les courants, car les valves fragiles sont très bien conservées, soit des individus fossiles appartenant alors à un biotope ancien.

Les zones riches en Ostracodes correspondent à des vases et des silts, celles qui en sont dépourvues à un substratum de sables le plus souvent éolisés repris ultérieurement par la mer (M. Vigneaux, *et al.*, 1971).

Nous voyons donc se matérialiser, cernée par des corps sableux éolisés sans Ostracodes, une zone de vasière à microfaune marine dans la partie centrale et à ensemble d'Ostracodes hétérogène à dominante euryhaline dans les zones septentrionale et méridionale. Ce schéma complexe résulte-t-il seulement de l'apport actuel d'espèces phytales et euryhalines en provenance de l'estuaire de la Gironde ou de la présence de formes fossiles d'âge holocène ? L'étude de carottes implantées dans cette zone doit apporter des éléments de réponse.

II. LES OSTRACODES DANS LES SERIES CAROTTEES

Les associations fauniques d'Ostracodes ont été inventoriées dans les nombreux carottages (Text-fig. 1) réalisés dans la région considérée. Nous allons les examiner suivant quatre radiales qui nous paraissent apporter les informations les plus précieuses.

II-1. Radiale septentrionale (Text-fig. 3).

D'Ouest en Est, les séries carottées montrent les associations suivantes:

Carotte C 6607 (1,40 m): alternance de sables fins jaunâtres et d'horizons sablo-vaseux. Ces derniers renferment une microfaune d'Ostracodes toujours caractérisée par l'association de type "A" précédemment décrite.

Carotte C. 6608 (2,20 m): sables jaunes grossiers toujours éolisés à galets et débris coquilliers dans la moitié inférieure, sans Ostracodes.

Carotte C. 6903.

3,50 à 3 m: sables grossiers, éolisés dans la partie supérieure, avec de nombreux galets; dépourvus d'Ostracodes.

3 à 2,10 m: sables coquilliers renfermant une association faunique hétérogène de type "B", au sein de laquelle le pourcentage des espèces marines est important. Présence de quelques formes oligohalines.

2,10 à 1,90 m: dépôt sablo-vaseux caractérisé par une association d'Ostracodes exclusivement marine de type "B".

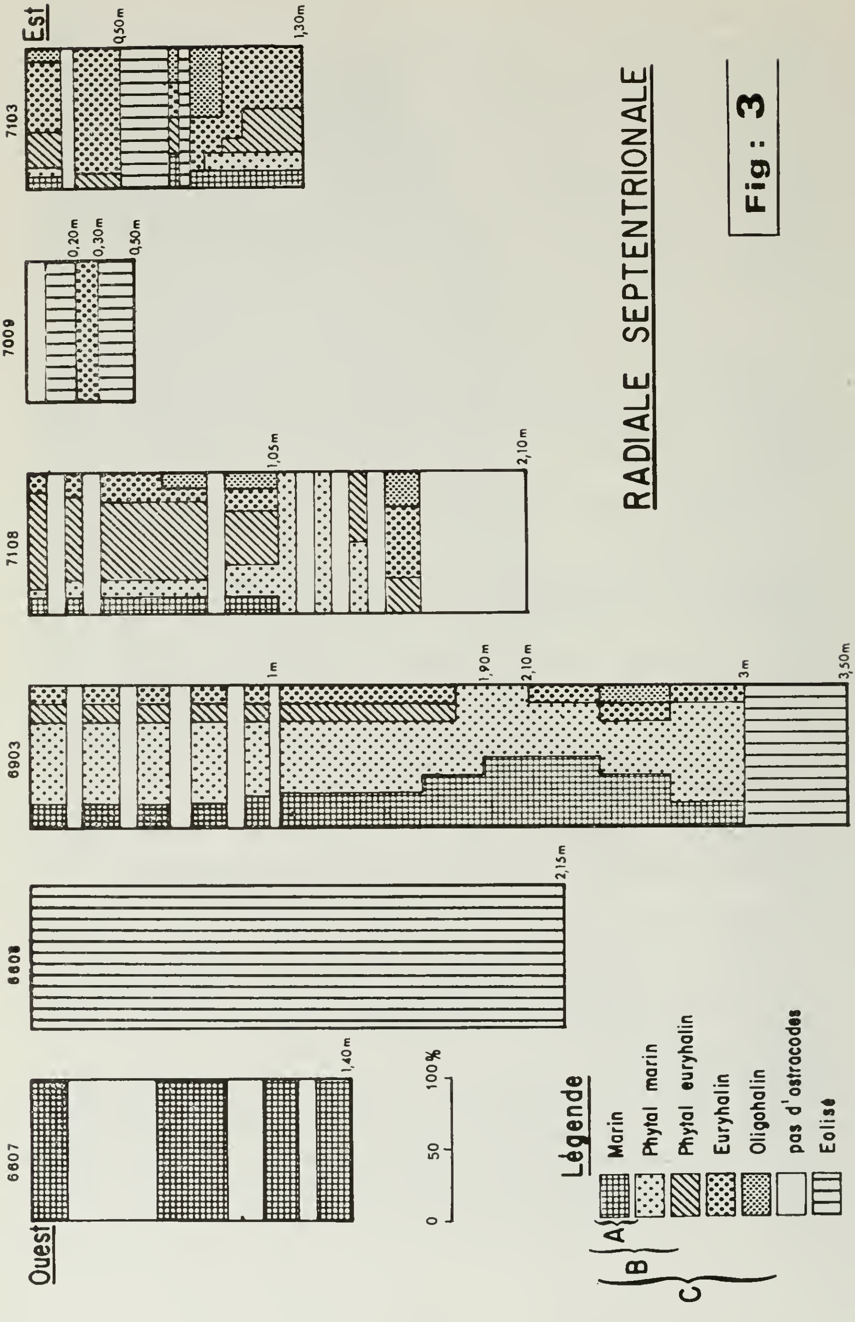
1,90 à 1 m: passage graduel de sables fins granoclassés à la base à des vases plastiques gris foncé au sommet. La faune est semblable à celle reconnue entre 3 m et 2,10 m.

1 à 0 m: alternance de silts fins sans Ostracodes et de vases silteuses renfermant des associations de types "B" et "C" avec prédominance des formes marines.

Carotte C. 7108:

2,10 à 1,05 m: vase caractérisée par l'association "C" à la base et "B" vers le sommet. Mais de nombreux horizons sont dépourvus d'Ostracodes.

1,05 à 0 m: sable très fin à la base, puis ensemble silto-vaseux renfermant l'association "C" avec des formes marines peu nombreuses.



RADIALE SEPTENTRIONALE

Fig: 3

Carotte C. 7009 (0,50 m) :sables gris, fins et homogènes, parfois éolisés. L'ensemble est azoïque, excepté entre 0,30 m et 0,20 m où la microfaune est euryhaline.

Carotte C. 7103 (1,70 m) : alternance de sables grossiers sans Ostracodes et de sables fins caractérisés par l'association faunique "C". Les formes marines sont toujours peu abondantes, tandis que les formes oligohalines prennent localement une certaine importance. Au-dessus de 0,50 m, l'association faunique est largement euryhaline.

La comparaison des successions reconnues dans ces diverses coupes nous amène à formuler les remarques suivantes:

Les sables éolisés sans Ostracodes reconnus au niveau du fond, existent aussi en profondeus (C. 6608). Ainsi, peut-on estimer que ce type de dépôt correspond à l'existence d'un cordon dunaire fossile. Ces sables grossiers se retrouvent dans certaines carottes (C. 6903, C. 7009, C. 7103) à des niveaux de plus en plus proches de la surface du fond au fur et à mesure que l'on se déplace vers l'Est. Ils permettent d'entrevoir l'existence d'une cuvette à flanc abrupt vers — 50 m environ et à pente douce à l'Est.

Ce cordon dunaire sépare deux types d'environnement: à l'Ouest un biotope de type infralittoral interne (C. 6607) ; à l'Est un milieu à faune complexe, dominée, de plus en plus nettement en allant vers la zone orientale, par le caractère estuarien (C. 6903, C. 7108, C. 7103).

En succession verticale, dans le partie occidentale (C. 6607), la faune marine évolue très peu. Par contre, à l'Est du cordon dunaire, on observe une modification qualitative et quantitative des associations fauniques dans le temps. Ainsi, dans la carotte C. 6903, la microfaune typique d'un milieu lagunaire à la base, montre une prédominance du caractère marin au sommet.

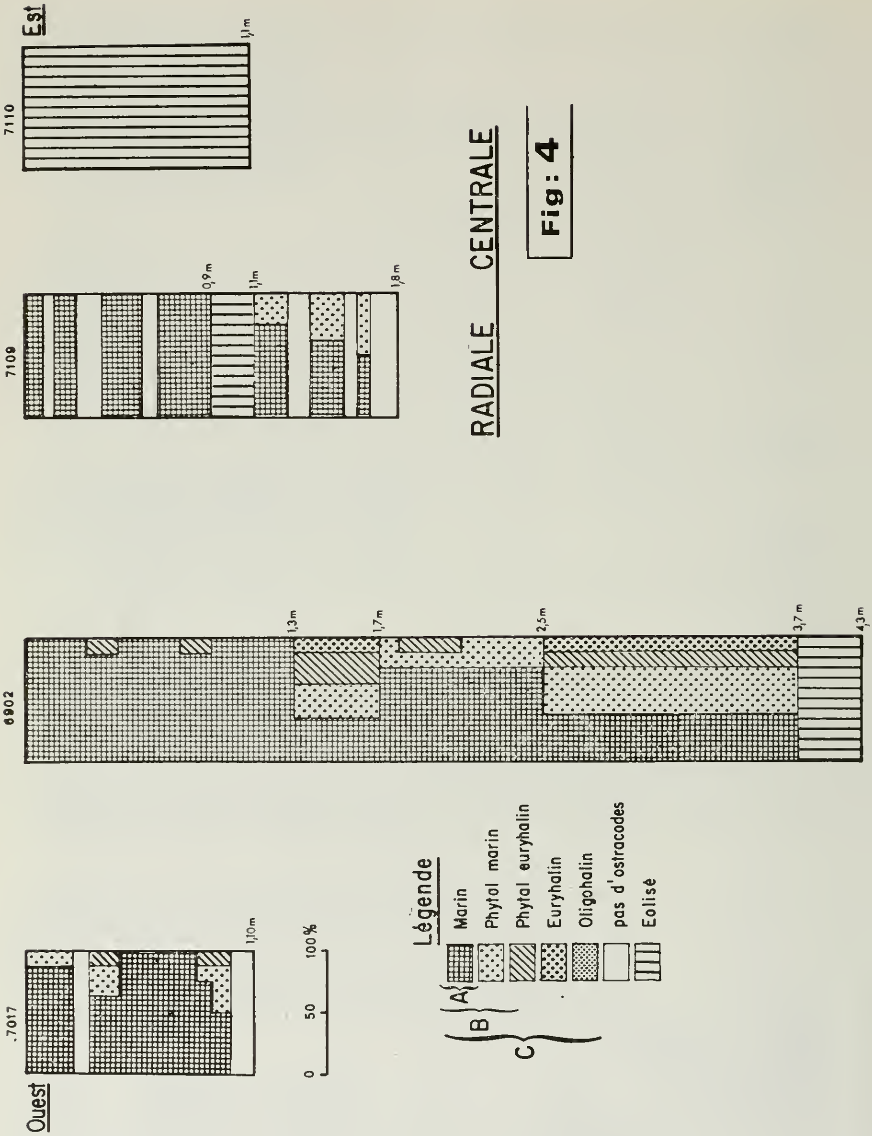
II-2. Radiale Centrale (Text-fig. 4).

Carotte C. 7017 (1,10 m) : vases homogènes, très plastiques dans lesquelles on trouve une microfaune de type "A", avec localement (vers 0,50 m) un très faible pourcentage d'espèces phytales sténohalines et parfois euryhalines.

Carotte C. 6902:
4,30 à 3,70 m: sables grossiers, roux, souvent éolisés, avec des galets, sans trace d'Ostracodes.
3,70 à 2,50 m: alternances de vase fine et de niveaux silteux à nombreux débris coquilliers et traces de bioturbation. L'ensemble faunique est caractérisé par l'exceptionnelle richesse qualitative et quantitative de l'association "C".
2,50 à 1.70 m: vases relativement fines à nombreux débris coquilliers. L'ensemble faunique exclusivement marin est de type "B".
1,70 à 1,30 m: vases avec quelques alternances silteuses. L'association faunique est semblable à celle reconnue entre 3,70 m et 2,50 m.
1,30 à 0 m: vases homogènes avec de rares coquilles et les traces de bioturbations; la faune est de type "A".

Une datation au 14 C réalisée entre 3,30 m et 3,10 m a donné un âge de 10 000 ans B. P. (M. Vigneaux, *et al.,* 1971).

Carotte C. 7109:
1,80 à 1,10 m: vase plastique homogène, dont quelques rares niveaux renferment une microfaune d'Ostracodes de type "B".
1,10 à 0,90 m: sables grossiers avec de nombreuses traces d'éolisation. pas d'Ostracodes.
0,90 à 0 m: vase brune très plastique et riche en matières organiques, renfermant une microfaune de type "A".



RADIALE CENTRALE

Fig: 4

Carotte C. 7110 (1,10 m) : sables moyens, jaunes, homogènes et souvent éolisés, dépourvus d'Ostracodes.

Dans les sédiments carottés de cette radiale, la faune possède un caractère marin accusé; les influences estuariennes sont pratiquement inexistantes ainsi qu'en témoigne l'absence totale de formes euryhalines et oligohalines.

A l'extrémité la plus orientale de la radiale, le dépôt correspond à un ancien "cordon dunaire" (C. 7110) analogue à celui matérialisé par la carotte C. 6608 de la radiale précédente.

En succession verticale, la microfaune de la carotte C. 7017 évolue très peu, comme celle de la coupe C. 6607. En revanche, dans la carotte C. 6902, si la base caractérise un milieu lagunaire, comme la C. 6903, la partie supérieure reflète un environnement marin de type infralittoral interne que l'on retrouve à l'Est (C. 7109).

Enfin, la datation de 10 000 B.P. à 3,20 m permet d'attribuer aux sédiments de C. 6902 un âge holocène.

II-3. Radiale méridionale 1 (Text-fig. 5).

Carotte C. 7017: voir radiale centrale.

Carotte C. 6910 (0,90 m) : Constituée par un ensemble sableux éolisé, sans Ostracodes.

Carotte C. 7001 (0,20 m) : ensemble sablo-vaseux renfermant une association de type "C" au sein de laquelle les espèces marines sont en pourcentage peu important et les formes oligohalines toujours présentes.

Carotte C. 7005:
1,80 à 1,55 m: vase compacte avec minces lits silteux; l'association faunique de type "C" comprend un pourcentage appréciable d'espèces marines et quelques formes oligohalines.
1,55 à 1,40 m: vase plastique homogène contenant une association marine de type "B".
1,40 à 1,20 m: sables fins à silts, et intercalations de vases. Association faunique "C" semblable à celle reconnue entre 1,80 et 1,55 m.
1,05 à 1,20 m: sédiments sablo-vaseux renfermant une faune marine de type "A".
1,05 à 0,65 m: vase plastique, un peu silteuse, correspondant à des dépôts sans Ostracodes à l'exception d'une association "C" (0,80 à 0,85 m).
0,65 à 0,10 m: vase plastique un peu silteuse et intercalations de sables fins, contenant un ensemble "C" avec un pourcentage important d'espèces marines et localement quelques formes oligohalines.
0,10 à 0 m: vase très plastique homogène à microfaune marine de type "B".

Une data tion au 14 cc entre 1,50 et 1,70 m a donné un âge de 6 400 ans B.P.

Carotte C. 7028 (1,10 m) : sables grossiers éolisés sans Ostracodes.

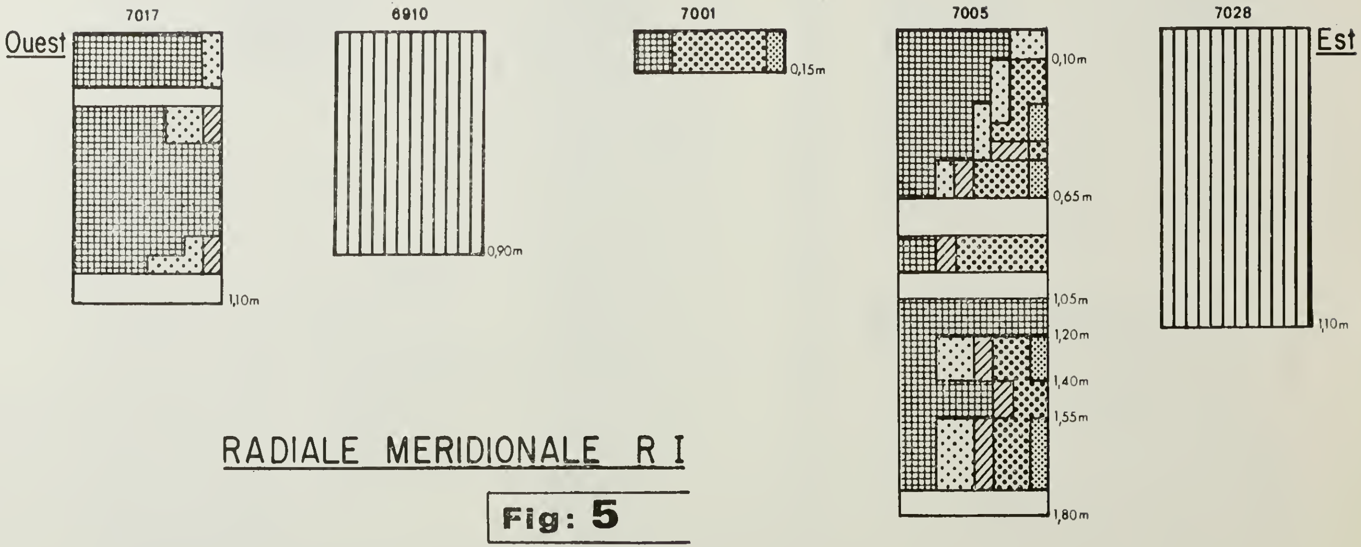
L'examen des faunes d'Ostracodes recueillies dans ces carottes permet de mettre en lumière les faits suivants:

Deux biotopes différents apparaissent: l'un à l'Ouest (C. 7017) suggérant une permanence marine; l'autre à l'Est (C. 7005) à caractère estuarien.

Séparant ces deux biotopes, la carotte C. 6910 confirme l'existence du cordon dunaire déjà mis en évidence dans la radiale septentrionale.

Vers — 20 m, les sédiments éolisés (C. 7028) suggèrent l'existence d'une zone dunaire alignée sur celle observée dans la radiale centrale.

En tenant compte de la datation au 14 C relative à la base de la



RADIALE MERIDIONALE R I

Fig: 5

C. 7005, on peut penser que l'environnement estuarien est relativement récent.
II-4. Radiale méridionale 2 (Text-fig. 6).

Carotte C. 7114 (1,45 m) : composée à la base et au sommet de vases très plastiques et dans la partie moyenne d'alternances de sables et de vases. La faune de type "A" est présente seulement dans les vases.

Carotte C. 7005 (1,80 m) : voir II-3.

Carotte C. 7112 (0,65 m) : la base et le sommet se composent de vases sableuses comprenant la faune de type "C" rencontrée dans la carotte C. 7005. La partie moyenne est constituée de sables jaunes grossiers et dépourvus d'Ostracodes.

Carotte C. 6908 (0,20 m) : vase sableuse compacte renfermant une faune pauvre de type "C".

Carotte C. 7007 (1,05 m) : galets à la base, surmontés de sables partiellement éolisés. Seuls les horizons sommitaux renferment quelques Ostracodes euryhalins.

Nous pouvons distinguer selon cette ligne:

— un domaine Sud-Ouest (C. 7114) à faune typique de la zone infralittorale interne.

— un domaine Nord-Est (C. 7005, C. 7112, C. 6908) où la faune présente un type estuarien sur toute l'épaisseur des sédiments.

— un cordon dunaire (C. 7007), déjà matérialisé (C. 7110, C. 7028) vers — 20 m.

Les informations fournies par ces deux dernières radiales semblent indiquer le passage direct à travers un cordon dunaire (C. 6910, C. 7028), d'un estuaire à la mer.

II-5. Si nous synthétisons les observations analytiques relatives à chaque radiale, nous pouvons formuler les conclusions suivantes:

Il existe suivant une coupe verticale une succession d'associations fauniques d'Ostracodes semblable à celle observée en surface depuis la zone centrale à microfaune marine homogène jusqu'aux parties septentrionale et méridionale dans lesquelles l'ensemble faunique est complexe.

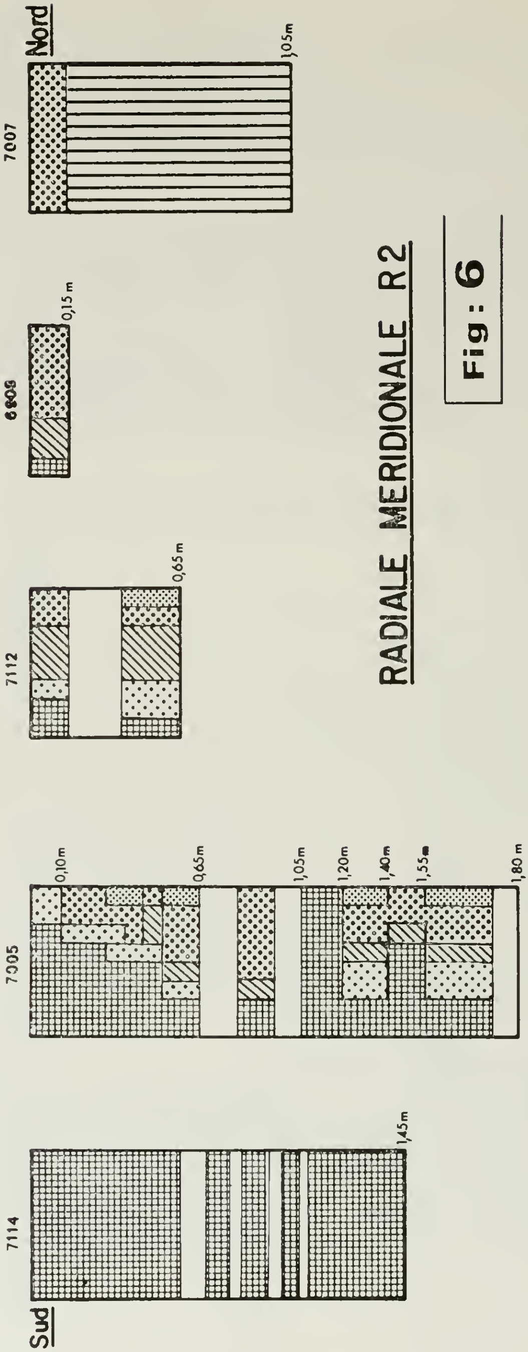
Les sédiments de surface éolisés, dépourvus d'Ostracodes, se poursuivent en profondeur. Ce phénomène d'éolisation prouve que ces sables étaient émergés avant la transgression holocène et appartenaient vraisemblablement à des dunes. Ces dernières semblent avoir formé une barrière importante à la transgression marine vers l'isobathe — 50 m (C. 6608, C. 6910), puis vers — 20 m en face de l'embouchure de la Gironde actuelle (C. 7110, C. 7109, C. 7007, C. 7028).

Les sédiments éolisés ont aussi été reconnus en carottes, sous une épaisseur plus ou moins grande, entre les cordons dunaires de — 50 m et — 20 m. Ceci tend à prouver l'existence d'une cuvette cernée par les dunes.

A l'Ouest du cordon dunaire de — 50 m, se rencontre (C. 6607, C. 7017, C. 7114) une microfaune homogène "A", typique d'un milieu infralittoral interne.

A l'Est et au Nord de ce même cordon, le caractère marin de la microfaune tend à s'estomper progressivement. Ainsi, dans la carotte C. 6902, l'association faunique est toujours marine; ce caractère est encore bien marqué dans la coupe C. 7109, mais il devient plus difficile à discerner dans le domaine plus oriental (C. 7108). Au Nord, les Ostracodes montrent toujours la dualité des influences marines et estuariennes (C. 6903). Toutefois, le cachet marin est prédominant.

Dans le partie méridionale, il semble que nous soyons à proximité d'une embouchure de fleuve, car nous avons un passage rapide du milieu marin



RADIALE MERIDIONALE R2

Fig : 6

(C. 7114) à un milieu estuarien. En effet, la carotte C. 7005 offre une faune complexe au sein de laquelle se manifeste constamment le conflit entre les influences marines et fluviatiles.

D'une manière schématique, la succession verticale des faunes indique un caractère marin de plus en plus franc au fur et à mesure que l'on se rapproche de la période actuelle. Le passage de l'environnement laguno-marin à celui de mer ouverte est particulièrement net et rapide dans la partie centrale (C. 6902). Cette évolution est moins marquée dans les zones septentrionale et méridionale et estompée près de la surface par la présence d'ensembles fauniques euryhalins incompatibles avec la position du prélèvement.

Nous sommes donc amenés à penser que ce domaine a évolué par étapes depuis un environnement continental et fluviatile jusqu'au domaine marin actuel. L'âge de 10 000 ans donné par le 14 C nous permet de situer de début de cette histoire à l'Holocène.

III. ESSAI DE RECONSTITUTION PALEOGEOGRAPHIQUE

Il est alors tentant de voir ce que la seule étude des Ostracodes peut apporter dans une reconstitution des paléogéographies successives de la zone considérée durant l'Holocène.

III-1. Si nous considérons la région à une période antérieure à 10 000 ans B.P., nous avons peu d'informations. En effet, seuls les sédiments de la C. 6902 (3,70-3,50 m) renferment des microorganismes marins de type infralittoral interne et phytal, et l'analyse lithologique montre que les sédiments de base suggèrent un delta de marée (M. Vigneaux *et al.,* 1971). A l'Ouest, le long de l'isobathe actuel — 50 m, les sables roux, grossiers, souvent éolisés, avec de nombreux débris coquilliers traduisent des milieux de plages en avant des cordons dunaires (C. 6910, C. 6608). Dans la région la plus occidentale, on note la permanence d'une faune marine typique d'un plateau continental sableux (C. 7017, C. 7114).

On peut donc imaginer (Text-figs. 7) qu'avant le début l'Holocène le rivage marin se situait vers — 50 m. En arrière de la plage, des dunes, semblables à celles du littoral aquitain actuel dessinaient des reliefs de faible amplitude. Un fleuve, qui se marque dans les sédiments par un delta de marée, atteignait directement la mer à travers les dunes. Vers l'Est, une plaine alluviale pouvait s'étendre en avant d'un second cordon dunaire situé aux environs de la cote — 20 m.

III-2. Avec le début de l'Holocène, la transgression flandrienne se poursuit en occupant la zone située immédiatement à l'Est de la barrière sableuse et donne naissance dans la partie centrale à une lagune marine. En effet dans la carotte C. 6902, on rencontre les formes caractéristiques du biotope phytal sténohalin associées aux formes d'origine océanique et à celles qui sont caractéristiques des biotopes sableux euryhalins.

D'un point de vue qualitatif et quantitatif cette microfaune d'Ostracodes ressemble à celle signalée par I. Yassini (1969) dans les chenaux du bassin d'Arcachon. Ainsi, peut-on penser que la faune de cette carotte est le témoig-

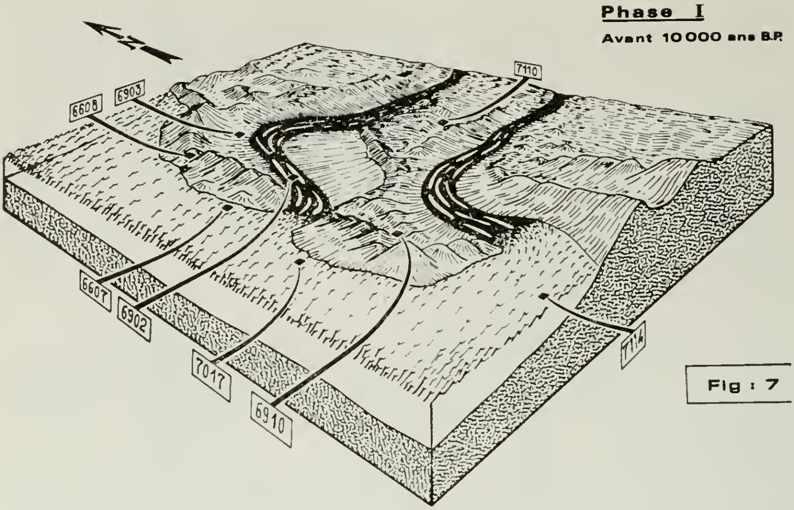


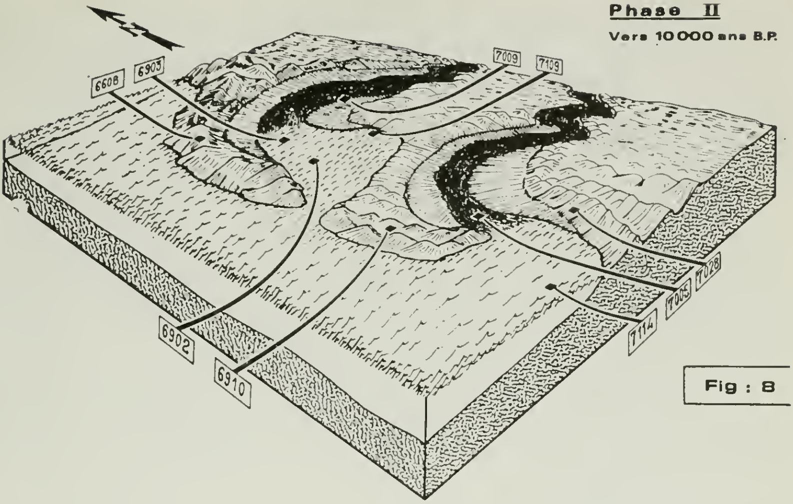
Fig : 7

nage d'un environnement de chenal peu profond à substrat sablo-vaseux, tapissé par les algues et largement alimenté par l'onde marine avec une salinité allant de 30 à 33%.

Dans la carotte C. 6903, les associations fauniques complexes de type "C" sont caractérisées par l'importance des formes euryhalines et la présence d'espèces oligohalines. Elles attestent ainsi du débouché d'une rivière dans une lagune (Text-fig. 8), dont l'extension est difficile à préciser: néanmoins, on peut la reconnaître à l'Est jusqu'aux carottes C. 7108 et 7109 et au Nord, au-delà de la carotte C. 6903.

III-3. Puis dans une étape ultérieure, la mer déborde les cordons dunaires occidentaux et modifie complètement (Text-fig. 9) le paysage précédent selon le schéma suivant:

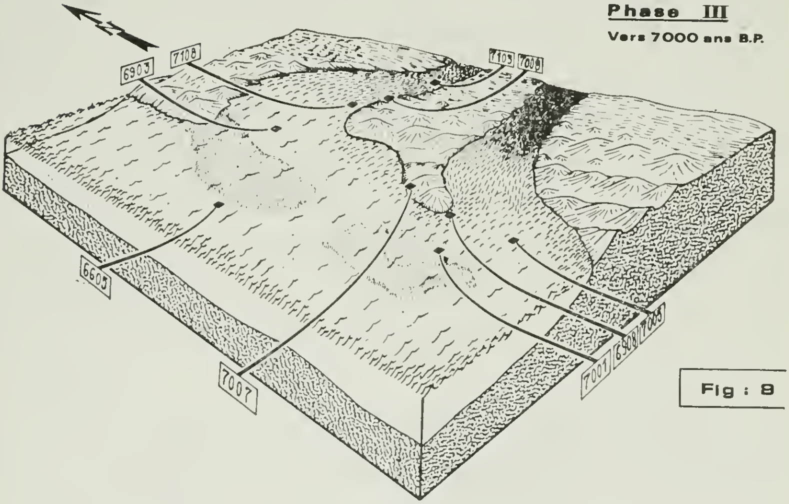
Dans le secteur central (carottes C. 6902, C. 7109) il y a passage rapide et sans transition de l'état lagune marine à celui de mer ouverte. On constate en effet un rapide déclin des formes phytales au profit des espèces marines de l'association "A". Il est évident que l'augmentation rapide de la tranche d'eau qui occupe cette région a pour conséquence de faire péricliter les algueraies qui s'étaient développées, et par là-même les Ostracodes qui vivaient. Ce fait semble en accord avec le taux de remontée important du niveau marin mis en évidence par A. Feral, (1970) entre 10 000 et 7 000 ans B.P. environ. De plus, on constate que la granulométrie de ces carottes devient



Phase II

Vers 10000 ans B.P.

Fig : 8



Phase III

Vers 7000 ans B.P.

Fig : 8

de plus en plus fine. Une "vasière" se forme donc très rapidement et fonctionne en tant que telle, probablement vers cette dernière date. L'absence de formes euryhalines et oligohalines dans ce secteur peut s'expliquer par le fait que le cordon dunaire Est (C. 7110, C. 7009) protégeait la lagune des arrivées d'eau douce.

Au Nord et au Sud, la microfaune d'Ostracodes présente des similitudes que traduit la présence de formes euryhalines et oligohalines. Ces formes sont les témoins des environnements "estuariens" qui se sont établis alors.

Dans le secteur septentrional, les plus anciennes empreintes de ce type d'environnement sont situés à l'Ouest (partie moyenne et supérieure de la carotte C. 6903) puis vers l'Est (carotte C. 7108 et C. 7103). On y reconnaît notamment les espèces des biotopes phytaux euryhalins semblables à ceux qui existent actuellement dans la partie aval de la Gironde entre la Coubre et Talmont (P. Carbonel, J. Moyes, J. P. Peypouquet, 1972).

Ce fait implique, que durant cette phase, et sur la trajectoire Ouest-Est définie ci-dessue, existaient des milieux euryhalins estuariens dont la salinité évoluait de 15 à 28% pour les zones les plus continentales à 28%-33% pour les plus marines.

Il est difficile de dater avec précision cette étape dans l'Holocène. Toutefois, en reprenant l'hypothèse précédemment émise par Feral, 1970 sur l'évolution de l'estuaire de la Gironde, on peut considérer qu'il y a environ 10 000 ans B.P., ce fleuve avait un régime dit à méandres. A partir de 10 000 ans B.P. par suite du taux de remontée du niveau marin particulièrement élevé (1,50 m par siècle en moyenne), le régime fluvial va se transformer complètement et devenir de type estuarien vers 7 000 ans environ. On peut donc admettre cette date pour l'établissement d'un estuaire dans cette zone.

Dans le secteur méridional, on constate l'absence de lagune marine. La zone de plate-forme continentale (C. 7114) communique avec une zone estuarienne très complexe (C. 7005) située au milieu d'un "couloir" dunaire (C. 6910, C. 7028). L'établissement de ce paysage date de 6 400 ans B.P. (Text-figs. 5, 6).

L'absence de faune d'âge antérieur à 6 400 ans B.P. dans cette région peut s'expliquer par le fait que nous sommes dans une zone de passage fluviatile relativement étroite ("couloir" dunaire, C. 7007, C. 7005, C. 7028). Ceci implique une mobilité des fonds incompatible avec l'établissement de biotopes phytaux favorables au développement des Ostracodes, ou avec le dépôt de microfaune transportée.

De la même manière que dans le secteur septentrional, on peut suivre le déplacement de ce type d'environnement dans les carottes C. 7112 et C. 6908 en direction de l'estuaire actuel de la Gironde. Mais, il est fort possible que le raccord ait pu s'effectuer avec les passes fossiles du chenal de Soulac datant de 6 000 ans B.P. signalé par A. Feral, (1970).

Que ce soit dans le secteur septentrional ou dans le secteur méridional, on constate la permanence du type estuarien tout le long des carottes C. 7005, C. 7013, C. 7108, C. 7112 et seule une faible épaisseur de sédiments au sommet de celles ci présente une faune au caractère marin infralittoral interne.

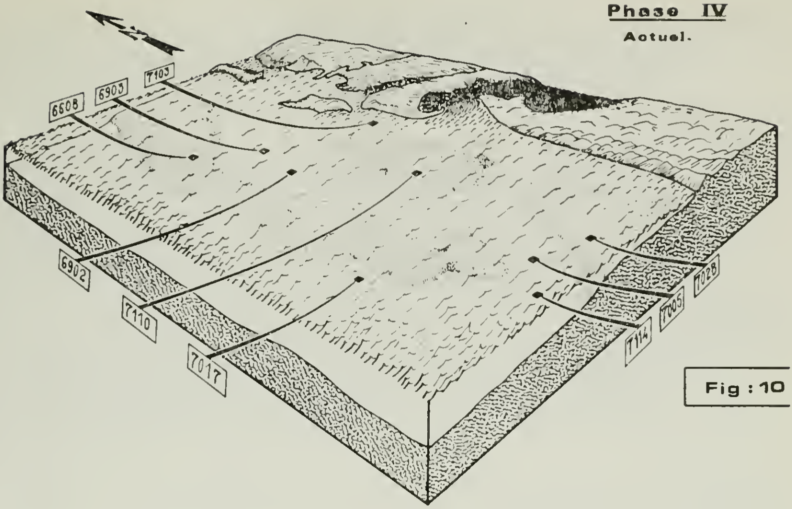


Fig : 10

Il semble que ce phénomène puisse expliquer dans une certaine mesure le fait qu'à partir de 5 000 ans B.P. le taux de remontée du niveau marin est inférieur à 0,25 m par siècle (A. Feral, 1970), ceci implique donc une évolution lente et un passage très graduel du régime estuarien au régime marin pour cette zone.

III-4. Dans une dernière phase, la mer franchit le cordon dunaire de — 20 m (carottes C. 7007, C. 7110, C. 7028) et repousse vers l'Est les domaines estuariens. En effet, la faune marine infralittorale interne "A", marquée toutefois par des apports euryhalins actuels en provenance de la Gironde (P. Carbonel, 1971), s'installe alors dans les secteurs septentrional et méridional de la zone étudiée. Finalement, l'onde marine atteint le littoral aquitain (Text-fig. 10) entaillé par un nouvel et unique estuaire entre Royan et le Verdon. C'est l'époque actuelle.

BIBLIOGRAPHIE

Carbonel, P.

1971. *Les ensembles fauniques d'Ostracodes récents de l'estuaire de la Gironde et du proche plateau continental. Relations avec les phénomènes hydrodynamiques. Intérêt dans la reconstitution des paléoenvironnements.* Thèse 3ème Cycle. Univ. Bordeaux I, 209 pp., XV pl., 37 fig.

Carbonel, P., Moyes, J. et Peypouquet, J. P.

1972. *Ostracodes du domaine phytal intertidal dans la partie aval de l'estuaire de la Gironde et dans la zone N.W. de l'île d'Oléron.* Bull. Inst. Géol. Bassin d'Aquitaine, Bordeaux. Vol. 12, pp. 191-194.

Feral, A.
1970. *Interprétation sédimentologique et paléogéographique des formations alluviales flandriennes de l'estuaire de la Gironde et de ses dépendances marines.* Thèse 3ème cycle. Univ. Bordeaux I, 158 pp., 62 fig., 2 tabl.

Vigneaux, M.
1971. *Bilan d'étude d'environment marin et applications dans le Golfe de Gascogne. Colloque International sur l'Exploitation des Océans, Bordeaux (France), Mars 1971,* CNEXO Paris, Thème III, tome 2, G. 1 05, 66 pp., 29 fig., 5 tabl.
1972. *Bilan cartographique des études effectuées sur le plateau continental aquitain au 28 Février 1972 par l'Institut de Géologie du Bassin d'Aquitaine.* Bull. Inst. Géol. Bassin d'Aquitaine, Bordeaux, No. Spécial, 1972, 25 pp., 5 figs., 13 cartes h.t.

Yassini, I.
1969. *Ecologie des associations d'Ostracodes du Bassin d'Arcachon et du littoral atlantique. Application à l'interprétation de quelques populations du Tertiaire aquitain.* Bull. Inst. Géol. Bassin d'Aquitaine, Bordeaux, No. 7, 1969, 288 pp., 39 pl., 3 fig., 54 tabl.

Pierre Carbonel,
Jean Moyes, et
Jean-Pierre Peypouquet,
Laboratoire de Géologie et Océanographie
Université de Bordeaux I,
Talence, France.

DISCUSSION

Dr. J. C. Kraft: The Holocene environmental reconstructions are very impressive. I am interested in a detailed listing of the supporting ostracode faunas. Are they available in the paper to be published?

Authors' reply: The species from the various environments are in the text.

Dr. H. Löffler: Are ostracodes absent from the eolian sands since transparency at that depth still would provide for algae attached to sand grains?

Authors' reply: At the bottom, the eolian sands are relatively fine-grained (1 mm) which is not favorable to the installation of algal biotypes, and hence phytal ostracodes. Moreover these sediments contain no silt and clay. Hence, there is no layer of organic matter and mud on the bottom. Therefore, continental shelf ostracodes of the internal-infralittoral zone can't develop.

These eolian sands represent ancient shore sands which were constantly reworked by tides. Ostracodes could not live in this unstable substrate.

Dr. G. Hartmann: As far as my experience goes, the shore sand is not at all populated by ostracods because of the movement of the sediments only the interstitial system is populated.

Authors' reply: We are of the same opinion as Dr. Hartmann. The coastal sands of the Bay of Biscay contain no ostracodes.

OSTRACODE BIOFACIES IN THE CAPE HATTERAS, NORTH CAROLINA, AREA

Joseph E. Hazel*
U. S. Geological Survey

ABSTRACT

Thirty-eight samples spaced on a grid around Cape Hatteras at depths of 15 to 90 meters contain a total of 126 species of ostracodes. The comparison of these samples on the basis of the presence and abundance of the species, using a multistate quantitative measure and principal coordinates analysis, allows the recognition of three biofacies and the position of the boundary between the Virginian and Carolinian faunal provinces. A Carolinian biofacies is present in the vicinity of Cape Hatteras in northern Raleigh Bay, on Diamond Shoals, and immediately east and north of the cape. The second biofacies assigned to the Carolinian Province occupies eastern and southern Raleigh Bay. A third biofacies is assigned to the Virginian Province and is found north and northeast of Cape Hatteras. The principal control on the major faunal discontinuity appears to be summer bottom temperature; the boundary between the provinces closely approximates the 22.5°C and 25.0°C isotherms for the warmest month.

BIOFACIES D'OSTRACODES AUX ENVIRONS DE CAPE HATTERAS, CAROLINE DU NORD

RÉSUMÉ

Trente huit échantillons pris à des profondeurs de 15 à 90 mètres, à distance régulière l'un de l'autre aux environs de Cape Hatteras contiennent au total 126 espèces d'Ostracodes. La comparaison de ces échantillons en considérant la présence et l' abondance des especes et en utilisant de coéfficient de corrélation (r) et l'analyse des coordonnées principales, permet de reconnaitre trois biofaciès et de tracer la frontière entre les provinces fauniques virginienne et carolinienne. Un premier biofacies carolinien a été trouvé aux environs de Cape Hatteras, dane la partie nord de Raleigh Bay, à Diamond Shoals, et immédiatement à l'est et au nord de Cape Hatteras. Un second biofaciès appartenant à la province carolinienne se trouve dans la partie est et sud de Raleigh Bay. Le troisième biofaciès qui fait partie de la province virginienne a été retrouvé au nord et au nord est de Cape Hatteras. La discontinuité faunique parait être occasionée principalement par la température estivale des fonds marins: les différentes provinces se touchent sur les isothermes de 22.5°C et 25°C du mois le plus chaud.

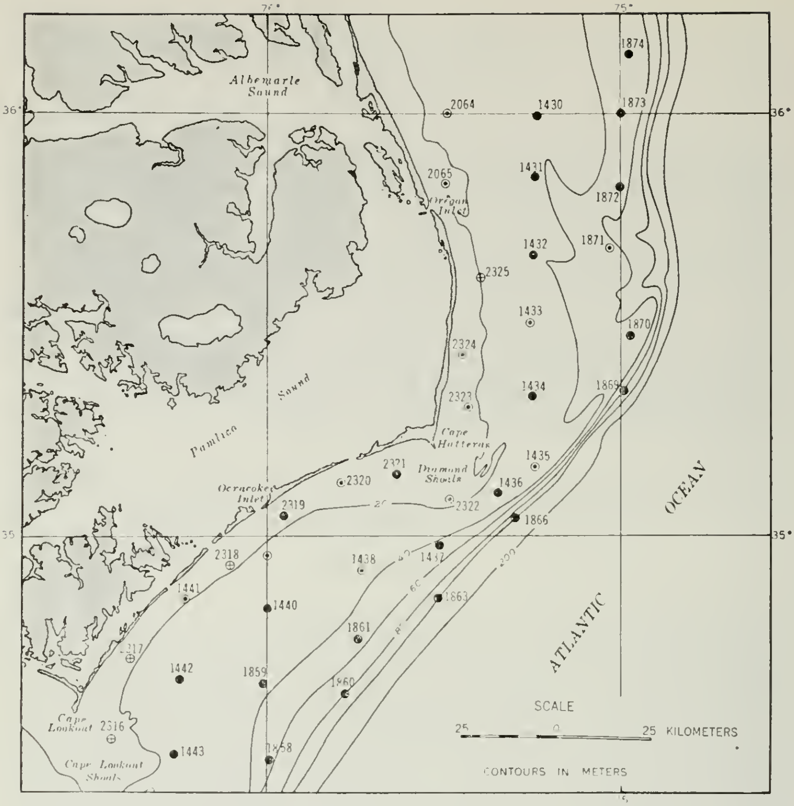
INTRODUCTION

It has been known for many years that in the Cape Hatteras, North Caroline, area (Text-fig. 1) many benthic invertebrates cease their equatorward or poleward expansion. Cape Hatteras has been designated a boundary between two faunal provinces by several authors (Hazel, 1970a, for a review). The most consistently used terminology for these provinces is Carolinian for the area south of the Cape and Virginian in the area to the north; the terms were first proposed by Dana (1953a,b). Until recently no attempts were made to determine the configuration on the continental shelf of this provincial boundary.

The primary purpose of the present paper is to document the distribution of similar ostracode assemblages on the continental shelf; similarity in this

---

*Publication authorized by the Director, U.S. Geological Survey.



Text-figure 1. — Location of the 38 collecting stations in the Cape Hatteras, North Carolina, area. Black dots, samples relatively rich in ostracodes; ccircled dot, ostracode density low; circled cross, samples barren. The nearshare area between Cape Hatteras and Cape Lookout is Raleigh Bay. Onslow Bay is the next embayed area to the south.

case is determined by utilizing counts of the species and a multistate quantitative similarity measure. Cluster (in R-mode) and principal coordinates analysis (in Q-Mode) were used to analyze the similarity matrices. Three major biofacies have been delineated using 38 samples containing 126 species (Text-fig. 1; table 1; table 2).

A secondary aspect of the study was to see if the patterns of biofacies could be related to macroenvironmental factors. It is shown that the major faunal boundary in the area is related to the distribution of summer bottom temperature.

A list of the more important species found in the study area is included.

ACKNOWLEDGMENTS

I am indebted to P. C. Valentine, U.S. Geological Survey, who in 1969 and 1970 collaborated in the identification of the ostracodes from most of the samples used in the present study as well as others from the Atlantic shelf (Valentine, 1971).

I also thank R. H. Benson and M. A. Buzas of the Smithsonian Institution for critically reading the manuscript.

RECENT PREVIOUS WORK

Cerame-Vivas and Gray (1966), utilizing marine macroinvertebrate occurrences in samples primarily from immediately south and north of Diamond Shoals and northeast of Oregon Inlet, qualitatively recognized three faunal areas near Cape Hatteras which they termed simply A, B, and C. Their area A, on the middle and inner shelf north and east of the cape, they considered to be inhabited by a southern extension of the arctic and boreal fauna. They also place their area A in the Virginian Province. (These two statements are incompatible; the Virginian Province is really climatically mild temperate, see Hall, 1964; Hazel, 1970a). Their area B, middle and inner shelf south of the cape, is one of ". . . mixed fauna which may receive components from the northern waters of area A and the tropical waters of area C, the latter being the larger contributor . . . there are other species characteristic of B itself," (Cerame-Vivas and Gray, 1966, p. 264). Cerame-Vivas and Gray pointed out that under certain winter wind conditions, cool waters of the Virginia Coastal Current penetrate into inshore Raleigh Bay and even into adjacent Onslow Bay. In such a situation, temporary populations of cryophilic species with planktonic larvae may appear in Raleigh Bay. Cerame-Vivas and Gray suggested that area B represents the Carolinian Province, and area C, on the outer shelf east and southeast of the cape, represents a northern extension of the "tropical" Gulf of Mexico and Caribbean fauna.

Maturo (1968), in a study of the bryozoans of the Atlantic shelf and slope, recognized two principal biofacies in the Cape Hatteras area. North and northeast of the cape he placed assemblages in the Virginian Province with essentially the same map configuration as that shown by Cerame-Vivas and Gray (1966). South of Cape Hatteras he was not able to differentiate two biofacies and recognized the Carolinian Province and Tropical Province. Maturo noted that 76 percent of the shelf bryozoans south of Cape Hatteras seem to reach their northern limit in the cape area. Using data given by Cerame-Vivas and Gray (1966), he calculated that 74.4 percent of the benthic invertebrates they studied that live south of the cape also ceased their northward expansion in the area.

Schnitker (1971) studied foraminifer assemblages in the cape area and concluded that the shelf assemblages of Raleigh Bay are intermediate in composition between those known from north of Cape Hatteras and those from farther south on the shelf. On the basis of dominant species he recognized nearshore, central shelf, and shelf edge-upper continental slope facies north of the cape in the southern Virginian Province, and central shelf and shelf edge-upper slope facies south of the cape.

Immediately south of the present study area, Day, Field, and Montgomery (1971) studied the benthic organisms collected from 10 stations in a southeast-trending transect across the shelf from the shoreline near Cape Lookout to a depth of 200 meters. They visited each station five times, took 85 samples, and compared the stations using multivariate techniques. They recognized an offshore fauna and an inshore fauna; the latter is best represented at depths of 10 to 20 meters. Between 20 and 39 meters, a marked faunal change was noted; an outer shelf fauna is developed at depths of 40 to 120 meters; an upper slope fauna is present below 140 meters and is best represented at depths of 160 to 200 meters. Day, Field, and Montgomery attributed the inshore-offshore faunal change to the effects of instability of temperature and water movements caused by waves inshore compared with the relative stability of these factors at offshore depths. It is interesting to note that Day and others did not corroborate the conclusion of Cerame-Vivas and Gray (1966), that the outer shelf assemblages represent the Caribbean Province. They found no obvious biogeographic differences that could not be attributed to local conditions.

Valentine (1971) and Hazel (1971) divided the Atlantic shelf from New Jersey to South Carolina into four major biofacies, using a cluster analysis technique and presence-absence data for 159 species of ostracodes in 115 samples. Three biofacies were recognized in the Cape Hatteras area; two of these, their biofacies 2 and 4, were thought to be thermally controlled, whereas the composition of biofacies 3 in the immediate vicinity of Cape Hatteras and disjunct to the south was believed to be related to other physical factors. The present study is an extension of this work in which the number of individuals per species was determined for the samples in Cape Hatteras area, and several samples were added.

DESCRIPTION OF THE AREA

Geography. — The area of this study comprises the Atlantic shelf off North Carolina from the latitude of Albemarle Sound to that of Cape Lookout and between the 15- and 90-meter isobaths. This is an area of approximately 10,000 km^2 (Text-fg. 1).

Off the two capes in the area, Hatteras and Lookout, are extensive shallow areas termed Diamond Shoals (off Hatteras) and Cape Lookout Shoals. The area between the two capes is Raleigh Bay. At Cape Hatteras the shelf is at its narrowest point on the coast of the United States north of 27°30′N. The change from shelf to slope varies from 60 to 100 meters depth in the area, being shallowest east of Cape Hatteras.

Water-Masses. — The following is summarized from Bumpus (1955) and Stefansson, Atkinson, and Bumpus (1971). Four water masses have been recognized in the general area. These have been termed Virginian Coastal Water, Carolinian Coastal Water, Carolinian Slope Water, and Gulf Stream Water.

Virginian Coastal Water is thought to be composed of an admixture of slope water and river effluents from areas north of Cape Hatteras. Carolinian Coastal Water is warmer and somewhat more saline and is composed of an admixture of effluents from streams south of Cape Lookout and of Gulf Stream Water. The middle and inner shelf waters of Raleigh Bay may represent Virginian or Carolinian Coastal Waters or an admixture of these depending on seasonal circulation patterns.

Gulf Stream Water occupies the outer shelf area and the area seaward of the shelf-slope break south of Cape Hatteras in the study area. Gulf Stream Water is warmer, more saline, and nutrient-poor, relative to coastal water. Underlying Gulf Stream Water on the slope and at times penetrating onto the shelf is Carolinian Slope Water. This water is colder than Gulf Stream Water and summer coastal water and is relatively oxygen-poor. It is thought to be of Caribbean origin.

Circulation. — Cape Hatteras is the focal point of the southerly flowing Virginia Coastal Current and the northerly flowing Carolina Coastal Current. Bumpus and Lauzier (1965) indicated that in spring, summer, and fall there is a southerly flow of water in inshore Raleigh Bay. This water is from the southerly flowing Virginia Coastal Current, and Stefansson, Atkinson, and Bumpus (1971) predicted that the maximum intrusion of Virginian Coastal Water into Raleigh Bay would be in late summer and spring when runoff from the northern rivers is greatest and when there is a concomitant period of northeasterly winds. The flow of Virginian Coastal Water into Raleigh Bay is weakened by southwesterly winds. Winds in the area are predominately from the south and southwest and from the northeast to northwest. Swells are dominantly from the northeast and east (U.S. Congress, House of Representatives, 1948; U.S. Army Corps Engineers, 1964).

Von Arx (1962, p. 344) discussed the vagaries in position of the Florida Current in the Cape Hatteras area. He pointed out that the position of the current maximum can oscillate offshore for a period of days, then approach the coastline, covering as many as 35 miles in 4 days; it then retreats to its mean position in 3 to 4 days. When the core of the current moves toward shore, so does a field of sloping isotherms. Water near the bottom can be left behind as the current retreats (von Arx, 1962; Blanton, 1971; Stefansson, Atkinson and Bumpus, 1971). The last authors considered the source of this water to be the Caribbean water mass underlying the Florida current and stated that the intrusions are partly wind controlled and favored by southerly or southwesterly winds as well as by stratification.

Temperature. — Northerly flowing warm currents and southerly flowing cool currents meet at Cape Hatteras. Thus, along the North Carolina coast from Bogue Island to Cape Hatteras, a distance of 50 statute miles, the average surface temperature for February changes from about 10°C to 15°C (Schroeder, 1966). In contrast, along the Atlantic Coast of Western Europe in February it averages 10°C at Brest, France, and 15°C at Tangier, Morocco, a distance of 1400 miles (data from Defant, 1961).

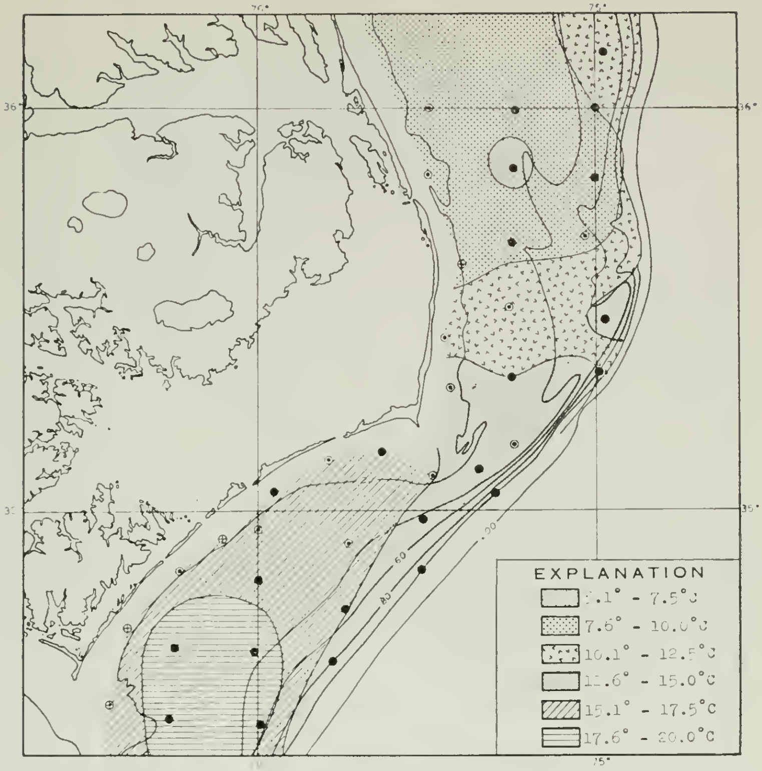
The confluence of cool and warm currents in the Cape Hatteras area precludes the development on the American Atlantic Coast of a climate even roughly similar to the classic warm-temperate zone of the eastern North Atlantic. That zone is inhabited by the assemblages of the Lusitanian faunal province which is found in the western Mediterranean and along the Atlantic Coast of the Iberian Peninsula and southwestern France. This fact has been often ignored, with the result that the southeastern coast of the United States has been referred to as warm temperate (for example, Johnson, 1934; Stephenson and Stephenson, 1954). Dana (1853a, b) placed his Carolinian Province in the warm-temperate zone; however, he was well aware of the pinching out of eastern Atlantic climatic regimes. He recognized a five fold division of the temperate zone, and his warm-temperate zone would be referred to as subtropical or outer tropical by most (for example, Hall, 1964). Valentine (1971) and Hazel (1971) indicated that a warm-temperate climate existed along the Middle Atlantic Coast during late Pleistocene and the Miocene-early Pliocene time.

In the study area during the warmest time of the year, August-September, the surface temperatures average between 25°C and 28°C (Schroeder, 1966; Walford and Wicklund, 1968). During the coldest month, however, the range in temperature of surface water over the shelf is much greater, being as low as 7.5°C in the north and as high as 20°C in Raleigh Bay.

Bottom temperatures, of course, are more important in understanding the distribution of benthic organisms. Recently, Walford and Wicklund (1968) presented bottom-temperature maps for the most of the Atlantic shelf. These authors constructed vertical monthly temperature profiles across alternate quarter degrees, plotting the averages for standard depths at the center of each quarter-degree square. The bottom temperatures were estimated from the monthly profiles, and maps with isotherms in 2.5°C intervals were drawn. The maps represent the only bottom temperature data available in a condensed form covering an extended period of time (50 years).

Text-figures 2 and 3 are bottom-temperature maps based on the average for the coldest and warmest month at each of the 38 stations of the present study. The data were taken from the 12 bottom-temperature maps of Walford and Wicklund (1968), placed on the sample base map (fig. 1), and contoured. These maps should be more useful in interpreting the distribution of organisms than maps for particular months.

The periodic influx of cooler Virginian Coastal Water into Raleigh Bay is not evident on these maps or on the surface-temperature maps provided by Schroeder (1966). The surface-temperature maps by Walford and Wicklund (1968, pls. 2, 3) for February and March, however, do show some indication of this. Occasionally, under the influence of persistent northeast winds, the temperatures in Raleigh Bay can become abnormally quite low. Stefansson and Atkinson (1967, p. 7, figs. 14, 20) indicated that in late February and early March of 1966, bottom temperatures in inshore Raleigh Bay averaged between about 5°C and 10°C. However, it was 20°C at one of their stations in outer

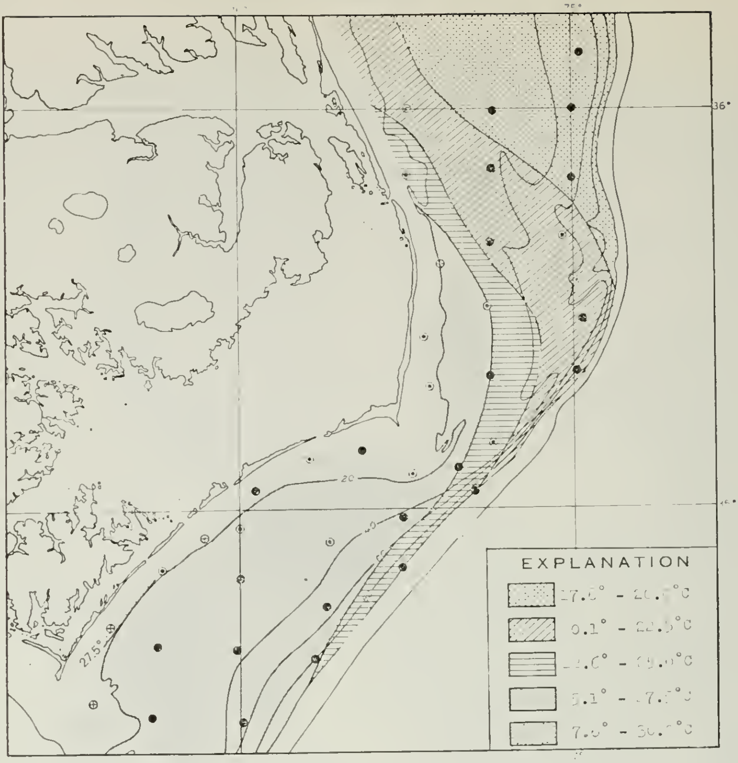


Text-figure 2. — Distribution of winter bottom temperature. Based on coldest monthly average bottom temperature at each station. Data from Walford and Wicklund (1968). Sample stations explained in Text-figure 1.

Raleigh Bay. The occasional influx of cooler waters into Raleigh and even Onslow Bay apparently allows some cryophilic species with planktonic larval stages to establish themselves outside their normal ranges (Wells and Gray, 1960; Cerame-Vivas and Gray, 1966). It is doubtful, however, if benthic species without planktonic larvae, such as ostracodes, could take advantage of short-term events such as this.

Bottom sediment. — Milliman (1972), Milliman, Pilkey, and Ross (1972), Milliman, Pilkey, and Blackwelder (1968), have indicated on a series of maps the major sedimentary patterns on the shelf in the present area of study. The samples used by those authors are in part the same as those used in the present study.

Milliman (1972) classified the bottom sediments seaward of Ocracoke Inlet and on Diamond Shoals as of questionable modern fluvial origin; the rest of the surficial sediments in the area are considered to be relict Pleistocene



Text-figure 3. — Distribution of summer bottom temperature. Based on warmest monthly average bottom temperature at each station. Data from Walford and Wicklund (1968). Sample stations explained in Text-figure 1.

and of continental origin. North and east of Cape Hatteras and over most of inner and central Raleigh Bay there is less than 5 percent carbonate in the sand-sized fraction. In southern and eastern Raleigh Bay, the carbonate percent increases to 5-25, with patches of higher percentages. In northern and eastern Raleigh Bay, the non-carbonate fraction is composed of subarkosic quartz sands; more orthoquartzitic sands predominate in southern Raleigh Bay.

Grain size of the bottom sediment is generally thought of as an important factor in influencing the composition of benthic assemblages. Data on the weight percent of material in each sediment-size grade from Phi 17 to Phi -10 for each sample are given by Hathaway (1971). These data have been grouped herein in the following manner:

Gravel	$\emptyset = < 0.0 = > 1.0$ mm
Coarse sand	$\emptyset = 0\text{-}1.0 = 0.5\text{-}1.0$ mm
Medium and fine sand	$\emptyset = 1.5\text{-}3.0 = 0.125\text{-}0.49$ mm
Very fine sand	$\emptyset = 3.5\text{-}4.0 = 0.0625\text{-}0.1249$ mm
Silt and clay	$\emptyset = > 4.0 = < 0.0625$ mm

The weight percents for each of these modal-size classes were normalized by taking the arcsin of the square root of the percentage and multiplying by two. Each station was then compared on the basis of the represented size-classes using the correlation coefficient (r) as a similarity measure and clustered by the unweighted pair-group method. The major clusters in the resulting dendrogram (Text-fig. 4) delineate grain-size bottom facies that can be mapped (Text-fig. 5). A principal components analysis of the same data resulted in essentially the same grouping of samples with 88 percent of the variation explained in the first two dimensions.

Diamond Shoals and the shelf immediately east of Cape Hatteras are covered by very fine sands (47 to 72 percent by weight) with very significant percentages (26 to 49) of medium and fine sand (cluster A in fig. 4; fig. 5). Cluster B is composed of the only two samples studied with significant amounts of silt and clay (16 to 24 percent); however very fine sand predominates (61-82 percent). One of these samples was taken at the shelf edge east of Cape Hatteras and the other in Raleigh Bay off southwestern Hatteras Island.

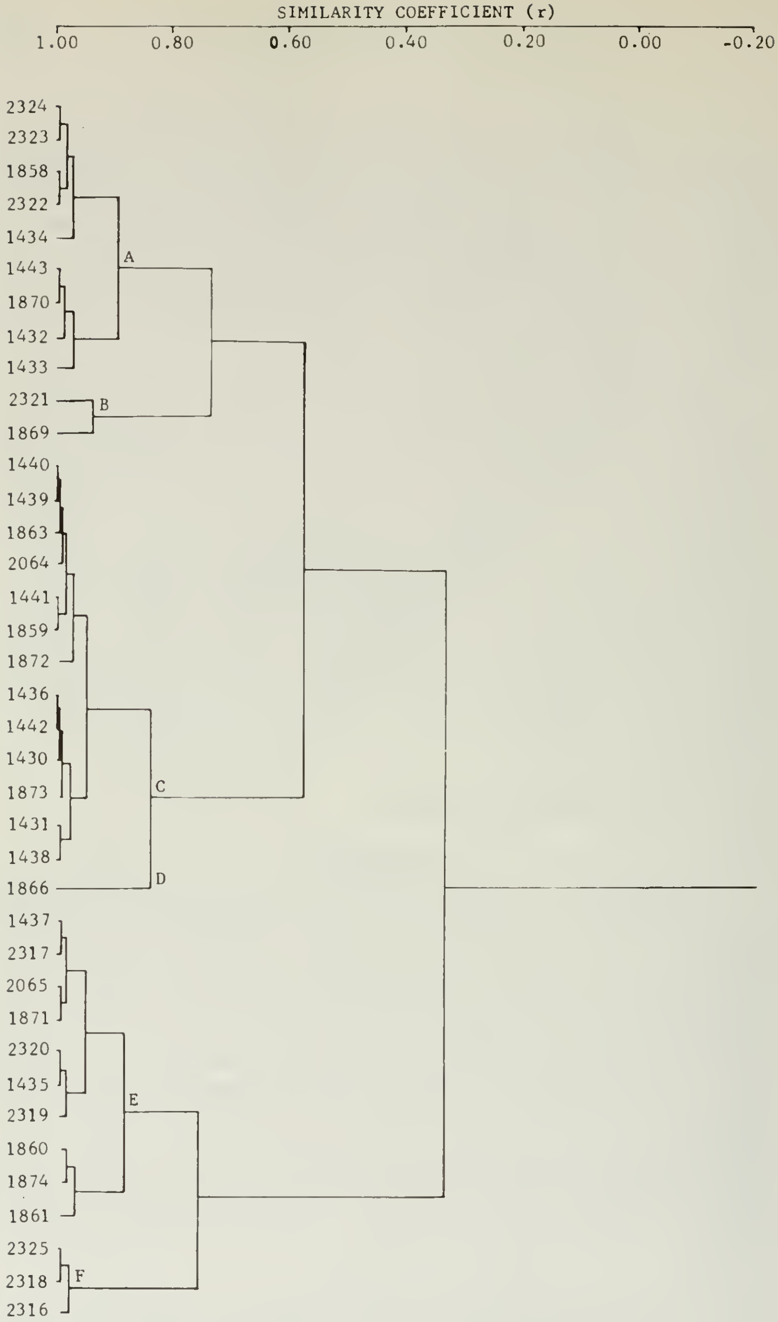
Inshore Raleigh Bay and Cape Lookout Shoals contain areas where coarse sand predominates (cluster F). Another area of coarse sand is off northern Hatteras Island. Large areas where coarse sand is mixed approximately equally with medium and fine sand (cluster E) are present in inshore Raleigh Bay, on Cape Lookout Shoals, and on the inner shelf north of Cape Hatteras. Patches of this sediment facies occur on the outer shelf south and north of Cape Hatteras.

Most of Raleigh Bay and the shelf north of Cape Hatteras is covered with medium and fine sand (cluster C).

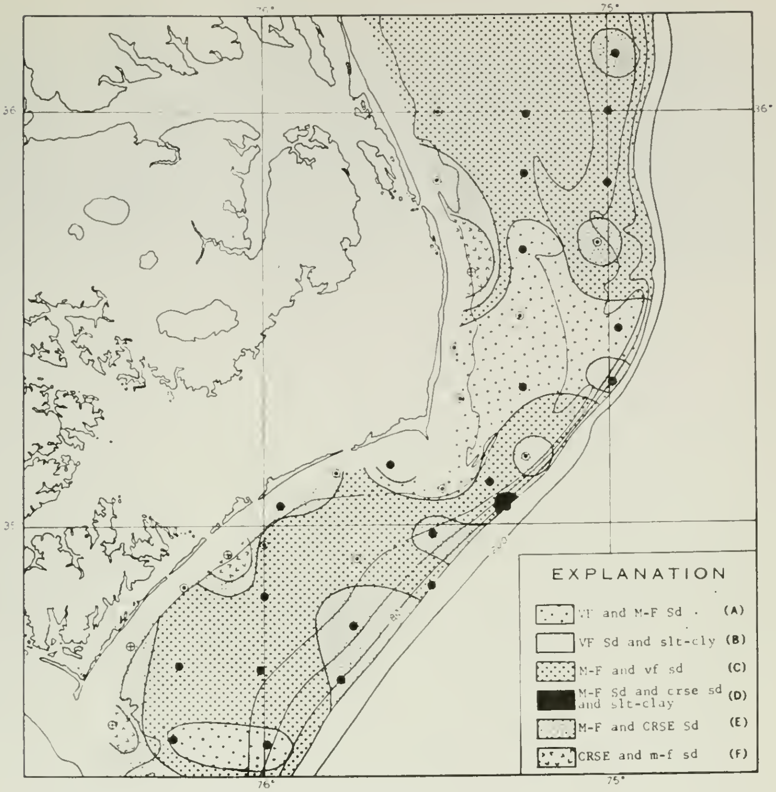
SAMPLING

The material used in this study was collected as part of the U.S. Geological Survey-Woods Hole Oceanographic Institution program to study the Atlantic continental margin. The 38 samples were taken on cruises of the R/V *Gosnold* (most samples) and R/V *Asterias* (a few of the shallower stations). Most of the sampling was done with a Campbell grab, which covers a bottom area of 0.6 square meters. The *Asterias* samples were taken with a smaller Smith-McIntyre grab. This material was subsampled for ostracodes and foraminifers and the sediment placed in alcohol or buffered formalin with Rose Bengal. Amounts of wet sediment varying from 30 to 200 cubic centimeters were screened on a 0.084 mm screen and dried. The carbonate part of the sand-sized fraction was separated, using a soap-float technique. The ostracodes were then picked from splits of the float. Four of the samples were barren (Table 1). All identifiable carapaces and valves of adults and juveniles were counted.

Because the samples were taken at different times of the year and in different years and because a biogeographic rather than ecologic interpretation was the goal, living and dead were counted together. Fossils were found in some samples; however, they were in general obvious because of what taxa



Text-figure 4.— Cluster analysis of the 38 stations using weight percents of modal grain sizes as variables. Grain-size data from Hathaway (1971) grouped as indicated. The correlation coefficient (r) was used as a similarity measure. Clustering was by the unweighted pair-group method. The weight percents were normalized by taking the arcsin of the square root of the percentage and multiplying by two. The clusters labeled A through F are mapped in figure 5.



Text-figure 5. — Bottom-sediment facies map based on major clusters (A-F) of figure 4. The capital and lower case letters in the explanation indicate the dominant and subordinate grain size classes, respectively. A more detailed breakdown of sediment composition can be found in Hathaway (1971); see also Milliman (1972). Sample stations explained in figure 1.

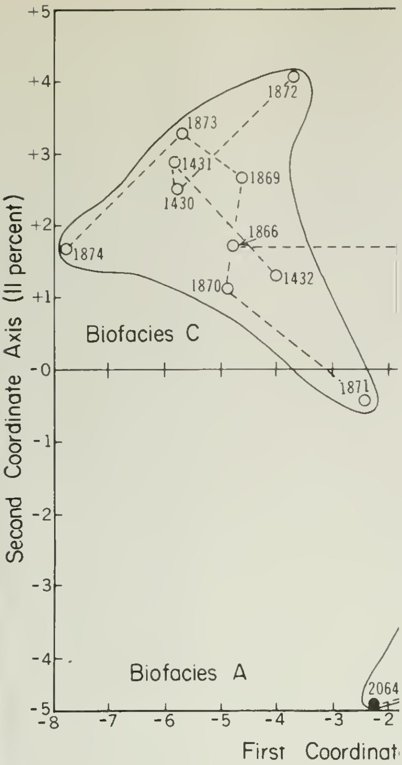
they represented and because of conditions of their preservation. No single dead shell was accepted as an occurrence unless the species occurred in other samples in the area. All corroded and blackened shells were ignored. Living specimens of all of the more common forms were found.

A wealth of information on the samples used, other than that given in Table 1, can be found in Hathaway (1971).

BIOFACIES ANALYSIS

Introduction. — In this report, stations that are similar to each other on the basis of the kinds and abundance of ostracodes present are delineated using the well-known correlation coefficient (r) as a similarity measure and prinicpal coordinates analysis (Gower, 1966; Blackith and Reyment, 1971).

Text-figure 6. — Principal coordinates analysis of 30 samples containing 126 species from the Cape Hatteras area. Eigenvalues and eigenvectors were extracted from a correlation matrix. Projections on the first three coordinate axes are shown. The first three axes account for 51 percent of the variation. No patterns that could be related to biogeography were evident in projections on six other axes. The dashed lines connect each sample to the sample with which it has the highest computed similarity. The three clusters of stations resulting from projections on the first two axes are considered to represent biofacies. Biofacies A and B represent the northern most part of the Carolinian Province and C the southernmost part of the Virginian Province. The biofacies are mapped in Text-figure 7.


Second Coordinate Axis (11 percent)
+5
+4
+3
+2
+1
-0
-1
-2
-3
-4
-5
-8
-7
-6
-5
-4
-3
-2
First Coordinat
Biofacies C
Biofacies A
1872
1873
1431
1869
1430
1866
1874
1432
1870
1871
2064

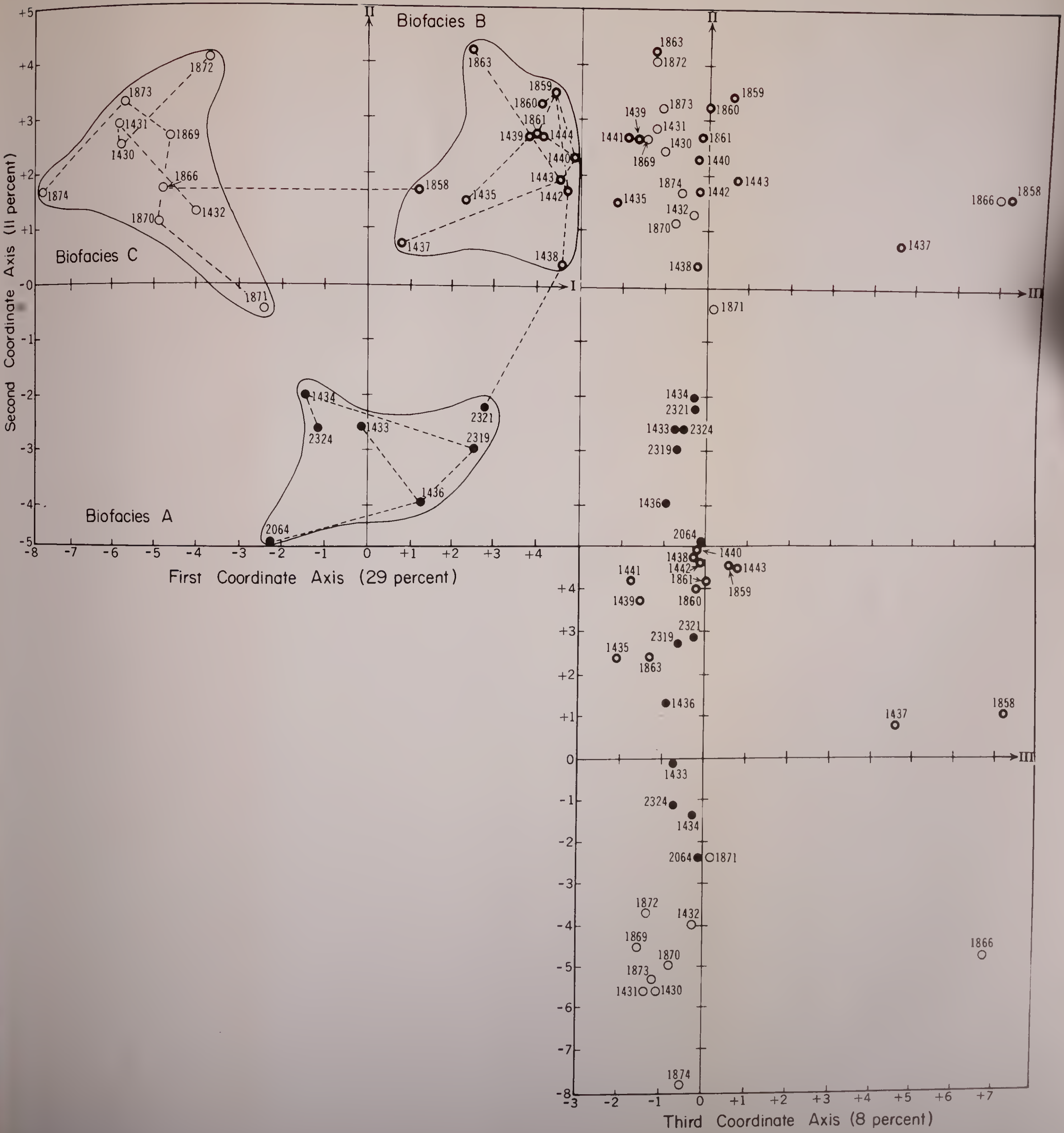

Biofacies B
Biofacies C
Biofacies A
Second Coordinate Axis (11 percent)
First Coordinate Axis (29 percent)
Third Coordinate Axis (8 percent)
I
II
III
1863
1872
1873
1431
1430
1869
1866
1874
1870
1432
1871
1859
1860
1861
1439
1444
1440
1443
1442
1858
1435
1437
1438
1441
1434
2324
1433
2321
2319
1436
2064

Table 1.- Location, depth, and temperature data. The winter and summer temperatures are average bottom temperatures for the coldest and warmest months and were calculated from the maps of Walford and Wicklund (1968); the ± indicates that the value given falls within a 2.5°C-point class (that is, ± 8.75 means the calculated value is between 7.50° and 10.00°). The values

Table 1.- Location, depth, and temperature data. The winter and summer temperatures are average bottom temperatures for the coldest and warmest months and were calculated from the maps of Walford and Wicklund (1968); the ± indicates that the value given falls within a 2.5°C-point class (that is, ± 8.75 means the calculated value is between 7.50° and 10.00°). The values for temperature instability are the standard deviations calculated using the bottom temperature averages for 12 months at each station.

Sample	Latitude north deg.	min.	Longitude west deg.	min.	Depth (meters)	Winter Temp. °C	Summer Temp. °C	Temp. Instab. s	Speci- mens	Species
Gos 1430	35	00	75	14	35	±8.75	±18.75	3.35	127	27
Gos 1431	35	51	75	15	32	6.25	21.25	4.41	194	42
Gos 1432	35	40	75	15	34	8.75	21.25	4.18	221	33
Gos 1433	35	31	75	15	30	11.25	25.00	4.21	54	22
Gos 1434	35	20	75	15	25	12.50	25.00	4.53	345	51
Gos 1435	35	11	75	15	27	13.75	23.75	3.19	50	17
Gos 1436	35	07	75	21	26	13.75	25.00	3.29	131	27
Gos 1437	34	59	75	31	44	13.75	26.25	3.30	95	29
Gos 1438	34	56	75	44	27	16.25	26.25	2.72	22	14
Gos 1439	34	58	76	00	20	16.25	26.25	4.09	40	14
Gos 1440	34	50	76	00	28	16.25	26.25	2.97	234	28
Gos 1441	34	51	76	14	18	16.25	27.50	4.10	84	21
Gos 1442	34	40	76	15	27	18.75	26.25	2.41	289	35
Gos 1443	34	30	76	17	32	18.75	26.25	2.74	302	36
Gos 1858	34	29	76	00	54	17.50	26.25	2.40	807	60
Gos 1859	34	40	76	01	33	18.75	26.25	2.53	222	31
Gos 1860	34	37	75	44	66	13.75	25.00	2.88	158	34
Gos 1861	34	46	75	45	41	15.00	26.25	3.25	1583	65
Gos 1863	34	51	75	31	86	13.75	23.75	2.94	92	30
Gos 1866	35	03	75	18	85	13.75	22.50	2.61	279	71
Gos 1869	35	21	74	59	70	12.50	21.25	2.89	896	81
Gos 1870	35	29	74	58	42	13.75	21.25	2.29	952	78
Gos 1871	35	41	75	02	43	8.75	21.25	3.72	37	15
Gos 1872	35	50	75	00	46	8.75	18.75	2.94	219	34
Gos 1873	36	00	75	00	44	10.00	18.75	2.46	325	45
Gos 1874	36	09	74	58	43	11.25	18.75	2.03	613	57
Gos 2064	36	00	75	30	23	8.75	21.25	4.06	16	11
Gos 2065	35	50	75	30	23	7.50	23.75	5.20	15	8
Ast 2316	34	32	76	26	16	16.25	26.25	3.31	0	
Ast 2317	34	43	76	23	16	16.25	27.50	4.23	0	
Ast 2318	34	56	76	06	16	16.25	26.25	3.93	0	
Ast 2319	35	03	75	57	17	16.25	26.25	4.35	195	28
Ast 2320	35	08	75	48	16	16.25	26.25	4.35	4	
Ast 2321	35	09	75	38	16	15.00	26.25	4.39	219	43
Ast 2322	35	07	75	29	16	15.00	26.25	3.74	52	24
Ast 2323	35	16	75	28	16	13.75	26.25	5.07	7	6
Ast 2324	35	26	75	27	15	11.25	26.25	5.78	19	15
Ast 2325	35	37	75	24	18	8.75	26.25	5.55	0	

The resulting major clusters of stations are considered to represent biofacies and can be indicated on a map. The biofacies are thus delineated in Q-mode and are mappable and meaningful if they form recognizable patterns. A species-versus-species comparison (R-mode cluster analysis) is used to indicate which individual species are closely associated with each other and help explain the patterns seen in Q-mode. The species composing the clusters formed in R-mode have no fixed geographic position, and the clusters themselves therefore have no *a priori* potential for mappability.

The approach to the delineation of bioassociational units is that of Buzas (1970, p. 113), Hazel (1970b), and others. In contrast to this is the methodology advocated by Kaesler (1966, 1969) in which biofacies are clusters formed in R-mode, and Q-mode clusters are referred to as biotopes. This is considered unsatisfactory herein, largely because I believe that biofacies should be mappable no matter how they are delineated, just as are bottom-sediment facies and lithofacies. A more flexible definition of the term biofacies than R-mode clusters is believed desirable. One application of this would be to Q-mode bioassociational groupings (Mello and Buzas, 1968, p. 749). A biotope is a physical and biological system of which a fauna and/or flora is a part; the biotope is not the fauna or flora itself and, therefore, cannot be defined directly by the comparison of samples composed only of biotic constituents.

Biofacies delineation. — From the 34 samples containing ostracodes, 126 species have been identified (Table 2) and 8894 specimens counted. Four samples were barren. Four contain very few specimens and were not used in the multivariate analyses. The remaining 30 samples were compared in Q-mode using principal coordinates analysis; figure 6 contains the results of ordination.

In Text-figure 6, three major clusters of stations result from projections on the first two coordinate axes which account for 40 percent of the variation. On the first coordinate axis, northern stations have high negative values and southern stations, high positive values. Stations from the immediate area of Cape Hatteras have intermediate values but overlap strongly with those to the south. The major biogeographic pattern in the area is outlined on this axis. On the second axis, the immediate cape area stations are delimited from those to the south. Little biogeographic information appears to be contained on the third or other axes.

The three groupings of stations on the first two axes are considered to represent biofacies, designated A, B, and C. The map distribution of these units is indicated in Text-figure 7.

Table 2. — Alphabetical listing of ostracode species found in Cape Hatteras area samples. The 76 more common species are indicated by numbers in parentheses following their names. These numbers are the code designation for the taxa in the R-mode dendrogram in figure 8; their occurrence and abundance can be found in figure 8. The occurrences of the rarer species are indicated in this table by the four-digit numbers following the species names; these numbers correspond to the sample numbers of table 1.

Many of the species in the list below have been recently illustrated by Valentine (1971). References, other than those containing the original descriptions, in which some of the above species have been illustrated, include Plusquellec and Sandberg (1969), Hazel (1967), Hulings (1966, 1967), Benda and Puri (1962), Engel and Swain (1967), Benson and Coleman (1963), Swain (1968), Puri (1958a,b), Hall (1965), Williams (1966), and Grossman (1967). That there has been relatively little work on American east coast Quaternary ostracodes is illustrated by the fact that about one half of the species delineated have not been formally proposed.

Actinocythereis dawsoni (Brady, 1870). (1)
A. sp. B. (2)
Argilloecia sp. A. 1423, 1874
A. sp. B. 1863
A. sp. C. 1860
Aurila laevicula (Edwards, 1944). 1442, 1858, 1861, 2321, 2322
Basslerites miocenicus (Howe, 1935). 1869, 2321
B. sp. A. 1869
B. sp. B. 1858
Bensonocythere americana Hazel, 1967. (9)
B. *arenicola* (Cushman, 1906). (10)
B. *whitei* (Swain, 1951). (12)
B. *sapeloensis* (Hall, 1865). 1869, 1870, 2322
B. sp. K. 1434, 1859
B. sp. M. (16)
B. sp. U. 1431
B. sp. CC. (14)
B. sp. EE. (13)
B. sp. FF. (15)
Bythocythere sp. A. (18)
B. sp. B. (19)
Campylocythere laeva Edwards, 1944. (20)
Caudites nipeensis Bold, 1946. 1860
Cushmanidea seminuda (Cushman, 1906). (22)
C. cf. *C. seminuda.* 1866
Cytherella sp. A. 1869
Cytherelloidea sp. A. 1443
Cytherois sp. A. 1861
Cytheromorpha newportensis Williams, 1966. (28)
Cytheropteron pyramidale Brady, 1868. (29)
C. *talquinensis* Puri, 1954. 1859
C. sp. A. 1861, 1869
C. sp. D. 1869
Cytherura elongata Edwards, 1944. (32)
C. *forulata* Edwards, 1944. (33)
C. *howei* (Puri, 1954). (34)
C. *pseudostriata* Hulings, 1966. (35)
C. *wardensis* Howe and Brown, 1935. (37)
C. sp. A. (38)
C. sp. B. (39)

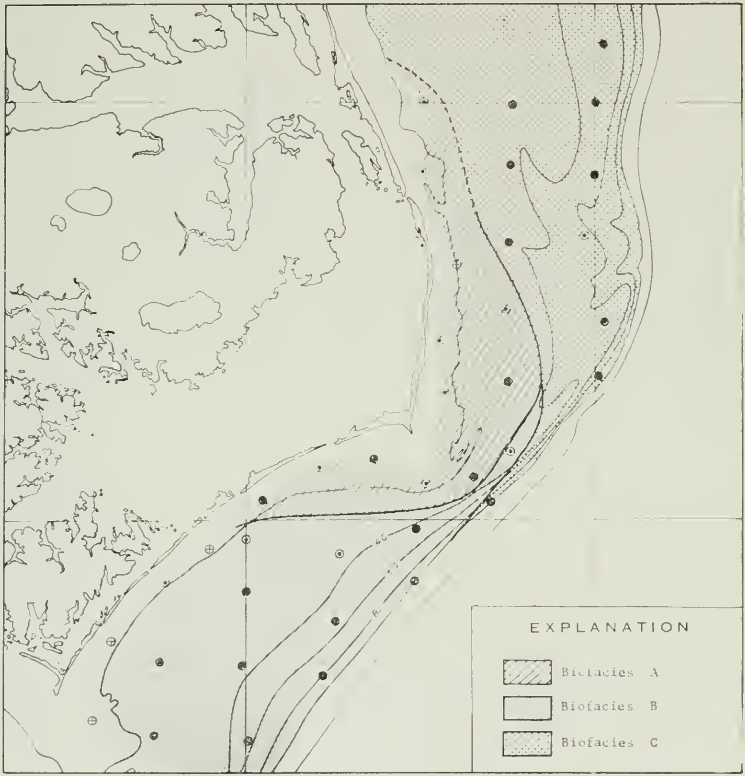
C. sp. C. 1431, 1434
C. sp. D. 1430, 1431, 1861, 1869
C. sp. E. 1869, 1870, 1874
C. sp. F. (43)
C. sp. G. (44)
C. sp. H. 1869
C. sp. J. 1434, 1870
C. sp. L. (36)
Echinocythereis margaritifera (Brady, 1868). (47)
E. planibasalis procteri (Blake, 1929). (48)
E. sp. A. (49)
Eucythere declivis (Norman, 1865). (50)
E. gibba Edwards, 1944. (51)
E. triangulata Puri, 1954. 1861, 1869
E. sp. A. 1865, 1870
Finmarchinella finmarchica (Sars, 1865). (54)
"Haplocytheridea" bradyi (Stephenson, 1938). (55)
Hulingsina americana (Cushman, 1906). (60)
H. glabra (Hall, 1965). (58)
H. rugipustulosa (Edwards, 1944). (59)
H. sp. C. (57)
H. sp. E. (61)
H. sp. F. (62)
H. sp. I. (63)
Jonesia cf. *J. acuminata* (Sars, 1865). 1863, 1869, 1870
Krithe sp. A. 1869
Leptocythere angusta Blake, 1929. (66)
Loxoconcha matagordensis Swain, 1955. 1861
L. reticularis Edwards, 1944. (70)
L. sperata Williams, 1966 (71)
L. sp. C. (68)
L. sp. H. (67)
Loxocorniculum postdorsolatum (Puri, 1960). 1434, 1869
Macrocyprina sp. A. 1860, 1863
M. sp. B. 1869
Macrocypris sp. E. 1869
Microcytherura choctawhatcheensis (Puri, 1954). (76)
M. sp. A. (77)
M. sp. B. 1432
M. sp. C. 1870, 2321
M. sp. D. 1430
Muellerina canadensis (Brady, 1870). (80)
M. lienenklausi (Ulrich and Bassler, 1904) s.l. (81)
Munseyella atlantica Hazel and Valentine, 1969. 1866
Neocaudites triplistriatus (Edwards, 1944). 1863
Neolophocythere subquadrata Grossman, 1967. (83)
Orionina bradyi Bold, 1963. 1861
Paracytheridea altila Edwards, 1944. (86)
P. rugosa Edwards, 1944. (87)
P. sp. A. (88)
Paradoxostoma delicata Puri, 1954. (89)
P. sp. A. 1861
P. sp. C. 1874
P. sp. D. 1860, 1861, 1870

Paranesidea sp. A. (92)
P. sp. D. 1860, 1869
Pellucistoma magniventra Edwards, 1944. (95)
P. sp. A. (96)
Phlyctocythere sp. A. (97)
P. sp. B. 1861, 1869
Pontocypris sp. A. 1860, 1861
Pontocythere sclerochilus (Tressler and Smith, 1948). 1870
P. sp. A. (23)
P. sp. B. (24)
P. sp. C. 1434, 1870
Propontocypris aff. *P. howei* (Puri, 1954). (101)
Proteoconcha gigantica (Edwards, 1944). (102)
P. multipunctata (Edwards, 1944). 1439
P. nelsonensis (Grossman, 1967). (104)
P. tuberculata (Puri, 1960). (105)
Protocytheretta danaiana (Brady, 1869). (106)
P. montezuma (Brady, 1869). (107)
Pseudocytheretta edwardsi Cushman, 1906. (108)
Pterygocythereis inexpectata (Blake, 1929). (109)
P. sp. A. (110)
Puriana floridana Puri, 1960. (111)
P. rugipunctata (Ulrich and Bassler, 1904). (112)
P. sp. A. (113)
P. sp. B. (114)
Radimella? floridana floridana (Benson and Coleman, 1963). (3)
"Sahnia" foveolata (Brady, 1870). (116)
"S." sp. B. (117)
"S." sp. C. (115)
Sclerochilus sp. A. 1870
S. sp. B. 1874
Xiphichilus sp. A. 1866

The dashed lines in the upper left plot of Text-figure 6 connect each sample to the one with which it has the highest computed similarity. The only three samples that do not link with any of the samples in their respective clusters are 1858 and 1866 of biofacies B and C, respectively, which have the highest resemblance to each other and 2321 of biofacies A which has its greatest similarity with 1438 of biofacies B. The relationship between 1858 and 1866 is expressed on the third coordinate axis and is caused by the mutual abundance of *Echinocythereis margaritifera* (Brady, 1868) (Text-fig. 8). However, in terms of the rest of the assemblage, 1858 and 1866 are consistent with the samples with which they are grouped on the first two axes. Sample 2321 has a slightly higher average similarity with the other samples placed in biofacies A than it does with those of biofacies B.

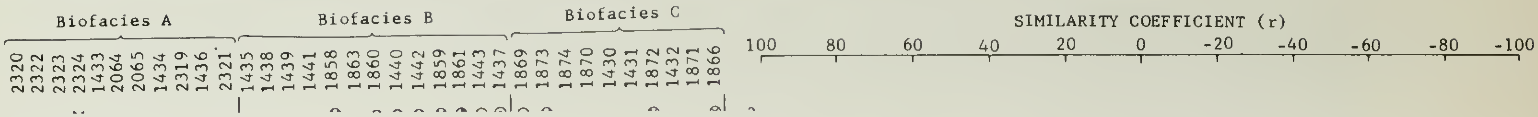
On the right in Text-figure 8, the samples of this study are grouped by biofacies. At the bottom in this figure is an R-mode dendrogram for virtually all of the 76 species that were found in more than two of the 30 samples used in the multivariate analyses. Opposite the endpoints of the dendrogram the occurrences of the species are plotted against the samples. Their relative abundance is indicated by symbols representing point classes of percent contribution on a geometric scale (except for the smaller samples for which an occurrence is indicated by an X). The figure thus serves as an occurrence chart and also as a base for interpreting the Q- and R-mode clusters.

Of the species that occur in biofaces A, relatively few are the principal contributors to the samples with significant numbers of specimens. The dominant elements (in terms of their relative abundance) are *Hulingsina americana* (Cushman, 1906), *Puriana floridana* Puri, 1960, and *Hulingsina* sp. E from the R-1 cluster of figure 8; *"Haplocytheridea" bradyi* (Stephenson, 1938) from the R-2 cluster; *Protocytheretta montezuma* (Brady, 1869), cluster R-3; and *Cytherura* sp. A, *Proteoconcha gigantica* (Edwards, 1944), *Hulingsina rugipustulosa* (Edwards, 1944), and *Paradoxostoma delicata* Puri, 1954, from clusters R-5 and R-6. Note that no species are restricted to this biofacies. Biofacies



Text-figure 7. — Map distribution of the biofacies delineated by principal coordinate analysis (Text-fig. 6). Biofaces A and B are considered to represent the northern part of the Carolinian faunal province and biofacies C, the southern part of the Virginian Province. Sample station explained in Text-figure 1.

Text-figure 8. — Occurrence, abundance, and associations of 76 ostracode species occurring in three or more samples. The R-mode dendrogram is based on a correlation matrix and clustered by the unweighted pair-group method. Code numbers are keyed to species listed alphabetically in Table 2. On the right in the figure the samples are grouped by biofacies. In the body of the figure the percent abundance of the species is indicated by symbols for all samples, except for those in which the numbers of specimens found were too few to make the percentages meaningful. Occurrences for species in latter group of samples are indicated by an X.


Biofacies A
Biofacies B
Biofacies C
2320
2322
2323
2324
1433
2064
2065
1434
2319
1436
2321
1435
1438
1439
1441
1858
1863
1860
1440
1442
1859
1861
1443
1437
1869
1873
1874
1870
1430
1431
1872
1432
1871
1866
SIMILARITY COEFFICIENT (r)
100
80
60
40
20
0
-20
-40
-60
-80
-100


Biofacies A
2320
2322
2323
2324
1433
2064
2065
1434
2319
1436
2321
Biofacies B
1435
1438
1439
1441
1858
1863
1860
1440
1442
1859
1861
1443
1437
Biofacies C
1869
1873
1874
1870
1430
1431
1872
1432
1871
1866
SIMILARITY COEFFICIENT (r)
100
80
60
40
20
0
-20
-40
-60
-80
-100
EXPLANATION
■ 32.0-63.9
● 16.0-31.9
◑ 8.0-15.9
⊗ 4.0-7.9
⊙ 2.0-3.9
· > 0-1.9
3
33
32
19
70
76
60
111
58
86
114
49
113
61
35
110
20
43
51
62
36
95
44
92
87
55
105
2
24
106
107
47
109
88
97
96
38
102
59
89
34
54
68
50
12
57
115
39
23
10
37
77
1
67
48
83
71
108
101
15
66
80
9
18
14
13
29
81
116
112
104
28
117
63
22
16
R-1
R-2
R-3
R-4
R-5
R-6
R-7
R-8
R-9
R-10
R-11

A has a map distribution in the Cape Hatteras area very similar to biofacies 3 of Valentine (1971) and Hazel (1971), which was defined using binary data and the Dice coefficient.

Most of the rest of the area south of Cape Hatteras is inhabited by the assemblages of biofacies B, which is characterized by high density and diversity; the dominant species appear in the R-1 through R-6 clusters of figure 8. The consistently occurring abundant species of biofacies B include *Cytherura forulata* Edwards, 1944, *Hulingsina americana* (Cushman, 1906), *Radimella? floridana floridana* (Benson and Coleman, 1963), *Puriana floridana* Puri, 1960, *Hulingsina* sp. E, *Cytherura* sp. L, *Pellucistoma magniventra* Edwards, 1944, and *Cytherura* sp. A. Several other species are consistent in their occurrence but are not as abundant. Biofacies A and B I believe represent biogeographic units within the subtropical Carolinian Province.

The assemblage composition of biofacies C is manifested in the large R-mode cluster of Text-figure 8 containing the labeled clusters R-7 through R-11. Note that relatively few of these species occur in biofacies A and even fewer in biofacies B. It is also evident that more cryophilic than thermophilic species are terminating their equatorward or poleward expansion in the Cape Hatteras area.

The dominant elements of biofacies C include *Puriana rugipunctata* (Ulrich and Bassler, 1904), *Muellerina lienenklausi* (Ulrich and Bassler, 1904), *Bensonocythere whitei* (Swain, 1951), *B. arenicola* (Cushman, 1906), *Cytherura wardensis* Howe and Brown, 1935, *Microcytherura* sp. A, *Loxoconcha* sp. H, *Loxoconcha sperata* Williams, 1966, *Pseudocytheretta edwardsi* Cushman, 1906, *Propontocypris* aff. *P. howei* Puri, 1954, *Leptocythere angusta* Blake, 1933, *Hulingsina* sp. I, *Protocytheretta danaiana* (Brady, 1869), *Hulingsina americana* (Cushman, 1906), *Cytherura forulata* Edwards, 1944, and others.

Discussion. — The use of species counts and a multistate quantitative similarity measure and principal coordinates analysis allows the clear delineation of the major ostracode biogeographic patterns in the Cape Hatteras area. In gross form, the three major biogeographic units delineated, biofacies A, B, and C, are very similar to those described for the area by Valentine (1971) and Hazel (1971), using most of the same samples and a binary (presence-absence) coefficient and cluster analysis. Therefore, if the most general structure is all that is desired, presence-absence data may be all that is necessary. This conclusion was also reached by Buzas (1972) in a study of foraminifer distributions.

The results with binary and multistate data in this area are similar partly because the area is the biogeographic endpoint for many cryophilic and thermophilic species. However, if the change in assemblages is manifested mainly by changing numerical dominance of species, this would be obscured by the use of binary data. Also, with ostracodes at least, once the organisms have been sorted for identification, they can be counted rather quickly. Therefore, in the modern environment where contemporaneity is assured (in contrast to paleobiogeography where larger units of time must be used), it is recommended that counts and multistate measures and classification systems be used to obtain the most information.

RELATIONSHIP OF BIOFACIES TO MACROENVIRONMENTAL FACTORS

General.—The 38 samples used in the present study lie in a 10,000-km^2 area. Therefore, they are quite inadequate for any aut- or synecological analysis. The data bank, however, I believe to be adequate for biogeographic purposes, and the biofacies delineated to be valid. In an open marine shelf environment, many abiotic factors such as salinity and available oxygen can be effectively eliminated as being of primary influence in controlling the faunal composition of biofacies.

The podocopid ostracodes are part of the microscopic wandering benthos and, for the most part, scavenge for food on the bottom or just below the sediment-water interface, or live on marine plants. If an adequate food supply is available, temperature and bottom-sediment size are commonly believed to be two primary factors controlling the distribution of species. One of the objects of this study was to see if the delineated biofacies composition could be shown to be largely controlled by either or both.

Temperature should have a more direct relationship to species distribution than other abiotic or biotic factors simply because, particularly for benthic species without planktonic larvae, the statement can be made that a species cannot live at a particular place if its thermal survival limits are exceeded or if temperatures needed for reproduction are not met (Hutchins, 1947; see Hazel, 1970a, for discussion as applied to ostracodes). Temperature exerts controls on species distribution before other abiotic and density-dependent factors become influential. Thus, even when it is understood that there is in a species both individual and deme adaption, and therefore variation with respect to tolerance of thermal fluctuation, temperature would tend to have a presence-absence effect. In contrast, such factors as available food, suitable substrate, and available light, are themselves generally gradational, and the effect on organisms of any of these factors would be manifested as changes in abundance.

Biofacies and bottom-sediment facies.—Text-figure 4, as discussed above, is a dendrogram based on grain-size data for the 38 stations in this study; Text-figure 5 indicates the map distribution of the bottom-sediment facies thus defined. A comparison of the biofacies map (Text-fig. 7) with the bottom-sediment facies map shows that there is no obvious correlation of particular biofacies with particular sediment facies. Thus, the type of substrate in this instance would seem to have minimal effect on the distribution of biofacies.

Biofacies and temperature.—A comparison of the isothermal map for the warmest month (Text-fig. 3) and the biofacies map (Text-fig. 7) suggests that summer temperature is the most important factor controlling the major faunal pattern seen, that is, the two major sample groupings on the first coordinate axis of Text-figure 6, which delineates the northern from the two southern biofacies in the area. The boundary between these major biofacies is near the 22.5°C and 25°C isotherms. All the stations assigned to biofacies C are on the cool side of the 25°C isotherm. That summer temperatures are the most important is graphically indicated in Text-figure 8. Note that many of the species of the R-1 through R-6 clusters, which contain the principal elements of biofacies A and B, also are found in biofacies C. In other words, many thermophilic species which are expanding their range from the south pass Cape Hatteras. In contrast, many of the species of the other major R-mode cluster, which contains the principal elements of biofacies C, are not found or are very rare at stations assigned to biofacies B and, to a lesser extent, biofacies A. Note that most of the biofacies A occurrences of cryophilic species are at stations 1434 and 1436 and that the calculated position of the 25°C isotherm is at these stations also. More cryophilic species, expanding their range from the north, terminate at Cape Hatteras than do thermophilic species; the warm bottom temperature in the cape area acts as an effective barrier to migration of northern forms.

In contrast, the summer maximum in most of the area of both biofacies A and B is between 25.0 and 27.5°C; thus summer temperature would seem not to be an important factor here. No clear-cut correlation is suggested by the map of winter isotherms either. Further, as mentioned above, biofacies A is similar in its map distribution to a biofacies defined on binary data by Valentine (1971) and Hazel (1971); that biofacies has a discontinuous distribution, occurring in nearshore Raleigh, Onslow, and Long Bays, particularly near inlets, and on Diamond, Cape Lookout, and Frying Pan Shoals. The composition of biofacies A appears to be related to physical characteristics associated with the shoals and inner parts of the bays. Tolerance to instability of substrate in the form of both turbidity and turbulence is probably most important.

REFERENCES

Arx, W. S. von
1962. *An introduction to physical oceanography.* Reading, Mass., Addison-Wesley, 422 pp.

Benda, W. K., and Puri, H. S.
1962. *The distribution of Foraminifera and Ostracoda off the Gulf Coast of the Cape Romano area, Florida.* Gulf Coast Assoc. Geol. Soc., Trans., vol. 12, pp. 303-341.

Benson, R. H., and Coleman, G. L., II
1963. *Recent marine ostracodes from the eastern Gulf of Mexico.* Kansas Univ., Paleont. Contr., 31, Arthropoda, art. 2, 52 pp.

Blackith, R. E., and Reyment, R. A.
1971. *Multivariate morphometrics.* London, Academic Press, 412 pp.

Blanton, Jackson
1971. *Exchange of Gulf Stream water with North Carolina shelf water in Onslow Bay during stratified conditions.* Deep-Sea Research, vol. 18, No. 2, pp. 167-178.

Bumpus, D. F.
1955. *The circulation over the continental shelf south of Cape Hatteras.* Amer. Geophys. Union, Trans. vol. 36, pp. 601-611.
Bumpus, D. F., and Lauzier, L. M.
1965. *Surface circulation on the continental shelf off Eastern North America between Newfoundland and Florida.* Amer. Geog. Soc., Serial Atlas Marine Environment, Folio 7.
Buzas, M. A.
1970. *On the quantification of biofacies.* North American Paleont. Convention, Chicago, 1969 Proc., Pt. B, pp. 101-116.
1972. *Biofacies analysis of presence or absence data through canonical variate analysis.* Jour. Paleont., vol. 46, No. 1, pp. 55-57.
Cerame-Vivas, M. J., and Gray, I. E.
1966. *The distributional pattern of benthic invertebrates of the continental shelf off North Carolina.* Ecology, vol. 47, No. 2, pp. 260-270.
Dana, J. D.
1853a. *Crustacea.* U.S. Exploring Expedition [Report], 1838-1842, vol. 14, pt. 2, pp. 690-1618.
1853b. *On an isothermal oceanic chart, illustrating the geographical distribution of marine animals.* Amer. Jour. Sci., ser. 2, vol. 16, pp. 153-167, 314-327.
Day, J. H., Field, J. G., and Montgomery, M. P.
1971. *The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina.* Jour. Animal Ecology, vol. 40, pp. 93-125.
Defant, Albert
1961. *Physical oceanography,* volume 1, New York, Pergamon Press, 729 pp.
Engel, P. L., and Swain, F. M.
1967. *Environmental relationships of Recent Ostracoda in Mesquite, Aransas and Copano Bays, Texas Gulf Coast.* Gulf Coast Assoc. Geol. Soc., Trans., vol. 17, pp. 408-427.
Gower, J. C.
1966. *Some distance properties of latent root and vector methods used in multivariate analysis.* Biometrika, vol. 53, No. 3/4, pp. 325-338.
Grossman, Stuart
1967. *Ecology of Rhizopoda and Ostracoda of southern Pamlico Sound region, North Carolina; Part 1, Living and subfossil rhizopod and ostracode populations.* Kansas Univ., Paleont. Contr., 44, Ecology, art. 1, pp. 1-82.
Hall, C. A.
1964. *Shallow-water marine climates and molluscan provinces.* Ecology, vol. 45, No. 2, pp. 226-234.
Hall, D. D.
1965. *Paleoecology and taxonomy of fossil Ostracoda in the vicinity of Sapelo Island, Georgia,* Report 4, Kesling, R. V., and others, *Four reports of ostracod investigations.* Ann Arbor, Univ. Michigan Press, pp. 1-85.
Hathaway, J. E.
1971. *Data file continental margin program Atlantic Coast of the United States;* vol. 2, *Sample collection and analytical data.* Woods Hole Oceanographic Institution, Ref. No. 71-15.
Hazel, J. E.
1967. *Classification and distribution of the Recent Hemicytheridae and Trachyleberididae (Ostracoda) off northeastern North America.* U.S. Geol. Sur., Prof. Paper 564, 49 pp.

1970a. *Atlantic continental shelf and slope of the United States — Ostracode zoogeography in the southern Nova Scotian and northern Virginian faunal provinces.* U.S. Geol. Sur., Prof. Paper 529-E, 21 pp.

1970b. *Binary coefficients and clustering in biostratigraphy.* Geol. Soc. America, Bull., vol. 81, No. 11, pp. 3237-3252.

1971. *Paleoclimatology of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina.* In Oertli, H. J. (ed.), *Paleoecologie ostracodes.* Centre Rech., Pau, Bull. 5 supp. 1, pp. 361-375.

Hulings, N. C.

1966. *Marine Ostracoda from the western North Atlantic Ocean off the Virginia Coast.* Chesapeake Sci., vol. 7, No. 1, pp. 40-56.

1967. *Marine Ostracoda from the western North Atlantic Ocean between Cape Hatteras, North Carolina and Jupiter Inlet, Florida.* Bull. Marine Sci., vol. 17, No. 3, pp. 629-659.

Hutchins, L. W.

1947. *The bases for temperature zonation in geographical distribution.* Ecological Monographs, vol. 17, pp. 325-335.

Johnson, C. W.

1934. *List of marine Mollusca of the Atlantic Coast from Labrador to Texas.* Boston Soc. Nat. Hist., Proc., vol. 40, No. 1, pp. 1-204.

Kaesler, R. L.

1966. *Quantitative re-evaluation of ecology and distribution of Recent Foraminifera and Ostracoda of Todos Santos Bay, Baja California, Mexico.* Kansas Univ., Paleont. Contr., 10, 50 pp.

1969. *Aspects of quantitative distributional paleoecology.* In Merriam, D. F. (ed.) *Computer applications in the earth sciences.* New York Plenum Press, pp. 99-120.

Maturo, F. J. S.

1968. *The distributional pattern of the Bryozoa of the east coast of the United States exclusive of New England.* Soc. Italiana Sci. Nat. e Museo, Atti vol. 108, pp. 261-284.

Mello, J. F., and Buzas, M. A.

1968. *An application of cluster analysis as a method of determining biofacies.* Jour. Paleont., vol. 42, No. 3, pp. 747-758.

Milliman, J. D.

1972. *Atlantic Continental Shelf and slope of the United States — petrology of the sand fraction of sediments, northern New Jersey to southern Florida.* U.S. Geol. Sur. Prof. Paper 529-J, 40 pp.

Milliman, J. D., Pilkey, O. H., and Blackwelder, B. W.

1968. *Carbonate sedimentation on the continental shelf, Cape Hatteras to Cape Romain.* Southeastern Geology, vol. 9, pp. 245-267.

Milliman, J. D., Pilkey, O. H., and Ross, D. A.

1972. *Sediments of the continental margin off the eastern United States.* Geol. Soc. America, Bull., vol. 83, No. 5, pp. 1315-1334.

Plusquellec, P. L., and Sandberg, P. A.

1969. *Some genera of the ostracode subfamily Campylocytherinae.* Micropaleontology, vol. 15, No. 4, pp. 427-280.

Puri, H. S.

1958a. *Ostracode Subfamily Cytherettinae.* Gulf Coast Assoc. Geol. Soc., Trans., vol. 8, pp. 183-195.

1958b. *Ostracode genus Cushmanidea.* Gulf Coast Assoc. Geol. Soc., Trans., vol. 8, pp. 171-181.

Sandberg, P. A.
1969. *Appendages and family placement of the ostracod genus Pellucistoma.* Jour. Paleont., vol. 43, No. 5, pp. 1174-1178.

Schnitker, Detmar
1971. *Distribution of Foraminifera on the North Carolina continental shelf.* Tulane Studies Geol. Paleont., vol. 8, No. 4, pp. 169-215.

Schroeder, E. H.
1966. *Average surface temperatures of the western North Atlantic.* Bull. Marine Sci., vol. 16, No. 2, pp. 302-323.

Stefansson, Unnsteinn, and Atkinson, L. P.
1967. *Physical and chemical properties of the shelf and slope waters off North Carolina.* Duke Univ. Tech. Rept., 230 pp.

Stefansson, Unnsteinn, Atkinson, L. P., and Bumpus, D. F.
1971. *Hydrographic properties and circulation of the North Carolina shelf and slope waters.* Deep-Sea Research, vol. 18, No. 4, pp. 383-420.

Stephenson, T. A., and Stephenson, Anne
1954. *Life between tide-marks in North America* — [Parts] IIIA, B, *Nova Scotia and Prince Edward Island.* Jour. Ecology, vol. 42, No. 1, pp. 14-45, 46-70.

Swain, F. M.
1968. *Ostracoda from the Upper Tertiary Waccamaw Formation of North Carolina and South Carolina.* U.S. Geol. Sur., Prof. Paper 573-D, 37 pp.

U.S. Army Corps of Engineers
1964. *Outer banks between Ocracoke Inlet and Beaufort Inlet, North Carolina.* U.S. Army Corps Engineers, Combined Rept., U.S. Army Engineer District, Wilmington, North Carolina, 26 pp., Appendices A-H.

U.S. Congress
1948. *North Carolina shore line, beach erosion study.* House of Representatives, U.S. Congress, 80th, 2d sess., House Doc. 763, 33 pp.

Valentine, P. C.
1971. *Climatic implication of a late Pleistocene ostracode assemblage from southeastern Virginia.* U.S. Geol. Sur., Prof. Paper 683-D, 28 pp.

Walford, L. A., and Wicklund, R. I.
1968. *Monthly sea temperature structure from the Florida Keys to Cape Cod.* Amer. Geog. Soc., Serial Atlas Marine Environment, Folio 15.

Wells, H. W., and Gray, I. E.
1960. *The seasonal occurrence of Mytilis edulis on the Carolina coast as a result of transport around Cape Hatteras.* Biol. Bull., vol. 119, pp. 550-559.

Williams, R. B.
1966. *Recent marine podocopid Ostracoda of Narragansett Bay, Rhode Island.* Kansas Univ., Paleont. Contr., 11, 36 pp.

Joseph E. Hazel,
U.S. Geological Survey,
Washington, D.C. 20244

DISCUSSION

Dr. R. A. Reyment: Several people have discussed quantitative studies during this meeting. One of the questions which has arisen is whether one should use factor analysis or not. I hope those who asked these questions were listening attentively to Dr. Hazel's paper, because he gave an excellent discussion of what may be considered the optimal method, that is, that of principal coordinates, proposed by J. C. Gower, for the problem which is frequently incorrectly or inaccurately treated by the factor analytical model of psychological or psychometrical work.

Dr. Hartmann: What was the percentage of amphiatlantic species in the different regions you studied?

Dr. Hazel: Of the 136 sublittoral species I identified in the Cape Hatteras area only three are amphiatlantic. These are *Finmarchinella finmarchica* (Sars, 1865), *Eucythere declivis* (Norman, 1865), and *Cytheropteron pyramidale* Brady, 1868. Of the about 200 podocopid ostracode species living in open marine sublittoral waters from Nova Scotia to South Carolina, only 21 seem also to occur in Europe and all but six of these are restricted to north of Cape Cod. Thus, only about 4% of the species found south of Cape Cod, which is the southern limit of the cold-temperat Nova Scotian faunal province, are amphiatlantic. In the Nova Scotian Province, however, about 33% of the species also occur in the eastern Atlantic.

The amphiatlantic species are of two basic types. Those such as *Baffinicythere emarginata* (Sars, 1865), *B. howei* Hazel, 1967, and *Finmarchinella barenzovoensis* (Mandelstam, 1957) live in the frigid Arctic province and penetrate equatorward into cold-temperate or northern mild-temperate waters. In contrast, species such as *Hemicythere villosa* (Sars, 1865), *Finmarchinella finmarchica* (Sars, 1865), and *Cythere lutea* Mueller, 1785, occur only as far poleward as the subfrigid provinces. These forms probably became amphiatlantically distributed during Pleistocene interglacial stages.

OSTRACODES OF THE MANGROVES OF SOUTH FLORIDA, THEIR ECOLOGY AND BIOLOGY

DIETMAR KEYSER
Zoologisches Institut und Museum, Hamburg

ABSTRACT

This is a preliminary report on the living ostracode population of the mangrove swamp area in South Florida. It deals mainly with the salinity range of some more abundant forms living in the oligo- and mesohaline region. The investigation shows that the border between the oligohaline and mesohaline at 4.5 o/oo salinity is distinct. It represents the upper limit for the freshwater-forms and the lower limit for nearly all of the halmyrobe species. Only two species have been found to cross this border: *Cyprinotus* sp. II and *Cyprideis ? beaveni* Tressler and Smith, 1948. A second limit might be the 10 o/oo salinity for some species accustomed to higher salinity. They are represented in this study by *Cytherura forulata* Edwards, 1944, *Reticulocythereis floridana* Puri, 1960, and *Reticulocythereis* sp. II. Besides *Cyprinotus,* another true brackish-water group of Cypridacea, is reported. The Thalassocypridini appear with three species of the genus *Parapontoparta* only in the halmyrobe region.

LES OSTRACODES DES MANGLIERS DU SUD DE LA FLORIDE LEUR ECOLOGIE ET LEUR BIOLOGIE

RÉSUMÉ

La plupart des ostracodes de la côte du golfe ne sont connus que par leur carapaces. Toutes les études écologiques faites dans cette région sont basées sur des espèces déterminées par cette origine. Il n'y a aucun doute de ce que les études écologiques de ce genre sont parfois problématiques.

Ce fut, donc, très important de compléter notre connaissances des ostracodes de la côte du golfe par l'investigation de populations vivantes d'ostracodes à travers des méthodes zoologiques.

L'auteur a échantillonné des ostracodes vivants pendant une période de deux années dans les marais à mangliers du sudouest de la Floride. Il était possible de receuillir un bon nombre de ces ostracodes connus uniquement par leurs carapaces jusqu'ici. Les descriptions exactes des portions mousses seront publiées plus tard.

Une investigation écologique intensive (salinité, température, substratum, et cétéra) fut faite sur le champ. Il est donc possible de décrire l'écologie de la plupart des espèces receuillies et de comparer ces résultats avec des études antérieures.

Le travail présente une description détáillée de l'écologie des ostracodes de manglier. Il montre clairement les résultats différents obtenus par des études faite faites avec des méthodes paléontologiques et zoologiques et les limites des études paléoecologiques.

INTRODUCTION

The ostracode fauna of the Gulf of Mexico has been described primarily in palaeontological papers. This means that the soft parts of most of the species of this region have not as yet been described. Secondly little is known about the ostracode fauna which inhabits the mangrove coasts in general. To solve both questions I have sampled the ostracodes of Southwest Florida, where one of the largest mangrove swamps is located. A study is now under way to describe the soft parts and ecology of the forms collected there. This paper is a preliminary report of some more abundant forms living in the oligo- and mesohaline parts of the mangroves. It deals with material which has been collected by a handnet with a mesh width of 0.2 mm on a monthly base from August 20, 1969 to April 4, 1970. The ostracodes have been picked living under a stereomicroscope. Text-figure 1 shows the localities where the samples in this study were taken.

The carapace morphology of most of the marine and brackish-water ostracodes of South Florida has been figured by Puri (1960). The morphology of the fresh-water ostracodes is partly known by a paper by Furtos (1936). Puri and Benda (1962) published a paper on ecology in which they used mainly dead animals to characterize four biofacies. King and Kornicker (1970) in Texas established three biofacies by the use of living ostracodes.

It seems that most of the workers are beginning to see that detailed ecologic data can only be gathered by the help of living specimen. Until recently an overall picture of the region in which one species lives was accepted, but from this, one is only able to say which physical and chemical data he can correlate with the abundance, when he is comparing the population of living animals.

MATERIAL

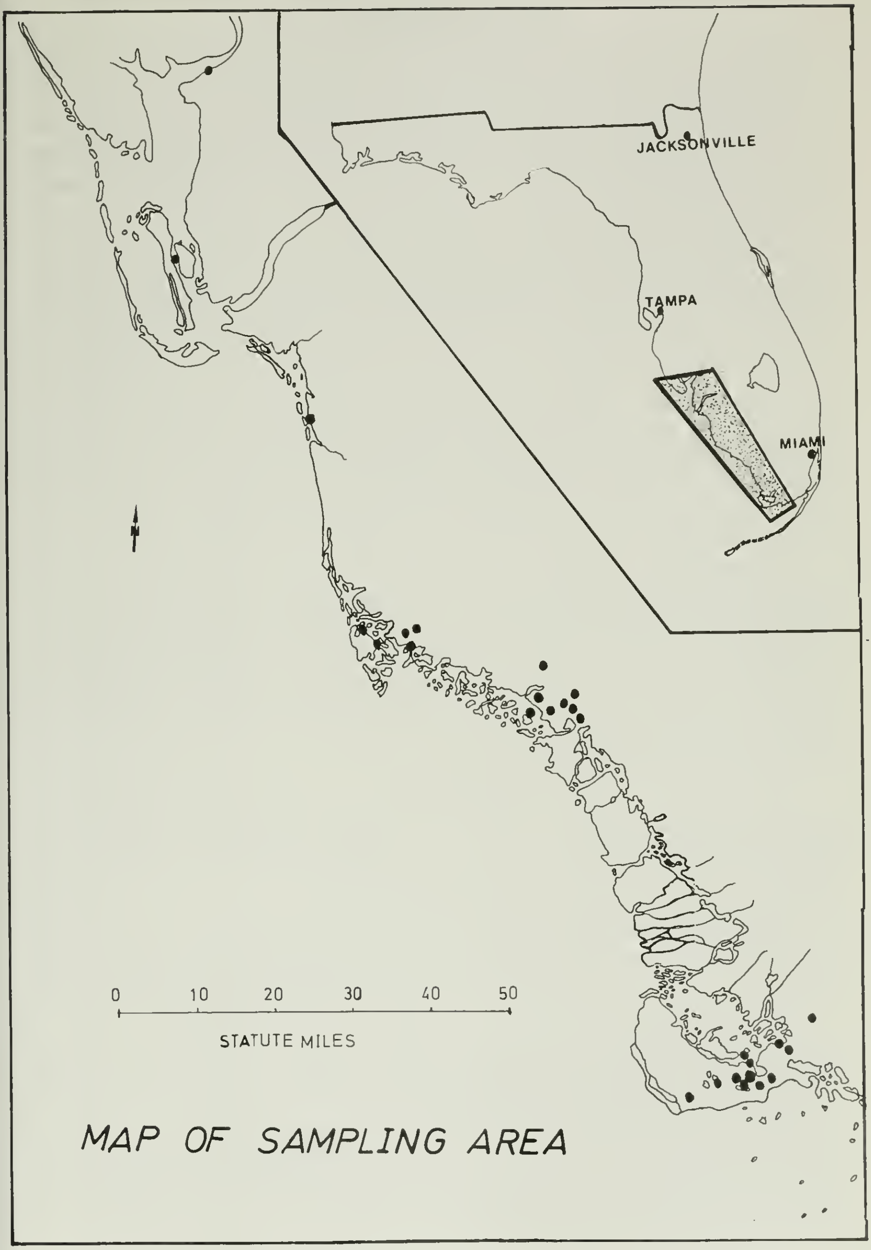
I found 20 species in the oligo- and mesohaline region of Southwest Florida. I could identify 14 of them, mainly by means of the carapace morphology. Seven of the species with five genera belong to the Cypridacea, while 13 species representing eight genera belong to the Cytheracea. These species are:

CYPRIDACEA:

Candona annae Méhes, 1941
Cypretta bilicis Furtos, 1936 (? = C. braevisaepta Furtos, 1934)
Cypria pseudocrenulata Furtos, 1936
Cyprinotus sp. II
Parapontoparta sp. A
Parapontoparta sp. B
Parapontoparta sp. C

CYTHERACEA:

Limnocythere ?sanctipatricii Brady and Robertson, 1869
Cyprideis ?beaveni Tressler and Smith, 1948
Cyprideis salebrosa van den Bold, 1963
?Haplocytheridea setipunctata (Brady, 1869)
Perissocytheridea ?bicelliforma Swain, 1955
Perissocytheridea ?brachyforma Swain, 1955
Aurila conradi (Howe and McGuirt, 1935)
Xestoleberis sp. A
Cytherura elongata Edwards, 1944
Cytherura johnsoni Mincher, 1941
Cytherura forulata Edwards, 1944
Reticulocythereis floridana Puri, 1960
Reticulocythereis sp. II


JACKSONVILLE
TAMPA
MIAMI
N
0 10 20 30 40 50
STATUTE MILES
MAP OF SAMPLING AREA

ECOLOGICAL AND ZOOGEOGRAPHICAL DISTRIBUTION OF CYPRIDACEA

Three species of the collected Cypridacea are already known from Florida (Furtos, 1936), but they were all reported from freshwater.

I found *Candona annae* Méhes only in the limnic and oligohaline zone (Text-fig. 2), and this species obviously does not tolerate higher salinity waters. Its distribution includes Massachusetts, Florida, and Columbia, South America.

Probably the limiting factor in *Cypria pseudocrenulata* Furtos and *Cypretta bilicis* Furtos (Text-fig. 2) is also salinity. These species are present in the oligohaline waters and two samples showed these forms in higher salinity water, but only in small numbers. *Cypria pseudocrenulata* has not been reported from brackish waters and neither has *Cypretta bilicis*. But *C. pseudocrenulata* might be synonymous to *Physocypria pustulosa* Sharpe, which has been mentioned by Swain (1955) in Texas lagoons.

Cyprinotus sp. II was present in oligo- and mesohaline conditions (Text-fig. 2). It probably tolerates higher salinity than the previous forms. This would be comparable to *Cyprinotus salinus* Brady, 1862, which is known to live mainly in oligo- and mesohaline water and only seldom in fresh water (Klie, 1938).

Another group of Cypridacea which was not encountered in fresh water is *Parapontoparta* sp. A, B, and C. To date they have not been reported from the Gulf Coast. The carapace shows some affinity to *Aglaiocypris*? figured by King and Kornicker (1970). Hartmann (1955) reported *Parapontoparta* from Brazil. Along with *Cyprinotus* this is the second group of Cypridacea which are found in the brackish-water region of the Gulf Coast. Probably all ostracodes which belong to the Thalassocypridini are true brackish-water forms and are never found in the fresh water.

All of the three species of *Parapontoparta* are swimming forms with a smooth translucent carapace. *Parapontoparta* sp. A (Text-fig. 2) is found on hard substrate covered by a small layer of soft or coarse detritus. The occurrence of this form in the present study is limited to the entire mesohaline, ranging in salinity from 4.2 o/oo - 18.6 o/oo.

Parapontoparta sp. B (Text-fig. 2) has a wider field of occurrence. I found it on silt, fine-medium sand and on mud. It seems that it does need some soft detritus, for I did not find it on sterile sand, silt or rock. The salinity range was from 4.2 o/oo - 20.9 o/oo.

Parapontoparta sp. C (Text-fig. 2) did not occur as frequently as the other forms. It was the only *Parapontoparta* found in oligo-, meso- and polyhaline waters. Detritus was also present.

The current affects these swimming forms more than burrowers, and I believe distribution of these animals is mainly influenced by currents. *Parapontoparta* sp. B tolerates some current, for I found only one specimen on mud but 15 in a channel with a strong tide current.

ECOLOGICAL AND ZOOGEOGRAPHICAL DISTRIBUTION OF CYTHERACEA

The only *Cytheracea* found in oligohaline waters was *Limnocythere ?sanctipatricii* Brady and Robertson (Text-fig. 3). King and Kornicker (1970) and Hulings (1958) reported *L. sanctipatricii* living in the α-mesohaline to the hyperhaline zone, so it is remarkable that the distribution in Southwest Florida is limited to the oligohaline. In only one station two specimens were found at a salinity of 12.2 o/oo. Therefore, it seems that this form is holeuryhaline.

Another euryhaline genus is *Cyprideis*. In Southwest Florida the most common mesohaline form is *Cyprideis ?beaveni* Tressler and Smith (Text-fig. 3). In some areas this species was found in such an abundance as to form an important element of the substrate. It occurs in oligo-, meso-, poly- and euhaline waters.

A second species, *Cyprideis salebrosa* van den Bold (Text-fig. 3), was present in only one sample, remarkably living in fresh water. Sandberg (1964) reported that living specimens occur, but he did not find one with appendages. Hartmann (personal communication) had some soft parts in his sample taken from the Rio de la Plata, but the salinity of this station is not known. Thus, it is questionable whether this species occurs living only in freshwater or also lives in brackish water.

Nearly as frequent as *Cyprideis ?beaveni* is ? *Haplocytheridea setipunctata* (Brady) (Text-fig. 3). This species is easily distinguished from other species of *Cyprideis* by means of their unique copulatory organ. This species obviously avoids the oligo- and α-mesohaline zone but is found continuously up to the euhaline. ?*Haplocytheridea setipunctata* is found only in sandy substrate. On this substrate *Cyprideis ?beaveni* can obviously not compete with ? *Haplocytheridea setipunctata. H. setipunctata* has been reported from the Gulf Coast and Atlantic Coast of North America.

Perissocytheridea ?brachyforma Swain (Text-fig. 3) is another brackish-water species, common in Floridian waters. It was found in the meso- and polyhaline zone in different types of substrate. It probably prefers harder ground, while *Perissocytheridea ?bicelliforma* Swain (Text-fig. 3) is often found in softer substrate, but also in the meso- and polyhaline district. *P. ?brachyforma* is very common in the Gulf and Caribbean but has not been reported from the Pacific Coast as has *P. ?bicelliforma.*

Aurila conradi (Howe and McGuirt) has also been reported from both coasts of the North American continent (Text-fig. 3). Living specimen were found at the transition to the oligohaline which concurs with the findings of Kornicker and Wise (1960). Their findings were that the salinity tolerance of *A. conradi littorala* Kornicker and Wise, 1960 is 6 o/oo to 65 o/oo below at a lower salinity it should become inactive. It prefers obviously hard ground which can be hard detritus, sand or sometimes rock or oyster reefs.

Xestoleberis sp. A (Text-fig. 4) was found at times to be associated

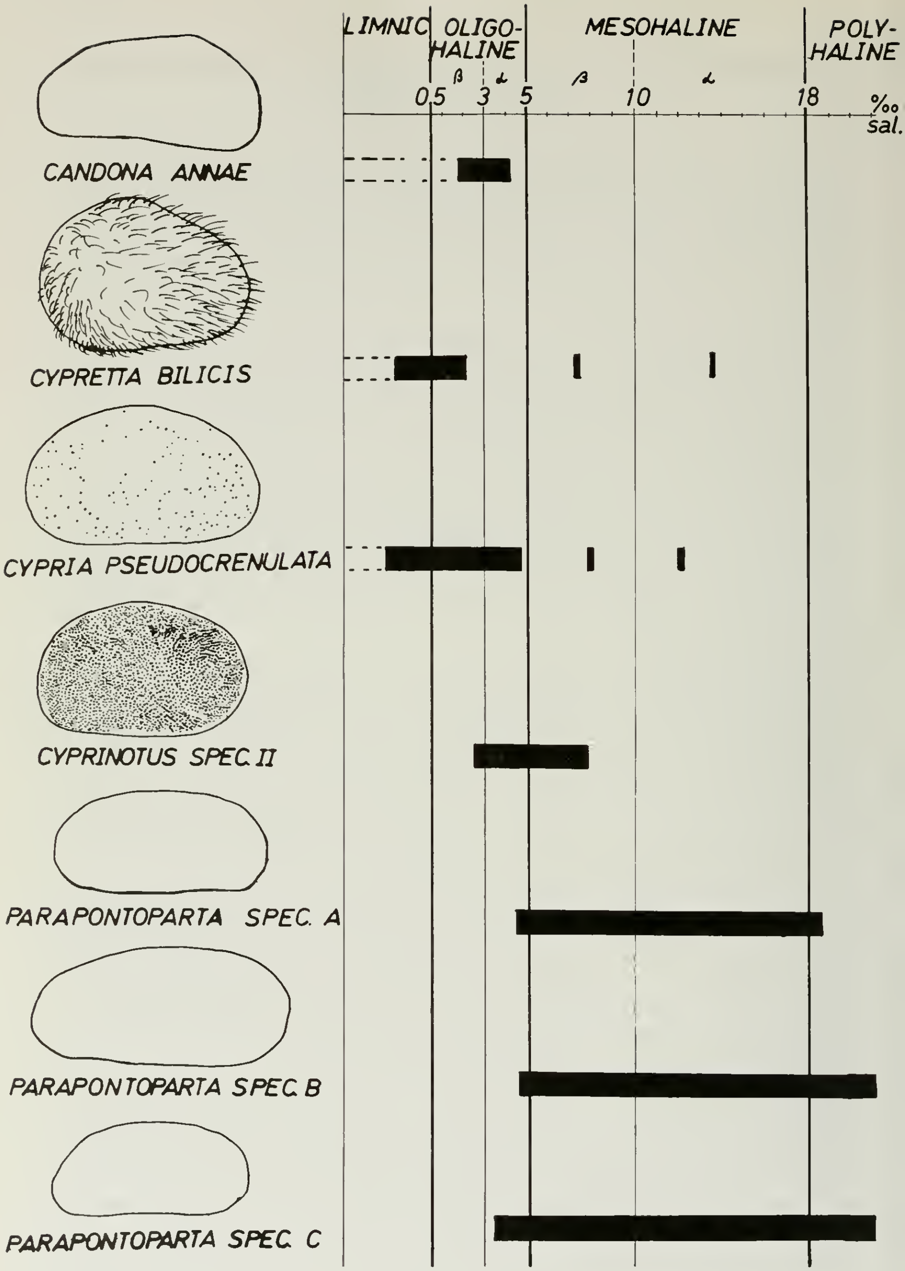


FIG.2 SALINITY RANGE OF CYPRIDACEA

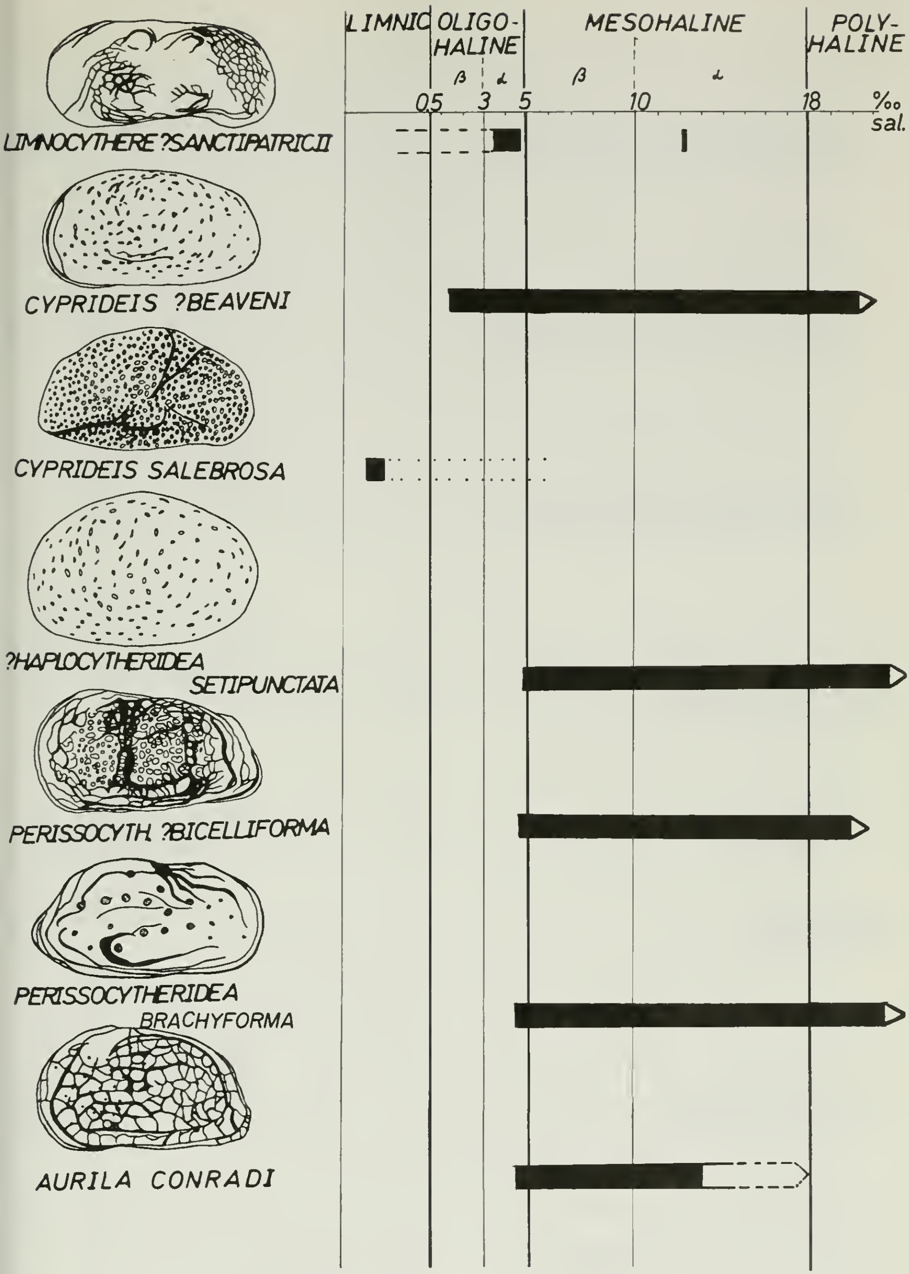


FIG.3 SALINITY RANGE OF CYTHERACEA

with *Aurila conradi. Xestoleberis* sp. A was present from mesohaline to polyhaline waters. It is remarkable that this form also lives at the transition to the oligohaline zone. This shows it also to be an euryhaline form. It does not occur in mud also comparable to *Aurila conradi.*

Three species of *Cytherura* were encountered in the mangrove region of Southwest Florida (Text-fig. 4). *Cytherura elongata* Edwards and *Cytherura johnsoni* Mincher were found in meso- and polyhaline waters, while *Cytherura forulata* Edwards was only present in α-mesohaline to euhaline samples. *C. elongata* was usually found to have larger number of individuals as the remaining species at the location. They all prefer the same substrate, mostly sand and some detritus. *C. elongata* and *C. forulata* are known from the Gulf Coast northwards to southern Virginia. *C. johnsoni* has also been reported from the Caribbean sea and the Pacific Coast.

Two species of brackish-water ostracodes are nearly unknown. Puri (1960) described one species as *Reticulocythereis floridana* Puri. I called the other *Reticulocythereis* sp. II (Text-fig. 4). Both are living in α-meschaline to polyhaline water, on sandy ground covered with some detritus. Both species occur together, the soft parts indicate different feeding habits.

RESULTS

This study represents the ecologic distribution of 20 brackish-water ostracode species, which were collected between August 20, 1969, and April 4, 1970, at a regular monthly interval in the mangrove region of Southwest Florida. The distribution has been examined mainly in the oligo- and mesohaline zone by examination of living specimens.

1) As typical limnic and oligohaline Cypridacea were identified *Candona annae* Méhes, *Cypretta bilicis* Furtos, and *Cypria pseudocrenulata* Furtos. The latter two have been found occasionally in mesohaline waters but are not believed to reproduce there.
2) A typical form of the Cypridacea in the α-oligo- and β-mesohaline is *Cyprinotus* sp. II.
3) As new for the Gulf Coast Cypridacea I have reported the genus *Parapontoparta.* Three species were found in the β-mesohaline and in the polyhaline exclusively, as previously known for the Thalassocypridini.
4) Only three species of Cytheracea were found in salinity lower than 4 o/oo: *Limnocythere ?sanctipatricii* Brady and Robertson, *Cyprideis ?beaveni* Tressler and Smith and only limnic *Cyprideis salebrosa* van den Bold.
5) *?Haplocytheridea setipunctata* (Brady), *Perissocytheridea ?bicelliforma* Swain, *Perissocytheridea ?brachyforma* Swain, *Aurila conradi* (Howe, and McGuirt), *Xestoleberis* sp. *A, Cytherura elongata* Edwards and *Cytherura johnsoni* Mincher showed clearly that they are not able to tolerate oligohaline waters.
6) The minimum salinity for *Cytherura forulata* Edwards, *Reticulocythereis floridana* Puri, and *Reticulocythereis* sp. II is the α-mesohaline.

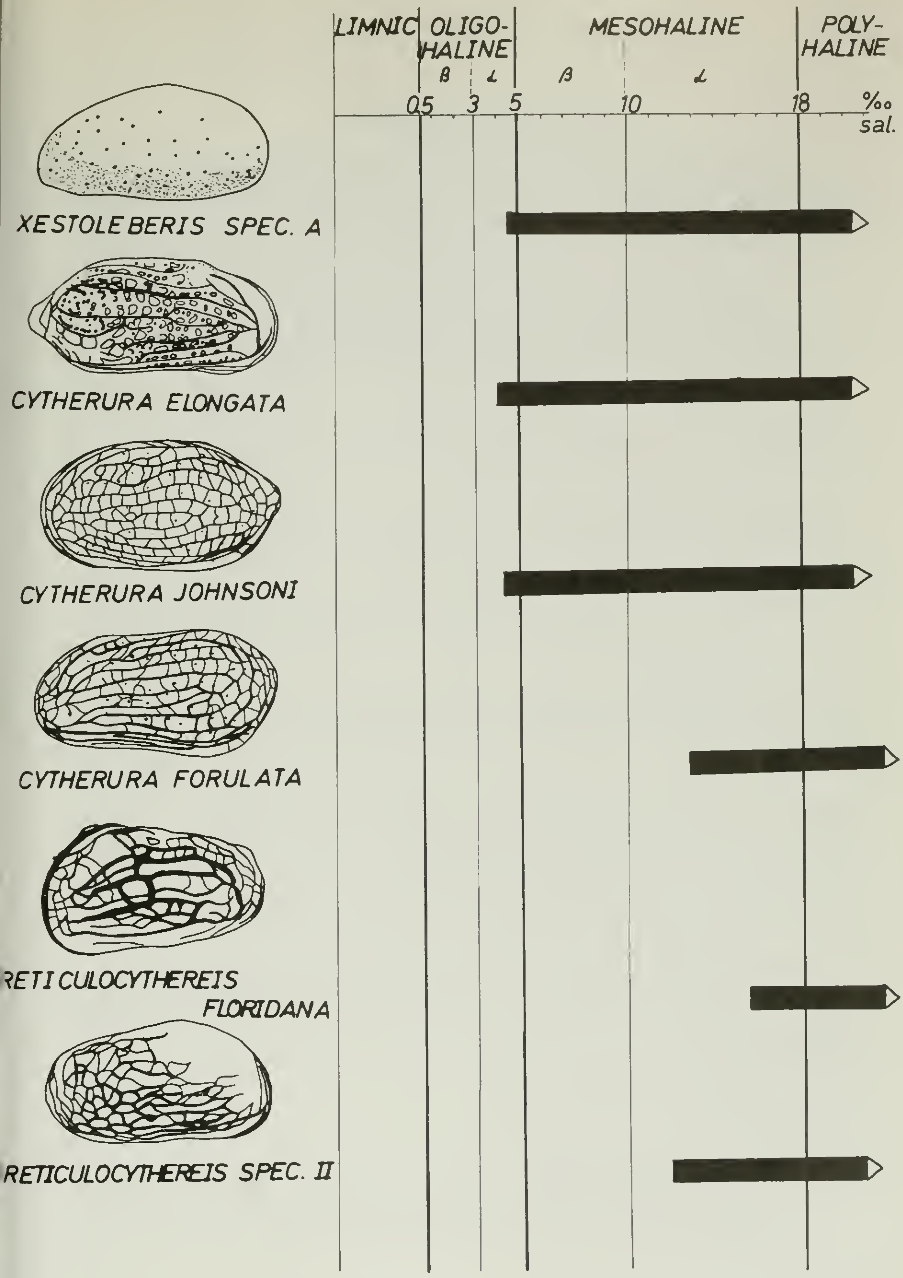


FIG.4 SALINITY RANGE OF CYTHERACEA

ACKNOWLEDGMENTS

I would like to thank Prof. Dr. G. Hartmann, Zoologisches Institut und Museum, Universität Hamburg, and Dr. H. S. Puri, Florida Department of Natural Resources, Bureau of Geology, Tallahassee, Florida, for the most valuable help during the study and the preparation of the manuscript. Gratitude is also expressed to the Florida Bureau of Geology and the Everglades National Park which made it possible to collect the material and were very helpful in many problems. I want to give my thanks also to the Florida State University which offered me the use of their instrumental facilities.

REFERENCES

Furtos, N. C.
1936. *Fresh-water Ostracoda from Florida and North Carolina.* American Mid. Nat., 17, pp. 491-522.

Hartmann, G
1955. *Neue marine Ostracoden der Familie Cypridae und der Subfamilie Cytherideinae der Familie Cytheridae aus Brasilien.* Zool. Anzeiger, Bd. 154, Heft 5/6, pp. 109-127.

Hulings, N. C.
1958. *An ecologic study of the Recent ostracods of the Gulf Coast of Florida.* Unpublished Dissertation Florida State University, Tallahassee, Fla.

King, C. E., and Kornicker, L. S.
1970. *Ostracoda in Texas Bays and Lagoons: An Ecologic Study.* Smithsonian Contrib. Zoology, No. 24, pp. 1-92.

Klie, W.
1938. *Ostracoda, Muschelkrebse.* In F. Dahl, *Die Tierwelt Deutschlands und der angrenzenden Meeresteile,* 34 (3), pp. 1-230.

Kornicker, L. S., and Wise, C. D.
1960. *Some Environmental boundaries of a marine ostracode.* Micropaleontology, 6 (4), pp. 393-398.

Puri, H. S.
1960. *Recent Ostracoda from the west coast of Florida.* Gulf Coast Assoc. Geol. Soc., Trans., vol. 10, pp. 107-149.

Puri, H. S., and Benda, W. K.
1962. *The distribution of Foraminifera and Ostracoda off the Gulf Coast of the Cape Romano area, Florida.* Gulf Coast Assoc. Geol. Soc., Trans. vol. 12, pp. 303-341.

Sandberg, P. A.
1964. *The ostracod genus Cyprideis in the Americas.* Stockholm Contrib. Geology, vol. XII, pp. 1-178.

Swain, F. M.
1955. *Ostracoda of San Antonio Bay, Texas.* Jour. Paleont., vol. 29, No. 4 (July), pp. 561-646.

Tressler, W. L., and Smith, E. M.
1948. *An ecologic study of seasonal distribution of Ostracoda, Solomons Island, Maryland, Region.* Chesapeake Biol. Lab., Pub. 71, pp. 3-57.

Dietmar Keyser,
Zoologisches Institut und Museum.
Hamburg,
Germany

DISCUSSION

Dr. L. S. Kornicker: I would like to commend you on an excellent paper. The question I have is whether you satisfied yourself by examining the West Coast specimens, that those you found on the East Coast and the West Coast were conspecific or are you relying on literature?

Mr. Keyser: At this moment I am still relying only on literature. But I agree that this is necessary, if one wants to give reliable zoographical data.

Dr. H. Löffler: I am glad that you put a question mark on *sanctipatricii*. For I don't think that your *Limnocythere* is *sanctipatricii,* which is known to be a cold water species.

Mr. Keyser: I think you are right, but I named it *sanctipatricii* for this species has been referred to in all papers I know of as *Limnocythere sanctipatricii.* The question mark should accentuate my disbelief that this is the same species as the European.

Dr. J. E. Hazel: I think that this work will be valuable not only in understanding mangrove environment but also in interpreting many Pleistocene deposits in Florida that have assemblages somewhat similar to what you described. I would like also to say that we have many of the same species in common, and we're not in all cases using the same names for them. We should get together and get the nomenclature sorted out.

Dr. H. Uffenorde: How close to the bottom-dwelling ostracodes did you measure salinity? In sheltered marginal marine environments a rapid decrease in salinity from bottom to top can be observed within a few decimeters. If there is any fresh water supplied by brooks, springs, or rain it may form a covering layer of fresh water.

Mr. Keyser: I used a portable conductivity meter. So I was able to measure the salinity directly above the bottom. To your other remark I would like to say, that the area in which I was sampling is a lagoonal type of environment, and there you find conditions which are mainly influenced by tidal currents and to a lesser extent by fresh water streams. King and Kornicker (1970) mentioned in a similar area that the bottom and surface salinity do not differ extensively, less than 1/10 of a part per thousand.

Dr. R. Reyment: My comment follows the preceding remark (by Uffenorde). As has been demonstrated by F. Manheim, R. Hallberg (1972; Diss. Univ. Stockholm), Hallberg and Reyment (Crustaceana, 1967), and Reyment (Bull. Geol. Univers. Instn. Upsala, 1969), the ecochemical conditions prevailing within the sediment (interstitial pore water) and in which many organisms live, including ostracodes, differ considerably from those existing in the supernatant water.

Dr. Uffenorde: I agree with Dr. Reyment's remarks. I fear we are heading the wrong way using methods developed by oceanographers to get data for areas a thousand and more times bigger than the ostracode habitat. This is true especially for measurements of oxygen saturation and redox potential.

THE FAMILY LEPTOCYTHERIDAE IN ARGENTINE WATERS

R. C. Whatley
Universidad Nacional de La Plata and University College of Wales
and
A. Moguilevsky
Universidad de Buenos Aires

ABSTRACT

Eight species, belonging to two genera of the Leptocytheridae, are herein recorded from the Argentine Continental Shelf and from adjacent littoral, estuarine, and lagoonal environments. Five of these species are new: *Leptocythere,* n. spp. A, B, *Callistocythere,* n. spp. A, B, C, but are not formally named or described here. Another species of *Leptocythere* is also left with open nomenclature. The geographical ranges of *L. patagonica* and *C. dispersocostata* previously recorded from Patagonia by Hartmann (1962), are extended northwards. Distributional and ecological data are given for each species and it is noted that the majority of species of both *Leptocythere* and *Callistocythere* are more phytal in their habit in these waters than is normal for the members of the two genera elsewhere. A note is also included on the known fossil history of the family in this part of South America.

RESUMEN

Se reconocen 8 especies, pertenecientes a 2 géneros de Leptocytheridae, en la Plataforma Continental Argentina y en ambientes adyacentes de tipo estuárico, litoral y de albufera. De estas especies, 5 son nuevas: *Leptocythere* n. spp. A, B, *Callistocythre* A, B, C, y una especies de *Leptocythere* se incluve bajo nomenclatcra abierta. Se amplía hacia el norte la distribución geografica de *L. patagonica* y *C. dispersocostata,* mencionada con anterioridad para Patagonia por Hartmann (1962). Se incluyen, además, detalles de la ecologia y distribución de cada una de las especies. Observándose que la mayoría de las especies de *Leptocythere* y *Callistocythere* de estas aguas son más comunmente epifiticos que otros miembros de los mismos géneros en otras regiones. Se incluyen algunas consideraciones sobre la historia geológica de la familia Leptocytheridae en este parte de America del Sud.

RÉSUMÉ

On reconnait 8 espèces, appartenent à 2 genres de Leptocytheridae, sur la plateforme continentale argentine et sur les milieux adjacents de type littoral estuaire ou lagune. De ces espèces, 5 sont nouvelles: *Leptocythere,* n. spp. A, B, *Callistocythere,* sp. A, B, C, et une espèce de *Leptocythere* est laissée dans une nomenclature ouverte. La distribucion géographique de *L. patagonica* et *C. dispersocostata,* mencionnées antérieurement en Patagonie par Hartmann (1962) s'étend vers le nord. De plus des détails concernant l'écologie et la distribution de chaque espèce ont été inclus. On peut noter que la plus grande partie des espèces de *Leptocythere* et *Callistocythere* en provenance de ces eaux sont plus communément epiphytiques que d'autres membres des mêmes genres en d'autres régions. On a égalment inclus une note sur l'histoire géologique les Leptocytheridae dans cette région d'Amérique du Sud.

INTRODUCTION

The present work forms part of a comprehensive monographic study concerning the taxonomy, ecology, and zoogeographical distribution of benthonic Ostracoda from the Argentine continental shelf and from adjacent littoral and estuarine environments. This study is based on samples collected by the Argentine Institute of Oceanography and the Hydrographic Service of the Argentine Navy, from the continental shelf and from the estuary of the River Plate (Río de La Plata) and samples collected by the authors, at various intervals during 1970 to 1972, from estuarine and littoral environments between the River Plate and Tierra del Fuego (Text-fig. 1). This latter sampling also embraces southern Chilean water, especially in the Straits of Magellan.

The sediment samples from the continental shelf have been collected by means of both "grab" and "dredge", and those from the littoral by standard techniques for collecting sediments and by the processing algae as described by Whatley and Wall (1969, p. 294). Sublittoral weed and sediments have been collected by dredging and by diving.

Relatively few works exist concerning the benthonic Ostracoda of Argentine and adjacent waters, and even fewer contain descriptions of the family Leptocytheridae. From the Argentine the only two species which have been described previously, both from Patagonia, are *Callistocythere dispersocostata* Hartmann, 1962, and *Leptocythere patagonica* (Hartmann, 1962), who also mentioned another, *Callistocythere* sp., also from Patagonia and Tierra del Fuego. The same author has described the following species from Brasil:

Callistocythere ornata (Hartmann, 1956)
Callistocythere sp. (Hartmann, 1956)
Callistocythere costata (Hartmann, 1956)
Mesocythere foveata Hartmann, 1956
Mesocythere elongata Hartmann, 1956
Mesocythere punctata Hartmann, 1956

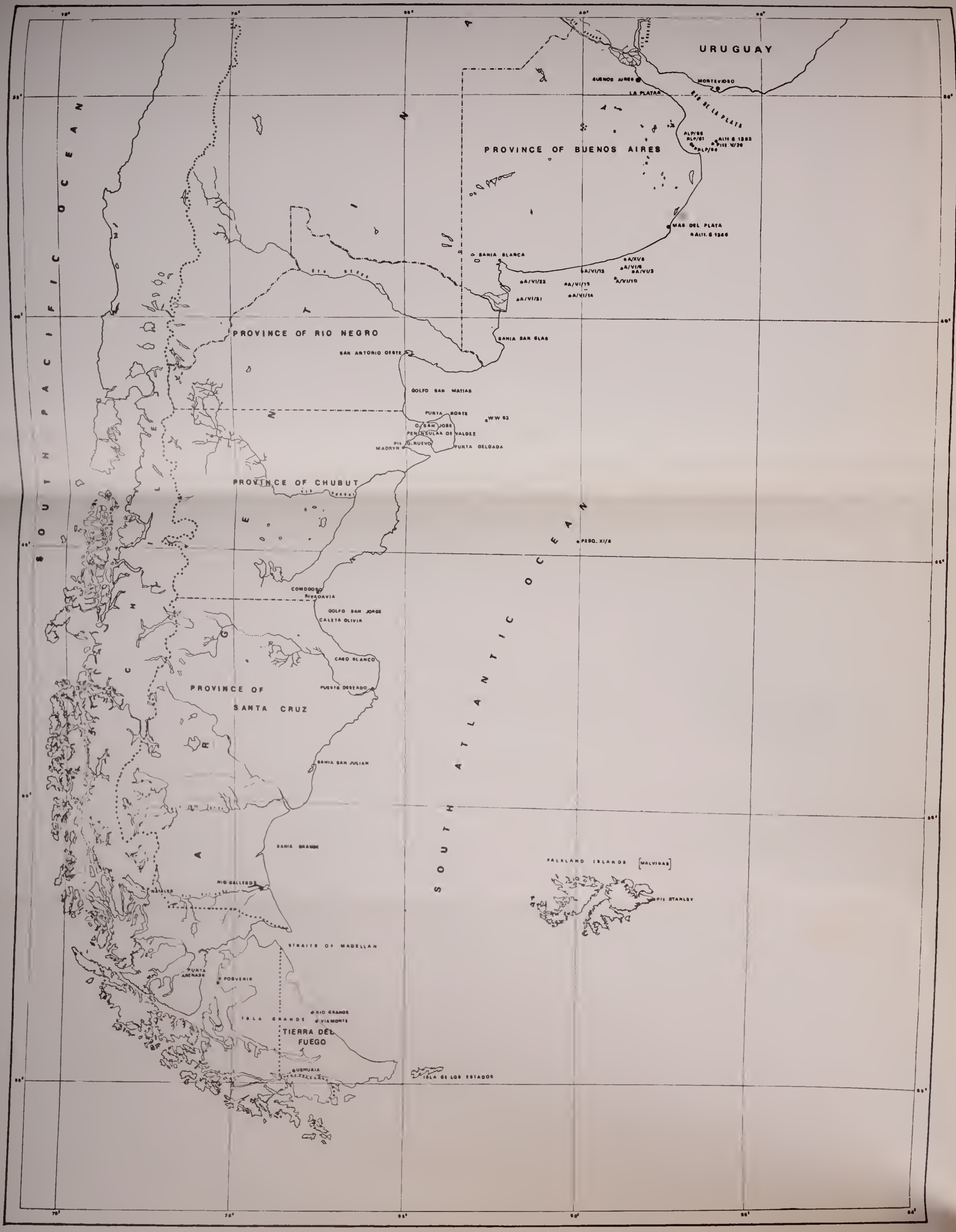
Ilyocythere Klie, is excluded from this list because the authors are of the opinion that it is probably synonymous with *Perissocytheridea* Stephenson. *Pericythere* is similarly excluded since, by virtue of its unbranched marginal pore canals and adont hingement, it would not seem to belong to the Leptocytheridae.

From Chile, Hartmann recorded both *C. dispersocostata* and *L. patagonica* (Hartmann, 1962) and also *C. fischeri* (Hartmann, 1961).

In the present study, three new species of *Callistocythere* and two of *Leptocythere* are added to the list for the family in these waters. Also, a further species of *Leptocythere* is left with open nomenclature.

That the family Leptocytheridae has a fossil history in the Argentine is evidenced by the occurrence of two species of *Mesocythere* in sediments of upper Oligocene/lower Miocene age from the eastern part of the Province of Santa Cruz, Patagonia, (Lic. Hugo Valicenti, personal communication), by the occurrence of *Callistocythere* in Miocene sediments from the Province of Entre Ríos (the material described by Rossi de Garcia (1966) as *Perissocytheridea littoralensis* is certainly *Callistocythere* as illustrated in Plate 2), and by the occurrence in Pleistocene and Holocene sediments in the Province of Buenos Aires of *C.*, n. sp. A (Whatley unpublished). All types and figured specimens


55°
URUGUAY
60°
A
65°
70°
75°


URUGUAY
MONTEVIDEO
BUENOS AIRES
LA PLATA
RIO DE LA PLATA
PROVINCE OF BUENOS AIRES
ALP/65
RLP/61
ALP/64
ALTI S 1363
PIII V/26
MAR DEL PLATA
ALTI. S 1346
A/XV/8
A/VI/8
A/VI/3
A/VI/12
A/VI/10
A/VI/13
A/VI/14
A/VI/23
A/VI/21
BAHIA BLANCA
BAHIA SAN BLAS
PROVINCE OF RIO NEGRO
SAN ANTONIO OESTE
GOLFO SAN MATIAS
PUNTA NORTE
WW 63
G. SAN JOSE
PENINSULAA DE VALDEZ
PTO MADRYN
G. NUEVO
PUNTA DELGADA
PROVINCE OF CHUBUT
PESQ. XI/4
COMODORO RIVADAVIA
GOLFO SAN JORGE
CALETA OLIVIA
CABO BLANCO
PUERTO DESEADO
PROVINCE OF SANTA CRUZ
BAHIA SAN JULIAN
BAHIA GRANDE
RIO GALLEGOS
STRAITS OF MAGELLAN
PUNTA ARENAS
PORVENIR
RIO GRANDE
VIAMONTE
ISLA GRANDE
TIERRA DEL FUEGO
USHUAIA
ISLA DE LOS ESTADOS
FALKLAND ISLANDS [MALVINAS]
PT. STANLEY
SOUTH ATLANTIC OCEAN
SOUTH PACIFIC OCEAN
ARGENTINA
CHILE

are deposited in the collections of the Department of Palaeontology, Museo de La Plata, to which the numbers quoted in the paper refer. Topotype or reference material has also been deposited in the British Museum (Natural History), the U.S. National Museum and the Argentine Museum of Natural Sciences, Buenos Aires.

ACKNOWLEDGMENTS

R. C. Whatley wishes to acknowledge the support of the Argentine Consejo Nacional de Investigaciones Científicas y Técnicas, and A. Moguilevsky the support of the Facultad de Ciencias Exactas y Naturales, University of Buenos Aires. The authors wish particularly to thank Lics. Maria Luz Piriz and Alicia Boraso for assistance in collecting and identifying algae and extend the same thanks to their companions on the 1971 expedition to Patagonia, especially to Sr. Miguel Manceñido for his services as diver and also for collecting the material on the cruise of the *Austral*. From the Hydrographic Service of the Argentine Navy, the authors have received many kindnesses and much valuable material and data. We wish particularly to acknowledge the help of Capt. Ascencio Carlos Lara, Teniente Osvaldo Bozzo, and Sr. N. Randich. Equally, we are extremely grateful to the Argentine Institute of Oceanography, Bahía Blanca, for all their assistance, especially from Ingeniero Alberto Lonardi and Lic. Felix Mouzo. Permission to use the facilities of the Argentine Centro de Investigaciones de Biología Marina del I.N.T.I., in Puerto Deseado and Ushuaia, kindly granted by the director, Dr. Oscar Kuhnemann, is gratefully acknowledged. Valuable discussions have been held with many workers in various fields but the authors particularly wish to mention Dr. Estaban Boltovskoy, Dr. Raul Santiago Olivier, Dra. Zulma Castellanos and Lic. Hugo Valicenti, who also helped with the photography. Lic. Lucy Costa and Sr. Jorge Mennucci have also helped the authors in many ways. The SEM photography was executed with the CONICET instrument. Finally, R. C. Whatley wishes to extend his warmest thanks to the British Council for financing his visit to Delaware and to his collegues in the University College of Wales, Aberystwyth, for their prompt response to many strange and varied requests.

GEOGRAPHICAL LOCATION AND DESCRIPTION OF THE SAMPLES

Although approximately 400 samples have been examined to date in our study of the Argentine benthonic Ostracoda, Leptocytheridae have only been found at the following 37 localities, of which 22 are littoral and the remainder on the continental shelf or from the entrance to the estuary of the River Plate (Text-fig. 1.)

a) *Littoral*

1) *Santa Elena.* Approximately 20 Km. north of Mar del Plata, Province of Buenos Aires. Red and green algae collected at low tide in February, 1971, from a lower eulittoral rock platform. The algae contained coarse to medium sand and shell fragments. Very exposed coast with strong wave action. *C.,* n. sp. A (dead) ♀.

2) *Playa Grande.* Mar del Plata, Approximately 38°S. Algae and sediment collected from a eulittoral rock pool immediately to the north of the Marine Biological Station, September 1970. *C.,* n. sp. A ♀, n.g. & sp. ♀, and *Leptocythere* sp. (all dead).

3) *Pocitos.* Approximately 30 Km. north of Bahía San Blas in the extreme south of the province of Buenos Aires at about 40°25'S. In this area, which is very sheltered by a series of offshore shoals and islands, exist a variety of littoral environments ranging from rock platforms and mud flats in the eulittoral and sublittoral, to dense clumps of *Spartina* growing in the upper eulittoral and in the littoral fringe.

PO/1. Fine sand and silt from roots of *Spartina. C.,* n. sp. A ♀ (live), *L.* n .sp. A ♂ ♀ juv. (live). January, 1971.

4) *Punta Ramírez.* Approximately 10 Km. south of the preceeding locality and similarly protected by offshore shoals and islands. Extensive eulittoral and sublittoral rock platform, with *Spartina* growing in the littoral fringe and upper eulittoral. The following samples collected in January, 1971, yielded Leptocytheridae.

PR/3. Upper sublittoral or lower eulittoral algae growing on stones at the bottom of a channel. *L.,* n. sp. A ♀ (dead).

PR/4. Eulittoral algae from rock pool. *C. dispersocostata* ♂ ♀ (live), *L.* n. sp. A ♂ ♀ (live).

PR/11. Upper eulittoral, *Ulva, Enteromorpha,* and sediment from a rock pool. *C. dispersocostata* ♂ ♀ (live), *C.,* n. sp. A ♀ (live), *C.,* n. sp. C ♀ (dead), *L.,* n. sp. A ♂ ♀ (live).

PR/13. Littoral fringe or extreme upper eulittoral. Sediment from around roots of *Spartina* growing in a shallow pool. *C. dispersocostata* ♂ ♀ juv. (live), *C.,* n. sp. C ♀ (live), *L. patagonica* ♀ (dead), *L.,* n. sp. A ♂ ♀ juv. (live), n.g. & sp. ♀ (dead).

5) *Arroyo Jabali.* Shallow muddy tidal ría-like inlet of the sea behind the village Bahía San Blas, Province of Buenos Aires, apparently without freshwater-connections and probably highly saline after protracted hot weather. January, 1971.

Ao/1. Algae and algal detritus collected from below low water mark. *C. dispersocostata* (dead), *L.,* n. sp. B (smooth form) ♂ ♀ juv. (live).

Ao/3. Fine sand and silt with much organic, particularly algal detritus, just above low water mark. *L.* n. sp. A ♂ ♀ juv. (live), *C.,* n. sp. A ♂ ♀ (live), *C.,* n. sp. C ♀ (live).

6) *San Antonio Oeste.* Province of Río Negro, approximately 40°40'S. Large ría immediately south of the town. Algal sample of *Bryopsis, Ceramium,* and *Ulva* from stones in the lower eulittoral at the base of a steep shingle beach, February, 1972. *L.,* n. sp. A ♂ ♀ juv. (live), *C. dispersocostata* ♂ ♀ (live).

7) *Las Grutas.* Province of Río Negro, a few Km. south of San Antonio Oeste. Eulittoral rock platform to the immediate south of the Esplanade. Leptocytheridae collected from the following samples in January 1971:

SA/1. Lower eulittoral. *Codium* from small rock pool. *C. dispersocostata* ♂ ♀ (live), *L.*, n. sp. A ♂ ♀ juv. (live), *C.* n. sp. C ♀ (live).

SA/2. Sediment of sand, small pebbles, and shell detritus from the same pool. *C. dispersocostata* ♂ ♀ juv. (dead). *L.*, n. sp. A ♂ ♀ juv. (dead). *C.*, n. sp. C ♀ (live).

SA/3. Assorted smaller algae, including *Polysiphonia, Ceramium,* and *Enteromorpha* from the same pool. *C. dispersocostata* ♂ ♀ (live), *C.*, n. sp. C ♀ (live). *L.*, n. sp. A ♂ ♀ juv. (live), *L. patagonica* ♀ (dead), n.g. & sp. ♂ (dead).

SA/5. Rhodophyceae from a number of lower eulittoral pools in the same area. *C. dispersocostata* ♂ ♀ (live), *C.*, n. sp. C ♀ juv. (dead) *L.*, n. sp. A ♂ ♀ juv. (live).

8) *Isla de Los Pájaros (Bird Island).* On the southern shore of Golfo San José, Península de Valdez, Province of Chubut, approximately 42°25'S. Eulittoral rock platform and mud flats on the mainland shore facing the island. Protected shore due to the presence of the Island. Leptocytheridae obtained from three of the nine samples.

BI/1. Algae from small 1-foot-deep rock pools in the upper eulittoral surrounded by tussocks of *Spartina. C. dispersocostata* ♀ (live), *L.*, n. sp. A ♂ ♀ juv. (live), *L. patagonica* ♀ (dead), *L.*, n. sp. B (smooth form) ♂ ♀ juv. January, 1971.

BI/5. *Corallina, Ulva,* and *Polysiphonia,* collected from three pools in the mid or lower eulittoral. *C. dispersocostata* ♂ ♀ juv. (live), *C.*, n. sp. A ♀ (live), *L.*, n. sp. A ♂ ♀ (live).

9) *Punta Norte.* Northern tip of Península Valdez? Province of Chubut, approximately 42°05'S. Exposed coastline with a lower eulittoral rock platform with dense algae beneath a steep shingle beach. Samples taken immediately to the south of the Elephant Seal *(Mirounga leonina)* colony administration buildings.

PN/1. *Blidingia* and *Porphyra* from rock platforms. *C. dispersocostata* juv. February, 1972.

10) *Caleta Valdez.* Elongate tidal lagoon separated from the sea by a shingle spit with a narrow entrance and apparently without fresh-water influence, on the eastward facing side of Península Valdez, Province of Chubut, at about 40°20'S. Sample of fine calcareous mud with algal debris taken from sublittoral. *C. dispersocostata* ♂ ♀ juv. (live), *L. patagonica* ♂ ♀ (live).

11) *Punta Delgada.* Southeastern tip of Península Valdez, 42°47'S. Extensive eulittoral rock platform terminated by a vertical drop to the sublittoral.

Pd/1. Assorted algae from upper eulittoral rock pool. *C. dispersocostata* ♂ ♀ (dead), *C.*, n. sp. C ♀ (live).

Pd/4. Green algae, principally *Enteromorpha,* from upper eulittoral rock pools. *C. dispersocostata* ♀ juv. (live), *L.*, n. sp. B (smooth form) ♂ ♀ (live).

Pd/7. *Codium* from lower eulittoral. *L.* n. sp. B ♂ juv. (live).

Pd/8. Red algae from upper eulittoral pools. *C. dispersocostata* ♂ ♀ juv. (live). *L.*, n. sp. B (smooth form) ♂ (live).

Pd/9. *Corallina* from the same pools. *C. dispersocostata* ♂ ♀ juv. (live) *L.*, n. sp. B (smooth form) ♂ juv. (live).

Pd/10. Mid-eulittoral Phaeophyta growing above "mattress" of *Corallina* and mussels. *C. dispersocostata* ♀ (live). January, 1971.

12) *Punta Ameghino.* On the northwestern shore of Golfo Nuevo, Province of Chubut, a few Km. N.E. of Puerto Madryn at about 42°37'S. Eulittoral rock platforms with many pools. Lower eulittoral algae, *Ceramium, Polysiphonia, Corallina, Codium vermilare,* and *Codium fragile. C. dispersocostata* ♂ ♀ juv. (live). February, 1972.

13) Bahía Solano. Algae collected from rock pools approximately midway between Caleta Córdoba and Pico Salamanca at about 45°42'S. and some 20-25Km. north of Comodoro Rivadavia, Province of Chubut. *C. dispersocostata* ♀ (live). *L.,* n. sp. B ♂ ♀ juv. (live), *L. patagonica* ♂ ♀ (live). March, 1972. (Collected by Lic. Hugo Valicenti).

14) *Caleta Olivia.* Province of Santa Cruz, wide bay a few Km. south of the town at about 46°30'S. Extensive eulittoral rock platform. Sediment sample of medium to coarse sand and shell debris from lower eulittoral channels in the rock platform. *C. dispersocostata* ♂ ♀ (dead), *L. patagonica* ♀ (dead). February, 1972.

15) *Puerto Deseado.* 47°45'10" S. Province of Santa Cruz. From several hundreds of eulittoral and sublittoral samples taken from within the Ría and from immediately outside it, from both algae and sediments, the following Leptocytheridae have been recorded: *C. dispersocostata* ♂ ♀ juv. (live), *L.,* n. sp. B ♂ ♀ juv., *L. patagonica* ♂ ♀ juv. (live).

16) *San Julián.* Province of Santa Cruz, at about 49°18'S. Large Ría without fresh-water influence. Immediately to the S.E. of the town, on the N. side of the Ría, steep muddy and stony eulittoral beach with, in the lower part, dense algal growth on stones. Sample of *Enteromorpha, Ceramium, Porphyra,* and a little *Ulva. L. patagonica* ♂ ♀ juv. (live). January, 1972.

17) *Monte León.* 50°18'S. Beach sample of sand and algal detritus. *C. dispersocostata* ♀ (dead).

18) *Río Gallegos.* Province of Santa Cruz, at about 51°38'S. Large estuary in which the tidal element is dominant. Sample of fine-grained lime mud taken at low water on the south bank of the estuary near the eastern limit of the town. *C. dispersocostata* ♀ (live). January, 1972.

19) *Cabeza del Mar.* Province of Magallanes, Chile at about 52°45'S. and some 55 km. north of Punta Arenas. Large shallow enclosed bay opening off from the west coast of the Straits of Magellan, with small tidal amplitude. Samples taken in the eulittoral immediately in front of Chorrillo La Lata Estancia. *Talusa parda, Ceramium,* and *Enteromorpha* with many epiphytes, growing on stones and also the adjacent sediment. *L. patagonica* ♂ ♀ juv. (live). *L.,* n. sp. B ♂ ♀ juv. (live). January, 1972.

20) *Puerto Porvenir.* Province of Magallanes, on the east side of the Straits of Magellan, in Chilean Isla Grande (Tierra del Fuego), at about 53°16'S. Narrow ría-like inlet with little fresh-water influence. Samples taken some 3 Km. west of the town on the northern side of the inlet, Rocky beach with algae growing on stones in the lower eulittoral, well protected by the narrow nature of the inlet and by dense growths of *Macrocystis* in the immediate offshore sublittoral.

Porv./2. Green algae, mostly *Cladophora,* from lower eulittoral. *L. patagonica* ♂ ♀ (live), *C. dispersocostata* ♀ (live). January, 1972.

21) *Estancia Viamonte.* Argentine Tierra del Fuego, on the northern coast of Isla Grande at about 53°56' S. and some 20-25 Km. S.E. of Río Grande, and

some 5 Km. east of the Estancia buildings. Very exposed coast with large tidal amplitude exposing wide mud and sand flats with isolated pebbles and boulders which bear algae.

Via/1. Eulittoral *Enteromorpha, L. dispersocostata* (live). January, 1972.

22) *Ushuaia.* Argentine Tierra del Fuego, on the northern coast of the Beagle Channel at about 54°50'S. From the large number of samples taken in this area January, 1972, Leptocytheridae were found in the following:

USH/4. From Bahia Golondrina, 5 Km. to the west of the town. *Macrocystis* holdfasts from the upper part of the sublittoral. *L. patagonica* ♂ ♀ (live).

USH/8. From the same locality, lower eulittoral *Enteromorpha. L. pataponica* ♂ ♀ (live), *C. dispersocostata* ♀ (live).

b) *Sediment samples from the continental shelf and from the estuary of the River Plate.*

1) *Almirante Saldanha/1252.* 36°05'S. 56°17'05"W. 23 Fm. Grab sample, fine to medium shelly sand. *M. foveata* ♀ (dead).

2) *Río de La Plata/59.* 36°11'S. 56°58'08"W. 3 1/2 Fm. Grab sample, silty mud with many broken shells. *C.* n. sp. A ♂ ♀ (dead), n.g. & sp. ♂ ♀ (dead).

3) *Río de La Plata/61.* 36°12'09"S. 56°58'08"W 3 1/4 Fm. Grab sample, fine silt and mud with small shells and comminuted shell fragments. n.g. & sp. ♂ ♀ juv. (dead). *C.,* n. sp. B ♂ ♀ (dead).

4) *Pesquería V/26.* 36°12'40"S. 56°24'08"W. 10 Fm. Grab sample, dark medium to fine sand with shell fragments. *M. foveata* ♀ (dead), *L. patagonica* ♀ (dead), *Leptocythere* sp. (dead).

5) *Río de La Plata/64.* 36°15'05"S. 56°55'05"W. 2 1/4 Fm. Grab sample, muddy silt with fine comminuted shell fragments. *C. dispersocostata* ♀ (dead), *C.,* n. sp. B ♂ ♀ (dead), *C.,* n. sp. A ♂ ♀ (dead), n.g. & sp. ♂ ♀ (dead).

6) *Almirante Saldanha/1245.* 38°11'S. 56°56'05"W. Grab sample, fine to medium poorly sorted sand with shell fragments. *M. foveata* ♂ ♀ (dead), *C.,* n. sp. A ♀ (dead).

7) *Austral/VI/8.* 38°41'S. 58°51'W. 80 feet. Dredge sample. Stones encrusted with polyzoa and serpulids, with corals, ascidians, shells, and some fine sand and silt. *C.* n. sp. A ♀ (live).

8) *Austral/VI/6.* 38°54'S. 58°47'W. 145 feet. Grab sample, medium sand. *C.* n. sp. A ♀ (live), n.g. & sp. ♂ ♀ (dead).

9) *Austral/VI/13.* 38°56'S. 60°03'W. 75 feet. Grab sample, very fine sand and silt, *C.,* n. sp. A ♀ (dead), *L.,* n. sp. A juv. (dead). n.g. & sp. ♂ ♀ (dead).

10) *Austral/VI/3.* 39°02'09"S. 58°24'05"W. 165 feet. Grey medium sand with a few shell fragments. n.g. & sp. ♂ ♀ (dead). Grab sample.

11) *Austral/VI/10.* 39°10'S. 50°05'W. 140 feet. Fine to medium shelly sand. n.g. & sp. ♂ ♀ (dead).

12) *Austral/VI/15.* 39°17'S. 60°27'W. 115 feet. Grab sample, fine sand with some shell fragments. n.g. & sp. ♂ ♀ (dead).

13) *Austral/VI/23.* 39°20′S. 61°40′W. 40 feet. Grab sample, fine sand. *M. foveata* ♀ (dead), *Leptocythere* sp. (dead), *L. patagonica* ♀ (dead), *C.,* n. sp. B ♀ (dead).

14) *Austral/VI/14.* 39°32′S. 60°20′W. 135 feet. Dredge sample, coarse to medium sand with many shells and fragments. *Leptocythere* sp. (dead).

15) *Austral/VI/21.* 39°45′S. 61°53′W. 45 feet. Grab sample, medium sand with some shell fragments. *C.,* n. sp. A ♂ ♀ (dead), *L.,* n. sp. A ♀ (dead), n.g. & sp. ♀ (live).

16) *West Wind/95.* 42°23′S. 62°43′W. 31 Fm. Grab sample, very fine sand to silt with many Foraminifera and comminuted shell fragments, n.g. & sp. ♀ (live).

17) *Pesqueria/XI/6.* 44°40′09″S. 60°04′09″W. 60 Fm. Grab sample, fine silty sand with large shell fragments. *L. patagonica* ♀ (dead).

SYSTEMATIC DESCRIPTIONS

Family **LEPTOCYTHERIDAE** Hanai 1954

Discussion. — Included in this family are the genera *Leptocythere* Sars, *Callistocythere* Ruggieri, *Mesocythere* Hartmann, and *Tanella* Kingma. The present paper concerns members of the first two.

Leptocythere and *Callistocythere* species are normally readily distinguishable and separable in that they differ in the following respects:

Callistocythere is shorter, wider, and more heavily calcified than *Leptocythere* and whilst the former is strongly ribbed and tuberculate or tuberculate, the latter is usually punctate or even smooth. The hinge of the two genera also differs in that in *Callistocythere* the hinge is more robust and contains, antero-medially in the left valve, two or more distinct denticles which are reflected in the opposite valve, whilst *Leptocythere* bears a single tooth antero-medially in the left valve which, if it is complemented in the right valve, this latter socket is always very weakly developed. The selvage locking "snap knob and pit mechanism of the ventral margin is always well developed in *Callistocythere* whereas it is absent, or only feebly developed in *Leptocythere.* Additionally the vestibulae of *Leptocythere* are discrete and better developed than in *Callistocythere,* which latter also exhibits less symmetrically developed marginal pore canals. Whilst both genera have essentially similar appendages, the posterior termination of the body of the females of *Leptocythere* is usually more rounded than that of *Callistocythere* which usually bear hooked, ventrally directed projections.

Whilst the majority of the species can be assigned to one or another of the two genera without difficulty, there exist a number of species which combine characteristics of the two genera and which are not really assignable. As pointed out by Wall (1969) *Cythere macallana* Brady, (1869) is morphologically intermediate between the two genera, although in summation of its biocharacters, it is probably slightly closer to *Leptocythere. L. patagonica* Hartmann and *C.*, n. sp. C are another two such forms. Such intermediate species are commonly responsible for the creation of new taxa, or for the restriction or expansion of existing generic diagnosis. For the present, the authors prefer to await a greater knowledge of the two genera, based on a restudy of existing species before advocating any of the possible alternatives.

Hanai (1957) also makes geographical and ecological distinctions between the two genera in considering *Callistocythere* as predominantly a marine warm water group and *Leptocythere* as a cold water brackish group. This is far too much of a generalization and there are very many exceptions to the rule. *C.*, n. sp. A, is for example, in the Argentine context, a warm water northern species, yet it is equally common in brackish environments as it is in marine ones. Indeed, in Holocene brackish lagoonal environments in the northern part of the Province of Buenos Aires, it formed the dominant part of the ostracode fauna, together with *Cyprideis, Paracytheroma,* and *Limnocythere.* (R. C. Whatley unpublished). Similarly, J. E. Whittaker (personal communication) records *Callistocythere* commonly in brackish-water environments along the English south coast, often in substantial numbers. Additionally. *C. dispersocostata* Hartmann, is in South American terms, a cold water southern species being commonly encountered in Tierra del Fuego and southern Chile. Such species as *Leptocythere tenera* (Brady & Norman) 1889, *Leptocythere* sp. 3 Whatley, Whittaker and Wall 1971), together with *Leptocythere* sp. recorded herein, are exclusively marine forms, often being restricted to relatively deep water. From this it would seem that whilst the majority of species of *Callistocythere* are marine and of low latitudes, and the majority of *Leptocythere* of high latitudes and able to tolerate reduced saline environments, there is probably much more biogeographical and ecological overlap of the two genera than previously thought.

Genus **LEPTOCYTHERE** Sars 1928

Leptocythere patagonica Hartmann, 1962

Plate I, figs. 1-3; Plate III, figs. 26, 27

1962. *Leptocythere patagonica* Hartmann, pp. 199-209, text-figs. 59-69.

Remarks. — This species is one of those which in many ways falls between the genera *Callistocythere* and *Leptocythere*. The posterior termination of the body of the female most closely resembles *Callistocythere*. It resembles *Leptocythere* in its shape and in the expression of sexual dimorphism and also in its ornament which is of fairly small uniform punctae. The weak "overprinted" reticulation, illustrated by Hartmann (1962, text-fig. 60), is very difficult to make out on most specimens but is certainly visible on some. The hinge is like that of *Callistocythere* and is very strongly developed with, anteromedially in the left valve, three strong teeth which are reflected in the antero-median element of the right valve. The ventral "snap knob and pit" locking device is more strongly developed than in other *Leptocythere* species herein described.

The marginal (radial) pore canals are less regularly symmetrical than in most *Leptocythere* species and consist anteriorly of three or four large proximal canals, of which the central is largest, which polyfurcate distally. The strong posterior rib is another feature more typical of *Callistocythere.* Another feature of interest in this species are the normal pore canals which although extremely large in size, are not apparently of sieve-type. The authors, whilst recognizing the fact that this species presents a mixture of the characteristics of *Leptocythere* and *Callistocythere,* have retained it within the former. The reasons for doing this are not profound, and it is realized that eventually it may be necessary with a better knowledge of both genera to perhaps erect a new taxon to accommodate such intermediate forms or to expand the original diagnosis of either *Callistocythere* or *Leptocythere* to accommodate them. It is also interesting to record that the instars very much more closely resemble *Leptocythere* than do the adults.

Material. — Several thousand specimens, of which the majority contain soft parts.

Dimensions. — All from Puerto Deseado.

	Length	Height
♀ LV MLP 11745/a	0.59	0.325
♀ RV MLP 11745/b	0.58	0.32
♂ RV MLP 11745/c	0.60	0.31
–1 Instar RV MLP 11745/d	0.52	0.29
–2 Instar Carapace MLP 11745/e	0.42	0.23
–3 Instar Carapace MLP 11745/f	0.34	0.20

The instars resemble *Leptocythere* more than does the adult. The –1 instar has, however, a hinge similar to but much weaker than the adult. All instars are punctate.

Distribution and ecology. — Hartmann (1962) recorded this species from Puerto Montt in Chile, in the Magellan Straits near Punta Arenas, and from Puerto Deseado, Province of Santa Cruz, Argentina; all from the eulittoral. In the present study this species can be shown to be principally eulittoral in its occurrence and although it does occur, usually as dead valves, north of Península Valdez, it is not common north of about 42°30′S. It has been found in the following samples:

a) Littoral
Punta Ramírez (dead)
Bird Island (dead)
Las Grutas (dead)
Caleta Valdez (live)
Bahía Solano (live)
Caleta Olivia (dead)
Puerto Deseado (live)
San Julián (live)
Cabeza del Mar (live)
Puerto Porvenir (live)
Ushuaia (live)

b) Continental Shelf
Pesquería/V/26 (dead)
Austral/VI/23 (dead)
Pesquería/XI/6 (dead)

It is probable that this species is entirely littoral and southern in its habit and the records from the north of Península Valdez and from the continental shelf, which are always of isolated dead specimens, are the product of post-mortem transportation. This species, is commonly phytal in its habit but has also been recovered live from eulittoral and sublittoral sedimentary environments in Puerto Deseado. It commonly inhabits "holdfasts" of *Macrocystis* which plants, due to their possession of "floats", are commonly distributed northwards by the prevailing northerly Malvinas current which could account for the occurrence of dead specimens as far north as 36°12′09″S (Pesq./v/26).

Leptocythere patagonica has not been recorded from environments of reduced salinity although in at least one locality, Caleta Valdez, its most northern live occurrence, it seems able to exist in waters which in summer are probably somewhat above the level of salinity of the adjacent sea. This species, unlike most other members of the Leptocytheridae herein discussed does not vary throughout its substantial latitudinal range in either size or ornamentation.

Leptocythere, n. sp. A Plate I, figs. 4-6; Plate III, figs. 1-7

Dimensions. —

	Length	Height	Width
LV MLP 11746	0.495	0.255	0.11

Material. — Approximately 1,500 live and 800 dead individuals.

Diagnosis. — A small to medium species of *Leptocythere* with ornament of small circular punctae and weak ribs, the latter being especially prominent anteriorly. Hinge weak and typical of the genus. Medium sulcus oblique and irregular.

Remarks. — This species is smaller than *L. patagonica,* and also differs in possessing finely punctate ornament without an "overprinted" reticulation. Additionally it does not possess a hinge reminiscent of *Callistocythere.* From *L.* n. sp. B it differs in its smaller size and more strongly and regularly punctate ornament. It is also more "northern" in its distribution than either of the above named species.

Distribution and ecology. — This species occurs very commonly in eulittoral environments between latitudes 40°S and 43°S., it is also recorded, much more rarely, on the continental shelf between about 38° and 39°S. It occurs in the following samples:

a) Littoral
Pocitos (live)
Punta Ramírez (live)
Arroyo Jabalí (live)
San Antonio Oeste (live)
Las Grutas (live)
Bird Island (live)
Punta Delgada (live)

b) Continental Shelf
Austral/VI/13 (dead)
Austral/VI/21 (dead)

Although in a number of localities it was collected live from sedimentary environments, except when the sediments are of fine grain, such as at Pocitos or Arroyo Jabalí, it is usually only encountered dead in such environments. The species is dominantly phytal in habit and has been found inhabiting a variety of weeds in eulittoral rock pools. The two records from the continental shelf, in both cases of single dead specimens, are thought to be the product of post-mortem transportation, probably by attachment to floating weed. Although there is some degree of variation in the ornamentation, some individuals being less strongly or less uniformly punctate than the majority, this does not seem to be linked, as it is with *L.* n. sp. B, to geographical or environmental factors. No size variation is apparent in this species, which, in the Argentine context, is a northern form, and throughout much of its range it is the only known species of the genus. In the southern part of its range it overlaps, in Península Valdez, with the smooth northern form of *L.,* n. sp. B, and to a lesser extent with *L. patagonica.*

Leptocythere, n. sp. B Plate I, figs. 7-11; Plate III, figs. 8-15, 20

Dimensions. —

	Length	Height	Width
L.V.	0.59	0.30	0.11

Material. — Approximately 400 live and 200 dead individuals.

Diagnosis. — *Leptocythere* of medium size with notable increase in strength of ornament and in size southwards throughout its range. Ornament varying from smooth to feebly punctate with highly variable ribs. Shell not strongly calcified. Hinge with antero-median and postero-median elevated areas in the left valve of which only the former is reflected in the right valve.

This species occurs as two distinct types, a "southern" form which is larger and ornamented with punctae (which increase in strength southwards) and a smaller, smoother "northern" form. These two clinal populations do not overlap and in no locality are they found occurring together. The penis of the males from each group is identical.

This species increases in size southwards as illutrated below by the following selected dimensions:

Lat. 42°25'S. (Bird Island)	Length		Height	
Smooth form	Range	Mean	Range	Mean
5 ♂ Carapaces	0.54-0.55	0.54	0.26-0.29	0.27
5 ♀ Carapaces	0.49-0.54	0.515	0.28-0.30	0.29
Lat. 47°45'10"S. (Puerto Deseado)				
Feebly punctate form				
3 ♂ Carapaces	0.58-0.59	0.58	0.29-0.30	0.30
3 ♀ Carapaces	0.55-0.57	0.56	0.31	0.31
Lat. 52°45'S. (Cabeza del Mar)				
More strongly punctate form				
3 ♂ Carapaces	0.58-0.60	0.59	0.29-0.31	0.30
3 ♀ Carapaces	0.58-0.59	0.58	0.31-0.32	0.32

This increase in size southwards is demonstrated by many other eurythermal Cytheracea in this study and is ascribed to the fact that in the colder waters of the south, species achieve maturity more slowly and as a consequence are able to grow larger. This species is somewhat reminiscent of *L. pellucida* (Baird), but differs in shape and size. It is larger, less strongly, and less regularly pitted than *L. n. sp. A,* and from *L. patagonica,* it differs in its more elongate shape, much less strongly calcified shell, in lacking strong ornament, and hinge structures similar to those of *Callistocythere.*

Ontogeny. — Juveniles are only rarely encountered, probably due to the fragile nature of the shell. The following dimensions are from Cabeza del Mar:

	Length	Height
–1 Carapace	0.49	0.26
–2 Carapace	0.42	0.25
–3 Carapace	0.38	0.24

Ecology and distribution. — This is essentially a "southern" littoral species which has not been recorded from the continental shelf. It is recorded from the following littoral localities:

a) Smooth form	b) Punctate form
Arroyo Jabalí (live)	Bahía Solano (live)
Bird Island (live)	Puerto Deseado (live)
Punta Delgada (live)	Cabeza del Mar (live)

The difference between the two forms of the species is emphasized by the disjunct nature of their distribution, in that between the southernmost occurrence of the smooth form, (Punta Delgada 42°47′S.) and the northernmost occurrence of the punctate form (Bahía Solano 45°42′S.), the species seems to be absent.

The smooth form appears to be restricted to algae in the eulittoral zone whilst the punctate form, although essentially similar in its habit, has also been recovered from eulittoral and sublittoral sediment samples at Puerto Deseado.

Leptocythere sp. Pl. I, fig. 12

Material. — Seven valves.

Remarks. — Because of the small number of specimens and because of their poor state of preservation, and because the species is probably only represented by juveniles, the taxonomic position of this form is uncertain. It may represent a new species of *Leptocythere* because the authors do not know of another species characterized by almost equally rounded end margins and by a smooth to weakly wrinkled shell surface. Because the hinge and inner lamella are only very feebly developed, it is thought that all the specimens are juveniles.

Dimensions. —	Length	Height
R.V. Playa Grande, Mar del Plata.	0.58	0.31
L.V. Austral/VI/14.	0.55	0.30

Distribution and ecology. — With the single exception of one valve from the sediment of a eulittoral rock pool from Playa Grande, Mar del Plata, this species is restricted to sediment samples, of medium to fine sand from the continental shelf between latitudes 36°12′40″S. and 39°32′S. and at depths ranging from 40 to 135 feet.

Genus **CALLISTOCYTHERE** Ruggeri, 1953

Callistocythere dispersocostata Hartmann, 1962 Plate I, figs. 13-15

1962. *Callistocythere dispersocostata* Hartmann: *in* Hartmann-Schroeder, Mitt. Zool. Mus., Hamburg, Ergans., 60, pp. 195-198, text-figs., 52-58.

Remarks. — This species, which is evidently closely related to *Callistocythere ornata* Hartmann) 1956, differs from all other species of the genus herein described in being more rounded antero-ventrally and mid-ventrally concave; in its irregularly ribbed and lobed and tuberculate ornament. In these features, and in its internal shell structure, it more closely resembles *C. littoralis* (Müller, 1894), the type of the genus.

Material. — Approximately 2,500 specimens of which about 1,000 contain appendages.

Distribution and ecology. — Hartmann (1962) originally described this species from eulittoral environments from the Pacific coast of northern and central Chile and also from Golfo Nuevo, Province of Chubut, in Argentine Patagonia. In the present study the species is almost ubiquitously encountered, often in great abundance, in littoral samples between 40°S. and 54°50′S. Whilst it has not been encountered in samples from the continental shelf, one single female valve was recovered from a sample in the mouth of the River Plate at 36°15′05″S. This latter record is thought to be an exotic one due to post-mortem transport by floating algae such as *Macrocystis*. This species is recorded from the following localities:

Río de La Plata/64 (dead)
Punta Ramírez (live)
Arroyo Jabalí (dead)
San Antonio Oeste (live)
Las Crutas (live)
Bird Island (live)
Punta Norte (live)
Caleta Valdez (live)
Punta Delgada (live)
Punta Ameghino (live)
Bahía Solano (live)
Caleta Olivia (dead)
Puerto Deseado (live)
San Julián (live)
Monte León (dead)
Río Gallegos (live)
Puerto Porvenir (live)
Estancia Viamonte (live)
Ushuaia (live)

In common with most of the Argentine Leptocytheridae this species is principally phytal in habit and in many localities it occurs live in some abundance on algae from eulittoral rock pools whilst from adjacent sedimentary environments it is only encountered as dead valves. However, this species in such localities as Caleta Valdez and Río Gallego is found living in muddy sediments and also from within the Ría at Puerto Deseado it may be encountered, probably living interstitially, in coarse sand and shell gravel environments in both the lower eulittoral and the sublittoral.

Dimensions (Puerto Deseado). —

	Length	Height
♀ LV MLP 11753/a	0.50	0.29
♂ LV MLP 11753/b	0.47	0.25
♂ Carapace MLP 11753/c	0.49	0.255
♀ Carapace MLP 11753/d	0.495	0.29
–1 Carapace MLP 11753/e	0.39	0.23
–2 Carapace MLP 11753/f	0.36	0.21
–3 Carapace MLP 11753/g	0.33	0.20

This material is somewhat shorter than the type material from Bahía Concepción, Chile, (♂ 0.49, 0.26; ♀ 0.50-0.53, 0.27), but the females are higher.

Callistocythere, n. sp. A Plate I, figs. 16-18; Plate II, figs. 1-3; Plate III, figs. 16-19, 22

Dimensions. —

	Length	Height	Width
LV.	0.38	0.21	0.09

Material. — Approximately 3000 live, dead and fossil specimens.

Diagnosis. — A new species of *Callistocythere* characterized by its ornament of large reticulae produced by the interaction of vertical and horizontal ribs, of which the vertical component is dominant dorsally and the horizontal component ventrally; by its possession of a strongly arched dorsal margin.

Remarks. — This species is smaller, more acuminate posteriorly and has a more regularly ribbed ornament than *C. dispersocostata* Hartmann, 1962. It also lacks the large lobes and tubercules which characterize the latter species. Also, although their ranges overlap in the limited area between about 40° and 42°S, the present species is a more northern form. *C.*, n. sp. A differs from both *C. ornata* (Hartmann, 1956) from the Brazilian Coast, and from *C.*, n. sp. C in its possession of an ornament of ribs rather than small reticulae. It differs principally from *C.*, n. sp. B in its much stronger ornament but is also longer, higher, more arched dorsally and has a more pronounced anterior cardinal angle. The present species is very close to *C. litoralensis* (Rossi de Garcia, 1966) from the Argentine Miocene but has a closer network of more delicate ribs and also differs in outline. It is thought, however, that this similarity is due to an ancestral relationship.

Distribution and Ecology. — This species is an abundant and often dominant member of the ostracode faunas of marine and brackish-water environments of the late Pleistocene and Holocene age in the northeastern coastal regions of the Province of Buenos Aires. Its known present day distribution is as follows:

a) Littoral
Santa Elena (dead)
Playa Grande (dead)
Pocitos (live)
Punta Ramírez (live)
Arroyo Jabalí (live)
Las Grutas (live)
Bird Island (live)

b) Estuary of the River Plate
and Continental Shelf
Río de La Plata/59 (dead)
Río de La Plata/64 (dead)
Pesquería/V/26 (dead)
Almirante Saldanha/1245 (dead)
Austral/VI/8 (live)
Austral/VI/13 (dead)
Austral/VI/21 (dead)

This species does not appear to extend in the littoral farther south than 42°S. It is notable for the fact that in the littoral it is quite catholic in its choice of substrates, being found almost as commonly in coarse sand and silt as it is on algae. It is evidently less phytal in habit than other Argentine species of the genus, with the exception of *C.,* n. sp. B. It is also, with the exception of a new genus and species, the most commonly encountered member of the family on the Continental Shelf.

C., n. sp. A and *C.,* n. sp. B are probably mutually exclusive, since they only occur together in one sample (Río de La Plata/64), and here the former species is only represented by a single specimen. The authors hope to better understand this relationship when they have investigated more samples from the estuary of the Río de La Plata and from the Uraguayan and Brazilian coasts.

Callistocythere, n. sp. B Plate II, figs. 4-5

Material. — Fifty-eight dead valves and carapaces, all adults.

Dimensions. —	Length	Height	Width
Female left valve	0.40	0.235	0.09

Diagnosis. — A species of *Callistocythere* characterized by its small to very small size; cardinal angle rounded in right but pronounced in left valves; ornament of dorso-lateral irregular ribs and ventro-lateral longitudinal ribs between which is an irregular smooth area, anterior terminal hinge element of the right valve distinctly lobate.

Remarks. — This species differs from *C.*, n. sp. A in its smaller size, straighter dorsal margin, less pronounced cardinal angles, and in possessing a smooth central unornamented area. Present evidence suggests that they are almost mutually exclusive as in only one sample (Río de La Plata/64) do they occur together and in this, *C.,* n. sp. A is represented by one specimen only. The present species differs from all other species of the genus known to the authors in possessing the smooth unornamented central area and the strongly lobed anterior terminal element in the right valve.

Ecology and Distribution. — This species has only been recovered from three samples and in all cases is represented by dead adults. A single female left valve was recovered from sample Austral/VI/23 at a depth of 40 feet in fine sand and the remainder of the material is from samples Río de La Plata 61 and 64 which are from fine muddy silt at depths of 31/4 and 21/4 Fm respectively. The known geographical range of the species is between 36°12'S. and 39°20'S. although the authors expect to encounter it in samples, yet to be picked from off the coasts of Uruguay and southern Brazil.

Callistocythere, n. sp. C Plate II, figs. 6-9; Plate III, figs. 23-25, 28

Dimensions. —	Length	Height	Width
LV.	0.425	0.24	0.09

Material. — Thirty-three ♀ specimens of which seven were dead.

Diagnosis. — *Callistocythere* characterized by shape and outline similar to *Leptocythere* but with hinge and another internal features typical of the genus. Ornament of irregular ribs, reticulae and tubercules, differently expressed in the two valves.

Remarks. — This species exhibits characteristics which place it between *Leptocythere* and *Callistocythere;* the ornament of ribs, reticulations and tubercules, the hinge and rather asymmetrical marginal pore canals are characteristics of the latter, whereas the very feebly developed ventral locking device, general shape, and outline are more characteristic of the former genus. It is, however, evidently very similar to *Callistocythere costata* (Hartmann, 1956) from Brasil. It differs however, in being more distinctly sulcate medianly and in possessing two vertical ribs which bound this sulcus anteriorly and posteriorly and a median longitudinal rib which bounds it ventrally. The present species also differs in being deeply sulcate postero-ventrally.

Distribution and ecology. — This species has only been found in the littoral where it occurs along the coast of the southern part of the Province of Buenos Aires, that of Río Negro and also part of Chubut, approximately between latitudes 40°30′S and 43°S. It occurs in the following localities:

Punta Ramírez (live)
Arroyo Jabalí (live)
Las Grutas (dead)
Punta Delgada (live)

Although recorded from Arroyo Jabalí in medium to fine sand and silt, this species is most commonly phytal in habit, being particularly associated with the genera *Ulva, Enteromorpha, Ceramium,* and *Polysiphonia.*

The authors are unable to account for the absence of males of this species throughout its distribution except perhaps by suggesting some different ecological requirements for the two sexes. All the females were recovered from eulittoral samples and it is possible that the males may be sublittoral in habit and could thus not be represented in this study which contains much fewer sublittoral than eulittoral samples. This would be aggravated by the fact that in no part of its range is the species of common occurrence.

Family **CYTHERIDEIDAE** Sars, 1925

Subfamily **NEOCYTHERIDEIDINAE** Puri, 1957

New genus and species

Plate II, figs. 12-18; Plate III, figs. 29

Remarks. — The present material contains only two live specimens and in these the appendages are too poorly preserved to describe. The authors are currently attempting to obtain living material of this spcies in order to describe the soft parts of the adult.

Dimensions.—	Length	Height	Width
Holotype from Ilha Bela, Brazil.	0.41	0.26	0.07
Adult			
♂ RV (Sample SA/5)	0.515	0.21	0.10
♂ Carapace (Sample Austral/VI/13)	0.53	0.215	0.19
♂ RV (Sample Río de La Plata/64) MLP 11760/c	0.53	0.21	0.11
♀ Carapace (Sample West Wind/95)	0.57	0.27	0.25
♀ RV (Sample Río de La Plata/61) MLP 11760/e	0.52	0.26	0.12
♀ Carapace (Sample Austral/VI/10)	0.58	0.265	0.245
−1 Instar.			
RV (Sample Río de la Plata/61)	0.45	0.20	
RV (ditto)	0.46	0.20	
LV (Sample A/VI/—)	0.48	0.21	
LV (ditto)	0.48	0.21	
−2 Instar.			
RV (Sample Austral/VI/6) MLP 11760/f	0.41	0.18	
LV (Sample Río de La Plata/59)	0.40	0.19	

The males are more elongate and more pointed posteriorly than the females and they are also, both actually and proportionally less high. The left valve is substantially larger than the right with strong ventral and postero-dorsal overlap. The surface of the shell, as can be seen in the illustrations, is intricately covered with small tubercles along the line of the ribs. Eye spot a small clear non-elevated patch. Normal pores very small and apparently open. Inner lamella wide, particularly anteriorly where there is a crescentic vestibule. A smaller vestibule also occurs posteriorly. Marginal (radial) pore canals few, long and slender; there are 8-10 anteriorly of which at least two bifurcate medially, the resulting rami of which may terminate as false canals. Between eight and ten canals which always occur as parallel pairs, occur posteriorly and postero-ventrally. Hinge lophodont. In the right valve the terminal elements are low smooth elevations, connected by a long smooth groove which is slightly widened at its distal extremities. The smooth terminal sockets in the left valve are very weak and are open to the anterior and interior. The adductors comprise an oblique line of four small scars, anterior to the most dorsal of which is a large heart-shaped scar, there is also a strongly incised fulcral pit.

Distribution and ecology.— In the present study this species has been recorded in sediments of the continental shelf with a lesser number of records from the littoral:

Littoral
Playa Grande (dead)
Punta Ramírez (dead)
Las Grutas (dead)

Continental Shelf
Almirante Saldanha/1252 (dead)
Río de La Plata/59 (dead)
Río de La Plata/61 (dead)
Pesquería V/26 (dead)
Río de La Plata/64 (dead)
Almirante Saldanha/1245 (dead)
Austral/VI/6 (dead)
Austral/VI/13 (dead)
Austral/VI/3 (dead)
Austral/VI/10 (dead)
Austral/VI/15 (dead)
Austral/VI/23 (dead)
West Wind/95 (live)

This species is evidently "northern" in character, ranging at least as far north as 23°45′S., and in the littoral as far south as 40°40′S., and on the shelf to 42°23′S.

DISCUSSION

It is notable that in Argentine waters, *Leptocythere* and *Callistocythere* in respect of the majority of the species encountered, are more phytal in their habit than those in other areas. Although species of the two genera are sometimes found in association with algae and marine angiosperms, this is usually in the form of "accidental" occurrences, by voluntary or involuntary migration from closely adjacent populations living on or within sediments. European species are usually found, both in marine and brackish environments, living on the surface, interstitially, or burrowing within the sediments. From all the various littoral stations collected in this work, samples of both sediments and algae have been taken. In some areas, such as Pocitos, Punta Ramírez, Arroyo Jabalí, Caleta Valdez, and Puerto Deaseado, Leptocytheridae have been recovered live from fine-grained sediments. These areas are all relatively sheltered and it is thought to be this factor which allows *Leptocythere* and *Callistocythere* to inhabit sedimentary environments in these cases. However, in these stations, where there are closely adjacent phytal environments, these latter always contain a much greater density of ostracodes (not only Leptocytheridae) than do the sediments. On the exposed rocky beaches and headlands along the coast, sediment samples from all parts of the littoral and sublittoral have, even from the bottom of deep and well-protected rock pools, failed to yield live Ostracoda. At the same stations, members of the Leptocytheridae occur almost ubiquitously, and frequently in substantial abundance in samples of algae.

This phenonmenon is not confined to the family under consideration. Of the 160 species isolated to date in the study we are undertaking on the Argentine benthonic Ostracoda, some 80% are restricted to the littoral, where, with the exception of such localities as mentioned above, there is an almost 100% dependence upon algae. Many other genera, such as *Argilloecia, Macrocypris, Paracypris,* and the majority of the Hemicytheridae, not normally considered as phytal species, are found on algae, in association with such well-known phytal forms as *Parakrithella, Xestoleberis,* Paradoxostomatidae. The authors, whilst realizing that this extreme dependence upon algae is undoubtedly a function of the interaction of many factors, consider that exposure is the primary cause, despite the fact that along the southern coasts of South America, westerly winds prevail.

Text-figure 1 gives the geographical distribution of the various species in both the littoral and the shelf. Whilst it is obvious that the area of Peninsula Valdez delimits the maximum northward extent of many "southern" forms, and vice versa, the authors prefer to delay the discussion of the disposition of ostracode faunal provinces along the Argentine coast, until they are able to publish their findings from the total fauna.

REFERENCES

Boltovskoy, E.

1964. *Provincias zoogeográficas de América del Sur y su sector antártica según los foraminíferos bentónices.* Boln. Inst. Biol. mar., Mar del Plata, 7, pp. 93-98.

Brady, G. S., and Norman, A. M.

1889. *A monograph of the marine and freshwater Ostracoda of the North Atlantic and of north western Europe. Section 1. Podocopa.* Scient. Trans. R. Dubl. Soc. N.S. 4 (2), pp. 63-270.

Hanai, T.

1957. *Studies on the Ostracoda from Japan. I Subfamily Leptocytherinae, new subfamily.* Fac. Sci. Tokyo Univ. Jour., Sec. 2., 10 (3), pp. 431-468.

Hartmann, G.

1956. *Weitere neue marine Ostracoden aus Brasilien.* In E. Titchak and K. H. W. Koepeke, *Beit. neotrop.,* Gustav Fischer Verlag., pp. 19-62.

1961. *Beitrag zur Ontogenie des Ostracodenschlossen (mit Beschreibung von 2 neuen Arten).* Z. W. Z., 165, pp. 428-452.

Hartmann-Schröder, G., and Hartmann, G.

1962. *Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besondered Berücksichtigung der Polychaeten und Ostracoden.* Mitteil. Hamburg. Zool. Mus. Inst., Ergánzungsband zu Band, 60, pp. 1-270.

Kingma, J. T.

1948. *Contributions to the knowledge of the Young-Cenozoic Ostracoda from the Malayan Region.* Thesis Univ. Utrecht, 119 pp.

Rossi de Garcia, E.

1966. *Contribución al conocimiento de los Ostrácodes de la Argentina. I Formación Entre Ríos, de Victoria, Provincia de Entre Ríos.* Rev. Asoc. Geol. Argentinea, 21, (3), pp. 194-208.

Sars, G. O.

1922-1928. *An account of the Crustacea of Norway.* Bergen Museum, 9, pp. 1-277.

Van Morkhoven, F. P. C. M.

1963. *Post-Palaeozoic Ostracoda. Their morphology, taxonomy, and economic use,* vols. I, II, Elsevier, Amsterdam, pp.

Wall, D. R.

1969. *The taxonomy and ecology of Recent and Quaternary Ostracoda from the southern Irish Sea.* Unpublished Ph.D. thesis, University of Wales.

Whatley, R. C. and Wall, D. R.

1969. *A preliminary account of the ecology and distribution of Recent Ostracoda in the southern Irish Sea.* In Neale, J. W. (ed). *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* Oliver and Boyd, Edinburgh, pp. 268-298.

Whatley, R. C., Whittaker, J. E., and Wall, D. R.
1971. *A taxonomic note on the genus Leptocythere Sars with particular reference to the type species.* Bull. Centre Rech. Pau-SNPA, 5 suppl. pp. 399-408.

R. C. Whatley,
Division Micropaleontología,
Facultad de Ciencias Naturales y Museo,
Universidad Nacional de La Plata,
Paseo de Bosque,
La Plata, Argentina
and
Department of Geology,
University College of Wales,
Aberystwyth,
Wales

A. Moguilevsky,
Depto. Biologia,
Facultad de Ciencias
Exactas y Naturales,
Universidad de Buenos Aires,
Ciudad Universitaria,
Pabellon 2, Pise 4, Nunez,
Capital Federal,
Argentina

DISCUSSION

Dr. G. Hartmann: You mentioned my species *Neocytherideis marchilensis archilensis* (it's wrong to place it in *Cushmanidea*). Did you see the marginal zone, and are you sure that it is not *Mesocythere foveata*?

Dr. Whatley: The ventral and posterior part consists of unbranched pore canals which occur in pairs. Dr. Sandberg has beautiful illustrations of this feature. Another interesting feature of this form is that it has a very deeply incised crescentic fucral furrow and fucral hole, but in some it is concentric very reminiscent of this other animal.

Dr. Hartmann: Did you have the soft parts?

Dr. Whatley: No, we had semi-mummified soft parts of these. I haven't found them living.

Description of Plate I

Figure

1-3. **Leptocythere patagonica** Hartmann, 1962
- 1. ♀ L.V. MLP. 11745/a. External view; × 46.6.
- 2. –1 Instar. R.V. MLP. 11745/d. External view; × 46.6.
- 3. ♂ R.V. MLP. 11745/c. External view; × 46.6.

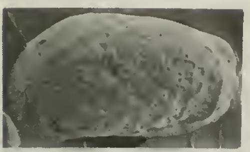
4-6. **Leptocythere,** n. sp. A
- 4. ♂ L.V. MLP. 11746. External view; × 60.
- 5. ♀ R.V. MLP. 11747/a. External view; × 60.
- 6. ♂ L.V. MLP. 11746. Detail of anteromedian normal pore canal and seta; × 2000.

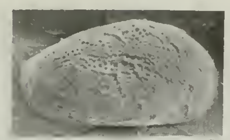
7-11. **Leptocythere,** n. sp. B
- 7. ♀ L.V. MLP. 11749/a. Detail of the extreme anteromedian part of the shell; × 333.
- 8. ♂ R.V. MLP. 11748. External view; × 63.3.
- 9. ♀ L.V. MLP. 11749/a. External view; × 63.3.
- 10. ♂ L.V. MLP. 11748. External view; × 63.3.
- 11. ♂ R.V. MLP. 11748. Detail of anterior; × 167.

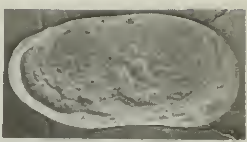
12. **Leptocythere** sp.
- 12. L.V. MLP. 11750. External view; × 46.6.

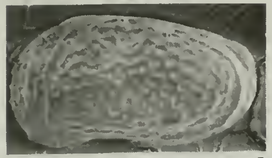
13-15. **Callistocythere dispersocostata** Hartmann, 1962
- 13. ♀ L.V. MLP. 11753/a. External view; × 60.
- 14. ♂ R.V. MLP. 11753/b. External view; × 60.
- 15. ♂ R.V. MLP. 11753/b. Detail of posterior; × 167.

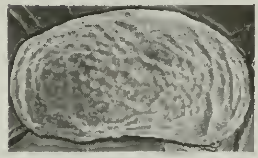
16-18. **Callistocythere,** n. sp. A
- 16. ♂ L.V. MLP. 11745. External view; × 83.3.
- 17. ♀ Carapace. MLP. 11755/g. External view; × 83.3.
- 18. ♂ R.V. MLP. 11754 External view; × 83.3.


1

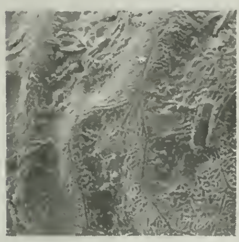

2

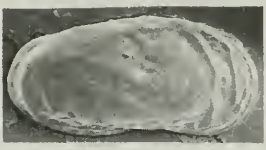

3

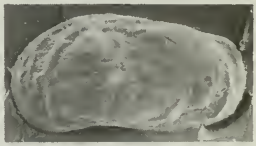

4

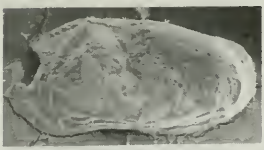

5

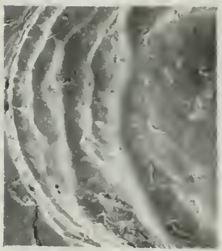

6

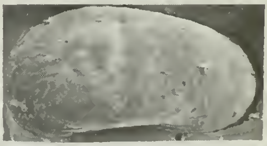

7

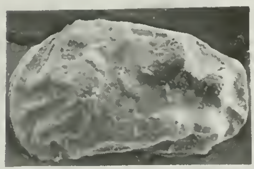

8

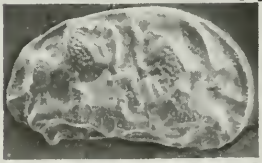

9

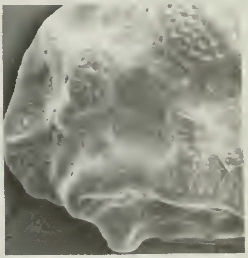

10

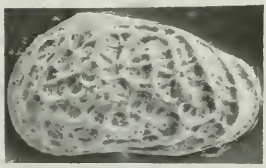

11

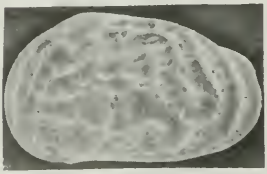

12

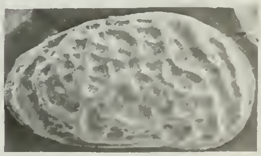

13


14


15


16


17


18

DESCRIPTION OF PLATE II

Figure

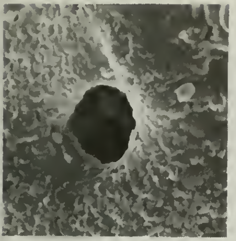
1-3. **Callistocythere,** n. sp. A
  1. ♂ R.V. MLP. 11759. Detail of normal pore canal; × 2666.
  2. ♂ L.V. MLP. 11759. Detail of posterior; × 266.
  3. ♂ R.V. MLP. 11759. Detail of anterior; × 266.

4, 5. **Callistocythere,** n. sp. B
  4. ♀ L.V. MLP. 11756. External view; × 76.6.
  5. ♂ Carapace. MLP. 11757/f. Right lateral view; × 76.6.

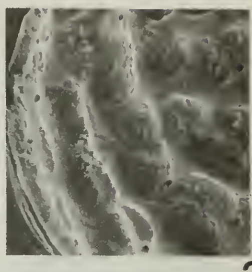
6-9. **Callistocythere,** n. sp. C
  6. ♀ R.V. MLP. 11758. Detail of pore canal and seta; × 2333.
  7. ♀ L.V. MLP. 11758. External view; × 66.6.
  8. ♀ R.V. MLP. 11758. External view; × 66.6.
  9. ♀ Carapace. MLP. 11759/a. External view; × 66.6.

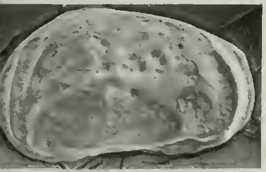
10, 11. **Callistocythere litoralensis** (Rossi de Garcia, 1966)
  10. ♀ R.V. External view. MLP. 11761/a. × 83.3.
  11. ♂ L.V. External view. MLP. 11761/b. × 83.3.

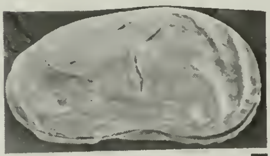
12-18. New genus and species
  12. ♂ R.V. MLP. 11760/c. External view; × 60.
  13. ♂ R.V. MLP. 11760/c. Detail of anterior; × 167.
  14. –2 Instar. L.V. MLP. 11760/f. External view; × 73.3.
  15. –2 Instar. L.V. MLP 11760/f. Detail of posterior; × 260.
  16. ♀ Carapace. MLP. 11760/e. External view; × 53.3.
  17. ♀ Carapace. MLP. 11760/e. Detail of anterior; × 167.
  18. ♀ Carapace. MLP. 11760/e. Detail of anterior; × 1666.

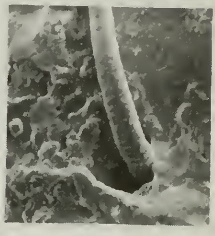

1

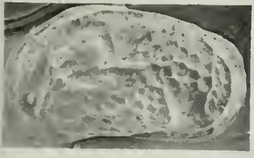

2

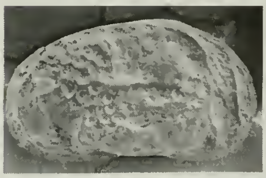

3

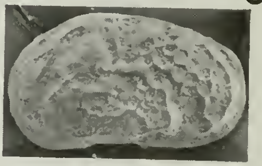

4

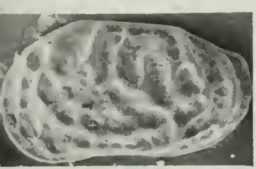

5


6

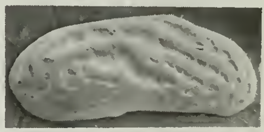

7


8


9

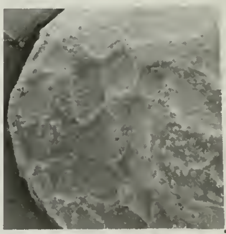

10

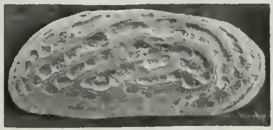

11


12

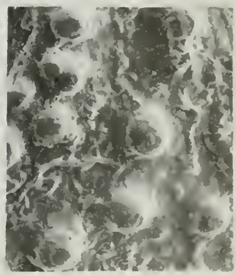

13


14


15


16


17


18

DESCRIPTION OF PLATE III

Figure

1-7. **Leptocythere,** n. sp. A
1. Holotype, ♂ MLP. 11746. Penis. Right inner lateral view; × 128.
2. Paratype. ♂ MLP. 11747/s. Second thoracic leg. Left outer lateral view; × 128.
3. Paratype. ♀ MLP. 11747/b. First thoracic leg. Right outer lateral view; × 128.
4. Holotype. ♂ MLP. 11746. First antenna. Right inner lateral view; × 128.
5. Paratype. ♂ MLP. 11747/s. Mandibles. Anterior view; × 128.
6. Topotype. ♀ L.V. Detail of anterior marginal area in transmitted light; × 71.5.
7. Holotype. ♂ MLP. 11746. Second antenna. Right inner lateral view; × 128.

8-15, 20. **Leptocythere,** n. sp. B
8. Holotype. ♂ MLP. 11748. Penis. Right outer lateral view; × 128.
9. Holotype. ♂ MLP. 11748. Second antenna. Left inner lateral view; × 128.
10. Holotype. ♂ MLP. 11748. Maxilla. Left outer lateral view; × 128.
11. Holotype. ♂ MLP. 11748. First antenna. Right outer lateral view; × 128.
12. Holotype. ♂ MLP. 11748. Mandibles. Posterior view; × 128.
13. Paratype. ♂ MLP. 11749/h. First Thoracic leg. Left inner lateral view; × 128.
14. Paratype ♂ MLP. 11749/h. Second thoracic leg. Left outer lateral view; × 128.
15. Holotype. ♂ MLP. 11748. Third thoracic leg.
20. Paratype. ♂ MLP. 11749/h. L.V. Detail of anterior and ventral marginal areas in transmitted light; × 71.5.

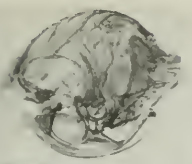
16-19, 22. **Callistocythere,** n. sp. A
16. Holotype. ♂ MLP. 11754. Penis. Left outer lateral view. × 128.
17. Paratype. ♀ MLP. 11755/a. Third thoracic leg. Left outer lateral view; × 128.
18. Paratype. ♀ MLP. 11755/a. First thoracic leg. Left outer lateral view; × 128.
19. Paratype ♀ MLP. 11755/a. Second thoracic leg. Right outer lateral view; × 128.
22. Holotype. ♂ MLP. 11754. First and second antennae. Right inner lateral view; × 128.

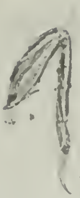
21. **Callistocythere dispersocostata** Hartmann, 1962
21. ♂ MLP. 11751. Penis. Right outer lateral view; × 128.

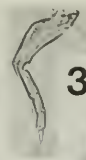
23-25, 28. **Callistocythere,** n. sp. C
23. Holotype. ♀ MLP. 11758. Posterior termination of the body; × 128.
24. Holotype. ♀ MLP. 11758. First thoracic leg. Right outer lateral view; × 128.
28. Holotype. ♀ MLP. 11758. First and second antennae. Left outer lateral view; × 128.

26, 27. **Leptocythere patagonica** Hartmann, 1962
26. ♂ MLP. 11793. Penis. Left outer lateral view; × 128.
27. ♀ R.V. Topotype. Detail of antero-median hinge element; approximately × 350.

29. New genus and species
29. ♀ R.V. MLP. 11760/e. Detail of anterior marginal area in transmitted light; × 120.

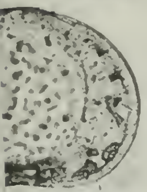

1


2

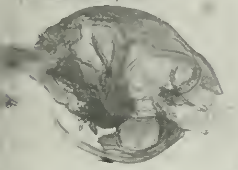

3


4

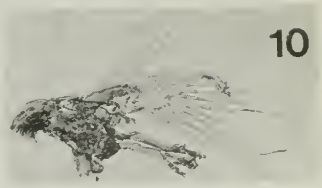

5

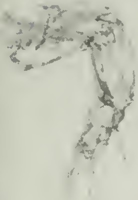

6


7


8


9

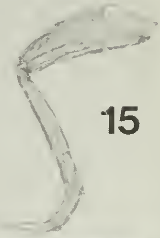

10

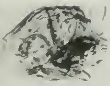

11


12


13


14

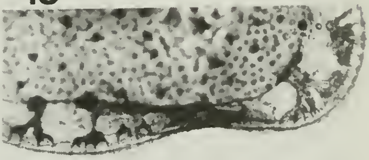

15


16


17

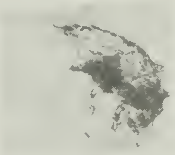

18


19

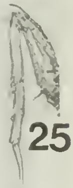

20

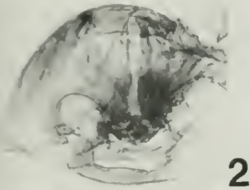

21


22


23

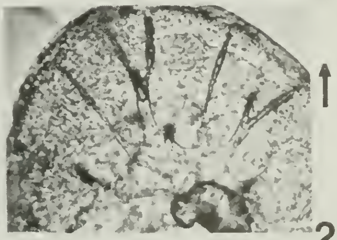

24


25


26


27


28


29

THE ULTRASTRUCTURE OF THE OSTRACODE (CRUSTACEA) INTEGUMENT

Raymond Holmes Bate
British Museum (Natural History)
and
Barbara Ann East
Imperial College

ABSTRACT

The ultrastructural detail of the ostracode integument [carapace + body cuticle] has been examined using both transmission and scanning electron microscopy. The ostracodes were either embedded in resin after decalcification and then sectioned on the ultramicrotome or examined as fractured surfaces in the scanning electron microscope. Although only a relatively small number of ostracodes have so far been examined the pelagic Myodocopida have so far exhibited only a lamellar organic carapace structure whilst benthic ostracodes of the Podocopida have exhibited a lattice structure. The body cuticle and the endoskeleton in living Podocopida are shown to have a lamellar chitin structure, the fibres of which exhibit parabolic curves in slightly oblique sections. This structure has been variously interpreted as being due to the chitin fibres curving down from one layer to the next or as being due to a helicoidal arrangement of the fibres through successive layers producing a parabolic curve as an artefact.

The distribution of lamellar and lattice chitin in the ostracode integument is considered to possibly reflect the mechanical requirement of the structure involved; a lamellar structure producing a flexible cuticle and a lattice structure a more rigid cuticle.

The ultrastructure of the ostracode integument is compared with the carapace detail known from other arthropod groups.

ZUSAMMENFASSUNG

Sowohl mit Hilfe des Elektronenmikroskopes als auch des Rasterelektronenmikroskopes wurde die Feinstruktur des Ostrakodenintegumentes (Gehäuse + Körperkutikula) untersucht. Die Ostrakoden wurden entweder entkalkt und in Kunstharz eingebettet und dann mit dem Ultramikrotom geschnitten, oder Oberflächenfragmente wurden mit dem Rasterelektronenmikroskop aufgenommen. Obgleich bisher nur eine verhältnismässig kleine Anzahl von Ostrakoden untersucht worden ist, kann gesagt werden, dass die pelagischen Myodocopiden nur eine lamellierte chitinöse Gehäusestruktur besitzen, während man bei den im Benthos lebenden Tieren in chitinöse Gitterstruktur vorfindet.

Die Kutikula des Gehäuses und das Endoskelett von recenten Podocopiden besitzt eine lamellierte Chitinstruktur, dessen Fasern in etwas schienfen Schnitten in parabolischen Kurven angeordenet sind. Diese Konfiguration wurde verschiedentlich interpretiert: einmal wurde angenommen, dasse die Chitinfasern sich kurvenartig von einer Schicht zur anderen erstrecken oder, dass durch eine schneckenartigspiralige Anordnung der Fasern durch aufeinanderfolgende Schichten eine parabolische Linie als Artefakt entstanden ist.

Die Verteilung von lamellarem und gitterförmigem Chitin im Integument der Ostrakoden könnte möglicherweise funktionellen Anforderungen entsprechen, wobei lamellierte Anordnung einer biegsamen Kutikula entspricht, während die gitterförmige zu einer steifern gehört.

Die Feinstruktur des Ostrakodenintegument wurde mit Gehäusestrukturen anderer Arthropodengruppen verglichen.

INTRODUCTION

In an earlier paper (Bate and East, 1972), we described the ultrastructure of the carapace of some ostracodes from both a palaeontological and a zoological point of view. As an extension of this investigation we are now proposing to discuss the ultrastructure of the whole integument, incorporating not only the carapace and the body cuticle (exoskeleton) but also that of the endoskeleton.

Although there is a wealth of published work on the ultrastructure of decapod crustacea (*e.g.,* Dennell, 1947, 1950, 1960; Drach, 1953; Bouligand, 1965; Kawaguti and Ikemoto, 1962, Skinner, 1962) and on insects (*e.g.,* Wigglesworth, 1933; Richards, 1951, 1952; Dennell and Malek, 1955a,b; Filshie, 1970; Locke, 1964; Neville, 1967, 1970; Neville and Luke, 1969a,b), there is an almost complete lack of similar data for the Ostracoda. Jørgensen (1970), although not the first to make reference to ultrastructural detail in the ostracode carapace, was certainly the first to write specifically on this subject. As yet unpublished, the work of M. Hounsome (University of Manchester) on freshwater ostracodes, has identified some of the structures which we record here. Certainly, despite the experimental difficulties which are experienced when dealing with animals as small as ostracodes, this type of study of the structure of the ostracode integument is bound to develop in the future.

The arthropod cuticle is covered on the outside by a non-chitinous epicuticle which appears to achieve its most complete development in insects where its essential function is to prevent dehydration. This is not, of course, the function of this layer in aquatic crustaceans and in ostracodes it is a relatively much thinner and more simple structure. The subject of this investigation is that part of the cuticle which underlies the epicuticle and which has been referred to as the procuticle by Richards (1951).

Electron microscopy of arthropod procuticle has clearly demonstrated it to consist of alternating dark and light bands which at first were considered to be of alternating dense and less dense material (Richards, 1951, p. 175). A fibrous structure within the layered cuticle had been observed in many instances and this was referred to as Balken (Richards, 1951, p. 192). Drach (1953), in an electron microscopical study of crustacean cuticle, interpreted the fibrous structure as consisting of horizontal fibres lying parallel to the carapace surface in the dark bands but lying oblique to the surface in the light bands. This interpretation is apparently supported by those cuticle sections which show parabolic fibres as in Plate 4, figure 13. Subsequently, however, this structure has been reinterpreted (Bouligand, 1965) as an artefact resulting from sectioning obliquely through the cuticle in which the fibres although horizontal in every layer, are in fact, oriented at various angles through successive layers. This cross-ply arrangement imparts considerable strength to the structure and although the chitin fibres never deviate from the horizontal, the overall trend is of a helicoidal spiral through successive layers. The importance of oblique sections lies, therefore, in elucidating this structure.

As stated by Neville (1967, p. 223) all arthropod cuticles are laminate in texture due to their secretion by a single layered epithelium. The disadvantage of such a structure is that it is weak when twisted (Neville, 1967, p. 218).

According to Locke (1964, p. 395) the lack of cross links is to be expected in cuticle requiring plasticity or elasticity rather than rigidity, although there is a mechanical strengthening in the lamellar structure due to the fibres of successive layers changing their orientation (Neville, 1967, p. 218). Thus, both the crustacean and the insect cuticles are known to consist of lamellae of chitin, the microfibrils (or in the case of Crustacea, bundles of them forming macrofibrils: Neville, 1970) of which are orientated parallel to the surface but at a gradually varying angle through successive layers. Although the parabolic effect, noticeable in many sections, was originally thought to be due to obliquely sloping fibres, this is not now generally considered to be the case in arthropods, although it has been observed in the tunicate, *Cynthia papillosa* (Neville, 1967, p. 225).

Although ostracodes are crustaceans they differ from decapods in the possession of a bivalve carapace. Indeed, within the arthropods as a whole, few groups possess a bivalve exoskeleton, the general pattern in those groups with a carapace being that of a cylindrical carapace covering the head, thorax and abdomen, from which only the appendages project. The notable exception to this, besides the Ostracoda, are the bivalved Branchiopoda on which no ultrastructural research has yet been conducted. Although such research has been undertaken on the decapods, the small size of most ostracodes has tended to stifle research in this direction. The present research project, investigating the ostracode carapace and body cuticle, was started in order to redress this omission. The results of this project to date are based on a study of the following ostracodes: order Podocopida — two Recent, fresh-water species *Cypridopsis vidua* (Müller, 1776) and *Heterocypris incongruens* (Ramdohr, 1808); one fossil (Cretaceous) fresh-water species, *Cypridea* sp. and one Recent, benthic marine species (*Moosella* sp.) from the Persian Gulf, (figured in Bate, 1971). Order Myodocopida — four Recent, pelagic species: *Conchoecia belgicae* (Müller, 1906); *Cypridina mediterranea* Costa, 1845; *Macrocypridina castanea* (Brady, 1897) and *Philomedes brenda* (Baird, 1850).

ACKNOWLEDGMENTS

This project was undertaken in the electron microscopy unit of the British Museum (Natural History); our thanks are due to Mr. Brian Martin, head of the unit, and to Mr. Colin Ogden for their help and the use of the facilities under their care. We should also like to record our thanks to Dr. A. C. Neville (Dept. Zoology, University of Oxford) and Dr. K. G. McKenzie for kindly reading the manuscript. Miss Margaret Austin printed the transmission electron micrographs and Mr. Roger Freeman, the scanning electron micrographs.

MATERIALS AND METHODS

Live material is preferable for this type of study, although not always possible to obtain. In order to facilitate this, laboratory cultures of two freshwater species: *Cypridopsis vidua* and *Heterocypris incongruens* were maintained. Initially these were used because, being less strongly calcified than the marine benthic species, their carapaces held together more satisfactorily after decalcification; decalcification being essential if sections for study by transmission electron microscopy are to be made. Unfortunately fresh material of the pelagic Myodocopida was not available for this study. Recently

Dr. M. V. Angel kindly made available an extensive collection of myodocopid ostracodes, thus permiting an extension of this investigation in the future.

Specimens of the Lower Cretaceous (Upper Purbeck) fresh-water genus *Cypridea* and of the Recent marine benthic ostracode *Moosella* sp. were both examined from acetate peel replicas shadowed with carbon and then coated with gold under vacuum; the specimens being initially embedded in TAAB Araldite. The specimens of *Macrocypridina castanea,* examined under the scanning electron microscope, were also embedded initially in TAAB Araldite prior to cutting the required section which was polished and then etched with 2% EDTA before coating with gold.

Thin sections were taken taken from ostracodes first decalcified by passing CO_2, for a minimum of three days, through the water in which they were living. The specimens were then killed and fixed with Palades buffered osmium tetroxide (2% OsO_4 with a phosphate buffer) for 20 minutes at pH 7.0. After two 30-minute changes of buffer the ostracodes were passed through 30% to 98% alcohol at 15 minute changes with two final changes of absolute alcohol. After an initial change of epoxypropane the specimens were kept overnight in 50/50 epoxypropane/TAAB Araldite. After embedding in Araldite the blocks were cured for two days at a temperature of 60°C. Sections were cut with a diamond knife on a Porter-Blum microtome and stained with uranyl acetate and lead citrate.

To test that the organic matrix referred to throughout this paper was composed of chitin, a chitosan test was carried out by Mrs. Carol Mayes on both Recent fresh-water and fossil (*Cypridea* sp.) ostracodes. This test (as described in Richards, 1951, p. 32) gave a positive chitin reaction.

Both thin sections and acetate peels were examined in an AEI.EM6B transmission electron microscope. Etched surface features were examined in the Cambridge Stereoscan scanning electron microscope.

RESULTS

The body cuticle of the fresh-water ostracodes, *Cypridopsis vidua* (Müller) and *Heterocypris incongruens* (Ramdohr) (Pl. 1, fig. 3; Pl. 2, figs. 5, 6, 7) is composed of lamellar chitin in which an outer, more electron-dense exocuticle may sometimes be observed (Pl. 2, fig. 7). Oblique sections (Pl. 2, fig. 5) reveal the parabolic structure indicative of successive layers being set at a slightly different angle to each other as described by Bouligand (1965). A two-layered epicuticle covers the outside of the body integument (Pl. 2, figs. 5, 7).

The carapace cuticle, in species belonging to the order Podocopida, is divided into an outer epicuticle (single layer, in *C. vidua* and *H. incongruens*); a median exocuticle composed of chitin fibres arranged in a lattice structure (Pl. 1, fig. 2) in which pore canals having a central filament have been observed (Pl. 1, fig. 1); and an inner endocuticle (Pl. 1, fig. 2) in which the chitin fibres are more finely developed and produce a more open reticulate structure.

Some sclerotisation of the outermost part of the exocuticle has been observed (Pl. 1, fig. 2), but only in the outer shell layer (outer lamella); the inturned layer (duplicature) or inner lamella does not show this (Pl. 1, fig. 2). As the section illustrated in Plate 1, figure 2 passes through the terminal edge of the valve it represents a double thickness of endocuticle and shows the repetition of the exocuticle. Sensory bristles, which arise from within the epidermal layer, extend in a rather uneven course through the shell to exit through a normal pore canal opening (Pl. 1, fig. 2, NPC). The bristle is here illustrated in cross section (Pl. 1, fig. 2,B). The reticulate structure of the organic matrix of the ostracode carapace, identified in living fresh-water ostracodes (*C. vidua* and *H. incongruens*), is recognisable in the fossil fresh-water *Cypridea* sp. (Pl. 2, fig. 4) (see also *Cypridea propunctata* in Bate and East, 1972) and in the Persian Gulf, cytheracean ostracode *Moosella* sp. (Pl. 3, fig. 11). The cross-lattice structure is clearly seen in both these illustrations.

Free swimming ostracodes of the order Myodocopida currently examined have a lamellar carapace structure (Bate and East, 1972) in which parabolic fibres have been observed in oblique section, for example, in *Conchoecia belgicae* (Pl. 3, fig. 8). Scanning electron micrographs of *Macrocypridina castanea* (Pl. 3, figs. 9, 10) also reveal a lamellar structure in which cross fibres are present (Pl. 3, fig. 9). The size of most myodocopid ostracodes enables some determination of the shell structure to be undertaken by ordinary light microscopy. By such means, illustrations of *Gigantocypris mülleri* (Harding, 1964), as well as our own examination of *Cypridina mediterranea* and *Philomedes brenda,* clearly show a layered (lamellar) structure in the carapace.

Histological preparations of podocopid ostracodes illustrate the ability of the endoskeleton to take up the stain (Haemalum Eosin; Masson's trichrome or Mallory's triple) to a much greater extent than does the carapace. Electron micrographs of the *C. vidua* endoskeleton (Pl. 4, figs. 12, 13) reveal a positive lamellar structure composed of microfibrils (Pl. 4, figs. 13, Mi) whilst that part to which the muscles are attached, the apodeme, has the microfibrils grouped to form thicker macrofibrils (Pl. 4, figs. 13, Ma); thus probably imparting greater strength to that region. Certainly the more densely layered chitin stucture of the body cuticle and of the endoskeleton makes them more clearly seen in this section (histological) than is the case for the more open lattice structure of the carapace. The helicoidal arrangement of the apodeme macrofibrils is clearly demonstrated by the parabolic pattern shown (Pl. 4, fig. 13).

STRUCTURE OF THE OSTRACODE INTEGUMENT

The cuticle or integument of the ostracode forms the exoskeleton of the animal and is either strengthened by calcification or remains unaltered. Sclerotisation does not appear to play a major role although it has been observed to affect the outer zone of the exocuticle (outer lamella only). As the body of the ostracode is protected within a bivalve carapace, there is no necessity to strengthen the body cuticle which, therefore, remains soft and unaltered.

Where elasticity of the cuticle is required rather than rigidity there is a considerable reduction in the number of cross-links present. As such, the cuticle covering the body (Pl. 1, fig. 3; Pl. 2, figs. 5, 7) has been observed to be a lamellar structure indistinguishable from the type recorded from decapods, although lacking the numerous pore canals commonly associated with decapod cuticle. Slightly oblique sections (Pl. 2, fig. 5) also reveal the parabolic pattern indicative of helicoidally arranged chitin fibres (Bouligand, 1965). The ostracode body cuticle is divisible into an outer (two-layered) epicuticle with a median (more electron dense) exocuticle and an inner endocuticle. It should be mentioned here, however, that not all sections illustrate an exocuticle layer. The appendage cuticle (Pl. 2, fig. 6) is a continuation of the body cuticle and is similarly layered, unlike that of the podocopid carapace which only shows a layered-structure in the selvage spine (Pl. 1, fig. 2) and in the hinge ligament (Bate and East, 1972).

The carapace of both *Cypridopsis vidua* and *Heterocypris incongruens* consists of an outer, clear, epicuticle layer beneath which the chitin matrix of the carapace consists of an open lattice structure of interlocking fibres in the exocuticle (Pl. 1, fig. 2) and a more open, reticulate structure in the endocuticle.

The fibres of the exocuticle are much thicker than those of the endocuticle, especially in the outer zone where sclerotisation renders them more electron-dense. In calcified ostracodes the exocuticle and endocuticle are both secondarily infilled by calcium carbonate crystals which not only infill the spaces between the chitin matrix but also incorporate fibres within their crystal structure (Bate and East, 1972). Owing to the fact that the fibres of the exocuticle are more densely packed than they are in the endocuticle, their structure is more readily understood as an interlocking matrix of chitin fibres. Although some suggestion of parallel layering (Pl. 1, fig. 2) may be observed, the basic lamellar structure of arthropods in which there is a helicoidal arrangement of fibres through successive layers, does not appear to be present in the carapace of ostracodes belonging to the Podocopida, although present in the body cuticle. Acetate peels of *Cypridea propunctata* (Bate and East, 1972) and *Cypridea* sp. (Pl. 2, fig. 4), both fossil fresh-water forms some 100 million years old, reveal a cross-lattice chitin structure similar to that of the living fresh-water Cypridacean species examined. Similarly, acetate peels of the marine cytheracean ostracode, *Mooseila* sp. (Pl. 3, fig. 11), from the Persian Gulf, reveal a cross-lattice structure within the shell, but here the body cuticle was not available for study. The ostracode carapace serves not only to protect the enclosed animal, but also acts as a rigid support structure from which the animal is suspended by means of numerous muscles. Although strengthened by calcification the basic organic matrix structure of the podocopid ostracode was probably evolved as a structure possessing rigidity in its own right and to this end there is a considerable increase in the number of cross-links. To further emphasize this point, the outer part of the exocuticle (Pl. 1, fig. 2) appears as a more electron dense layer due to sclerotisation; a strengthening process not really necessary in species later calcified unless functioning as an intermediary phase between moulting and calcification, a period when the carapace is normally soft.

As in decapods where sclerotisation occurs, pore canals of a secretory nature (differing from the normal pore canals which are larger and may have a sensory function) are required to carry tanning fluids (polyphenols) through to the outer surface. Canals almost certainly carrying out this function have been observed in the exocuticle of *Cypridopsis vidua* (Pl. 1, fig. 1) and, as these arise from the epidermal layer, it follows that they must extend through both the endo- and exocuticle, though not necessarily opening through the epicuticle. They have not yet been definitely identified from within the endocuticle.

The carapaces of *Conchoecia belgicae* Müller, *Philomedes brenda* (Baird), *Cypridina mediterranea* Costa, and *Macrocypridina castanea* (Brady) have been examined and found to possess a lamellar structure similar to that found in decapods and in the body cuticle and endoskeleton of podocopid ostracodes.

Because of their size, the layering within the myodocopid ostracode carapace is often visible under ordinary optical light microscopy (see Harding, 1964, and for general comments on myodocopid cuticle, Kornicker, 1969). The electron microscopical study of *Conchoecia belgicae,* Bate and East, 1972) confirmed the layered-structure of the cuticle in which oblique sections (Pl. 3, fig. 8) show the parabolic pattern of helicoidally arranged fibres. In *Macrocypridina castanea,* which is only poorly calcified, some cross fibres have been observed (Pl. 3, fig. 9) within the structure although their orientation is probably exaggerated due to pulling apart of the layers at that point. According to Iles (*in* Harding, 1964) the delicate shell of *Conchoecia* is probably kept in a state of turgor through the hydrostatic pressure of the haemocoelic fluid situated between the inner and outer lamellae. Rigidity in myodocopid ostracodes could be achieved, therefore, in spite of an elastic layered-structure, by this hydrostatic pressure, in contrast to the more rigid lattice structure observed in the podocopid ostracodes which do not appear to employ hydrostatic pressure.

Within the anterior half of the ostracode body there is developed an internal support structure, the endoskeleton, to which appendages are attached. In *Cypridopsis vidua* this structure is rectangular in cross section with extensions (apodemes) for the attachment of muscles (Pl. 4, figs. 12, 13). Electron micrographs of the endoskeleton reveal a lamellar chitin structure (Pl. 4, figs. 12, 13) in which the microfibrils are so arranged as to produce a parabolic pattern in oblique section (Pl. 4, fig. 13), bottom left of illustration. In the apodeme, the microfibrils are bunched together to form much thicker macrofibrils (Pl. 4, fig. 13), a feature which was first recognised in Crustacea by Neville, 1970, and may have a mechanical significance. The helical arrangement of both the micro- and the macrofibrils of the endoskeleton identifies this structure as being composed of typical lamellar crustacean cuticle.

DISCUSSION

The body cuticle and endoskeleton of *Cypridopsis vidua,* the body cuticle of *Heterocypris incongruens* (order Podocopida), and the carapace of *Macrocypridina castanea, Conchoecia belgicae, Philomedes brenda,* and *Cypridina mediterranea* (order Myodocopida) are constructed of lamellar chitin, appearing as alternating light and dark bands in transverse section. In slightly oblique sections a parabolic pattern appears, indicating that the chitin fibres in this type of structure are arranged in the helicoidal spire as interpreted by Bouligand (1965) and Neville (1970). Thus the lamellar or layered chitin structure present in the Ostracoda is structurally identical to that of decapod Crustacea and insects.

The carapaces of *Cypridopsis vidua* and *Heterocypris incongruens* (Podocopida) have a cross-lattice or reticulate chitin structure. This is also apparent in the carapace of the fossil cypridacean genus *Cypridea* and in that of the Recent cytheracean ostracode *Mooslla* sp. Although some sort of layering appears to be present within the lattice structure, as seen in the exocuticle of *Cypridopsis vidua,* it has not been possible to identify a helicoidal arrangement of the chitin fibres and, indeed, the fibres may not be horizontally arranged, but, as in the tunicate *Cynthia papillosa,* be directed obliquely to any layering which might be present. Such a structure, according to Picken (1940) would possess considerable mechanical strength and would not readily split if stretched in any direction. This would clearly be of considerable advantage to a benthic ostracode even allowing for secondary calcification.

A lamellar chitin structure as present in the larger decapod Crustacea is retained in those parts of the ostracode body where some flexibility is required. The retention of the lamellar structure in the myodocopids examined is probably related to their pelagic mode of life in which a heavily calcified carapace would be a serious weight disadvantage; rigidity of the carapace possibly being attained through internal fluid pressure. In benthic ostracodes the carapace is subjected to different environmental stresses than is that of pelagic species and it is conceivable that the necessity of providing a rigid carapace for the support of the body and for withstanding external stresses was responsible for the development of a cross-lattice or reticulate structure. This is not too difficult to accept when one considers that in the majority of arthropods the carapace forms a straightforward exoskeletal sheath covering an elongate, segmented body. In the ostracode, however, two lateral flaps of tissue, arising from the dorsal part of the body, secrete a bivalved carapace between which is suspended a saclike body. There is thus a considerable morphological difference between the ostracodes and other arthropods although the conchostracans, a group of fresh-water crustaceans having a superficial resemblance to bivalve Mollusca, also possess a bivalve carapace the ultrastructural detail of which is as yet unknown. Clearly, the investigation of this group of crustaceans is essential in this context and it is proposed to undertake this in due course.

REFERENCES

Bate, R. H.

1971. *The distribution of Recent Ostracoda in the Abu Dhabi Lagoon, Persian Gulf.* In Oertli, H. J. (ed.): Paléoécologie Ostracodes Pau, 1970, Bull. Centre Rech. Pau-SNPA, vol. 5, suppl., pp. 239-256.

Bate, R. H., and East, B. A.

1972. *The structure of the ostracod carapace. Lethaia,* 5, pp. 177-194.

Bouligand, Y.

1965. *Sur une architecture torsadée répandue dans de nombreuses cuticules d'arthropodes.* C. r. hebd., Séanc. Acad. Sci., Paris, 261, pp. 3665-3668.

Dennell, R.

1947. *The occurrence and significance of phenolic hardening in the newly formed cuticle of Crustacea Decapoda.* Proc. Roy. Soc. B, 134, pp. 485-503.

1950. *Epicuticle of blowfly larvae.* Nature, 165, p. 275.

1960. Chapter 14: *Integument and exoskeleton.* In Waterman, T. H. (ed.), *The physiology of Crustacea,* vol. 1, *Metabolism and growth,* Academic Press, London and New York, xvii + 670 pp.

Dennell, R., and Malek, S. R. A.

1955a. *The cuticle of the cockroach Periplaneta americana. II. The epicuticle.* Proc. Roy. Soc. B., 1943, pp. 239-257.

1955b. *The cuticle of the cockroach Periplaneta americana. III. The hardening of the cuticle: impregnation preparatory to phenolic tanning.* Proc. Roy Soc. B, 143, pp. 414-426.

Drach, M. P.

1953. *Structure des lamelles cuticulaires chez les Crustacés.* C. r. hebd. Séanc. Acad. Sci., Paris, 237, pp. 1772-4.

Filshie, B. K.

1970. *The fine structure and deposition of the larval cuticle of the sheep blowfly (Lucilia cuprina).* Tissue and Cell, 2, pp. 479-498.

Harding, J. P.

1964. *Crustacean cuticle with reference to the ostracod carapace.* Pubbl. staz. zool. Napoli, 33 suppl., pp. 9-31.

Jørgensen, N. O.

1970. *Ultrastructure of some ostracods.* Bull. geol. Soc. Denmark, 20, pp. 79-92.

Kawaguti, S., and Ikemoto, N.

1962. *Electron microscopy of the integumental structure and its calcification process during molting in a crayfish.* Biol. Jl. Okayama Univ., 8, pp. 43-58.

Kornicker, L. S.

1969. *Relationship between the free and attached margins of the myodocopid ostracod shell.* In Neale, J. W. (ed.) *The Taxonomy, Morphology and Ecology of Recent Ostracoda.* Oliver and Boyd, Edinburgh, ix + 553, 109-135.

Locke, M.

1964. *The structure and formation of the integument in insects.* Chapter 7 In Rockstein, M. (ed.) *The physiology of Insecta,* 3, Academic Press, London and New York, pp. 379-470.

Neville, A. C.

1967. *Chitin orientation in cuticle and its control.* In *Advances in Insect physiology,* 4, Academic Press, London and New York, pp. 213-286.

1970. *Cuticle ultrastructure in relation to the whole insect.* In Neville, A. C. (ed.) *Insect ultrastructure,* 5, London, pp. 17-39.

Neville, A. C., and Luke, B. M.
1969a. *Molecular architecture of adult locust cuticle at the electron microscope level.* Tissue and Cell, 1, pp. 355-366.
1969b. *A two-system model for chitin-protein complexes in insect cuticles.* Tissue and Cell, 1, pp. 689-707.

Picken, L. E. R.
1940. *The fine structure of biological systems.* Biol. Rev., 15, pp. 133-167.

Richards, A. G.
1951. *The integument of arthropods.* Univ. Minnesota Press, Minneapolis, 411 pp.
1952. *Studies on arthropod cuticle. VIII. The antennal cuticle of honeybees, with particular reference to the sense plates.* Biol. Bull., 103, pp. 201-225.

Skinner, D.
1962. *The structure and metabolism of a crustacean integumentary tissue during a molt cycle.* Biol. Bull., 123, pp. 635-647.

Wigglesworth, V. B.
1933. *The physiology of the cuticle and of ecdysis in Rhodnius prolixus [Triatomidae, Hemiptera]; with special reference to the function of the oenocytes and of the dermal glands.* Quart. Jour. Mic. Soc., 76, pp. 269-318.

Raymond Holmes Bate,
Department of Palaeontology,
British Museum (Natural History),
London, SW7,
England

Barbara Ann East,
Department of Chemical Engineering,
Imperial College,
London, SW7,
England

DISCUSSION

Mr. D. Keyser: I found during my studies on functional sieve pores a different structure of the shell. It consists of a thin outer chitinous layer, a thick calcified zone and a well-developed inner chitinuous layer followed by the body cavity, which extends in the valves. Could the differences be due to a different method or preparation for the transmission electron microscope?

Dr. Bate: Transverse sections through the carapace of several ostracodes have failed to show the inner and outer chitin layers referred to by Mr. Keyser. This is not a question of the method of preparation as fractured valves examined in the scanning electron microscope [see Bate and East, 1972, fig. 2A,B] have similarly failed to show these layers. The ostracode valve is an organic (chitin) structure secondarily calcified — the calcification extending across the total thickness of the shell, only a thin outer epicuticle layer being uncalcified. I have observed that when removing an ostracode from its carapace, the inner lamella falls back and adheres to the inside of the valve. This chitin, inner lamella, could be mistaken as being an inner chitin layer of the outer lamella. At the present time we have no other explanation to put forward as detailed examination of the carapace structure does not as yet support the contention that the ostracode valve is a layer of calcium carbonate sandwiched between two layers of chitin.

Dr. R. H. Benson: In the paper by Peter Sylvester-Bradley and myself of last year, we were able to show that there is a foliated inner structure of the carapace wall, and a laminar structure on the external part of many of the marine ostracodes. The calcified lamella is formed from a sort of lath structure, like courses of bricks. Apparently in freshwater the foliation of the shell wall tends to become less well organized and is massive. This may have something to do with relation of the fact that in marine forms these concentric layers follow the general shell structure. Its departure from the general curvature of the shell decreases from the outside where the structure has the greatest relief, to the inside where it is parallel to a smoother or more rounded surface. In other words, where reticulation occurs on the outer part, the laths follow these structures up, in, and around the murae or the wall structures and then they diminish and become more and more parallel to the curvature of the inner side.

There is another interesting difference I have found. That is as the "outer lamella", so called, approaches the outer margin it then continues inward as an infold, similar to that reported by Kornicker, and still with the horizontal layering following on into what used to be called the duplicature. Dr. Kornicker and Dr. Harding pointed out that in the myodocopids this was a continuous structure. Now I have been able to show this occurring in the podocopids, and I noticed that Dr. Oertli has similarly found that these horizontal layers of the outer lamella come down toward the outer margin and turn in on the infold but that they do not necessarily follow the chitinized inner lamella or vestment. They turn and run out into the features of the selvage the lists, and so forth, like outcrops. In other words, in a fracture section taken across the free margin the horizontal layers follow the structure of the outer lamella, diminishing toward the inside of the shell, making a turn at the margin very abruptly, and then outcrop into the lists and the selvages. Only the tiniest amount goes on into the body cavity. The turn is so sharp, I believe that where the radial pores go through, that changes in orientation of the C-axes of the crystals of calcite are responsible for the appearance of a zone of concrescence as is seen under light microscopes.

Dr. Bate: The structure Dr. Benson refers to in his paper concerns the recognition of an outer laminar layer and an inner foliated layer seen in transverse carapace sections of *Henryhowella asperrima.* This structure relates to the arrangement of the calcium carbonate crystals and is totally different to the organic matrix of the valve studied in our work. Indeed, as we have shown previously [Bate and East, 1972, p. 188] the organic matrix does not limit the crystal growth to the species available within the chitin structure but passes through the crystal structure [Bate and East, 1972, fig. 5A, B.] I believe that it is this organic matrix structure which will eventually provide the answers to such questions as "are the myodocopids more primitive than the podocopids?" and "is the structure of the organic matrix related to the phylogeny of the ostracod or is it environmentally controlled?" The observations of Benson and Sylvester-Bradley that the laminar calcareous layer does not continue on the duplicature is of interest in that it parallels our observations concerning the tanned part of the outer lamella which likewise does not continue onto the duplicature.

POSTSCRIPT

Professor R. Dennell [Manchester University] recently demonstrated in the cuticle of the shore crab that parabolic fibres are not artefacts but represent fibres actually curving down from one lamellar layer to the next. This is opposite to the interpretation of both Bouligand and of Neville but is in agreement with Drach's original interpretation of these structures. Dennell is supported in his study by the results of Dr. J. Dalingwater [Manchester University], currently working on fossil arthropod cuticle. Their evidence is convincing. Accordingly we would ask the reader to keep an open mind as to which of these two interpretations is correct as far as the ostracode is concerned. Personally we would be happier with Dennell's interpretation of the structure illustrated here in Plate 4, figure 13 as being due to parabolic fibres rather than being the result of an oblique section producing an artefact.

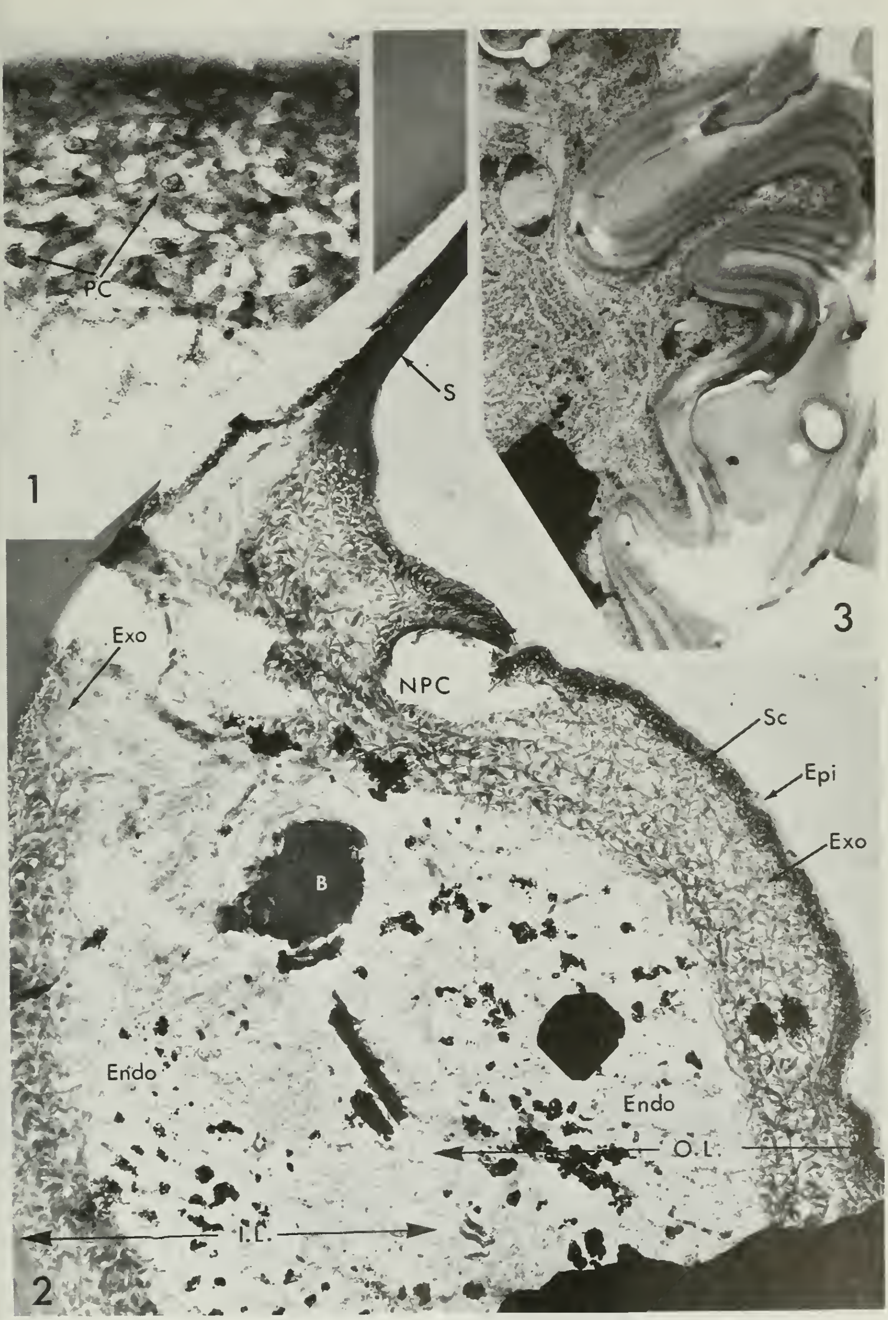
EXPLANATION OF PLATE 1

Figure

1. Transmission electron micrograph of thin section through carapace exocuticle of *Cypridopsis vidua* [transverse section]. Secretary pore canals [PC] with a central filament, are seen in cross section; × 40,000.

2. Transmission electron micrograph of thin section through the free margin [valve edge] of *Cypridopsis vidua* carapace [transverse section]. The double thickness of the carapace in this region is due to the outer lamella of the carapace turning under on the inside to form the inner lamella. Both inner and outer lamellae are divided into an outer epicuticle, a median exocuticle and an inner endocuticle. The sclerotised outer zone of the exocuticle is not developed in the inner lamella.
B — sensor bristle; Epi — epicuticle; Endo — endocuticle; Exo — exocuticle; I.L. — inner lamella; NPC — normal pore canal aperture; O.L. — outer lamella; S — selvage spine; Sc — sclerotised layer; × 10,270.

3. Transmission electron micrograph of transverse section through lamellar body cuticle in *Heterocypris incongruens;* × 10,790.


PC
S
1
3
Exo
NPC
Sc
Epi
Exo
B
Endo
Endo
O.L.
I.L.
2

EXPLANATION OF PLATE 2

Figure

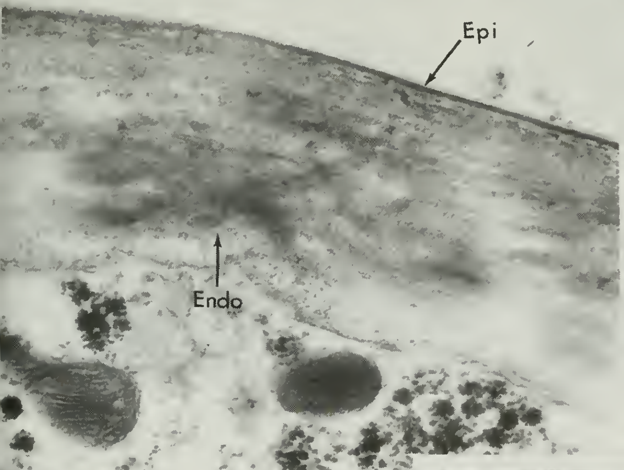
4. Transmission electron micrograph of acetate peel replica of a Lower Cretaceous *Cypridea* sp. carapace [transverse section]. Surface etched by 2% EDTA prior to replication, chitin fibres [CF] standing out in relief from the grey background of calcium carbonate; × 11,050.

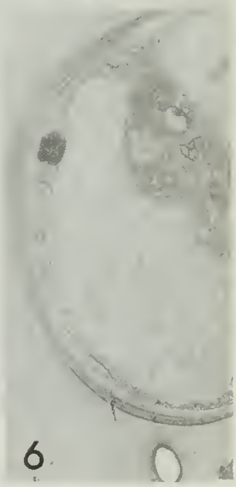
5. Slightly oblique transverse section through body cuticle of *Heterocypris incongruens* [transmission electron micrograph] to show parabolic artefact indicative of helicoidally arranged chitin fibres. Epi — epiculticle composed of two layers, the inner layer being the more electron dense. Endo — endocuticle showing parabolic pattern of chitin fibres; × 29,080.

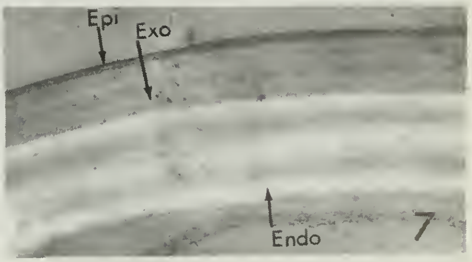
6. Transverse section through antenna of *Cypridopsis vidua* to show lamellar structure of cuticle [transmission electron micrograph]; × 6,027.

7. Transverse section through body cuticle of *Heterocypris incongruens* [transmission electron micrograph] to show lamellar structure of typically banded appearance.
   Epi — epicuticle; Endo — endocuticle; Exo — exocuticle; × 31,170.


CF
4


Epi
Endo
5


6


Epi
Exo
Endo
7

Explanation of Plate 3

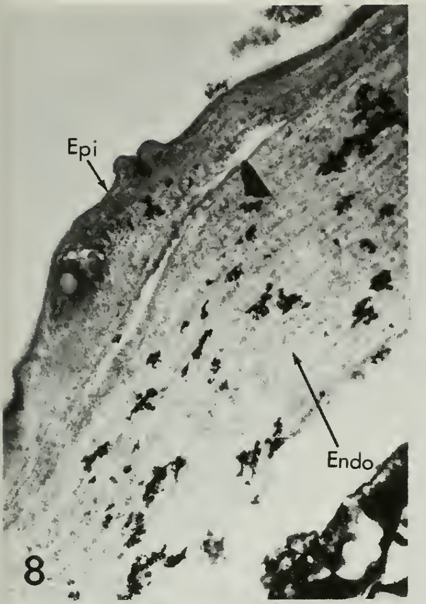
Figure

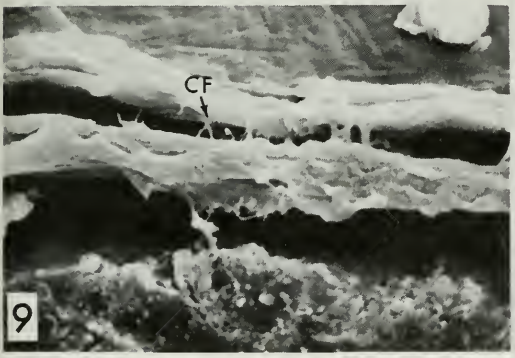
8. Slightly oblique transverse section through *Conchoecia belgicae* carapace [transmission electron micrograph] showing parabolic artefact due to helicoidally arranged chitin fibres. Epi — epicuticle; Endo — endocuticle; × 15,560.

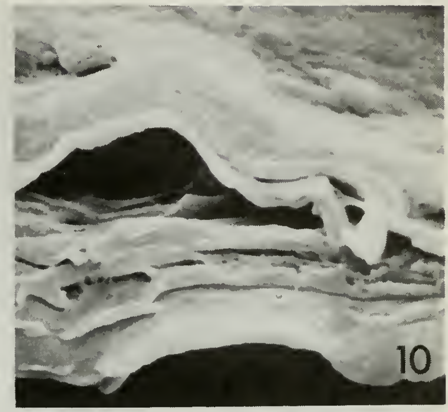
9. Transverse section through *Macrocypridina castanea* carapace [scanning electron micrograph] showing lamellar structure with some cross fibres where the layers have pulled apart, possibly due to the grinding process employed. The chitin fibres [CF] would probably not have this precise angle of orientation in life, the position being exaggerated towards the verticle; × 1,600.

10. Transverse section through *Macrocypridina castanea* carapace [scanning electron micrograph] to show layered structure of the outer lamella. As in figure 9, the outer lamella has parted along the centre line; × 4,000.

11. Transmission electronmicrograph of acetate peel replica of cytheracean ostracode [genus *B* sp.] carapace to show lattice structure of the chitin fibres [CF]; × 19,000.


Epi
Endo
8


CF
9


10


CF
11

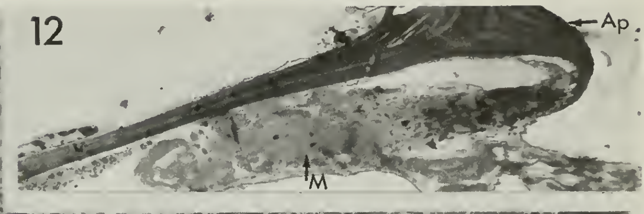
EXPLANATION OF PLATE 4

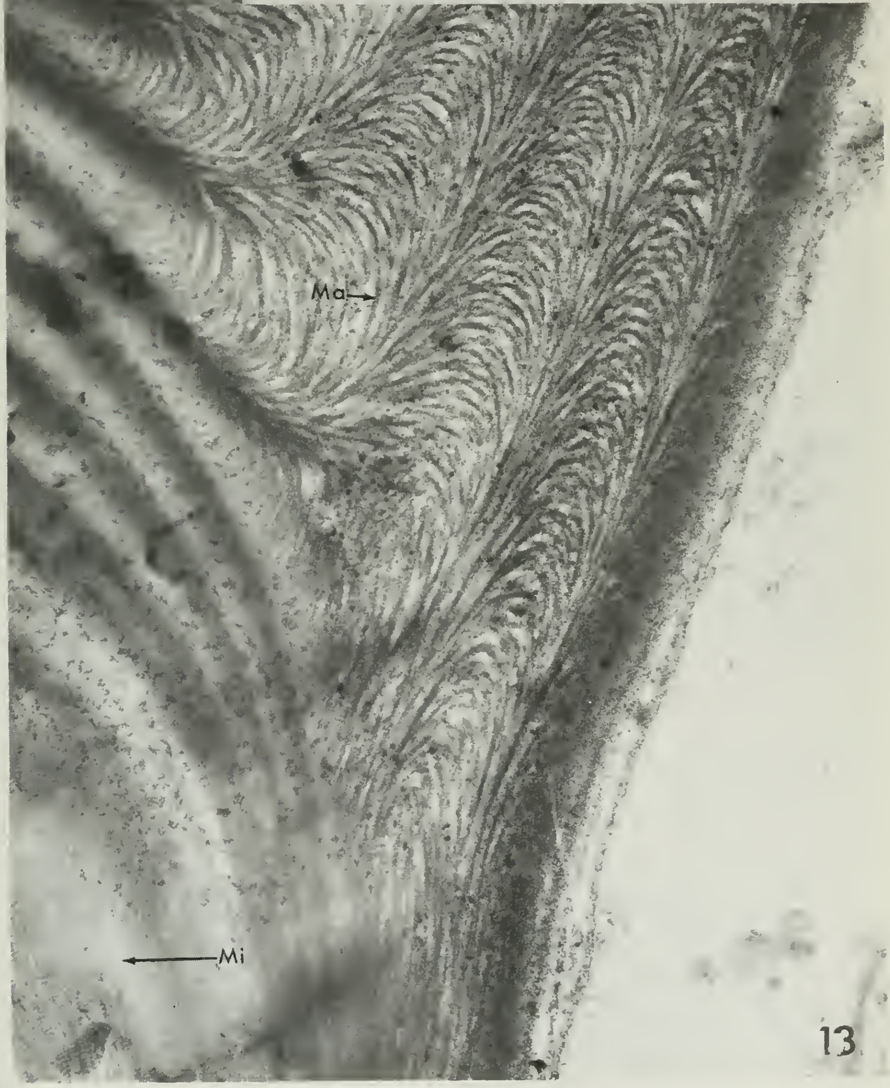
Figure

12. Longitudinal section through part of the endoskeleton of *Cypridopsis vidua* [transmission electron micrograph] to show the relationship of the apodeme [Ap] to the lower bar of the endoskeleton and to the body muscle [M]; × 2,950.

13. Enlarged view of part of endoskeleton and base of apodeme [longitudinal section through *Cypridopsis vidua*] showing the microfibrils [Mi] which form the layered structure of the endoskeleton and the larger macrofibrils [Ma] which form the apodeme structure. The slightly oblique section through the apodeme very clearly illustrates the parabolic artefact of macrofibrils arranged helicoidally through successive layers; × 31,330.

12





13

THE CONSERVATION OF OSTRACODE TESTS — OBSERVATIONS MADE UNDER THE SCANNING ELECTRON MICROSCOPE

H. J. Oertli
Société Nationale des Pétroles d'Aquitaine
Pau, France

ABSTRACT

Examination under the scanning electron microscope of the fractures of ostracode tests shows that in general the organic ("chitinous") layers which, in the living state, envelop the thick, calcite middle layer are preserved. These layers play a role of prime importance in the (good) conservation of the shells. If, for various reasons, they are partially damaged or removed, the middle layer — composed of crystallites whose shape and arrangement are fairly irregular — is brought to the surface which leads to a "badly conserved" appearance on the one hand, and on the other, opens the test to rapid destruction (these crystallites form a relatively loose-knit network). The degree of conservation of the fossilized tests is linked above all to the diagenetic factors affecting the sediment.

LA CONSERVATION DU TEST DES OSTRACODES OBSERVATIONS AU MICROSCOPE ELECTRONIQUE A BALAYAGE

RÉSUMÉ

L'examen au microscope électronique à balayage de surfaces de fracture du test d'Ostracodes fossiles montre qu'en général, les couches organiques ("chitineuses") qui enveloppent, à l'état vivant, l'épaisse couche médiane calcitique restent conservées. Elles ont un rôle primordial dans la (bonne) conservation des coquilles. Si, pour des raisons diverses, elles sont partiellement altérées ou enlevées, la couche médiane— composée de cristallites à forme et arrangement assez irréguliers — se trouve ramenée à la surface, d'où un aspect "mal conservé" d'une part, et un risque de destruction rapide d'autre part (ces cristallites formant un réseau relativement lâche). Le degré de conservation de ces tests fossiles est lié surtout aux facteurs diagénétiques qui affectent le sédiment.

INTRODUCTION

During the study of ostracodes we note differences in the state of preservation of the tests of the specimens : some are perfectly preserved, the surface is gleaming, the patterns of ornamentation, if any, stand out clearly; others — sometimes within the same sample — are dull, the sculptures are more or less blunted. The whole range of conservation can be observed, right up to the "indeterminable" stage. There are a great many factors which could affect the conservation of the tests, and it is almost impossible to state exactly which part each factor plays. If the factors are at work during the "life" phase, or they are at least syn-sedimentary (wear by movement on the substratum, attack by parasitic organisms) — they come into action more particularly sooner or later after the burial of the organism (circulation of attacking waters, stress due to compaction or the tectonic movement of the sediments — the second parameter being able to back up the first). The problem to solve was what was responsible, from the microstructural point of view, for the difference in the "well preserved" and "poorly preserved" appearance. Is poor conservation due to surface corrosion? To a change caused by recrystallization? To the mineralogical composition? A reply to these questions should enable a greater understanding of the behaviour of the tests during fossilization and the diagenesis of the sediments.

I should like to thank the management of the SNPA and the Head of the Geology Department, Centre de Recherches, Mr. Kulbicki, for giving me the opportunity to work on this subject. My colleagues (J. Le Fèvre, M. Hamaoui, J. L. Rumeau, Mrs. Aubert) have given me their invaluable assistance by their critical reading of the manuscript and their suggestions.

STUDY METHODS

A series of ostracode specimens obtained from sediments of varying ages (Mesozoic, Tertiary, Recent) was examined. To obtain results which could be directly compared, observations were generally made on two identical valves of the same species, one with a glossy, "well conserved" surface, the other with a dull, "poorly conserved" surface.

I ought to add that both well and poorly conserved specimens are only infrequently found in one and the same sediment sample. When this occurs, it is perhaps an indication that the group is made up of specimens which have not all lived in that place, or that some of them have been subject to "destructive" influences after death (for example, contact with attacking interstitial water), or again that the association is really a composition of several successive "micro-environments", contained in the same sample.

First of all, the exteriors of the valves to be studied were examined at a small magnification, to identify the specimens, and, at a greater magnification, for microtopography. Then, the same specimens were broken, using a needle, and the surfaces of the fractures were studied. The observations presented here are based on the study of nearly 1000 SEM photos (Stereoscan), taken by the author.

RESULTS

As was to be expected, the great magnifications of the external views already showed remarkable differences: solid surface, relatively smooth, in case of good conservation; a surface more or less rough and granular in the opposite case (Plate 1). But what accounts for the "solid surface"? The examination carried out on the fractures held some surprises. Some sort of set arrangement of the mineral particles which make up the test might have been expected. But although there is clearly a very thin external layer and a thin internal layer, the "vital part" of the test seems to lack a very regular structure (apart from the exceptions which shall be discussed further on). Indeed, the non-crystallized grains (crystallites) which form the thick middle layer of the test are most often arranged in a very irregular way. In some cases, they are globular and relatively consistent in size (but able to weld together) (Pl. 2, figs. 2, 3); in other cases, flat components form compact, laminated layers, sometimes towards the interior of the same fracture (Pl. 2, fig. 4; Pl. 3, fig. 2). Recrystallization may cause the formation of quite large (pseudo-) crystals and bring about a fairly extensive metamorphosis of the test (Pl. 2, figs. 5-8; Pl. 8). It seems very difficult to pinpoint the moment when such transformations took place. According to Sylvester-Bradley (1971, pp. 96, 98, 99), neo-formations can be observed after a short treatment in an ultrasonic cleaner.

With regard to the thin external and internal layers, they are very easily distinguishable in well-conserved specimens (see, for example, Plates 3 and 4). They have either an amorphous appearance, or are made up of very small grains, compressed into one or several compact layers; the external layer can form a sort of skin or cuticle covering the surface like a sheet. No doubt, these layers correspond to the "chitinous internal and external layers" (Hartmann, 1966, p. 39); their organic chemical nature moreover, often causes a marked reaction on the electron beam: higher production of secondary electrons, much greater luminosity than that produced by the calcitic layer. Hartmann (*op. cit.*) uses the term "chitin" in its broadest sense, as our knowledge as to its exact chemical composition does not allow us to be more precise. He mentions the waxy nature of the external layer, which corresponds exactly to some of our illustrations (*e.g.*, Pl. 8, fig. 4). The more granular structure in other cases (*e.g.*, Pl. 7, fig. 5) is due perhaps to a partial calcification. In Sylvester-Bradley & Benson (1971, figs. 1-4 and 47), the calcitic layer is called the "foliated layer" and the organic layer (internal) the "laminar layer". The latter is reported to be found sometimes also on the exterior, and to form the lining of the transverse canals (p. 251); but the authors assume that it is calcified as well (p. 282). Following Bate & East (1972), the thin outer layer would most probably be what they called the epicuticle.

The comparative examination of the surface of the fractures of specimens both badly and well conserved, showed that poor conservation resulted from the removal, partial or complete, of the organic external layer, by erosive or corrosive agents (in this note, I am not speaking of the network of organic meshes inside the calcareous layer, partly due to the subject chosen — in which the interior network is rarely of importance — and partly because when using scanning electron microscopy, these organic meshes are often not visible without special preparation). Nevertheless, careful examination of the fractures shows here and there shreds of matter which cause a higher production of secondary electrons, and it is probable that these are indeed organic matter (for example, Plate 2, figs. 4, 7). Thus the surface is reduced to the interior of the thick calcitic layer with its heterogeneous elements and texture, which accounts for the rough appearance with loss of gloss (cf. Plates 4 and 5).

The partial or complete disappearance of the external layer certainly facilitates the attack, that is to say the partial or total dissolution of the test, due to the rather loose-knit conglomeration of the basic components of the middle layer and the absence of an external protection layer.

The part played by "erosion" in the destruction of the test seems minimal compared with that of corrosion. Indeed, the shape of the ostracode shells would lead to selective abrasion, that is, abrasion of the most exposed parts; however, the destruction seems to be more or less even over the entire surface. Supposing, therefore, that bad conservation is due essentially to chemical phenomena, this may lead us to believe that these effects of corrosion are proof of a water-sediment interaction.

To my knowledge, only five publications, to date, have dealt with the structure of the test of ostracode fossils by electron microscopy — without studying, however, the differences in their conservation: Jørgensen, 1970, Sylvester-Bradley and Benson, 1971, Sylvester-Bradley, 1971, Langer, 1971, Bate and East, 1972. I should like to quote the passage in Jørgensen, which my results have confirmed (p. 84): "The micrographs (. . . .) reveal that the crystal units generally show no morphological orientation. In view of the optical orientation of the mineral matter of the valves, the general lack of morphological orientation appears striking". Langer, too, observes that "meist findet man aber nur ein Haufwerk äusserlich irregulär geformter kryptokristalliner Kalkkörner." (1971, p. 183). This absence of orientation contrasts with the more or less laminated structure of the test of the Foraminifera, for example (Pessagno and Miyano, 1968; Towe and Cifelli, 1967; Reiss and Luz, 1970; Wood, 1949; and others) or with the molluscs (Wise and Hay, 1968), whose formation, however, is completely different.

This research, centered on the problem of "conservation", has given rise in passing to some observations which seem of interest, but which the time available has not permitted me to go into more fully. If I bring them up here, it is not to present results but rather to talk of certain observations and to raise questions on which to reflect.

MARGINAL ZONE

An inner lamella, slightly or not calcified, in the marginal zone stands out very clearly in a section, as might be expected (Pl. 6, figs. 1, 2). When it is thick and highly calcified, there are two variations: either it lies in juxtaposition — as if glued — to the outer lamella (Pl. 6, figs. 3-5), or it is closely linked to the latter (Pl. 6, figs. 8, 10).

In all the cases studied, the calcified portion of the inner lamella is recognizable by its structure and its different crystallization: the crystallites are arranged more or less perpendicularly to the surface of the lamella. In certain cases, this lamella is crossed by layers of a different consistency (organic layers ? — see Pl. 6, figs. 8, 10).

It is obvious that such sections are excellent for the study of different types of marginal pore canals.

ARRANGEMENT OF THE CRYSTALLITES

I have already mentioned the somewhat "disordered" arrangement of the crystallites within the calcitic layer, except in the calcified part of the inner lamella and with the other obvious exception of secondary crystallization. In certain cases, however, an arrangement practically parallel to the surface can be observed. In much the same way, a stricter arrangement exists around the tubercules, spines, and other ornamental features, where the stratification follows the relief, rather like folds; on this subject, see also Sylvester-Bradley and Benson (1971, p. 251).

The lateral pore-canals either traverse the test without affecting its microstructure (setting aside the internal arrangement of the canal which is fairly complex where sieve-plates are concerned), or they affect the surrounding area as if they had pierced the test from the interior towards the exterior, like a diapir. The "chitinous" coating of these canal walls is often conserved (for example, Pl. 7, fig. 2).

RECRYSTALLIZATION

The secondary crystals in the test are easily recognized by their size, often very large, their arrangement — in islets or druses, or by contrast in broad beaches (Plate 3) — and by their "cancerous appearance".

Recrystallization may be confined to parts of the calcitic layer of the test, or absorb the test wall (Pl. 8, figs. 5-8) and even extend beyond it quite considerably (Pl. 9, figs. 1-3) (it is striking to note that sometimes the organic cortex remains preserved even when in direct contact with freshly formed crystals, proof of its different chemical nature (see Pl. 8, figs. 3, 4).

In other cases recrystallization is limited to the internal cast without affecting the test itself (Pl. 9, figs. 4, 5).

TRANSPARENCY

What accounts for the fact that within a well-conserved faunal association, one specimen is perfectly transparent, while another is opaque, milky? I have indeed tackled this problem, but the number of observations made up to now is still insufficient for me to make anything more than suppositions. In comparing the sections of test fragments from specimens of the same species, there seems to be evidence that the crystallites of transparent specimens do not differ either in size or arrangement from the opaque ones (Pl. 10, figs. 1, 2). It is a striking fact that even highly heterogeneous test structures detract in no way from the perfect transparency. The surface of the transparent specimens is always relatively smooth, not granular, which could seem to be a determining factor in the matter of transparency [on this subject, see also J. W. Murray (1967), who concludes, following his experiments on Foraminifera, that interstitial water of pH 7,0 attacks the wall, producing thereby a milky or white appearance]. But among the opaque specimens, there are some with a very smooth surface, as shown on Plate 10, figure 10, and comparable to Plate 10, figure 4, which are not transparent, but simply glossy. These examples show that there are still a good number of problems to solve.

REFERENCES

Bate, R. H., and East, B. A.
1972. *The structure of the ostracode carapace.* Lethaia, 5, pp. 177-194.

Jørgensen, N. O.
1970. *Ultrastructure of some ostracodes.* Bull. Geol. Soc. Denmark, 20, pp. 73-92, 7 pls.

Langer, W.
1971. *Rasterelektronenmikroskopische Beobachtungen über den Feinbau von Ostracoden-Schalen.* Paläont. Z., 45, 3/4, pp. 181-186.
1971. *Über einige Feinstrukturen von Muschelkrebsen aus dem westfälischen Miozän* (Jung-Tertiär). Natur Heimat, 31, 2, pp. 70-74.

Murray, J. W.
1967. *Transparent and opaque foraminiferid tests.* Jour. Paleont., vol. 41, No. 3, p. 791.

Pessagno, E. A., and Miyano, K.
1968. *Notes on the wall structure of the Globigerinacea.* Micropaleontology, vol. 14, No. 1, pp. 38-50.

Reiss, Z., and Luz, B.
1970. *Test formation pattern in planktonic foraminiferids.* Rev. Españ. Micropaleont., vol. 2, No. 1, pp. 85-96.

Sylvester-Bradley, P. C., and Benson, R. H.
1971. *Terminology for surface features in ornate ostracodes.* Lethaia, vol. 4, No. 3, pp. 249-286.

Sylvester-Bradley, P. C.
1971. *The reaction of systematics to the revolution in micropaleontology, in* Heywood, V. H. (ed.) ; *Scanning Electron Microscopy,* pp. 95-111.

Towe, K. M., and Cifelli, R.
1967. *Wall ultrastructure in the calcareous Foraminifera: crystallographic aspects and a model for calcification.* Jour. Paleont., vol. 41, No. 3, pp. 747-762.

Wise, S. W., and Hay, W. W.
1968. *Scanning electron microscopy of Molluscan shell ultrastructure. I. Techniques for polished and etched sections. II. Observations of growth surfaces.* Amer. Microsc. Soc., Trans., vol. 87, No. 4, pp. 411-418; pp. 419-430.

Wood, A.
1949. *The structure of the wall of the test in the Foraminifera; its value in classification.* Quart. Jour. Geol. Soc. London, 104, 414, pp. 229-255.

H. J. Oertli,
S.N.P.A.,
Centre de Recherches,
64001 Pau,
France

DISCUSSION

Dr. I. G. Sohn: The paper suggests a possible explanation of the silicification phenomenon. The outer layer is replaced by silica which seals and preserves the specimen.

EXPLANATION OF PLATE 1

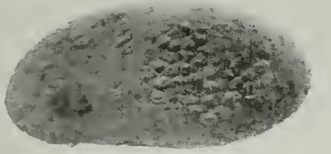
Surfaces (good and poor conservation).

Figure

1-4. **Cyamocytheridea punctatella** (Bosquet, 1852).
Rupelian, Delémont (Canton of Berne, Switzerland).
1-2. Left valve, well conserved; × 55 and × 550 (Ref. 70543/43 and /44).
3-4. Left valve, poorly conserved; × 55 and × 550 (Ref. 70543/45 and /46).

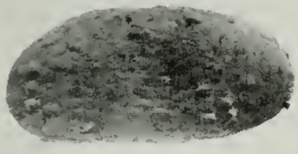
5-8. **Cytheridea pernota** Oertli and Key, 1955.
Rupelian, Delémont (Canton of Berne, Switzerland).
5-6. Right valve, well conserved; × 55 and × 550 (Ref. 70543/39 and /40).
7-8. Right valve, poorly conserved; × 55 and × 550 (Ref. 70543/41 and /42).

The enlargements are all of the central part of the valves.

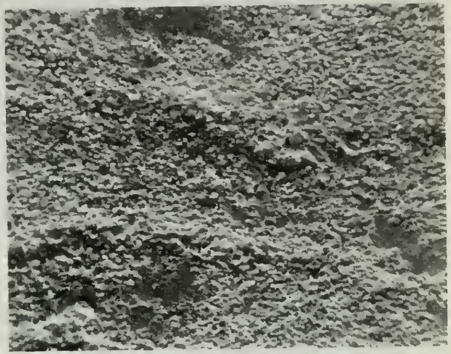


1

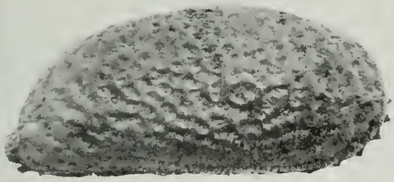
2



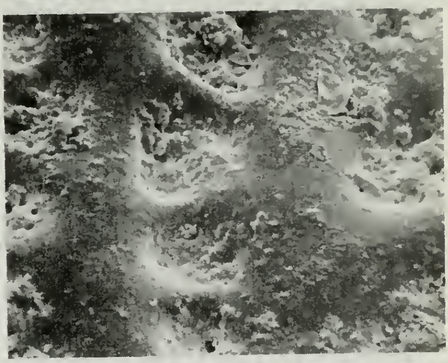
3



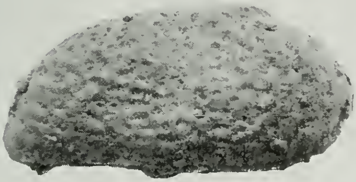
4



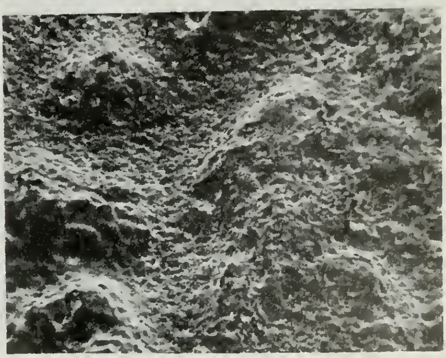
5



6

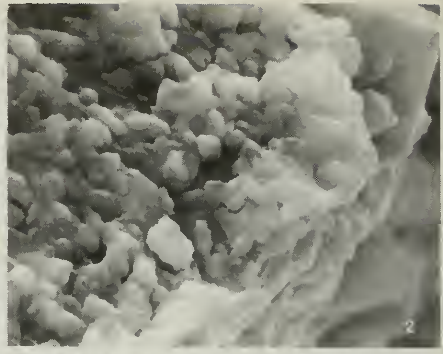


7

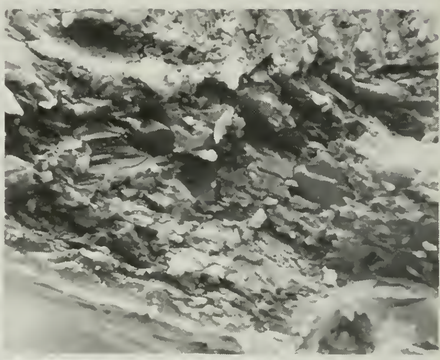


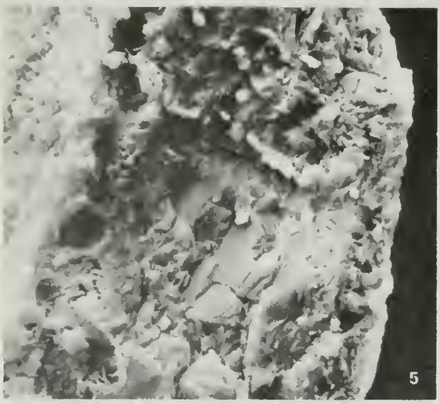
8

1



2





5

6

7

8

EXPLANATION OF PLATE 2

Morphology of the test components (see also Plate 7).

Figure

1-3. Crystallites of relatively consistent size.
1. **Cytheridea** sp. Well-conserved specimen. Paleocene, Cerisols (Dept. Ariège, France); × 2700 (Ref. 69139/17).
2-3. **Cytheridea variepunctata** Oertli, 1956. Poorly preserved specimen; Rupelian, Delémont (Canton of Berne, Switzerland); × 3800 (Ref. 70553/22 and /21).
2. Shows a fairly loose arrangement of the crystallites; in fig. 3, the grains are also welded together (same specimen).

4-6. Amorphous crystallization with laminar fracture (see also Plate 3, fig. 2) **Schuleridea perforata** (Roemer, 1938).
Poorly conserved specimen. Lutetian, Villiers-St.-Frédéric (Dept. Yvelines, France); × 1650, × 830, × 1650 (Ref. 70547/34, /21, /20).

7-8. Recrystallizations within the test (see also Plates 8 and 9).
7. Pyrite crystals having "absorbed" part of the test (to the left); and "metamorphosed" another part (to the right). Note the presence of the "chitinous covering" (cf. Plates 3 and 8). **Bythocypris** ? sp.; middle Paleocene, Libya; × 1370 (Ref. Polaroid 71515).
8. Crystallization of calcite, near to outer edge. **Fastigatocythere fullonica** (Jones, 1884); Upper Bathonian, Boulogne-sur-Mer (Dept. Pas-de-Calais, France); × 1340 (Ref. 71550/24).

EXPLANATION OF PLATE 3

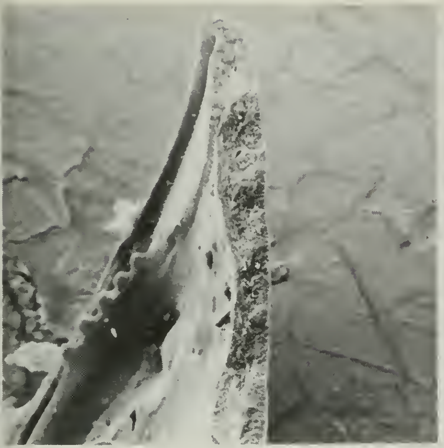
External layer ("cortex") (see also Plates 4 and 5).

Figure

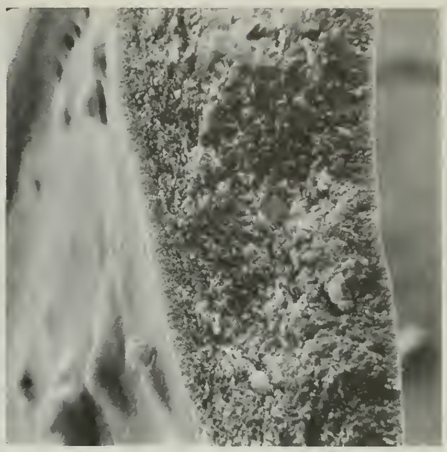
1-4. **Schuleridea perforata** (Roemer, 1838)
Lutetian, Villiers-St.-Frédéric (Dept. Yvelines, France). Successive magnifications; × 165, × 765, × 3800, × 41000. (Ref. 70547/15; /13; /8; /4). Left valve of a well-conserved specimen. The border zones (external and internal sides of the valve) are made up essentially of small crystallites, while the middle layer shows quite a rough, amorphous crystallization (fig. 2) — which, however, does not detract in any way from the transparency of the test. See also Plate 10, figure 9.
Note the organic external layer — which in well-conserved specimens can be observed both on the exterior and in the interior of the test — is made up of a row of very uniform grains (fig. 3 and 4).

5. **Cytherella** cf. **ovata** (Roemer, 1841).
Well-conserved specimen. Albian, section Apt-Gargas (Dept. Vaucluse, France); × 3060 (Ref. 70559/11). Another view of the "cortex", here a little less regular.

6. **Cytheridea variepunctata** Oertli, 1956.
Moderately well-conserved specimen. Rupelian, Delémont (Canton of Berne, Switzerland); × 3600 (Ref. 70553/29). The "chitinous" external layer, whose components have in part merged to form a sort of pellicle, is still well conserved to the right, but to the left impairment is setting in.



1

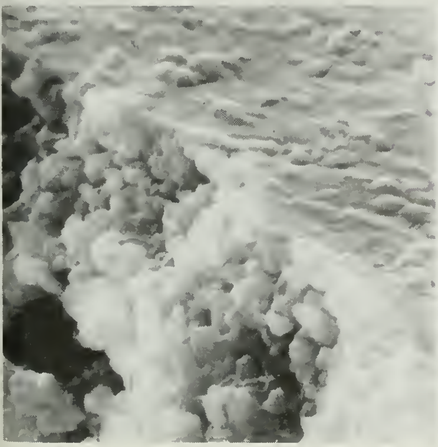


2

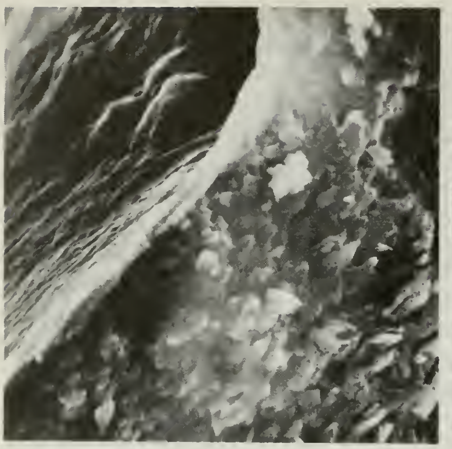
3

4

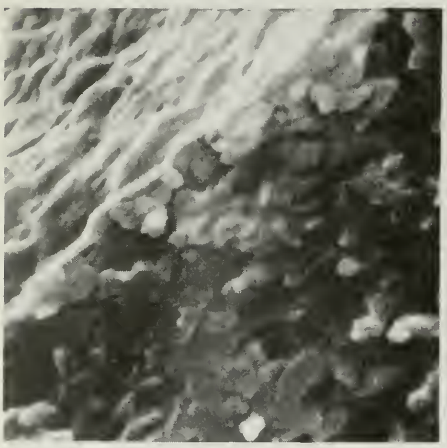
5



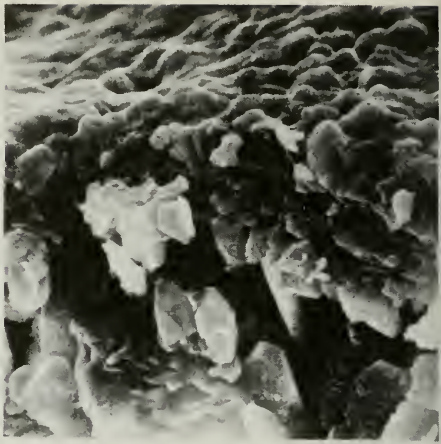
6



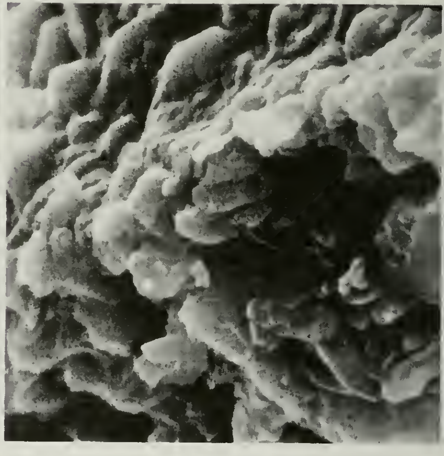
1



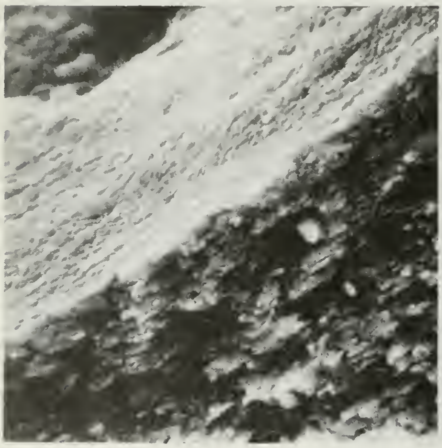
2



3



4



5

6

EXPLANATION OF PLATE 4

External layer ("cortex").

Good conservation (left half of the plate) — poor conservation (right half) (see also Plates 3 and 5).

Figure

1, 2. **Fastigatocythere fullonica** (Jones, 1884).
Well-conserved specimen. Upper Bathonian, Boulogne s/Mer (Dept. Pas-de-Calais, France). × 3300 and × 6600 (Ref. 71550/12 and /5). Relatively rigid "chitinous" cortex, but supple enough to withstand fracturing better than the interior of the test (fig. 1; see also Plate 5, fig. 2).

3, 4. Same species and sample, poorly conserved specimen.
× 3300 and 6600 (Ref. 71550/22 and /18). The "chitinous" external pellicle has become very thin, clearly revealing the hillocks of underlying crystallites; in certain places (left part of fig. 4), the pellicle has completely disappeared.
Note the crystals of neoformation (fig. 3 — see also Plate 8).

5, 6. **Cytheridea variepunctata** Oertli, 1956.
Well (fig. 5) and poorly (fig. 6) conserved specimens. Rupelian, Delémont (Canton of Berne, Switzerland). × 1530 (Ref. 70553/16 and /17). "Cortex" of tightly packed grains, nearly aligned in the external layer (fig. 5), practically entirely missing in the specimen on the right (fig. 6).

EXPLANATION OF PLATE 5

External layer ("cortex") (see also Plates 3 and 4).

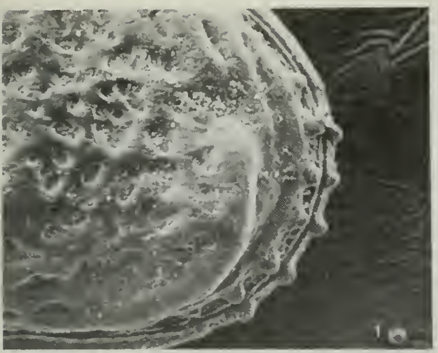
Figure

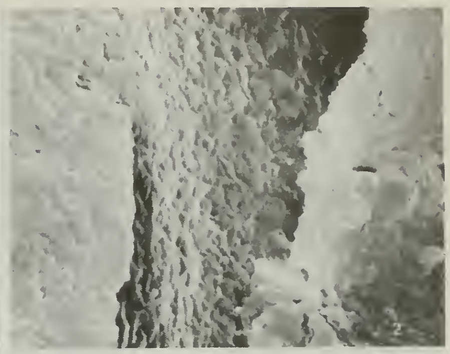
1, 2. **Cytheridea** sp.
Well-conserved specimen. Paleocene, Cerisols (Dept. Ariège, France); × 126 and × 1260 (Ref. 69140/8 and /22). Resistance of the external layer (see also Plate 4, fig. 1). The anteromedian area of the specimen shown here has been placed for 1 minute in an HCl solution. Fig. 1: before attack; Fig. 2: central area of the picture after attack. The acid has created a cavity, revealing the angular to rounded crystallites of the interior of the test. The "chitinous" external layer is visible to the left, and even more so to the right, where it overhangs.

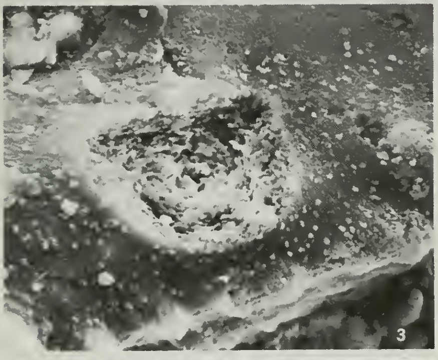
3, 4. **Hermanites** sp.
Well conserved specimen. Same stratum; × 820 and × 3850 (Ref. 69136/7 and /12). Detail of the surface, with cavity due to the artificial removal of a spine. Fig. 4 shows — at a slightly different angle — the left part of the cavity (angular crystallites, loosely arranged; external layer of small, subrounded grains in a compact layer).

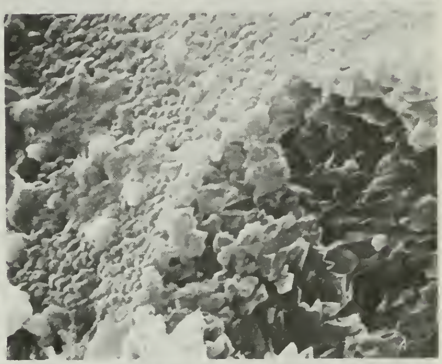
5. **Cytherella** cf. **ovata** (Roemer, 1841).
Poorly conserved specimen. Albian; Gargas-Apt section (Dept. Vaucluse, France). × 2820 (Ref. 70559/18).

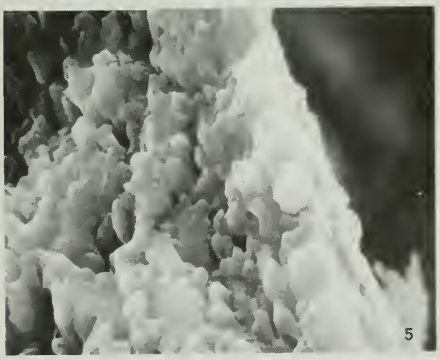
6-8. **Cytheridea variepunctata** Oertli, 1956.
Poorly conserved specimen. Rupelian, Delémont (Canton of Berne, Switzerland); × 385, 770 and 3850 (Ref. 70553/18, /20, /23). In these two species, the external layer has practically disappeared. In fig. 5, the crystallites towards the exterior still show good cohesion; in fig. 8, they are beginning to separate.

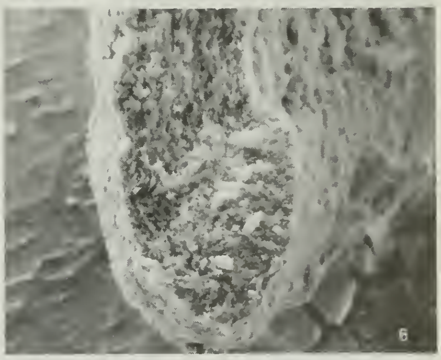

1


2


3


4

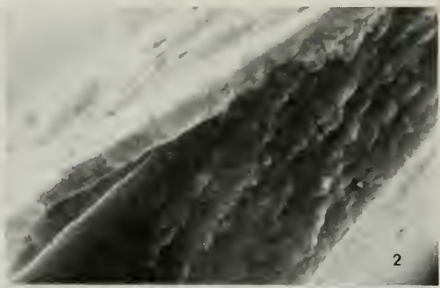

5


6

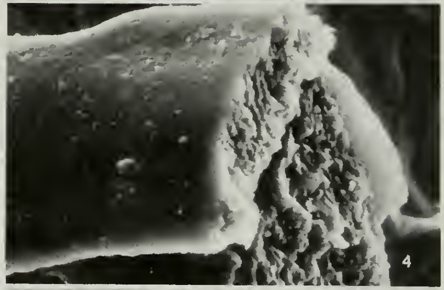

7


8

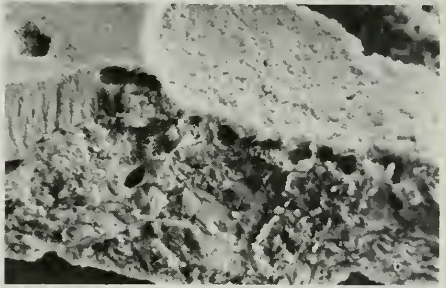

1


2

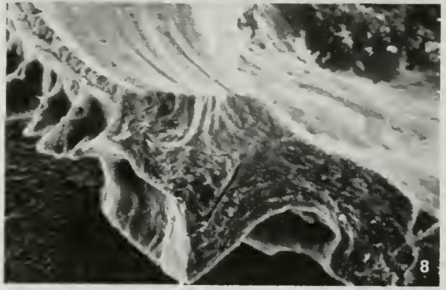

3

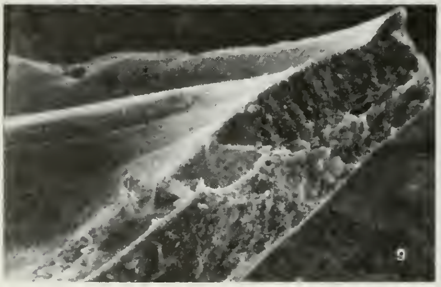

4

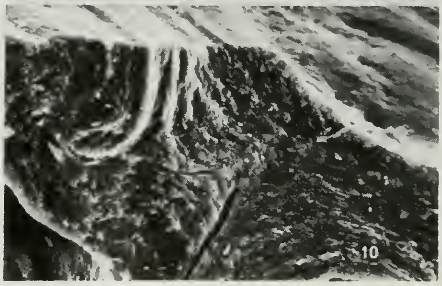

5


6


7


8


9


10

EXPLANATION OF PLATE 6

Observations on the marginal zone.

Figure

1-4. **Falunia** ? sp.
Well-conserved specimen. Subrecent; W Kiskalesi, Içel (Turkey); × 1200, 2850, 550 and 1260 (Ref. 71536/23 and /24; 71531/18; 71536/25). In Figures 1 and 2 (anterior marginal zone), the thin inner lamella can be clearly distinguished from the outer lamella; its formation and chalky appearance are much like the "cortex" of the external layer (clearly visible in the centre of Figure 2). In Figures 3 and 4 (ventral marginal zone), the inner lamella lies side by side with the outer lamella. Note its internal structure (perpendicular arrangement of the crystallites — see especially fig. 4) and the flap of the external layer (on the right of fig. 4).

5-7. **Schuleridea perforata** (Roemer, 1838).
Poorly conserved specimen. Lutetian; Villiers-St.-Frédéric (Dept. Yvelines, France); × 165, × 375 and × 1650 (Ref. 70547/23, /22 and /27). The inner lamella is very compact and can be clearly distinguished from the outer lamella.

8, 10. **Echinocythereis** sp.
Well-conserved specimen. Subrecent; N Atlantic (64°45′N, 29°06′W; 568 fathoms); × 750 and × 550 (Ref. 71531/12 and /13). The inner lamella is closely linked to the outer lamella, but still has a ± perpendicular structure, intersected here by secondary (chitinous ?) lamellae which penetrate fairly deeply into the interior; these lamellae form the septa on the surface.

9. **Cytheretta** sp.
Well-conserved specimen. Lutetian; Villiers-St.-Frédéric (Dept. Yvelines, France); × 285 (Ref. 71077/27). Contact inner/outer lamella.

EXPLANATION OF PLATE 7

Special arrangements of the crystallites

Figure

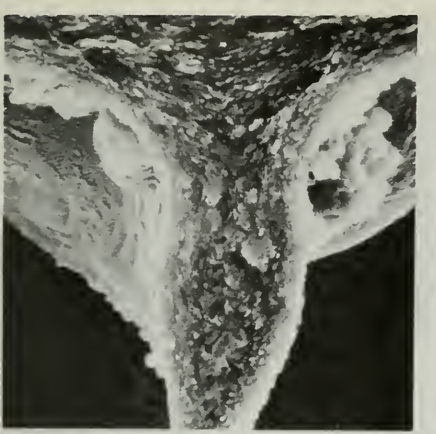
1. **Echinocythereis** sp.
Well-conserved specimen (section through a spine). Subrecent; N Atlantic (64°45'N, 29°06'W; 568 fathoms). × 565 (Ref. 71531/16).

2. **Hermanites** sp.
Poorly conserved specimen (section through a crest; the external surface is below). Paleocene, Cerisols (Dept. Ariège, France); × 3600 (Ref. 69143/9). In the ribs, nodules, knobs, spines, the arrangement of the crystallites is subparallel to the surface; the "movement" begins well below the jagged formations (see top of fig. 1.)

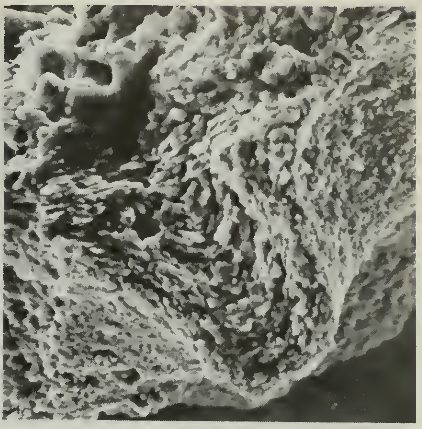
3. **Loxoconcha** sp.
Well-conserved specimen. Subrecent; W Kiskalesi, Içel (Turkey); × 1320 (Ref. 71536/34). Lateral pore canal (sieve form) running through the test without affecting the arrangement of the crystallites (outside edge: towards the bottom).

4, 5. **Bradleya** sp.
Fairly well-conserved specimen. Subrecent; Persian Gulf; × 1420 and × 1200 (Ref. 71550/43 and 71577/6). Lateral pore canal (sieve form) running through the test, having a marked effect on the arrangement of the crystallites ("diapir"). Outside edge, towards the bottom (opening blocked by "chitinous" material) in fig. 4, towards the top in fig. 5. — Note the laminar arrangement of the crystallites and the canal's coating of organic matter partially conserved.

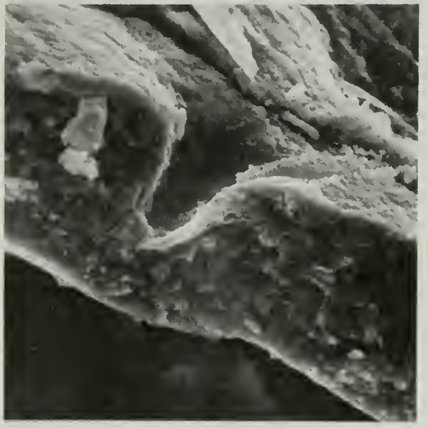
6. **Fastigatocythere fullonica** (Jones, 1884).
Well-conserved specimen. Upper Bathonian, Boulogne s/Mer (Dept. Pas-de-Calais, France); × 685 (Ref. 71550/3). Same feature: lateral pore canal in "diapir" form (outside towards the left).



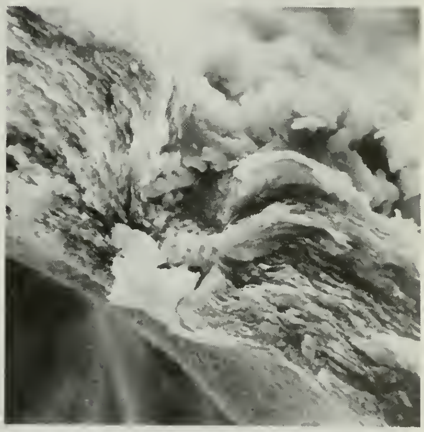
1



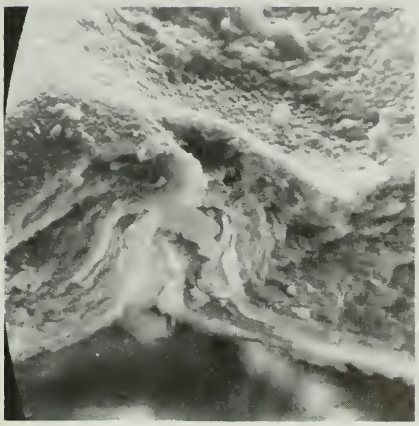
2



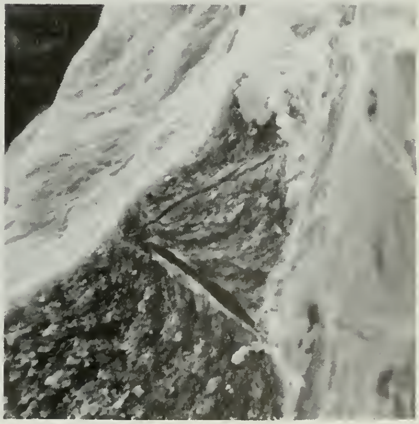
3



4



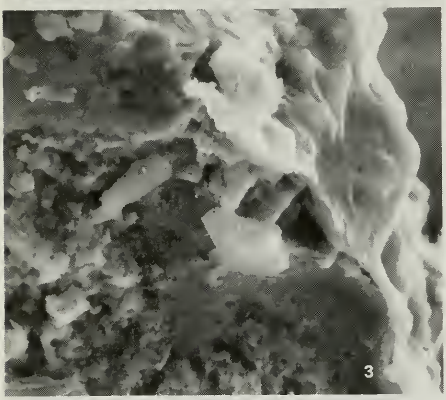
5

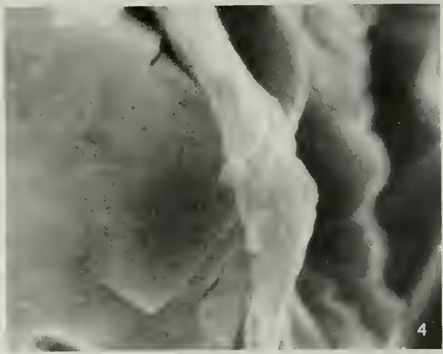


6


1

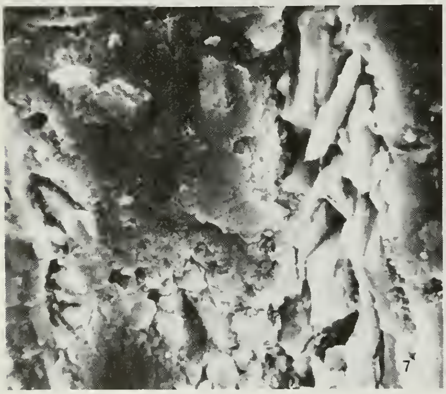

2


3


4


5


6


7


8

EXPLANATION OF PLATE 8

Recrystallizations and fillings (see also Plate 9).

Figure

1. **Hermanites** sp.
Poorly conserved specimen. Paleocene, Cerisols (Dépt. Ariège, France); × 355 (Ref. 69144/10).

2. **Fastigatocythere fullonica** (Jones, 1884).
Moderately well conserved specimen. Upper Bathonian, Boulogne s/Mer (Dept. Pas-de-Calais, France); × 1320 (Ref. 71550/21). Partial recrystallization of the test (see also Plate 2, fig. 6 and Plate 4, fig. 2).

3, 4. **Bythocypris** ? sp.
Pyritised specimen, not very well conserved. Paleocene; bore-hole in Libya; × 1425 and × 7100 (Ref. 71515/4 and /5). Recrystallization by pyritisation. Note that in spite of the "metamorphosis", the "chitinous" external layer has remained intact in places (see also Plate 2, fig. 5 and Plate 9, figs. 1, 2).

5-8. **Bythocypris** ? sp.
Poorly conserved specimen. Paleocene; bore-hole in Libya; × 67, × 340, × 1370 and × 685 (Ref. 71506/38; /41; /40 and /43). The test has been almost entirely destroyed by the crystallization (marcasite ?). Views of the surface (fig. 5: whole specimen; fig. 6: rear area; fig. 7: central area; fig. 8: medio-ventral area).

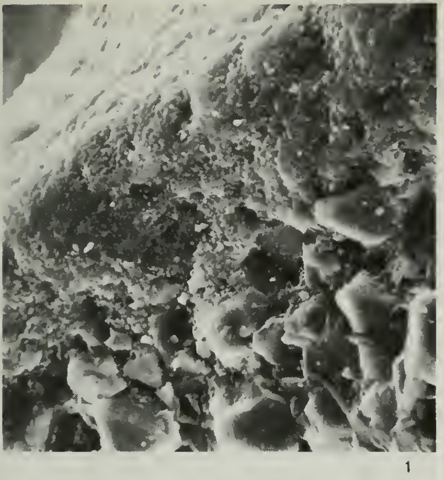
EXPLANATION OF PLATE 9

Figure

1-3. **Bythocypris** ? sp.
Pyritised specimen. Paleocene; bore-hole in Libya; × 1260, × 137, × 840 (Ref. 71506/26, /29, /32). Crystallized internal cast. In certain places, recrystallization does not attack, or only slightly the test itself (fig. 1), in others, the crystals reach and pass through the surface (figs. 2, 3; see also Plate 8).

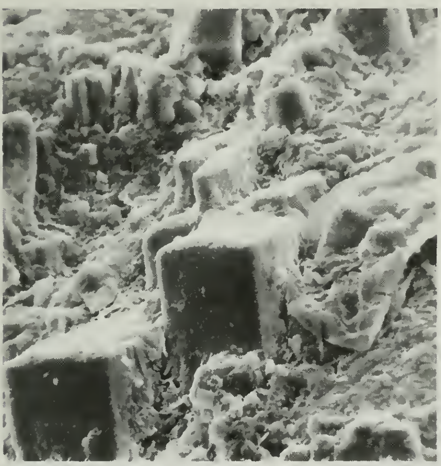
4, 5. **Bythocypris** ? sp.
Moderately well conserved specimen. Tertiary, Iran; × 55 and × 275 (Ref. 70550/20 and 70550/21). The test has been partially removed, thereby revealing, in the centre, crystals of gypsum; however, this crystallization has not attacked, strictly speaking, the test.

6, 7. **Fabanella** cf. **boloniensis** (Jones, 1882).
Fairly well conserved specimen. "Infravalanginian" near Brouco, Lisbon region (Portugal); × 1200 and 600 (Ref. 71577/51 and /52). In this case, too, the filling of the carapace has not affected the structure of the wall.

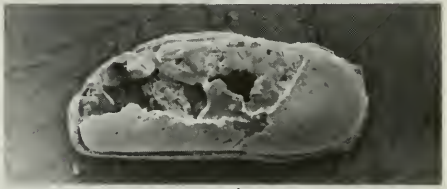


1

2 ↑



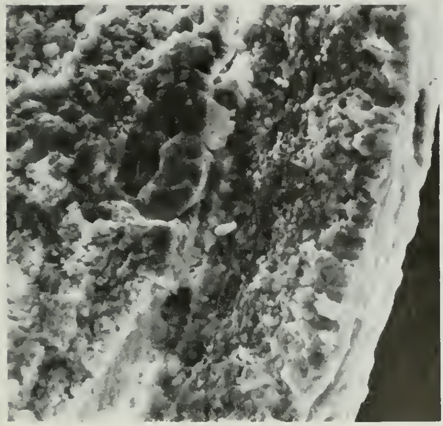
3



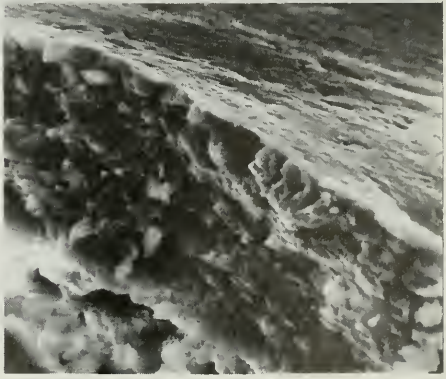
4 ↑

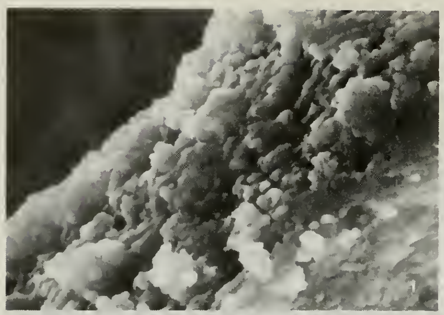
5 ↑

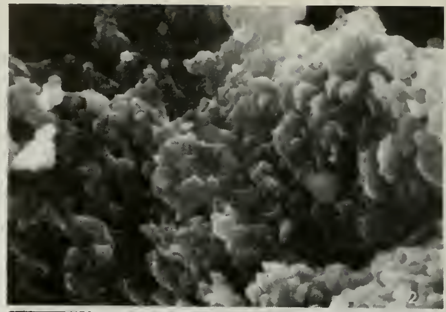
6



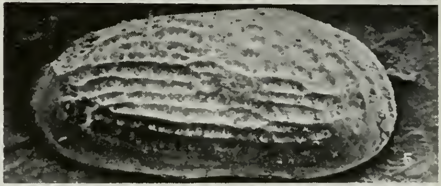
7 ↓

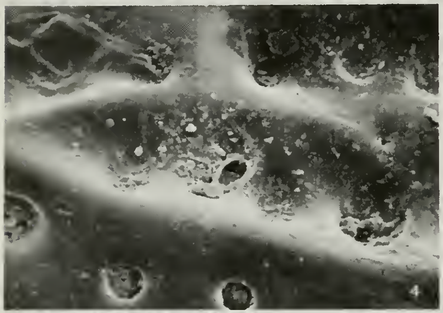


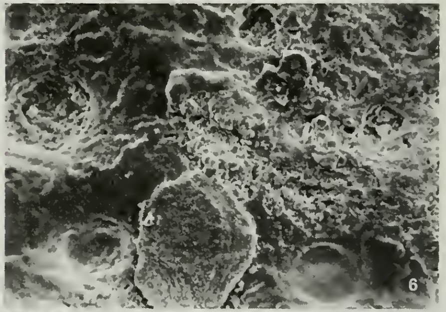

1




3

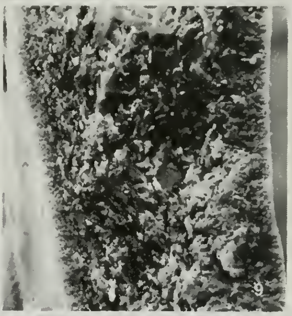

5


4


6


7


8


9


10


11

EXPLANATION OF PLATE 10

Transparency — opacity. Lustre — dullness.

Figure

1, 2. **Falunia** ? sp.
Transparent and opaque specimens. Subrecent; W Kiskalesi, Içel (Turkey); × 3300 (Ref. 71536/26 and /30). Apparently, the internal structure of both forms is the same.

3, 4.
Same specimen as fig. 1, before fracturing, external view; × 55 and × 550 (Ref. 71517/35 and /36).

5, 6.
Same specimen as fig. 2, before fracturing, external view; × 55 and × 550 (Ref. 71517/37 and /38). There seems to be some evidence that the shape of the surface is responsible for the degree of transparency.

7, 8. **Bradleya** sp.
Surface of transparent (7) and opaque (8) specimens. Subrecent, Persian Gulf; × 2830 (Ref. 71577/11 and /9). Comparison of these two photographs would seem to confirm the important role played by the surface.

9. **Schuleridea perforata** (Roemer, 1838).
Translucent specimen. Lutetian; Villiers-St.-Frédéric (Dept. Yvelines, France); × 770 (Ref. 70547/13). The very inhomogeneous internal structure of the test does not detract in any way from its perfect transparency!

10, 11. **Fabanella** cf. **boloniensis** (Jones, 1882).
Surface of opaque specimens, glossy (10) and dull (11); "Infravalanginian", Brouco, Lisbon region (Portugal); × 1200 (Ref. 71577/19 and /17). Very striking differences in the fine morphology of the surface.

APPLICATION OF THE ELECTRON MICROPROBE ANALYZER TO THE STUDY OF THE OSTRACODE CARAPACE

H. Meade Cadot, Roger L. Kaesler, and W. R. van Schmus
University of Kansas

ABSTRACT

Preliminary electron microprobe analysis of specimens of Holocene marine Ostracoda suggests that variation in concentration of $MgCO_3$ in calcite of the carapace varies markedly from the outside to the inside of the carapace of individuals in some taxa and remains relatively constant in others. Superimposed on this individual and phylogenetic variation is a tendency to secrete calcite with less magnesium in cold water than in warm water. Because of early diagenesis, electron microprobe analysis is not suggested for study of fossil or subfossil specimens until the effects of diagenesis are more thoroughly understood.

L'APPLICATION DE L'ANALYSEUR MICROPROBE ÉLECTRONIQUE A L'ÉTUDE DE LA CARAPACE OSTRACODE

RÉSUMÉ

L'analyse préliminaire, par le microprobe électronique, des spécimens Holocene Ostracoda marin, suggère que la variation dans la concentration de Mg CO_3 dans le calcite de la carapace, diffère d'une maniere marquante de l'extérieur à l'intérieur de la carapace des spécimens individuels des taxa, et cette variation reste relativement constante dans d'autres spécimens. Il y a une tendence à sécréter le calcite avec moins de magnésium dans l'eau chaude, qui est superposée sur cette variation individuelle et phylogénique. A cause de la diagénèse hâtive, l'analyse microprobe électronique est à déconseiller pour l'étude des spécimens des fossiles ou des sous-fossiles jusqu'à ce que les effets de la diagénèse soient mieux compris.

INTRODUCTION

The composition of calcite in the skeletons of many marine organisms has been shown to be dependent upon environment and phylogeny. Magnesium is the major ion that substitutes for calcium in calcite. In biogenic calcite, the amount of magnesium carbonate may range from nearly 0 to about 25 mole percent! Chave (1954) first examined calcite of the ostracode carapace in an X-ray diffraction study of a mixture of species from six Holocene environments. He was able to show a positive correlation between water temperature and mole percent $MgCO_3$ in calcite, but because he studied mixed samples, he was not able to isolate the effects of phylogeny or taxonomic affinity. In a later study, Foster (1959) (see also Foster and Benson, 1958) was unenthusiastic about results from X-ray diffraction studies, partly because of the small amount of material in the ostracode carapace.

Since the work of Chave (1954), environmental factors that influence the substitution of magnesium for calcium have been widely discussed (Lowenstam, 1963; Dodd, 1967), but no new data have been added to support hypotheses about the ostracode carapace. Principal current hypotheses are that magnesium substitution in biogenic calcite is controlled largely by phylogeny, temperature, and rate of growth. The latter two of these are factors that are probably highly correlated with each other in many organisms.

Moberly (1968) demonstrated that rate of growth may be an important factor controlling concentration of magnesium in calcite. Both algae and bivalves incorporate more magnesium into their skeletal material during times of rapid growth than during times of slow growth. Whether this applies to Ostracoda is open to question. Unlike most calcite-secreting organisms, ostracodes secrete their carapaces very rapidly following ecdysis rather than growing continuously. Therefore, seasonal changes in temperature will not affect the composition of calcite within a single carapace. It does not follow, however, that Moberly's (1968) hypothesis is incorrect — only that variations within an ostracode carapace are due to some cause other than seasonal variations.

The purpose of this paper is to present preliminary results of an investigation using electron microprobe analysis of the composition of calcite of the ostracode carapace (see also Cadot, *et al.,* 1972). Specifically, we have investigated 1. distribution of magnesium within carapaces, 2. phylogenetic control of magnesium concentration by studying several individuals from the same taxon from many different environments, and 3. enviromental control, especially the effects of temperature.

On the basis of electron microprobe analysis, we have reached some conclusions, but we hasten to emphasize that they are tentative and that additional work is now underway to test these ideas. Three sources of variation in mole percent $MgCO_3$ have been identified: 1. variation within individual carapaces, 2. variation between carapaces collected from warm and cold water, and 3. variations due to phylogeny — that is, marked differences between individuals from distantly related genera from the same environment. By far the greatest variation in mole percent $MgCO_3$ occurs within calcite of individual carapaces rather than between carapaces collected from warm and cold water. However, within a single genus, differences between specimens from different environments may correlate with differences in water temperature. Finally, in order to learn about primary distribution of $MgCO_3$ in the carapace it is important to study specimens that still contain soft parts. Especially in cold water, early diagenesis of the calcite may result in a redistribution of magnesium throughout the carapace or a loss of magnesium from high magnesium calcite.

METHODS OF ANALYSIS

The electron microprobe analyser is an instrument somewhat akin to the scanning electron microscope in which the characteristic X-ray spectra generated by an electron beam are analyzed for wavelength and intensity. "To a first approximation, the intensity of a given characteristic X-ray line A_K of the element A is proportional to the concentration of the element A in the mineral" (Keil, 1967, p. 6).

Electron microprobe analysis is well suited for study of concentration of magnesium in biogenic calcite because the analysing beam can be focused to a diameter of only a few microns. Because the electron beam can be so finely focused, it is possible to analyze the composition of calcite at several points in a traverse across the ostracode carapace. In our study, a spot size of 6 to 8 microns was used in order to minimize decomposition of the calcite being analyzed. The "probe tracks" at which calcite was analyzed are clearly visible in some of the figures in Plate 1. Moreover, because specimens are studied in polished section using X-rays, the danger of contamination from external sources is virtually eliminated.

Lipps and Ribbe (1967) concluded that "analysis to planktonic foraminiferal tests using an electron microprobe is limited by the nature of the specimens whose thin and porous walls make reliable quantitative results difficult to obtain." Our pilot study has shown that good data can be obtained from ostracodes with a microprobe because the calcite is dense and not porous. Our analytical error is probably less than 5 percent and is certainly less than 10 percent.

Details of the operating procedure were reported by Cadot, *et al.* (1972).

DISCUSSION

Table 1 shows the number of ostracodes analyzed and the number of analyses of each species. Approximate water temperature, mean mole prcent $MgCO_3$, and the coefficient of variation of the analyses with 95 percent confidence limits are also shown. Part of this information is summarized graphically in Text-figure 1 in which the concentration of $MgCO_3$ of seven ostracode valves is shown along transects from the outside to the inside of the valves. Although the results reported below are from analyses of single valves, they are generally supported by multiple analyses of other specimens of the same species from the same locality.

VARIATION WITHIN CARAPACES

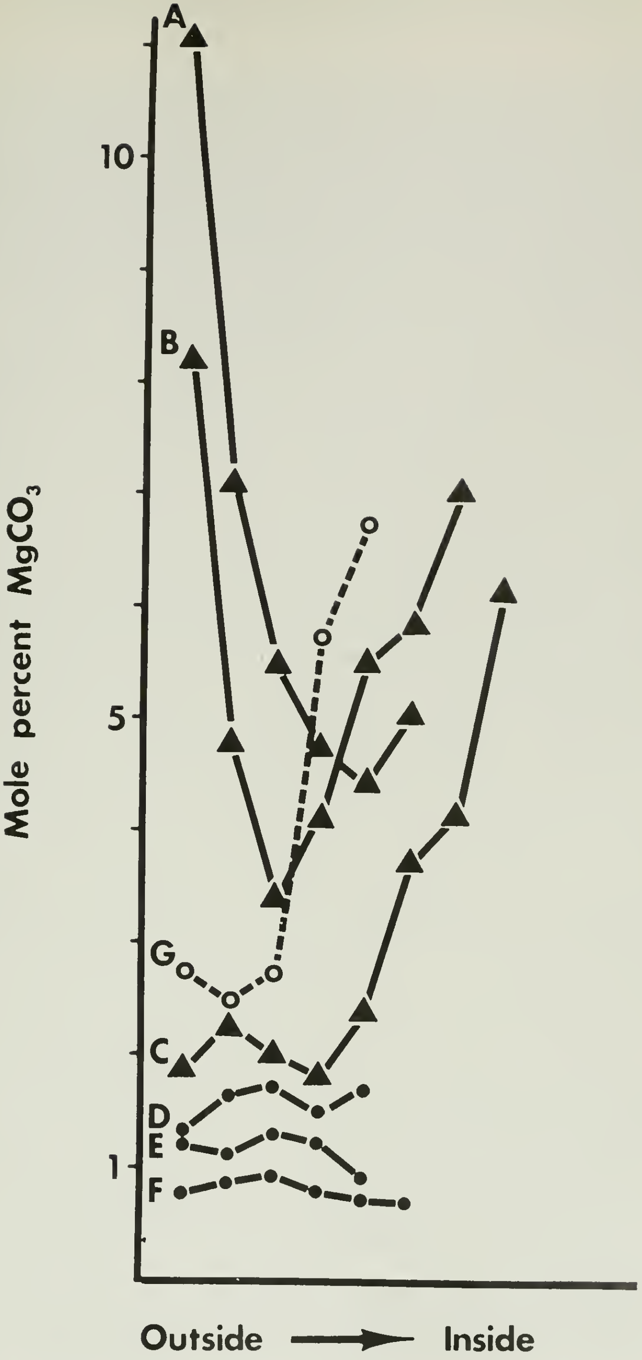
For those specimens studied, the greatest variation in concentration of $MgCO_3$ within carapaces was found in species of *Bairdia* (Pl. 1, figs. 1, 2). In Text-figure 1, transects A, B, and C represent concentrations of $MgCO_3$ in valves of three different species of *Bairdia* from different places. Note the tendency for a high $MgCO_3$ content in the inner portion of all three transects and in the outer part of transects A and B.

Transects D, E, and F show the concentration of $MgCO_3$ in three specimens of *Krithe* (Pl. 1, fig. 3), again from three different areas. In comparison to the *Bairdia* species, specimens of *Krithe* show almost no variation in concentration of $MgCO_3$ within individual carapaces.

Transect G shows the concentration of $MgCO_3$ in a specimen of *Macrocypris* from the deep, cold water of the Tasman Sea. Text-figures 5 and 6 of Plate 1 show the polished sections of two specimens of *Macrocypris* from cold water. The concentration of $MgCO_3$ shows a marked discontinuity between the low-magnesium calcite on the outside of the carapace and the high-magnesium calcite on the inside. This discontinuity may coincide with the layering of calcite in the carapace that is shown in Plate 1, figures 5 and 6.

Table 1. Ostracoda analyzed and results, with 95 percent confidence limits of coefficients of variation (modified from Cadot, Van Schmus, and Kaesler, 1972).

	Locality	Temp.	Mean Mole % $MgCO_3$	Coeff. of Var.	No. of Spec.	No. of Analyses
Podocopina						
Cytheracea						
Xestoleberis sp.	Bermuda	26°C.	3.73	9.77± 5.36	4	9
Krithe producta	St. of Magellan	7°C.	1.59	11.07± 5.03	3	12
Krithe sp.	Tasman Plateau	4°C.	1.17	13.47±12.04	1	5
Krithe sp.	Tasman Sea	2°C.	0.82	8.44± 4.13	2	10
Echinocythereis sp.	St. of Magellan	7°C.	1.08	10.58± 5.81	1	9
Bairdiacea						
Bairdia sp.	Philippines	28°C.	5.51	36.33±14.85	1	17
Bairdia sp.	Bermuda	26°C.	5.24	25.01± 3.26	4	130
Bairdia sp.	Tasman Plateau	4°C.	2.82	48.33±17.90	1	23
Cypridacea						
Macrocypris sp.	Tasman Sea	1°C.	3.97	42.86±19.98	1	19
Argilloecia meridionales	St. of Magellan	7°C.	7.24	8.80± 4.82	1	9
Platycopina						
Cytherellidae						
Cytherella sp.	Tasman Plateau	1–2°C.	4.62	38.09±19.24	2	12
TOTAL					21	255



Text-figure 1. Mole percent $MgCO_3$ measured in transects from outside to inside surface of carapace. A. *Bairdia* sp., Philippines; B. *Bairdia* sp., Bermuda; C. *Bairdia* sp., Tasman Sea; D. *Krithe producta,* Strait of Magellan; E. *Krithe* sp., Tasman Plateau; F. *Krithe* sp., Tasman Sea; G. *Macrocypris* sp., Tasman Sea.

We believe that statements about the concentration of $MgCO_3$ in the ostracode carapace must be based on a consideration of the appreciable variation and possible zonation that may be present within a carapace. Clearly the mean value of $MgCO_3$ in transect F conveys more information that the mean concentration in, say, transect B where the $MgCO_3$ is bimodally distributed. We hope that work now in progress will help provide a coherent picture of the amount of variation in $MgCO_3$ likely to occur in individual carapaces.

VARIATION WITH ENVIRONMENT

In the specimens studied, the concentration of $MgCO_3$ varied with temperature so as to support Chave's (1954) hypothesis. Transects D, E, and F (Text-fig. 1) represent analyses of *Krithe* from progressively cooler water — the Strait of Magellan, the Tasman Plateau, and the Tasman Sea respectively. With very little overlap, the specimens from warmer water have more $MgCO_3$ in their carapaces.

Among the specimens of *Bairdia* studied, the variation is not so straightforward. Transects A, B, and C through specimens from progressively cooler water, the Philippines, the Bermuda Islands, and the Tasman Sea, respectively, trend toward less $MgCO_3$ in cooler water. This trend is superimposed on the high variability of the $MgCO_3$ concentration found in *Bairdia*. The cold-water form (transect C, Tasman Sea) departs from the high-low-high pattern of $MgCO_3$ concentration prevalent in transects through valves from warmer water. It is suggested that this result may indicate that calcite in the outer part of valves of *Bairdia* and possibly other genera may be in equilibrium with sea water when it is secreted or, perhaps, later in the animal's life.

VARIATION DUE TO GENETIC DISSIMILARITY

An indication of variation due to genetic difference has been observed. Based as it is on our very small sample size, it must be regarded as highly tentative. Interpretation is further complicated by the fact that neither *Krithe* nor *Macrocypris* is a typical member of its respective superfamily. Moreover, many of the specimens studied have come from the abyssal environment, the fauna of which is only now becoming well understood. Nevertheless, Text-figure 1 and Table 1 both show that cytheraceans may have a somewhat lower coefficient of variation than either the bairdiaceans or the cypridaceans. If this indication is real and is supported by further study, it will mean that individual cytheracean ostracodes show less variation in $MgCO_3$ concentration through their carapaces than other ostracodes. In addition, the possible zonation of low- and high-magnesium calcite in *Macrocypris* suggests a basic difference in the means of secreting carapace material between cypridaceans and some other ostracodes.

Unfortunately, electron microprobe analysis appears to be ill-suited to the study of fossil or subfossil material, especially from cold water. Early diagenesis of the calcite may result in lowering the $MgCO_3$ concentration, just as the outer part of the studied specimens of *Bairdia* and *Macrocypris* from cold water all had low concentrations of $MgCO_3$. Alternatively, magnesium may be redistributed throughout the carapace. The principal evidence for this suggestion comes from study of the specimen illustrated in Plate 1, figure 5 (not included in Table 1). This specimen was without soft parts when it was collected, and it shows a much more uniform concentration of $MgCO_3$ than specimens of *Macrocypris* containing soft parts. Its coefficient of variation was 17.22 compared to 42.86 for the specimen illustrated in Plate 1, figure 6 from the Tasman Sea. The mean value of $MgCO_3$ concentration was nearly the same for both specimens, suggesting redistribution of $MgCO_3$ throughout the carapace with diagenesis.

ACKNOWLEDGMENTS

The analyses were performed in the microprobe laboratory of the Division of Meteorites, Smithsonian Institution, Washington, D.C. We gratefully acknowledge the use of these facilities and the assistance of C. Obermeyer, J. Nelen, and E. Jarosewich. Research was supported in part by N.S.F. grants GB-4446, GA-12472, and GV-25157 to The University of Kansas and by a faculty travel grant from the University. All specimens studied will be deposited with The University of Kansas Museum of Invertebrate Paleontology.

REFERENCES CITED

Cadot, H. M., Van Schmus, W. R., and Kaesler, R. L.
1972. *Magnesium in calcite of marine Ostracoda.* Geol. Soc. America, Bull., vol. 83, pp. 3519-3521.
Chave, K. E.
1954. *Aspects of the biogeochemistry of magnesium, 1. calcareous marine organisms.* Jour. Geol., vol. 62, pp. 266-283.
Dodd, J. R.
1967. *Magnesium and strontium in calcareous skeletons: a review.* Jour. Paleont., vol. 41, pp. 1313-1329.
Foster, G. L.
1959. *The constituents and their structural arrangement in ostracode carapaces.* University of Kansas, unpublished M.S. Thesis, 88 pp.
Foster, G. L., and Benson, R. H.
1958. *The constituents and their structural arrangements in ostracode carapaces (abstr.).* Geol. Soc. America, Bull., vol. 69, pp. 1565.
Keil, K.
1967. *The electron microprobe X-ray analyzer and its application in mineralogy.* Fortschritte der Mineralogie, vol. 44, No. 1, pp. 4-66.
Lipps, J. H., and Ribbe, P. H.
Electron-probe microanalysis of planktonic foraminifera. Jour. Paleont., vol. 41, No. 2, pp. 492-496.
Lowenstam, H. A.
1963. *Biological problems relating to the composition and diagenesis of sediments.* In: Donnelly, J. W., edit., *The earth sciences. Problems and progress in current research.* Rice University Semicentennial Pubs., Chicago, Chicago University Press, pp. 137-195.

Moberly, R.
1968. *Composition of Mg-calcite of algae and pelecypods by electron microprobe analysis.* Sedimentology, vol. 11, pp. 61-82.

H. Meade Cadot,
Roger L. Kaesler,
and
W. R. van Schmus,
Department of Geology,
University of Kansas,
Lawrence, Kansas 66045

DISCUSSION

Dr. H. Löffler: Can you use strontium in an analysis of this type?

Dr. R. Kaesler: We could use strontium, but the difficulty with using it is that strontium is substituted in the aragonite lattice much more readily than in the calcite lattice. So it is not likely to be terribly abundant in an ostracode carapace. We would like also to look at some heavy metals such as zinc, cadimium, and mercury.

Dr. P. Sandberg: It would be interesting to make a comparison between your results and those of Dr. Oertli on relative states of carapace preservation.

Dr. R. Kaesler: Yes, the very recent carbonate work is demonstrating that this diagenesis may occur early sometimes and it can happen without any apparent change in the way things look.

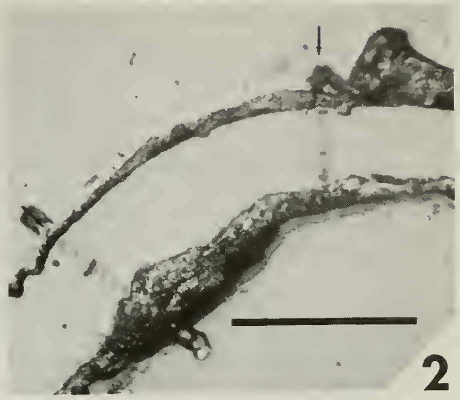
Explanation of Plate 1

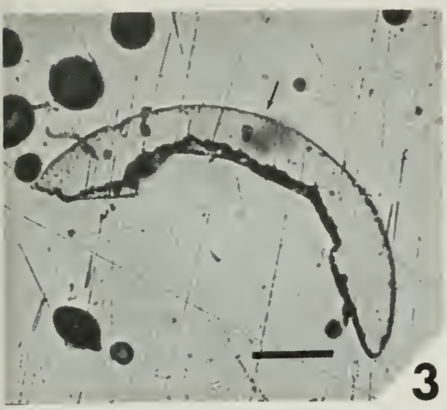
Scale on all figures indicates 100 microns; arrows indicate direction of microprobe traverse.

Figure

1. **Bairdia** sp.
   Specimen from Bermuda; oblique section; representing Bairdiacea.
2. **Bairdia** sp.
   Enlargement of Figure 1 showing two transects of microprobe analyses.
3. **Krithe** sp.
   Specimen from the Tasman Sea; lateral cross section; representing Cytheracea.
4. **Cytherella** sp.
   Specimen from the Tasman Sea; lateral cross section; representing Cytherellidae.
5. **Macrocypris** sp.
   Specimen from Tasman Plateau; without soft parts when collected; may have undergone slight diagenesis.
6. **Macrocypris** sp.
   Specimen from Tasman Sea; longitudinal cross section; representing Cypridacea.

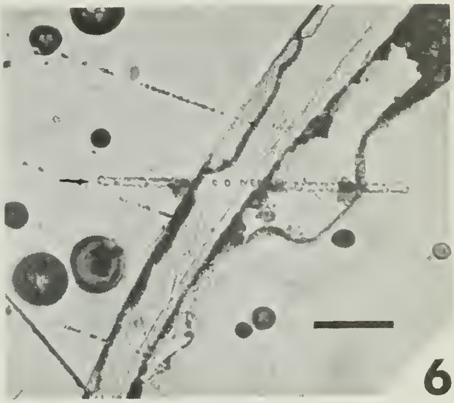

1


2


3


4


5


6

Cadot, Kaesler, and Van Schmus, Plate 1

THE CHITINOUS SKELETON AND ITS BEARING ON TAXONOMY AND BIOLOGY OF OSTRACODES

Knud Schulz
Zoologisches Institut und Zoologisches Museum, Hamburg

ABSTRACT

In the present paper the author discusses the systematical value of the ectoskeleton of ostracodes.

This skeleton is composed of different chitinous rods and apodemes, which lie embedded in the surface of the body wall and serve mainly as a support for extremities, an attachment for certain muscles, and a screen, resp., support for other organs of the soft body.

The morphological studies of the author show clearly:

1. The chitinous skeleton is of great importance for taxonomy and relationship of ostracodes.
2. It is possible to homologize many different parts of the skeleton in higher systematical units, for example Cyprididae (-acea) and Cytheridae (-acea). According to that there is a chance of specifying the natural relationship of higher systematical units.
3. The finer morphology is of generic or even specific rank and value.
4. Some chitin features seem to be influenced by the biology of the species concerned, especially by their mode of locomotion and food intake.

LE SQUELETTE CHAITONNEUX ET SON RAPPORT SUR LA TAXONOMIE ET LA BIOLOGIE DES OSTRACODES

RÉSUMÉ

Dans le travail actuel, l'auteur discute la valeur systématique de l'écto-squelette des ostracodes.

Ce squelette se compose de plusieurs verges et apodèmes chaitonneux, qui demeurent enfoncés dans la surface du mur corporel, et qui servent d'appui, principalement, pour les extrémités, un point de rattachement pour certains muscles, et un écran (*resp.*) d'appui pour d'autres organes du corps mous.

L'étude morphologique de l'auteur montre clairement:

1. Le squelette chaitonneux est d'une grande importance pour la taxonomie et classification des ostracodes.
2. Il est possible d'homologiser bien des parties différentes du squelette dans des unités systématiques supérieures. Par exemple, Cyprididae (-acea), et Cytheridae (-acea). Selon cela il existe l'occasion de spécifier la relation naturelle des unités systématiques supérieures.
3. La morphologie fine est de rang et valeur générique, et même spécifique.
4. Quelques traits du chaitin semblent être influencés par la biologie de l'espèce en question, surtout par leur mode de locomotion et d'ingestion alimentaire.

INTRODUCTION

Ostracodes differ from most other crustaceans by the lack of a solid armour of the soft parts. It must have been completely reduced during their long phylogeny. There is only a thin cuticle left on the body wall which can sometimes be strengthened by more or less strong muscle fibres below. The carapace represents a very effective protection against the harassment of the environment. It suspends the soft body within its valves by the aid of the adductor muscle. On the other hand there were evolving two different skeletal constructions during the ostracode phylogeny which could form attachment points for appendages and certain muscles or could serve as a support for the soft body itself.

CHITINOUS SKELETON

The first skeletal system is composed of different chitinous rods and lies embedded in the surface of the body wall. It supports the soft body especially in its ventral regions, gives abutment to several muscles and a stable base to the extremities.

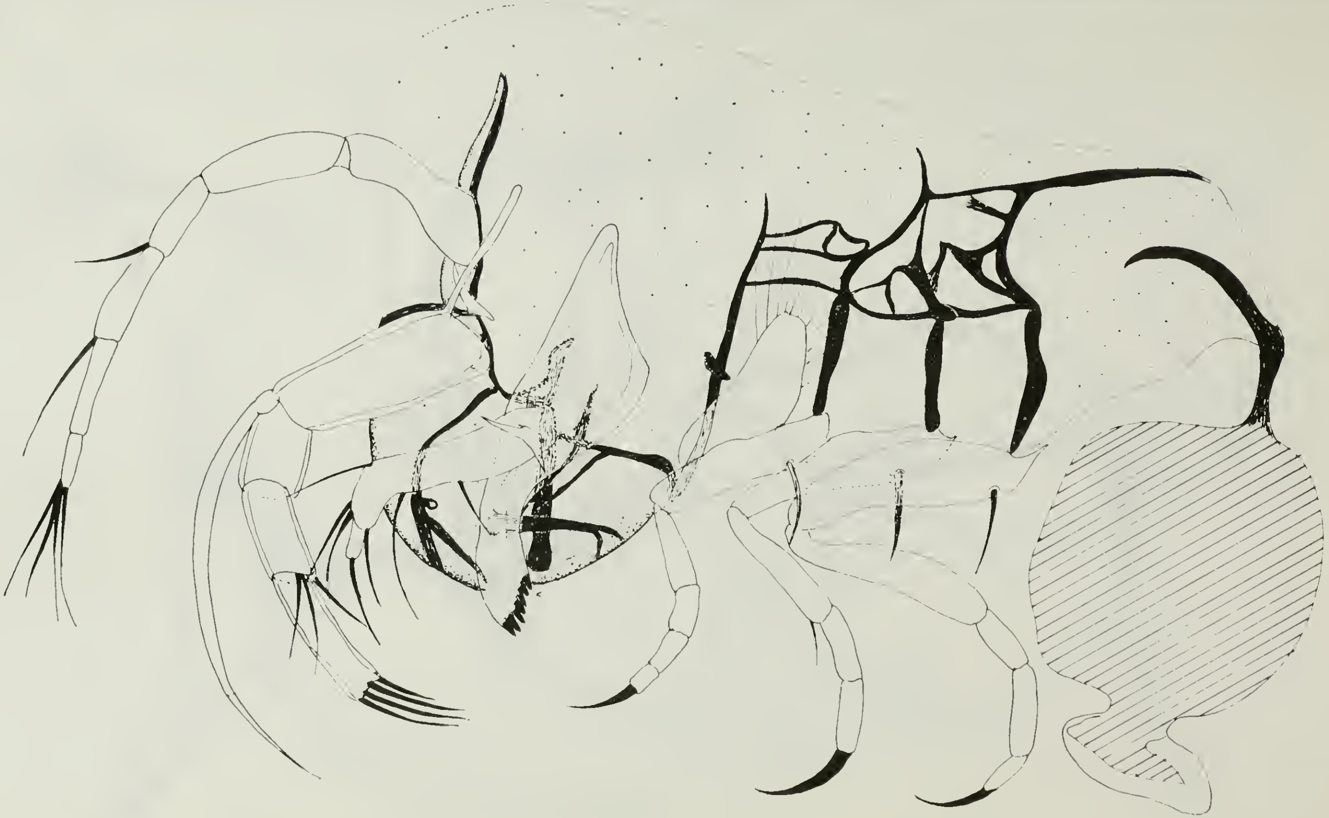
The other skeletal system, the endoskeleton, is completely encased within the body and often composed of a chitinous plate located in the centre of the body. This endoskeleton is of great importance for the suspension of the soft body from the carapace by a series of strong muscles. It is not proved in all ostracode taxa yet, but it is likely to be widespread.

The external framework of the skin is divided into two sections, the so-called headcase and the thoracic framework. The latter represents the base for the trunk-limbs, furca, and copulatory organ. The thoracic framework does not exist in all ostracode groups. As an example one can take the framework of a cytherid, *Semicytherura nigrescens* Baird, 1838 (Text-fig. 1). The headcase is heavy chitinized and represents a two-piece capsule (Text-fig. 2). Its anterior helmet-shaped division encloses the forehead and upper lip and serves as an attachment for the first and second pair of antennae. The posterior part of the headcase begins at the mouth entrance and contains the hypostome or sternum which is the base for the mandibles, maxillae, and sometimes other extremities. The sternum and upper lip are fused together by the lower lip in such a way that both parts show only little freedom of movement in case of food intake.

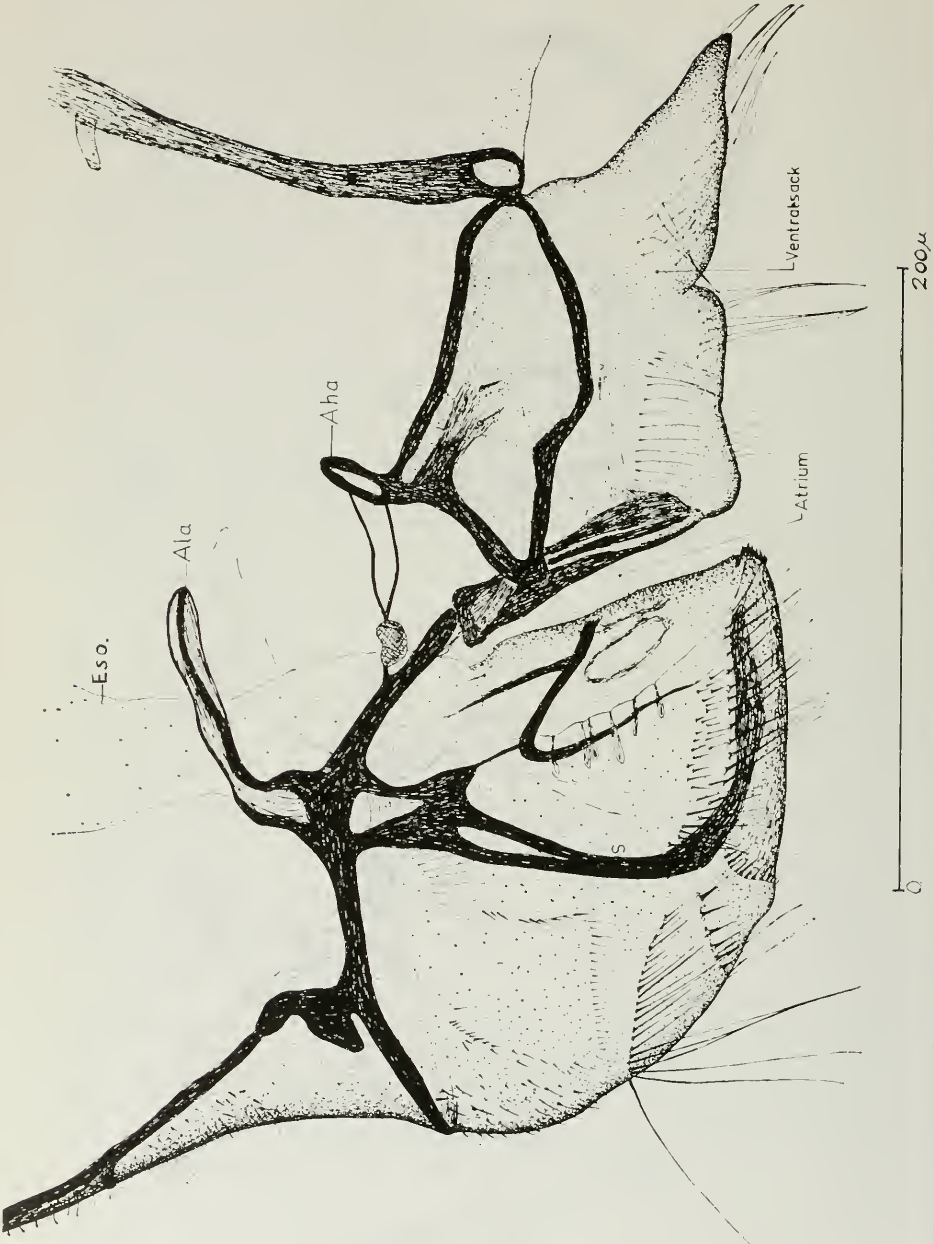
The headcase contacts the adductor muscle tendon by means of two strong apodemes in such a way that it is fixed in a certain place. The "antenno-labral apodeme" (Ala) arises from the lateral part of the upper lip, while the "anterior-hypostomal apodeme" (Aha) arises from the dorsal region of the sternum (Text-figs. 2-5).

The chitinous skeleton of the trunk is well developed in only few ostracode taxa [such as Platycopa, Cytheridae (-acea)], see Text-fig. 1). In most cases there cannot be noticed a special attachment for the thoracic limbs. The furca merely often has its own chitinous rod as a point of attachment for its muscles. There seems to exist a correlation between a crawling locomotion, the total lack of a dorsal muscular system of the soft body, and the occurrence of such a chitinous skeleton of the trunk in some ostracode taxa.

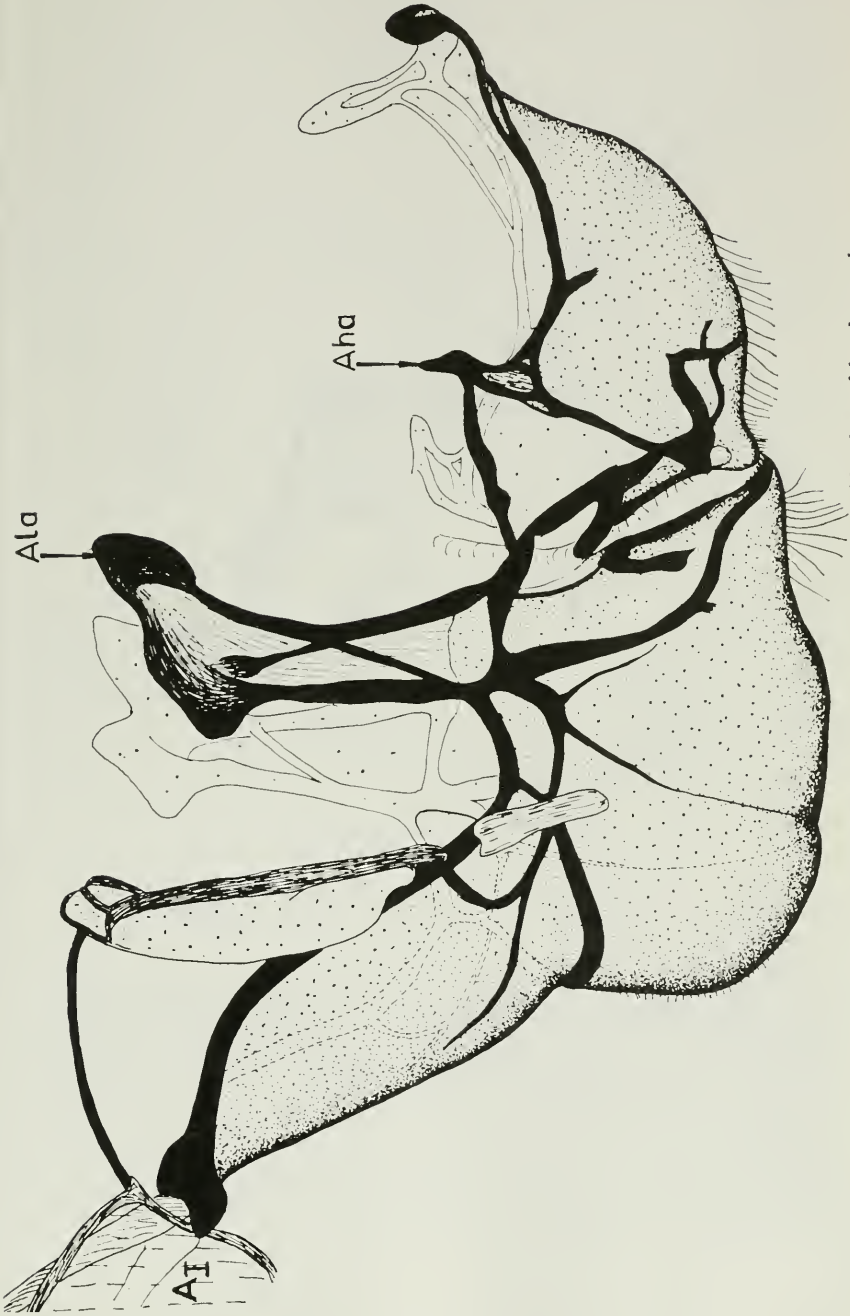
My own morphological studies show clearly that position and shape of skeletal elements of cytherids, cypridids, and darwinulids are constant features within the species and very little exposed to any modification (Text-figs. 2, 3, 4). Moreover there is a good chance of homologizing certain skeletal elements within the subfamilies of those groups, except in the sucking mouth of the paradoxostomatids, where upper lip, lower lip, and sternum are so perfectly fused, that there is still no chance of homologizing.



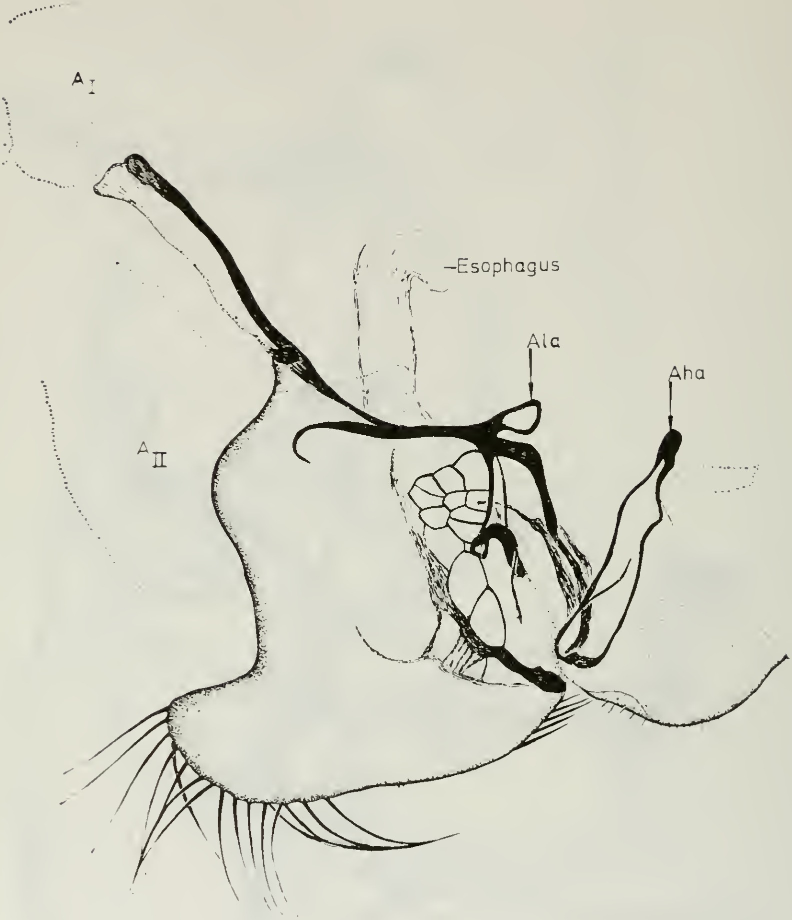
Text-figure 1.—*Semicytherura nigrescens* Baird, 1838. Chitinous Skeleton of male soft body.



Text-figure 2. — *Cyprideis torosa* (Jones, 1850). Side-view of head-capsule.



Text-figure 3. — *Heterocypris salina* (Brady, 1862)—Side-view of head-capsule.



Text-figure 4. — *Darwinula* sp. — Side-view of head-capsule.

In general it is safe to say that with the chitinous skeleton there turns up a new area of features which can be of great value for taxonomy. With help of these structures there may be a better opportunity of clarifying the relationship of ostracode families such as cytherids, cyprids, darwinulids, and their subfamilies than has been possible by means of the carapace and appendages. A comparison with specimens of these three groups shows, that the forming of the chitinous skeleton is not induced by functional needs but could be traced back to a general basic form, which might be represented by the Platycopa. It looks by way of example as if the phylogenetic distance between cytherids and cypridids is not very great.

To demonstrate this we can take the rake-shaped organ of the Cyprididae (-acea) and the lower lip of Cytheridae (-acea) or Darwinulidae (-acea) as representing homologous organs (see fig. 6-11). *Heterocypris,* for example, has remarkably big teeth whereas in many other cypridid taxa they occur very small. These teeth correspond to a row of teeth respectively more or less strong bristles in the group of the cytherids (see fig. 8-11). *Cyprideis* has a number of small teeth which can just as well be of great value for the transportation of food particles into the atrium. *Hirschmannia, Hemicythere,* and *Semicytherura* show only a row of hairs.

On the other hand there can be noticed a striking likeness in the lower lips in different ostracode families. In other words, these structures can easily be recognized as homologous organs. Moreover the lower lip, *e.g.,* can serve as a good diagnostic structure for classifying some cytherid or cypridid taxa. (In this respect it is interesting to notice that *Semicytherura* (Cytheridae) shows more affinities to *Paradoxostoma* than to most other cytherids.

The main skeletal elements of headcase or trunk are often of generic, sometimes even specific rank. On the other hand various species of one genus often differ only slightly in chitinous structures, *e.g.,* there occur some secondary rods within the skeleton which can be decisive. A sexual dimorphism can only have an effect on the construction of the thoracic skeleton, the headcase of both sexes are of total conformity.

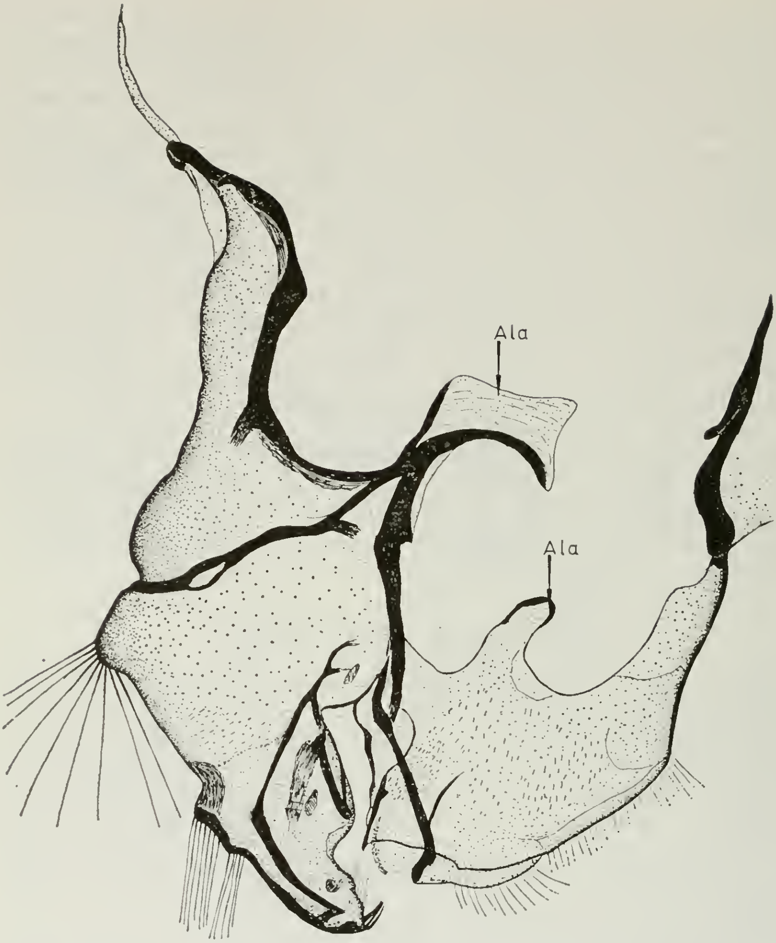
RELATIONSHIPS TO HABITS

The ostracode mode of life shows more or less morphological effects on the general equipment of the chitinous skeleton. Thus, there is often to be observed a reinforcement of skeletal structures in bottom dwelling or burrowing cytherids. The shape of their headcase is more ball-like than the same structure of algae-living ostracodes. Hence it appears as a functional accommodation to a stronger or weaker mechanical stress on the skeleton of these different ostracodes.

Swimming ostracodes like cypridids require considerable space for their antennae. Therefore, in this group the first antenna is attached to the top of the forehead. It looks as if this is a secondary adaptation.

The sucking mouth of the cytherid *Paradoxostoma* can be seen as a functional adaptability to the different mode of food intake. The upper lip and sternum are rigidly fused and the mandibles are enclosed within the headcase.

The character of the teeth which are located at the mouth entrance of cytherids and cypridids (mentioned above) seems to be influenced by the nature of food. Hairs and bristles on the surface of the headcase show similar variations, but the function of these elements is not absolutely clear.

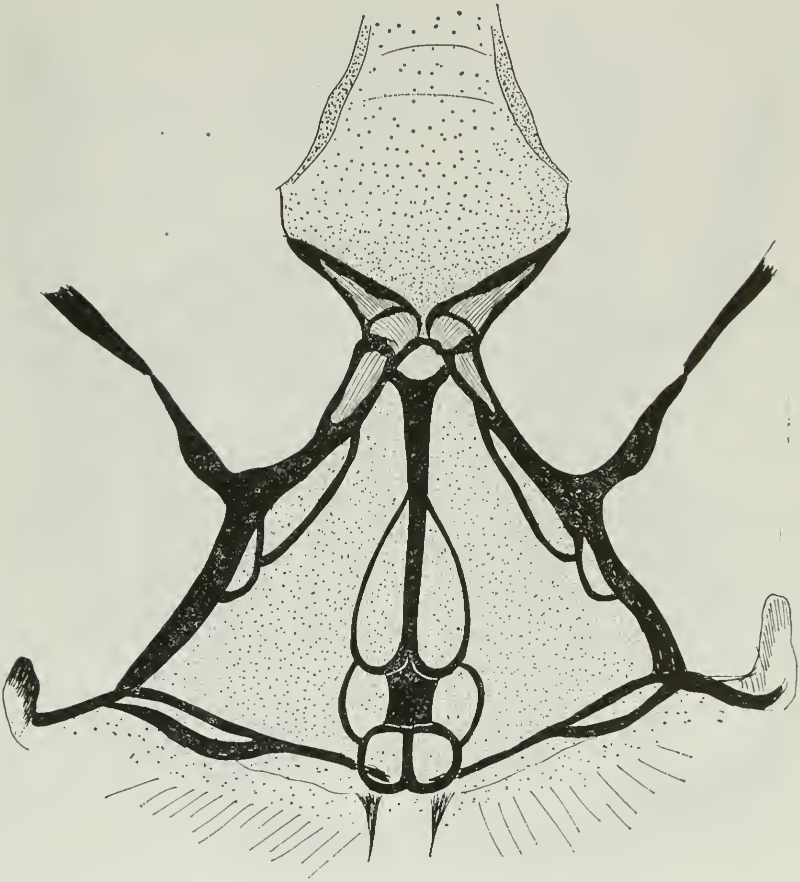


Text-figure 5. — *Bairdia* sp. — Side-view of head-capsule.

CONCLUSION

We see that with the chitinous skeleton there appears a new field of characteristic features, which can be, in addition to descriptions of carapace and soft body, of great value for taxonomy. It may be helpful in answering phylogenetic questions which are not yet solved.

Knud Schulz,
Zoologisches Institut und Zoologisches Museum,
Hamburg,
Germany



Text-figure 6. — *Darwinula* sp. — Lower lip.

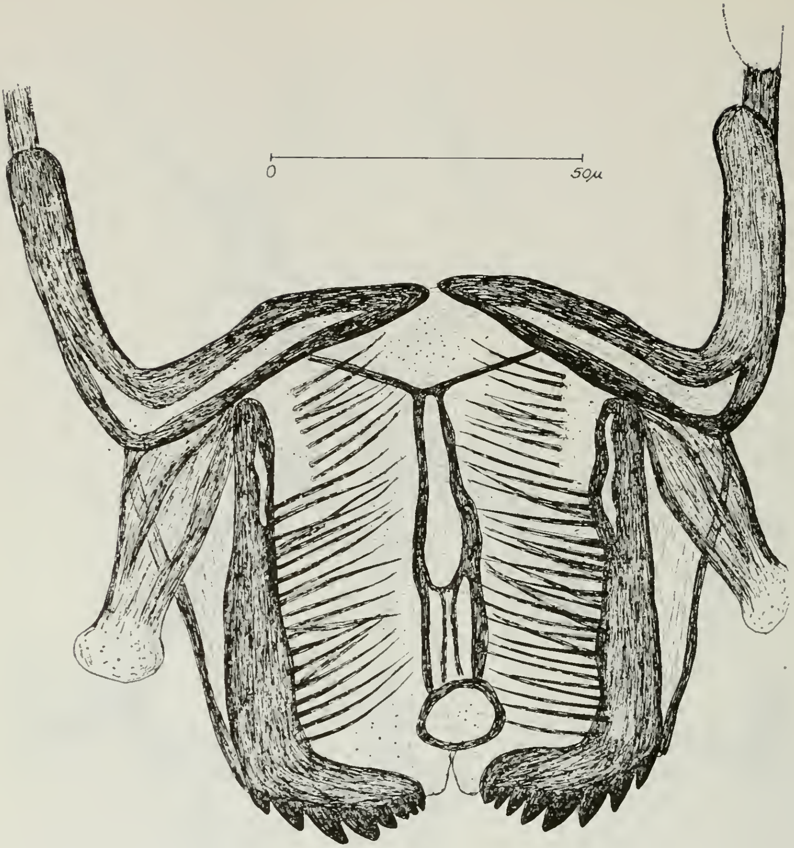
DISCUSSION

Dr. I. G. Sohn: How did you dissect the specimen to see the structures?

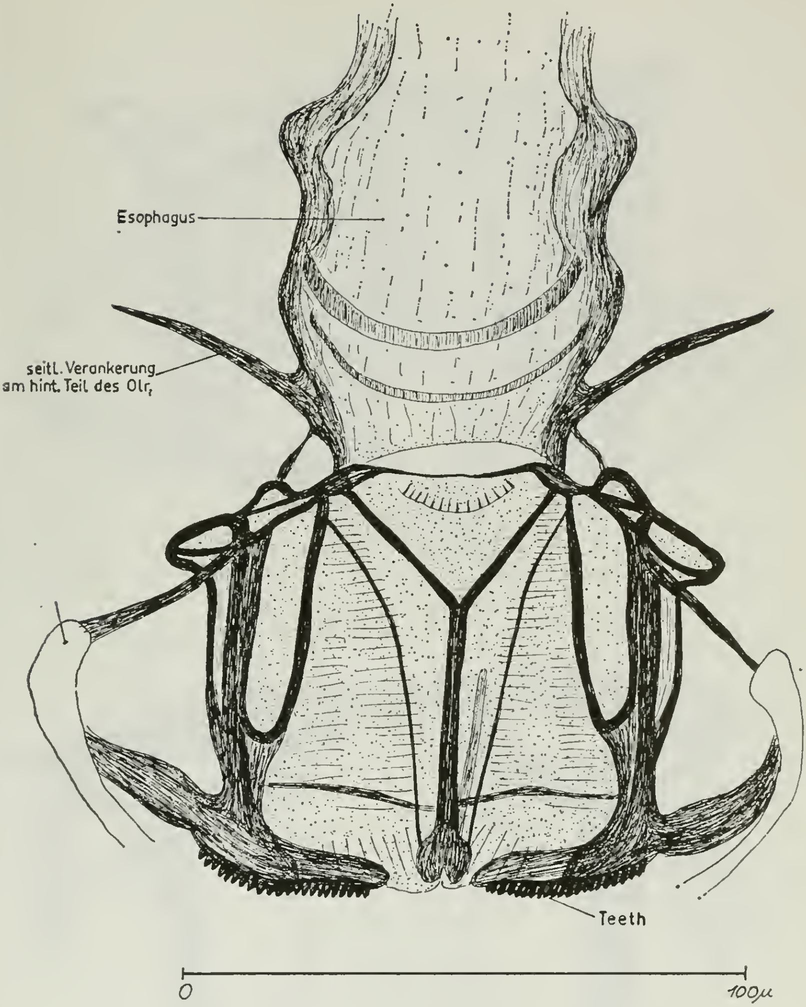
Mr. K. Schulz: I heated the body in liquid potassium-hydroxide, stained it afterwards with "Direct Deep Black" and dissected the structures under a stereo-microscope with fine minute needles.

Dr. R. Maddocks: I'd like to know whether you work at all with the chewing apparatus?

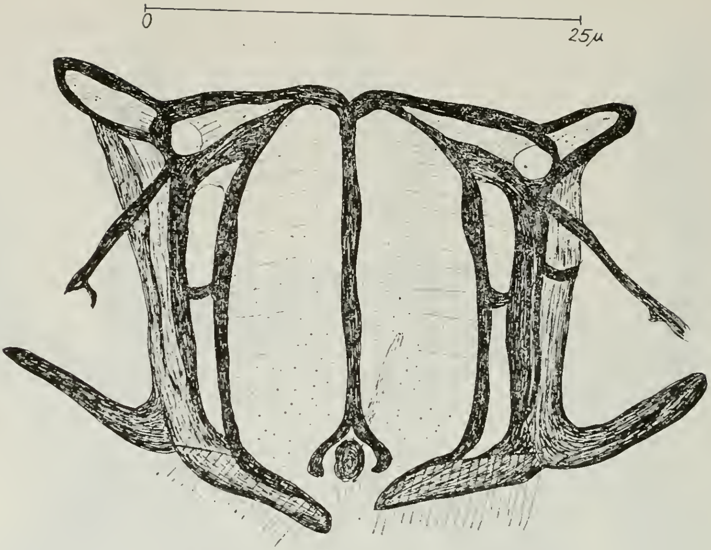
Mr. Schulz: Yes, but only with chitinous parts of upper lip, lower lip, and sternum. I have not worked on the attachments of muscles and their function in that region yet.



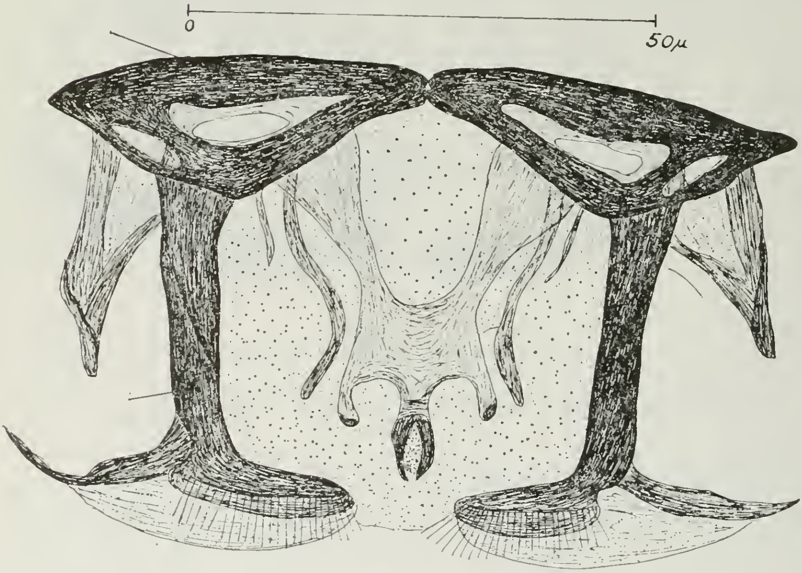
Text-figure 7. — *Heterocypris salina* (Brady), 1862) — Lower lip.



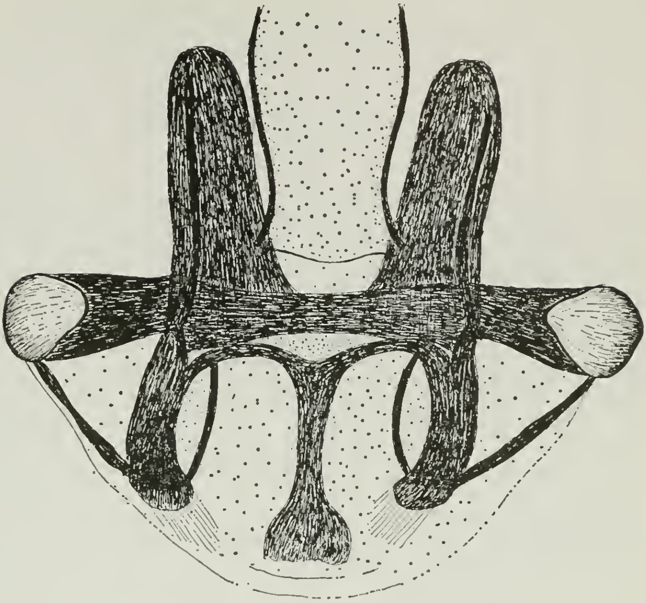
Text-figure 8. — *Cyprideis torosa* (Jones, 1850) — Lower lip.



Text-figure 9. — *Hirschmannia viridis* (O. F. Müller, 1785) — Lower lip.



Text-figure 10. — *Hemicythere villosa* (G. O. Sars, 1865) — Lower lip.



Text-figure 11. — *Semicytherura nigrescens* (Baird, 1835) — Lower lip.

BIOFACIES AND MICROSTRUCTURE OF HOLOCENE OSTRACODA FROM TIDAL BAYS OF DELAWARE

FREDERICK M. SWAIN AND JOHN C. KRAFT
University of Delaware,
and
University of Minnesota

ABSTRACT

Ostracoda of the tidal bays of southern Delaware occur in four presently recognized biofacies: (1) silty clay bay biofacies representing most of the area, *Leptocythere* spp.; (2) silty organic clay tidal-river biofacies with *Cyprideis* and *Perissocytheridea;* (3) tidal bay sand biofacies with *"Haplocytheridea"* and *Campylocythere;* (4) tidal marsh mud biofacies with *Cytherura.*

The relatively weak calcification of the ostracodes and correspondingly heavy chitinization in the tidal bay collection makes possible a study of features of the carapace cuticle, *i.e.,* epicuticle, and underlying procuticle. The epicuticle, here interpreted as being deposited as polyphenolic material by secretory setae, may reflect minute irregularities in the underlying calcified procuticle, such as pits and nodes. Surface hexagonal patterns of 0.2 micron diameter may represent heteroaromatic structure of epicuticle material.

In *Cytherura* spp. epicuticle is laid down in plates that join along reticulating surface ridges.

The outer surface of the procuticle is variously smooth, nodose, punctate, heterolabyrinthic or vermiculolabyrinthic. Further work is necessary to evaluate taxonomic usefulness of these variations but some characteristic patterns seem to occur.

A variety of sieve plate patterns is represented in this collection. In *Loxoconcha* and *Cytheromorpha,* secretory setae are located so as to cover entire surface with epicuticle coating. The normal pore setae in *Cytherura* having crateriform rims are believed to represent secretory setae. The sieve plates in some cytheracean ostracodes may serve for emission of repellent or attractant substances or both.

Parasitic diatoms scattered over surface of one species of the collection resembling a *Monoceratina* undergo progressive burial by epicuticle. They provide nodosity to this ostracode shell. Other examples of attached algae or bacterial filaments can be recognized in the collection.

LES BIOFACIES ET LA MICROSTRUCTURE DES OSTRACODES HOLOCENES DANS LES BAIES RELEVANTES DE LA MER, DANS L'ETAT DE DELAWARE

RÉSUMÉ

Les ostracodes des baies maritimes du sud de Delaware se trouvent dans quatre biofacies actuellement reconnues:

1. Les biofacies des baies de sol glaiseux et limonneux, représentant la plupart de la zône, *Leptocythere* spp.;

2. Les biofacies de sol glaiseux limonneux et organique, maritimes et fluviales, avec *Cyprideis* et *Perissocytheridea*;

Les biofacies de baie maritime de surface sableuse, avec *"Haplocytheridea"*, et *Campylocythere;*

4. Les biofacies de boue et de marécage, relevantes de la mer, avec *Cytherura.*

La calcification relativement faible des ostracodes et la chitinisation correspondemment forte dans la collection des baies maritimes rend possible l'étude des traits du cuticle du carapace, c'est-à-dire épicuticle, et la procuticle se trouvant par dessous. L'épicuticle, interprété ici comme étant déposité comme du matériel polyphénolique par des sétae secrétoires, pourrait réflêter des irrégularités minutieuse dans dans le procuticle calcifié qui se trouve par dessous, telles que des noyaux et de noeuds. Des formations héxagonales de 0,1 micron de diamètre représentent une structure hétéroaromatique de matériel de l'épicuticle, possiblement.

Dans *Cytherura* spp., l'épicuticle est situé en plaques qui se joignent au long de rides de surface réticulantes.

La surface extérieure du procuticle est quelquefois sans rides et contient par fois des noeuds. Elle peut aussi être punctate, hétérolabyrinthique, ou vermiculolabyrinthique. Il faudra encore du travail pour l'evaluation de l'utilité taxonomique. de ces variations, mais quelques formations caractéristiques semblent se mettre en évidence.

Une variété de formations de plaque en crible est représentée dans cette collection. Dans *Loxoconcha* et *Cytheromorpha,* les setae secrétoires sont situées de facon a couvrir la surface entière d'un résidue d'épicuticle. Les setae normales des pores dans *Cytherura,* ayant des jantes cratériformes sont censés représenter des setae secrétoires. Les plaques en crible dans quelques ostracodes Cytheriques peuvent servir dans l'émission des substances de répulsion ou d'attraction, ou pour toutes les deux.

Des diatômes parasitiques situés sur la surface de l'une des espèces dans la collection, se ressemblant à une *Monoceratina* subissent une sépulture progressive par l'épicuticle. Ils pourvoient à cet ostracode de la nodosité dans sa conche. D'autres exemples d'algues et de filaments bactériaux rattachés sont reconnaissables dans la collection.

INTRODUCTION

A small fauna of about 20 species of Ostracoda was collected from tidal bays in southern Delaware. The species are listed, together with their distribution and environmental characteristics, in Table 1.

Specimens of each species have been studied by scanning electron microscopy and some of the features noted are discussed herein. In most instances the specimens of the assemblage are poorly calcified and in many the epicuticle is better developed than is typical of many marine ostracode assemblages, features which are unique enough to warrant a consideration of details of these carapace features.

ACKNOWLEDGMENTS

The work was supported by National Science Foundation Grant No. GP-5604 to Kraft. William Osborn assisted with field work. Takako Nagase assisted with the preparation and scanning electron microscopy of the specimens. Dr. L. S. Kornicker and Dr. R. H. Bate kindly read the manuscript.

OSTRACODE BIOFACIES

Most of the ostracode-bearing samples studied were silty clay from Indian River Bay; a few other samples contained ostracodes in sand and marsh mud in that bay. In Rehoboth Bay and Little Assawoman Bay several samples of sand and silt contained ostracodes. Table 1 shows the data at each collecting station.

Silty Clay Bay Biofacies. (Localities IR 177, 178, 181, 182, 208, 209, 212, 223, 227, 245, 247, 264, 268, RB 270, LA 282, 284). This material is characterized by pH values of 7.1 to 7.6 and Eh values of —250 to +125 mv. Salinity is 28 to 30 o/oo. The sediment originated as mineral and organic detritus carried in by the tidal rivers. The ostracode species of this biofacies are:

Leptocythere aff. *L. castanea* Sars, 1866 (Pl. 4, figs. 7 a, b; Pl. 5, figs. 1 a, b).
L. aff. *L. pellucida* (Baird, 1850) (Pl. 3, figs. 1 a, b)
L. aff. *L. crispata* (Brady, 1868) (Pl. 4, figs 6. a-c, 8 a, b)
L. aff. *L. angusta* Blake, 1933 (Pl. 4, figs. 5 a, b)
L. cf. *L. nikraveshae* Morales, 1966 (Pl. 4, figs. 2 a, b, 3 a, b, 4 a, b)
Monoceratina? aff. *M.? stimulea* (Schwager, 1866) (Pl. 5, figs. 7 a-e)
Echinocythereis? aff. *E.? clarkana* (Ulrich and Bassler, 1904) (Pl. 5, figs. 2 a, b)
Eucythere sp. (Pl. 2, figs. 7 a, b)
Cytherura vestibulata Hall, 1965 (Pl. 1, figs. 4 a, b, 5 a-c, Pl. 2, figs. 1 a-d)
C. aff. *C. corensis* Grossman, 1967 (Pl. 2, figs. 2 a-c, 3 a, b)
Cylindroleberis psitticina Darby, 1965 (Pl. 4, figs. 1 a, b)

A species that occurs in this biofacies as well as in others of the area is *Cytheromorpha* aff. *C. curta* Edwards, 1944 (Pl. 3, figs. 2 a-d, 3 a-c, 4 a-f).

Silty Organic Clay Tidal River Biofacies. (Localities IR 228, PC 197).

The silty clays of Indian River and Pepper Creek contain:

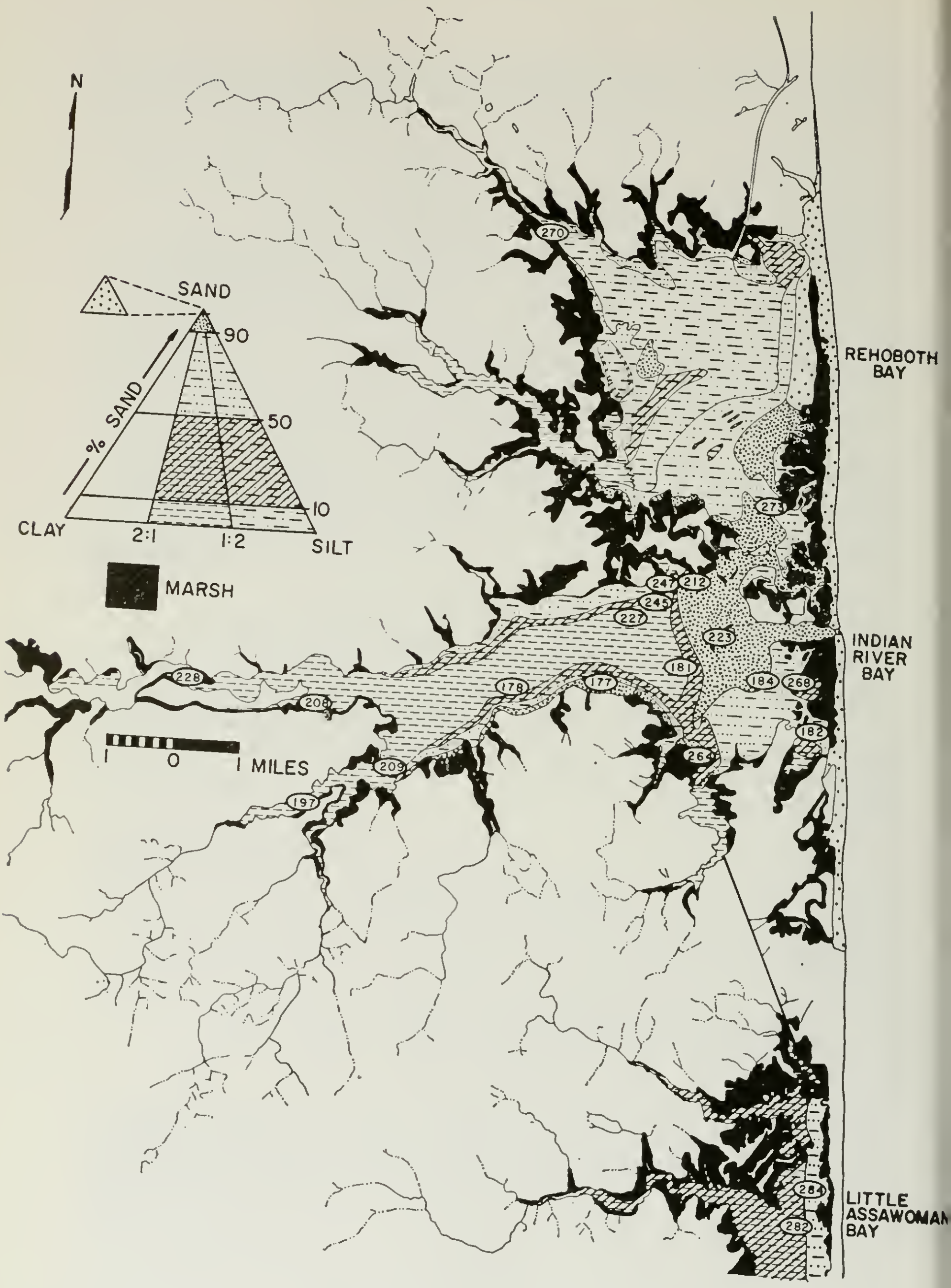
Cyprideis aff. *C. locketti* (Stephenson, 1938) (Pl. 2, figs. 5 a-c)
Perissocytheridea brachyforma Swain, 1955 (Pl. 1, figs. 1 a-f)

The pH of the muds in this environment is 7.4 to 7.45 and the Eh is —105 to — 200 mv. The salinity is 6 to 12 o/oo. These species seem to be primarily detritus feeders. *Loxoconcha purisubrhomboidea* Edwards, 1944 (Pl. 5, figs. 4 a-c, 5 a-c) and *Cytheromorpha* aff. *C. curta* Edwards, 1944, are also present in the tidal river muds.

Tidal Bay Sand Biofacies. (Localities IR 184, RB 273). The sand-bottom areas of Indian River Bay and Rehoboth Bay are characterized by stands of marine algae (*Ulva* and others) on which the ostracodes occur. The pH values of the environment are 7.9 to 9.99 and the Eh values are +109 to +211 mv. The salinity is 30 o/oo+. The species of the sand biofacies are:

Eucythere aff. *E. triangulata* Puri, 1954 (Pl. 2, figs. 6 a-c)
Proteoconcha? *multipunctata parva* (Edwards, 1944) (Pl. 5, figs. 6 a-c)
Paradoxostoma aff. *P. hodgei* Brady, 1870 (Pl. 5, figs. 3 a, b)
Haplocytheridea aff. *H. setipunctata* (Brady, 1867) (Pl. 1, figs. 2 a, b, 3 a, b)

Tidal Marsh Mud Biofacies. (Locality Ir 212) One species, *Cytherura* cf. *C. forulata* Edwards, 1944 (Pl. 2, figs. 4 a, b) was found in the *Spartina* marsh muds bordering Indian River Bay. The area is characterized by pH value of 7.45 and Eh of —140 mv; the salinity was not measured. The ostracode here is believed to be a detritus feeder.



Text-figure 1. — Bottom-sediment types and ostracode collecting localities in southern Delaware. Sediments mapped by Kraft and students.

Table 1. Ostracoda from Tidal Bays of Delaware
IR, Indian River Bay; PC, Pepper Creek; RB, Rehoboth Bay; LA, Little Assawoman Bay

Station	Location	Sediment Type	pH	Eh(mv)	Ostracoda
177	IR	Silty clay	7.32	+125	*Echinocythereis? aff. E.? clarkana* (U and B) *Leptocythere* aff. *L. castanea* Sars
178	IR	Silty clay	7.28	+ 15	*Leptocythere* cf. *L. nikraveshae* Morales
181	IR	Silty clay	7.35	—120	*Leptocythere* aff. *L. castanea* Sars *Leptocythere* cf. *L. nikraveshae* Morales
182	IR	Silty clay	7.1	— 15	*Monoceratina?* aff. *M? stimulea* (Schwager)
184	IR	Sand	8.45	— 10	*Proteoconcha ? multipunctata parva* (Edwards)
208	IR	Silty clay	7.40	—240	*Cytheromorpha* aff. *C. curta* Edwards; *Eucythere* sp.
(near mouth of the river)					
209	IR	Silty clay	7.30	—250	*Leptocythere* aff. *L. pellucida* (Baird)
212	IR	Marsh mud	7.45	—140	*Cytherura* cf. *C. forulata* Edwards
223	IR	Sand	7.90	+115	*Eucythere* aff. *E. triangulata* Puri, *Paradoxostoma* aff. *P. hodgei* Brady
227	IR	Silty clay	7.35	—150	*Leptocythere* cf. *L. nikraveshae* Morales *Leptocythere* aff. *L. angusta* Blake
228 (Indian River)	IR	Silty clay	7.45	—200	*Cyprideis* aff. *C. locketti* (Stephenson) *Cytheromorpha* aff. *C. curta* Edwards *Loxoconcha* cf. *L. purisubrhomboidea* Edwards
245	IR	Silty clay	7.6	— 75	*Cytherura vestibulata* Hall
247	IR	Sandy silty clay	7.5	+120	*Cytherura vestibulata* Hall
264	IR	Sandy silty clay			*Cytherura vestibulata* Hall, *Loxoconcha* cf. *L. purisubrhomboidea* Edwards, *Leptocythere* aff. ***L. crispata*** (Brady)
268	IR	Sandy clay	n.d.	n.d.	*Leptocythere* aff. *L. crispata* (Brady)
197	PC	Silty clay	7.4	—105	*Perissocytheridea brachyforma* Swain
270	RB	Sandy silt	7.03-7.63	— 42 —199	*Cytherura* cf. *C. corensis* Grossman
273	RB	Silty sand	7.61-9.99	+109 +211	*Haplocytheridea* aff. *H. setipunctata* (Brady)
282	LA	Silty, sandy clay	7.52-7.70	— 75	*Cylindroleberis psitticina* Darby
284	LA	Silty, sandy clay	7.59	—100	*Cytheromorpha* aff. *C. curta* Edwards

SURFACE TEXTURAL FEATURES OF SHELL

Ostracode shell structure. — The ostracode shell-structure nomenclature herein conforms to that discussed by Bate and East (1972, and this volume) and consists of the following.

1. Epicuticle, thin uncalcified outer organic covering of part or all of ostracode carapace; little or no development of structure appears to occur in the epicuticle, but it may reflect structures in the underlying procuticle; organic matter is nonchitinous.

2. Procuticle-exocuticle, a relatively thin chitin-impregnated layer, calcified in most ostracodes, stained pink by Haemalum Eosin, underlying epicuticle; calcite crystals may terminate outward in several projecting patterns; *i.e.,* reticulate-labyrinthic, nodose-labyrinthic, heterolabyrinthic, or exocuticle may be smooth-surfaced; represents outer part of procuticle of Richards (1951); not present in all ostracodes, particularly in some myodocopids.

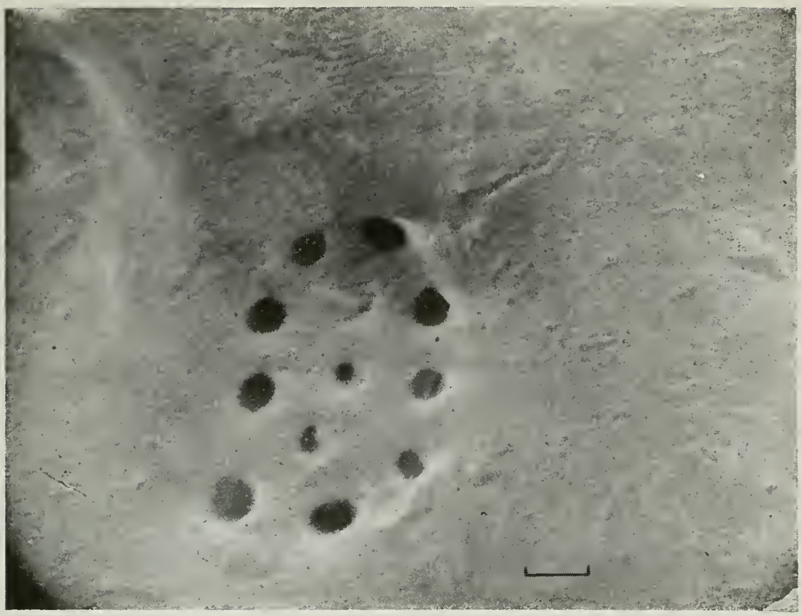
3. Procuticle-endocuticle; forms inner part of procuticle; present in all ostracodes and is calcified in most; composed of a lattice of elongate chitin fibres stained purple by Haemalum Eosin (Bate and East, 1972, and this volume); may contain pigment granules which give characteristic color patterns to certain ostracodes; overlies directly the epidermal cells of the ostracode animal.

In the present discussion the material underlying the epicuticle will all be referred to as procuticle, because of the difficulty in distinguishing exo- and endocuticle in lateral-view photographs of the carapace.

The ostracode animal may have at least two different kinds of setae emerging from pores in the procuticle. These may be large, thick, stiff and springlike in nature, or soft and appear to be fluid-filled in the living animal. After death the latter setae collapse (Pl. 3, fig. 3 c). The stiff setae have a protective function and in several instances are branched in the procuticle for further strength (*Bairdia, Cypridopsis*). The smaller setae are thought to be sensory and may also be secretory or other small setae may be only secretory. It is not clear whether two distinct types of these smaller setae may occur in the same individual (Omatsola, 1970, 1971).

One function of certain types of setae is suggested by the writers to be secretion of the epicuticle. The chitinous procuticle of the ostracode is secreted by the epidermal cells, either entirely or mainly before molting, with calcification occurring after molting (Bate and East, 1972). The secretion of epicuticle involves a different biochemistry than that of the procuticle as it is composed of lipids and polyphenols rather than chitin.

Features of the epicuticle. — Epicuticle is believed to be represented in most, if not all of the specimens studied here, but is not developed over entire exterior of carapace in several instances. It is not known whether certain areas that lack epicuticle in these specimens have lost it after death or whether it was never present. For example, in *Haplocytheridea* aff. *H. setipunctata* (Brady) (Pl. 1, figs. 2b, 3b) epicuticle (dark areas) is lacking in the pit



Text-figure 2. — Part of surface of shell of *Cytheromorpha* aff. *C. curta* Edwards from Locality 284, Little Assawoman Bay, Delaware, showing close-packed polygonal structure of cuticle surface around a sieve plate. Bar represents approximately 1 micron.

areas (light areas) in specimens that still had appendages when collected. One of the functions, perhaps the main one, of the biochemically resistant epicuticle is probably to protect the bacteria-susceptible chitin of the procuticle from decay during life of the animal by continuing to lay down epicuticle where needed. Consistent absence of epicuticle in the pits of *H. setipunctata* may indicate an old individual no longer able to supply epicuticle requirements.

The nodosity of the epicuticle seen in *Perissocytheridea brachyforma* Swain (Pl. 1, figs. 1 b, c, f), *Cytheromorpha* aff. *C. curta* Edwards (Pl. 3, figs. 4 c, d) and minute pits in *Leptocythere* cf. *L. nikraveshae* Morales (Pl. 4, fig. 2 b) are here considered to be structures reflected from the underlying procuticle surface. More sparsely nodose epicuticle surfaces as in *Haplocytheridea* aff. *H. setipunctata* (Pl. 1, figs. 2 b, 3 b) and in *Eucythere* aff. *E. triangulata* Puri are less certainly reflected from the underlying procuticle; they may represent stockpiles of epicuticle substance that are used for repair of the epicuticle if needed.

One feature of the epicuticle not reflected from the procuticle is the close-packed hexagonal pattern seen on part of the surface of *Cytheromorpha* (arrows Pl. 3, figs. 2 b, 3 c, 4 c). This pattern having individual diameters of hexagonal structures about 0.2 microns (Text-fig. 2) is superimposed on the minutely nodose pattern of diameter about 0.1 micron (1,000° Å). The hexagons may represent either the aromatic structure of the epicuticle or microbial or mineral growths on epicuticle surface; the former explanation seems the more plausible. The epicuticle may have undergone partial condensation in those areas, thus reflecting the aromatic nature of the layer.

In *Cytherura vestibulata* Hall (Pl. 1, figs. 4b, 5b; Pl. 2, fig. 1 b), some *C.* cf. *C. corensis* Grossman (Pl. 2, fig. 3b), and *C.* cf. *C. forulata* Edwards (Pl. 2, fig. 4b) epicuticle, and perhaps the underlying procuticle also, is apparently laid down in plates the margins and intersections of which lie along the narrow ridges of the valve surface. As two kinds of normal pores occur in *C.* cf. *C. corensis* (Pl. 2, fig. 3b) it is not clear which one or both may contain setae that are involved in epicuticle formation. As discussed below, the pores that have raised rims around them may be the secretory pores.

In one specimen of *Cytherura* cf. *C. corensis* (Pl. 2, figs. 2b, c) epicuticle appears to have been smeared-on irregularly perhaps to cover filamentous bacterial growths on surface.

Epicuticle occurs in platelike fashion with marginal rims around some sieve plates in *Loxoconcha* cf. *purisubrhomboidea* Edwards (Pl. 5, figs. 5b, c). The burial of diatoms attached to the surface of *Monoceratina*? aff. *M.*? *stimulea* (Schwager, 1866) seems to be accomplished by laying down of epicuticle.

Features of the procuticle. — The outer surface of the procuticle in the specimens studied here, in many instances as seen reflected in the overlying epicuticle is variably smooth, nodose, pitted, spongy, or irregular. It is uncertain whether the surface is formed of a matrix of chitin and calcite of which both, or only the calcite, are involved in the surface textural variations. In several instances in which epicuticle remains on part of the valve surface (Pl. 1, fig. 2b; Pl. 2, fig. 7b; Pl. 4, fig. 4b; Pl. 5, fig. 5b), there seems to be primary roughness and irregularity of the outer surface of the procuticle that is not entirely reflected in the epicuticle.

Classification of the variations of procuticle surface texture of less than one micron is difficult, but the writers suggest the term labyrinthic for these non-smooth surfaces, with modifying terms of nodose (Pl. 3, figs. 4 c-e), spongy (Pl. 4, fig. 2b, 4b), heterolabyrinthic (irregularly) (Pl. 2, fig. 7b), and vermiculolabyrinthic (winding and branching furrows). The latter type was not found in the present specimens but occurs in fresh-water *Candona* and *Darwinula* and in marine *Pontocythere* (*Hulingsina*). It should be emphasized that these features are 1 to 2 orders of magnitude smaller than the surface ornamental features generally described on Ostracoda.

Features of seta pores and sieve plates. — Normal pores in which seta are associated with sieve plates in the present collection occur in *Perissocytheridea brachyforma* Swain, *Haplocytheridea* aff. *H. setipunctata* (Brady), *Cytheromorpha* aff. *C. curta* Edwards, *Cyprideis* aff. *C. locketti* (Stephenson), *Eucythere* aff. *E. triangulata* Puri, *Loxoconcha* cf. *L. purisubrhomboidea* Edwards, *Echinocythereis*? cf. *E.*? *clarkana* (Ulrich and Bassler), and perhaps in *Proteoconcha* ? *P. multipunctata parva* (Edwards). In the *Perissocytheridea* (Pl. 1, fig. 1b, f) the sieve plates lying on the ventral slope are smaller than those of the main valve surface.

The sieve-plate setae occur both centered and uncentered in the plate and in the *Cyprideis* both types occur in the same specimen. In the *Haplocytheridea* the setae seem to be mostly centered; in the *Loxoconcha* mostly uncentered, in the *Cytheromorpha* centered, in *Eucythere* aff. *E. triangulata* centered and in the *Echinocythereis* ? uncentered. No physiological significance can at present be attached to these variations, but they may be useful taxonomically as observed by others (Puri and Dickau, 1969; Sandberg and Plusquellec, 1969; Omatsola, 1970).

The setae in *Loxoconcha* cf. *L. purisubrhomboidea* and *Cytheromorpha* aff. *C. curta* (Pl. 5, fig. 5b; Pl. 3, fig. 4f) are arranged closely enough to each other to be able to cover the entire surface and presumably are secretory setae that function to produce the epicuticle. In the former species these setae rise from sieve plates while in the latter species they appear to be distinct from the larger sieve plate setae. Perhaps the sieve plate setae in *Loxoconcha* serve more than one function.

Two kinds of normal pores occur in the *Cytherura* of this collection; neither of which is associated with a sieve plate. The larger pores (Pl. 2, fig. 3b) lack crateriform rims whereas the smaller pores have calcified rims. The setae of the latter type of pore are here suggested to be secretory setae for epicuticle.

The proximally knurled setae (Pl. 1, fig. 1, d, e; Pl. 5, fig. 4c) are suggested to be of sensory function.

Although the function of the sieve plates and of the large noncratered pores in *Cytherura* remains speculative they may serve as sites of emission of attractant or repellent substances or both.

SYMBIOTIC OR PARASITIC ATTACHED ALGAE

In *Monoceratina*? aff. *M.*? *stimulea* Schwager specimens of the diatom *Cocconeis* sp. are attached to the surface (Pl. 5, figs. 7c, d, e), in varying stages of preservation. It appears that the diatoms were in the process of being covered by epicuticle secretions when the specimens were collected. The diatoms in this case contribute to the ornamental pattern of the ostracode as node-formers.

Other instances of diatoms attached to ostracode valves were noted (Pl. 4, fig. 7b), but burying of these was not observed to take place except in *Monoceratina*? Several examples of filamentous algae? on fresh-water ostracodes and a few marine ostracodes studies by the writers have been seen but in the present collection attached algae other than diatoms are relatively rare. In *Cytherura* cf. *C. corensis* Grossman (Pl. 2, figs. 2b, c) there are filamentous structures on the valve surface that may be algal. In the illustrations it appears that the filamentous structures were rather hurriedly covered by an irregular coating of epicuticle.

CONCLUSIONS

The Ostracoda discussed herein are typical of oligohaline tidal bays having pH values that fall in the general 7-8 range and negative Eh values, the latter indicating reducing conditions. The assemblage as a whole is dominated by *Leptocythere* spp. and *Cytherura* spp. Tentatively, four biofacies are recognized: (1) silty clay bay biofacies with species of *Leptocythere, Cytherura* and others, the principal biofacies of the area; (2) silty organic clay tidal river biofacies with a species of *Cyprideis* and of *Perissocytheridea;* (3) a tidal bay sand biofacies with species of *Eucythere* and of *Paradoxostoma* and *Haplocytheridea;* and (4) tidal marsh mud biofacies with a species of *Cytherura.*

Epicuticle is well developed in most of the specimens and calcification is rather poorly developed as a reflection of the lime-poor environment. Incomplete epicuticle in definite shell areas such as in pits of *Haplocytheridea* cf. *H. setipunctata* may be characteristic of old individuals in which secretory setae are not able to supply needs for new epicuticle.

Assuming that epicuticle serves to protect procuticle and that secretory setae can replenish damaged epicuticle, small mounds of epicuticle in *Haplocytheridea* and *Eucythere* and craterlike only partly calcified deposits around normal pores in some species studied here are suggested as stockpiles for repair purposes. Very small close-packed hexagonal structures about 0.2 microns in diameter occur either as part of, or on, the surface of the epicuticle, the origin of this structure is uncertain but it may be the crystal structure of the epicuticle that has undergone partial condensation.

In some *Cytherura* and covering the sieve plates in *Loxoconcha,* epicuticle, and perhaps underlying procuticle, seem to have been formed in plates with distinct boundaries.

The procuticle surface, presumably the calcified portion, essentially, is irregular in some ostracodes. The irregularities result in a labyrinthic pattern of the exposed procuticle after weathering of the epicuticle. The patterns exhibited by the surface are variously characterized here as: punctate, or spongy, nodose, heterolabyrinthic, or vermiculolabyrinthic. The labyrinthic surface seems to be more typical of non-marine and brackish-water ostracodes than of marine forms.

Setae, suggested to be secretory for the epicuticle, occur closely spaced in *Cytheromorpha* aff. *C. curta* Edwards, and *Loxoconcha* cf. *purisubrhomboidea* Edwards. In the former species the setae are not associated with sieve plates and do not have knurled sensory bases and perhaps are unifunctional, in the latter species the sieve plate setae may be polyfunctional. In *Cytherura* both large, unrimmed, and smaller, rimmed, normal pores bear setae. The smaller-pore setae are suggested to be rimmed with epicuticle material and calcite and to be the secretory setae.

Diatoms in progressive stages of being covered over by epicuticle were noted in a species of *Monoceratina*? These are in part regularly spaced, as if by design, on the valve surface. Other possible algal filaments covered by epicuticle were noted on a *Cytherura* sp.

REFERENCES

Bate, R. H., and East, B. A.
1972. *The structure of the ostracod carapace.* Lethaia, vol. 5, pp. 174-194.

Omatsola, M. E.
1970. *Podocopid Ostracoda of the Lagos Lagoon, Nigeria.* Micropaleontology, vol. 16, pp. 407-445, pls. 1-13.
1971. *Campylocythereis, a new genus of the Campylocytherinae (Ostr., Crust.) and its muscle scar variation.* In Colloquium on the Paleocology of Ostracodes. Oertli, H. J. (ed.), Bull. Cent. Rech. Pau-SNPA, vol. 5, suppl. pp. 101-123, 4 pls.

Puri, H. S., and Dickau, B. E.
1969. *Use of normal pores in taxonomy of Ostracoda.* Gulf Coast Assoc. Geol. Soc. Trans., vol. 19, pp. 353-367, pls. 1-6.

Richards, A. G.
1951. *The integument of arthropods. Minneapolis,* Univ. of Minn. Press, 411 pp.

Sandberg, P. A., and Plusquellec, P. L.
1969. *Structure and polymorphism of normal pores in cytheracean Ostracoda (Crustacea).* Jour. Paleont., vol. 43, pp. 514-521.

Frederick M. Swain,
Department of Geology,
University of Delaware,
Newark,
Delaware 19711, and
Department of Geology and Geophysics
University of Minnesota,
Minneapolis 55455

John C. Kraft
Department of Geology
University of Delaware
Newark, Delaware 19711

DISCUSSION

Dr. L. S. Kornicker: Were the specimens you dealt with living when collected? Is the decalcification caused by their residing in a reducing mud after their death, or did the living animals have little calcification? If the former, one might ask whether the ostracodes from sediments with positive Eh were as decalcified as those in sediments having negative Eh. Were the illustrated specimens living or empty when collected?

Dr. Swain: Nearly all the specimens discussed and illustrated contained soft parts or remnants of the soft parts when collected. The poor calcification we believe is a primary feature and not due to decalcification after death. The point you raise as to the possible effect of Eh on the shells after burial is an interesting one, which we are not able to answer at the present time. In general, however, negative Eh conditions in accumulating sediments seem to favor preservation rather than destruction of calcareous shells.

Explanation of Plate 1

Figure

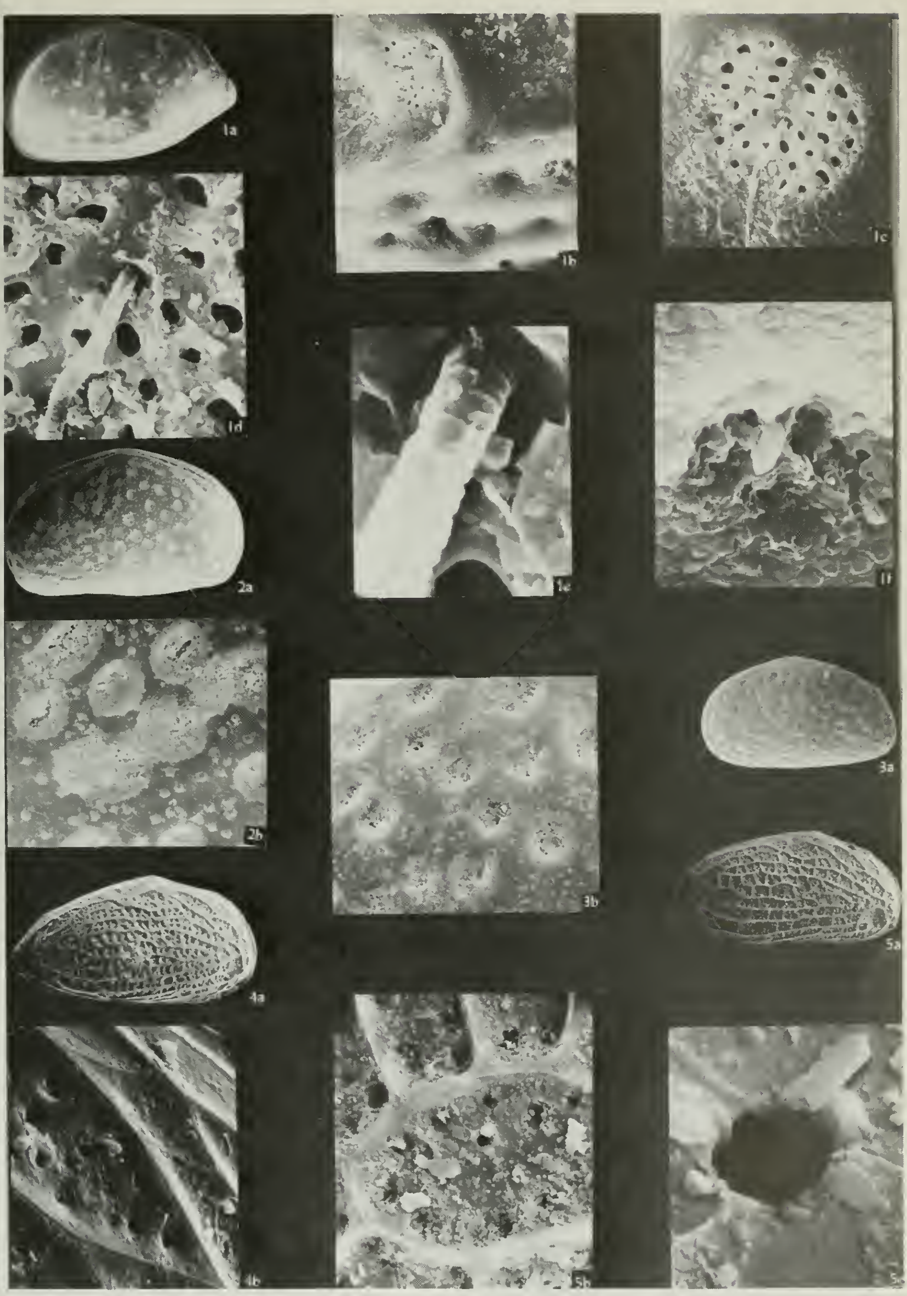
1a-f. **Perissocytheridea brachyforma** Swain.
a. Left side of shell; × 56. b. Enlargement of midventral surface showing a sieve plate, sensory seta, and studded or finely nodose labyrinthic surface due to projection of portions of calcified procuticle into epicuticle; × 568. c. Enlargement of sieve plate with a median septum at base of which lies the sensory knurled seta; × 1,118. d, e. Enlargements of knurled seta; × 2,795 and × 11,180 respectively. f. Enlargement of a ventrally located sieve plate of smaller size than preceding; × 2,795. Locality 197, Pepper Creek, Delaware.

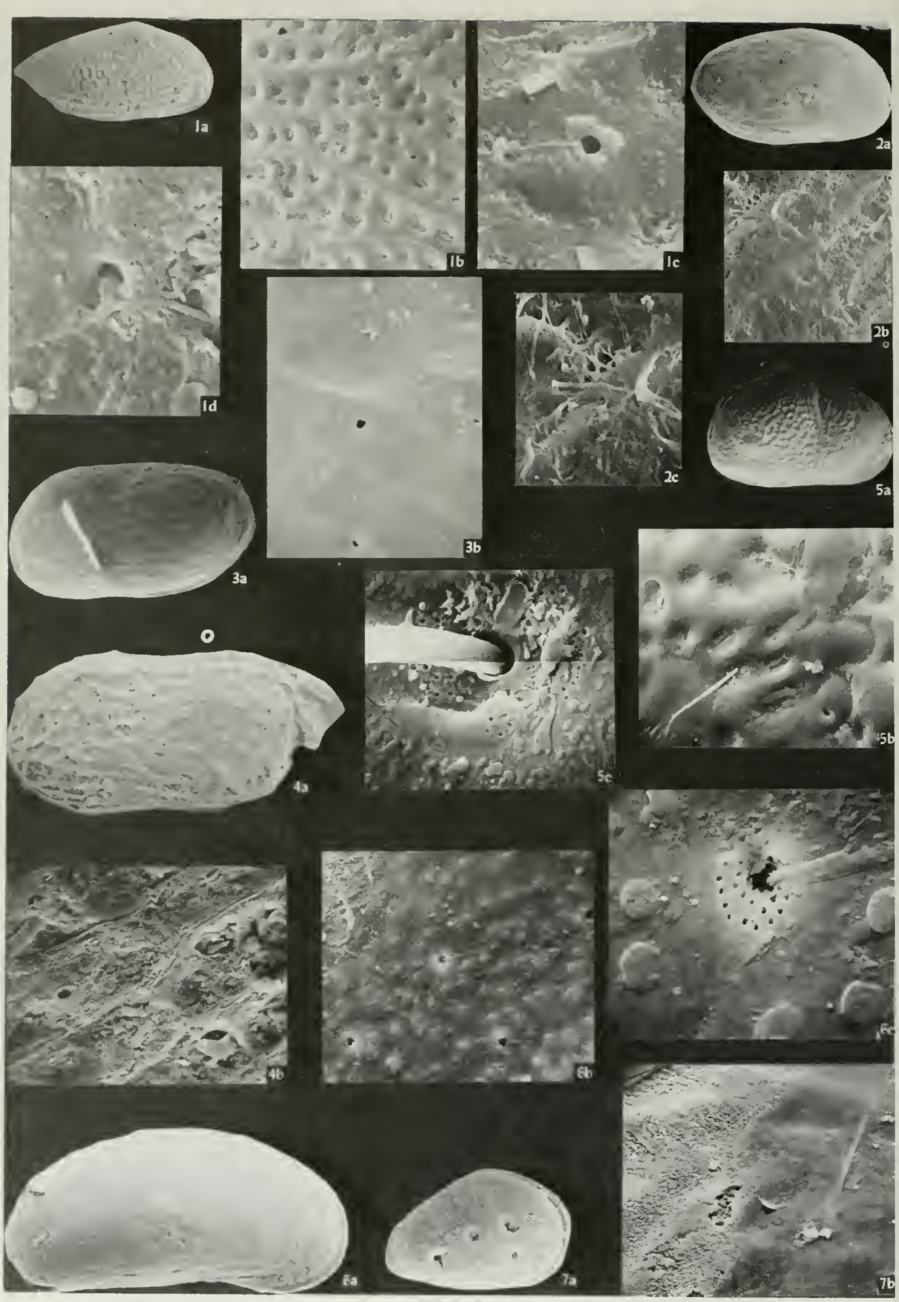
2a, b. **Haplocytheridea** aff. **H. setipunctata** (Brady).
a. Right side of shell; × 47. b. Enlargement of surface showing crowded pit areas that in part contain setae and poorly preserved sieve plates and sparsely nodose interpit areas that represent projections of procuticle into epicuticle; around and in pits epicuticle absent and surface of procuticle is exposed; × 227. Locality 273, Rehoboth Bay, Delaware.

3a, b. **Haplocytheridea** aff. **H. setipunctata** (Brady).
a. Left side of shell; × 47. b. Enlargement of surface of shell; × 227, showing depressions that in part contain poorly preserved sieve plates, and sparsely nodose interspaces; epicuticle interpreted as forming surface of interspaces; underlying procuticle exposed in pits. Locality 273, Rehoboth Bay, Delaware.

4a, b. **Cytherura vestibulata** Hall.
a. Right side of male shell; × 103. b. Enlargement of part of anterodorsal surface showing normal pores and lines of intersection of plates of epicuticle and perhaps of the underlying procuticle in narrow surface ridges; × 1,030. Locality 245, Indian River Bay, Delaware.

5a-c. **Cytherura vestibulata** Hall.
a. Right side of female shell; × 86. b. Enlargement of median surface; × 860, showing normal pores and intersection of plates of epicuticle and perhaps of the underlying procuticle in narrow surface ridges; surface covered with epicuticle; × 4,300. Locality 264, Indian River Bay, Delaware.


1a
1b
1c
1d
1e
1f
2a
2b
3a
3b
4a
4b
5a
5b
5c


1a
1b
1c
2a
1d
2b
2c
5a
3b
3a
4a
5c
5b
4b
6b
6c
6a
7a
7b

EXPLANATION OF PLATE 2

Figure

1a-d. **Cytherura vestibulata** Hall.
a. Exterior of right male valve; × 81. b. Enlargement of part of median surface showing intersections of plates of epicuticle and underlying procuticle along narrow ridges and some normal canals; × 473. c. A normal pore and seta with a thickened rim; × 2,236. Locality 247, Indian River Bay, Delaware.

2a-c. **Cytherura** cf. **C. corensis** Grossman.
a. Right side of shell; × 97. b. Enlargement of part of median surface; × 559, showing epicuticle, with fibrous chitin of outer part of procuticle reflected beneath it. c. Further enlargement of part of same surface; × 989. Locality 270, Rehoboth Bay, Delaware.

3a, b. **Cytherura** cf. **corensis** Grossman.
a. Left side of shell; × 97. b. Enlargement of part of surface showing junction of plates of epicuticle and underlying procuticle along narrow surface ridges, and normal pores of two types: (1) large with little or no development of raised rims and (2) small with raised crateriform rims; × 473. Locality 270, Rehoboth Bay, Delaware.

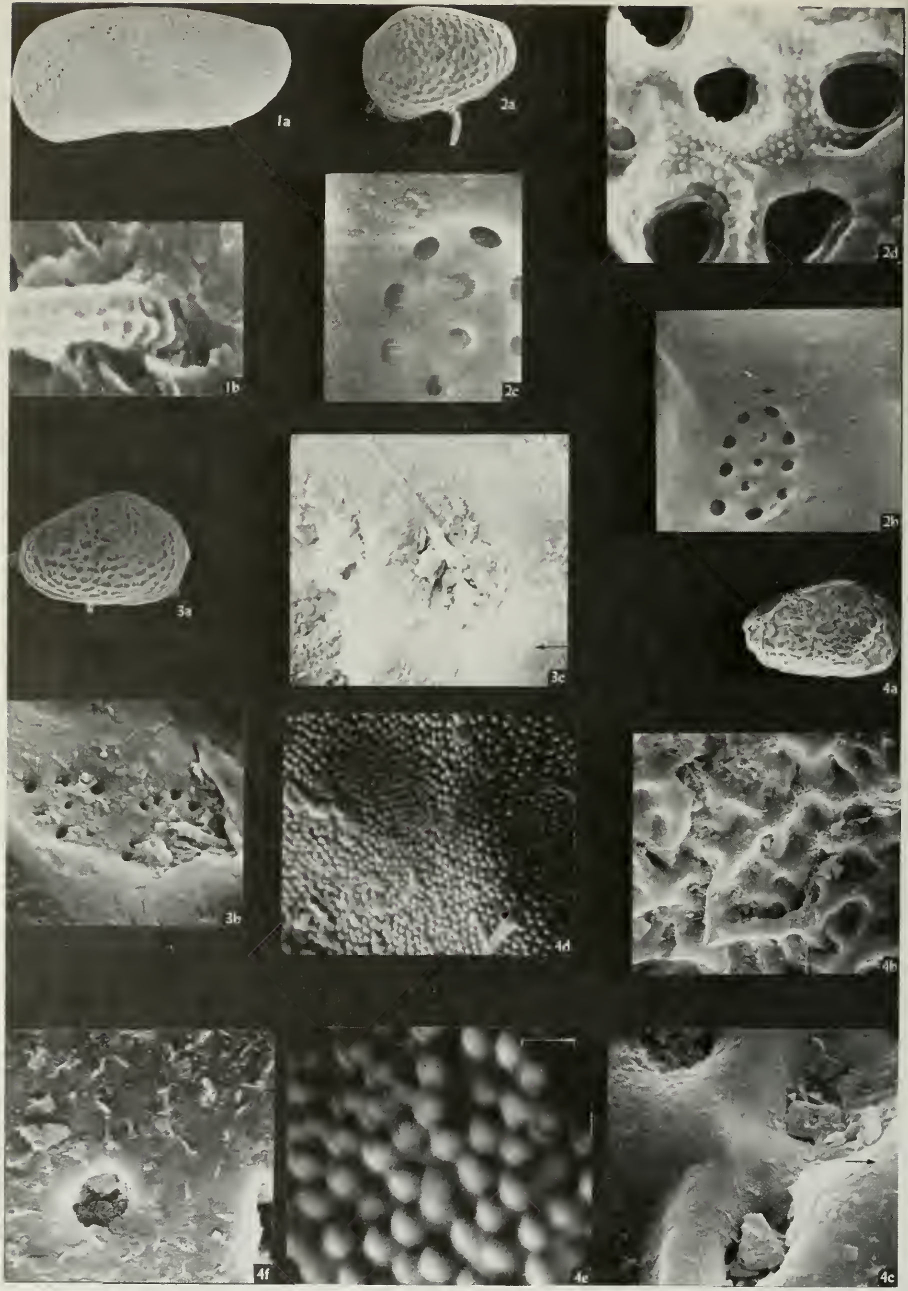
4a, b. **Cytherura** cf. **C. forulata** Edwards.
a. Left side of an imperfect shell; × 99. b. Enlargement of part of surface showing normal canals and junction of plates of epicuticle and underlying procuticle along crests of narrow surface ridges; × 507. Locality 212, Indian River Bay, Delaware.

5a-c. **Cyprideis** aff. **C. locketti** (Stephenson).
a. Right side of shell; × 25. b. Enlargement of part of surface showing sieve plate areas and normal pore seta of simple and branched type; × 249. c. Enlargement of a sieve plate area, normal pore and seta; surface covered with epicuticle; × 2,494. Locality 228, Indian River, Delaware.

6a-c. **Eucythere** aff. **E. triangulata** Puri.
a. Exterior of right valve; × 99. b. Enlargement of part of surface showing sieve plates, normal pores, and setae; × 507. c. Enlargement of a sieve plate area; surface covered here by epicuticle; × 2,494. Locality 223, Indian River Bay, Delaware.

7a, b. **Eucythere** sp.
a. Right side of probably immature setose shell; × 99. b. Enlargement of surface showing epicuticle, the underlying exocuticle, and possibly a small portion of endocuticle near center of picture; × 512. Locality 208, Indian River Bay, Delaware, near mouth of Indian River.

Plate 3



EXPLANATION OF PLATE 3

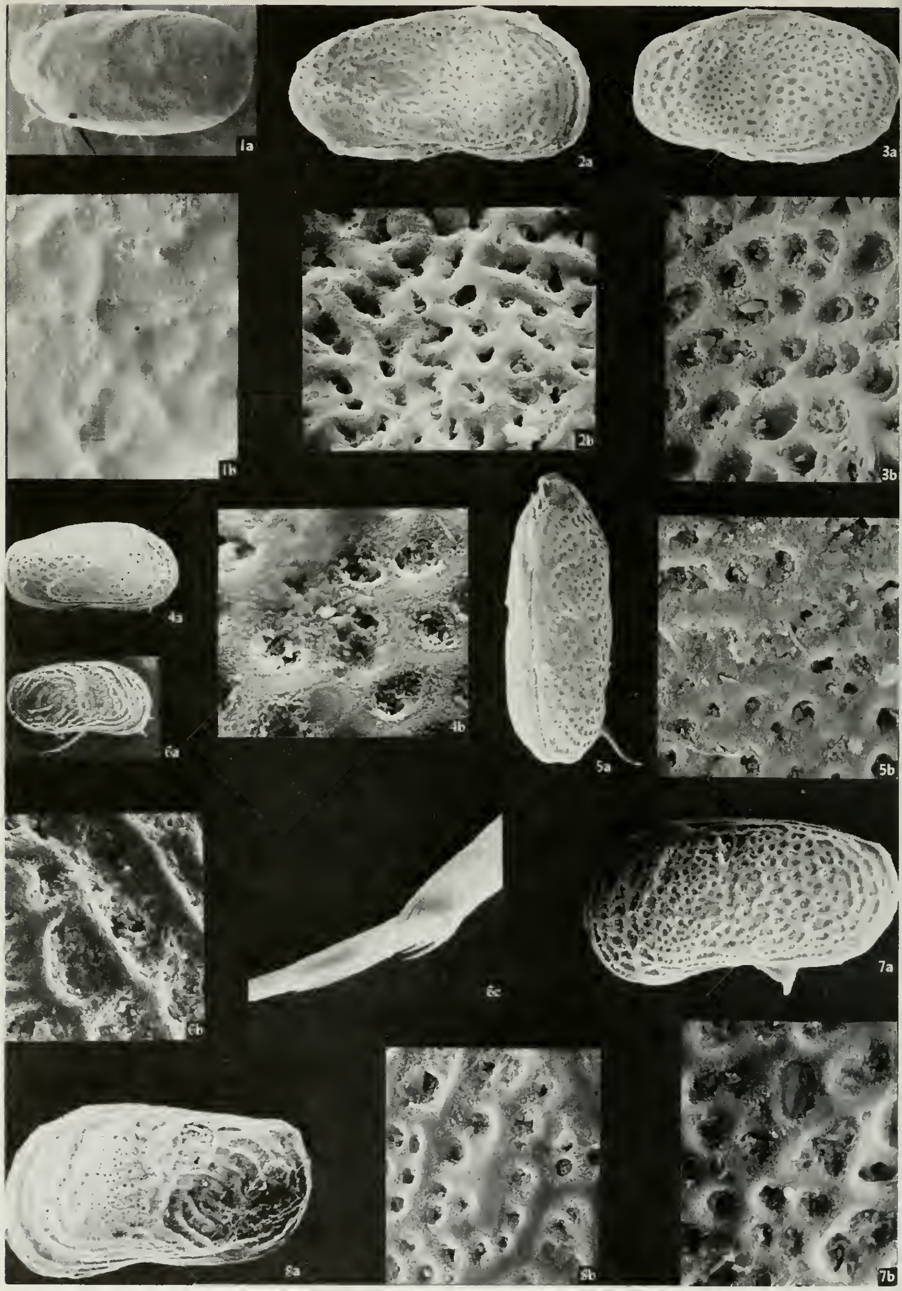
Figure

1a, b. **Leptocythere** aff. **L. pellucida** (Baird).
a. Left side of shell; × 85. b. Enlargement of seta, knurled proximally; × 8,084. Differs from *L. pellucida* in having sinuous longitudinal ridge. Specimen appears to have a heavily developed epicuticle. Locality 209, Indian River Bay, Delaware.

2a-d. **Cytheromorpha** aff. **C. curta** Edwards.
a. Left side of shell; × 86. b. Enlargement of part of surface showing a sieve plate area, scattered secretory setae, and the close-packed polygonal structure of the cuticle surface around the sieve plate; × 2,150. c. Further enlargement of sieve plate, × 4,300 showing minute nodose cuticular structure of sieve plate surface and a few secretory setae. d. Further enlargement of a different sieve plate showing details of nodosity of cuticle surface; × 9,890. It appears that the nodose structures are reflected in epicuticle from underlying procuticle. Locality 284, Little Assawoman Bay, Delaware.

3a-c. **Cytheromorpha** aff. **C. curta** Edwards.
a. Right side of shell; × 100. b. Enlargement of a sieve plate area; × 2,408, showing part of a seta on right side of sieve plate and minute nodose structure reflected in epicuticle from underlying procuticle. c. Part of surface around a normal pore and seta (knurled proximally), and both nodose and polygonal structure of cuticle; × 2,408. Polygonal structures interpreted as being structure of epicuticle. Locality 228, Indian River, Delaware.

4a-f. **Cytheromorpha** aff. **C. curta** Edwards.
a. Right side of weakly calcified somewhat shrunken shell; × 99. b. Enlargement of part of surface; × 512. c. Enlargement of part of area of preceding showing minute polygonal structure of epicuticle, minute nodose structure of procuticle and secretory setae; × 2,537. d. Enlargement of nodose and polygonal structures and setae; × 10,320. e. Enlargement of nodes showing small ridges on some of them; × 51,170. f. Part of surface in a different area showing a normal pore and numerous secretory setae; × 512. Locality 208, Indian River, Delaware.


1a
2a
3a
1b
2b
3b
4a
4b
5a
5b
6a
6b
6c
7a
8a
8b
7b

EXPLANATION OF PLATE 4

Figure

1a, b. **Cylindroleberis psitticina** Darby.
a. Left side of shell; × 47. b. Enlargement of part of surface; × 882, showing surface epicuticle. Locality 282, Little Assawoman Bay, Delaware.

2a, b. **Leptocythere** cf. **L. nikraveshae** Morales.
a. Right side of a collapsed shell; × 112. b. Enlargement of part of surface; × 538, showing areas of smooth epicuticle underlain by spongy-textured procuticle. Locality 181, Indian River Bay, Delaware.

3a, b. **Leptocythere** cf. **L. nikraveshae** Morales.
a. Left side of a partly collapsed shell; × 99. b. Enlargement of part of surface of shell showing spongy surface of procuticle and intervening pits lined with smooth epicuticle?; secretory setae occur in several places; × 516. Locality 227, Indian River Bay.

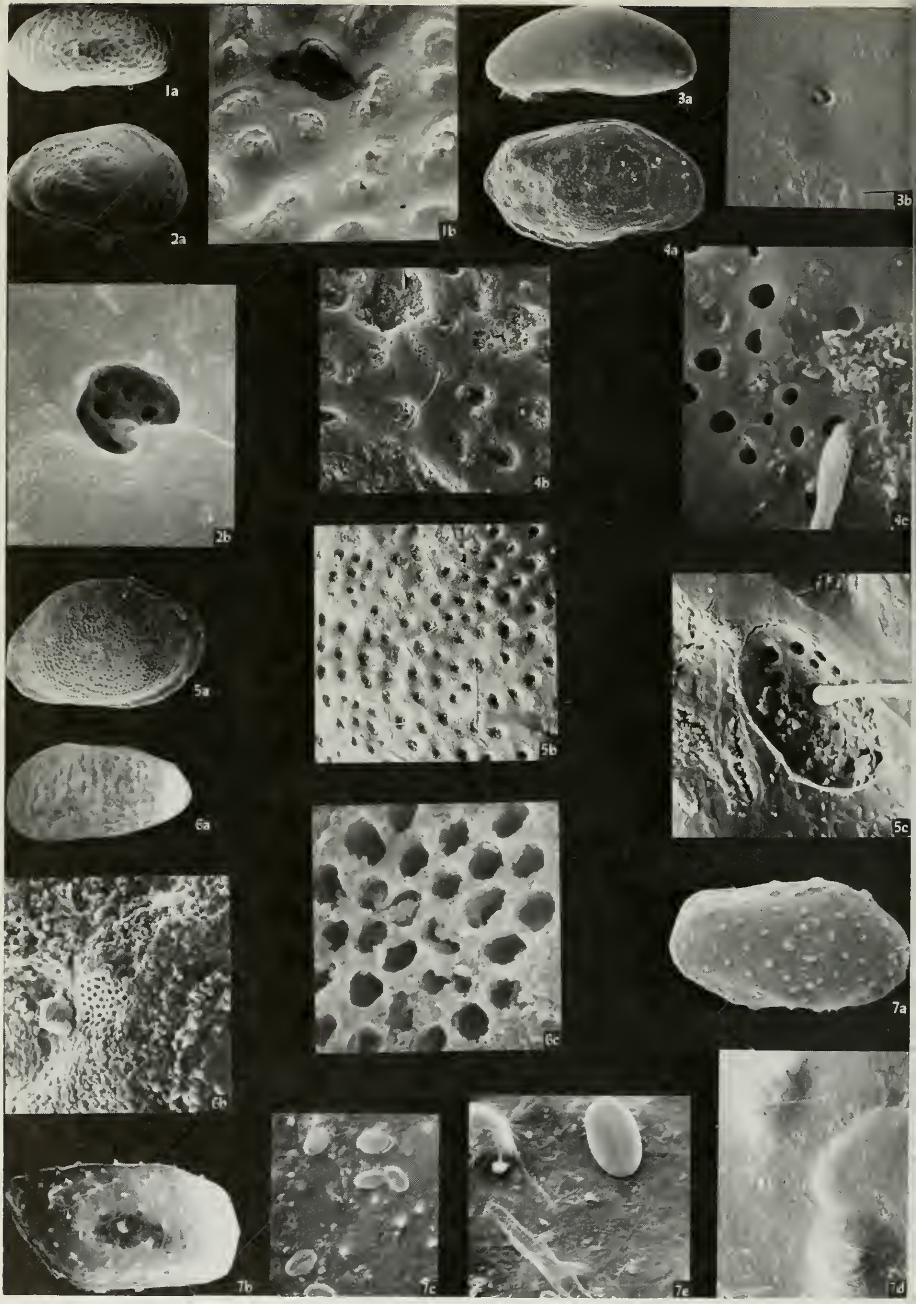
4a, b. **Leptocythere** cf. **L. nikraveshae** Morales.
a. Right side of shell; × 56. b. Enlargement of part of surface; × 560, showing areas of epicuticle, procuticle and secretory setae. Locality 178, Indian River Bay, Delaware.

5a, b. **Leptocythere** aff. **L. angusta** Blake.
a. Dorsal view of shell; × 99. b. Enlargement of part of surface; × 516, showing roughened surface of procuticle and secretory setae. Locality 227, Indian River Bay, Delaware.

6a-c. **Leptocythere** aff. **L. crispata** (Brady).
a. Right side of shell; × 43. b. Enlargement of part of surface of shell; × 434, showing areas of epicuticle on ridges and underlying procuticle. c. Part of first thoracic leg; × 869, showing setose fringe on outside lateral margin. Locality 264, Indian River Bay, Delaware.

7a, b. **Leptocythere** aff. **L. castanea** Sars.
a. Left side of shell; × 108. b. Enlargement of part of surface showing irregular outer surface of procuticle; × 538. Locality 177, Indian River Bay, Delaware.

8a, b. **Leptocythere** aff. **L. crispata** (Brady).
a. Left side of shell; × 97. b. Enlargement of part of surface showing epicuticle to be smooth on ridge crests, wrinkled on slopes of depressions and terminating around normal pores; × 473. Locality 268, Indian River Bay, Delaware.


1a
1b
2a
2b
3a
3b
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
7e
7d

EXPLANATION OF PLATE 5

Figure

1a, b. **Leptocythere** cf. **L. castanea** Sars.
a. Left valve exterior; × 56. b. Enlargement of part of surface, showing smooth areas of epicuticle, as well as roughened areas that reflect structure of underlying procuticle; × 560. Locality 181, Indian River Bay, Delaware.

2a, b. **Echinocythereis**? aff. **E.** ? **clarkana** (Ulrich and Bassler).
Immature shell. a. Right side of shell; × 110. b. Enlargement of normal pore, sieve plate and part of proximally knurled seta; × 5,160, also showing minutely nodose epicuticle. Locality 177, Indian River Bay, Delaware.

3a, b. **Paradoxostoma** aff. **P. hodgei** Brady.
a. Left side of shell; × 99. b. Enlargement of surface showing epicuticle, normal pore with narrow rim, and seta; × 2,365. Locality 223, Indian River Bay, Delaware.

4a-c. **Loxoconcha** cf. **L. purisubrhomboidea** Edwards.
a. Right side of male shell; × 45. b. Enlargement of part of surface; × 450, showing elongate sieve plate, normal pore and distal part of proximally knurled seta; × 4,515; epicuticle surface is shown. Locality 264, Indian River Bay, Delaware.

5a-c. **Loxoconcha** cf. **L. purisubrhomboidea** Edwards.
a. Left side of female shell; × 50. b. Enlargement of part of surface showing smooth but incomplete epicuticle, underlying granular procuticle, pits, sieve plates, normal pores and setae; × 247. c. Detail of a sieve plate, normal pore and seta, and rimlike margin of epicuticle around sieve plate; a few chitin fibers in procuticle appear in lower part of photograph; × 2,473. Locality 228, Indian River, Delaware.

6a-c. **Proteoconcha** ? **P. multipunctata parva** (Edwards).
a. Left side of shell; × 45. b. Enlargement of part of surface, showing roughened surface of calcified procuticle, and a sieve plate; × 989. c. Detail of sieve plate; × 4,515. Locality 184, Indian River Bay, Delaware.

7a-e. **Monoceratina** ? aff. **M.**? **stimulea** (Schwager).
a. Right side of male ? shell; × 56. b. Right side of female ? shell; × 56. c. Enlargement of part of surface of 7a, showing surface of epicuticle and adhering specimens of *Cocconeis* in several stages of covering by epicuticle and of dissolution; × 516. d. Enlargement of part of surface of another specimen; × 559, showing patterned nature of epicuticle that may have been caused in part by previous attachment of diatoms and two *Cocconeis* in different stages of entombment and dissolution. e. Enlargement of part of surface of 7b showing unburied (upper right) and buried (upper left) *Cocconeis;* × 593. Locality 182, Indian River Bay, Delaware.

AN INTRODUCTION TO THE NUMERICAL PHYLOGENY AND CLASSIFICATION OF PARADOXOSTOMATID OSTRACODA, INCLUDING A REDESCRIPTION OF *MACHAERINA TENUISSIMA* (NORMAN, 1869)

Kenneth G. McKenzie
Riverina College N.S.W., Australia
and
Roger L. Kaesler
University of Kansas

ABSTRACT

Using 30 characters from 23 genera of paradoxostomatid Ostracoda, a phenetic study was conducted as a prelude to a proposed numerical cladistic study. The method to be used in the numerical study is discussed, and *Machaerina tenuissima* (Norman) is redescribed.

UNE AVANT-PROPOS A LA PHYLOGÉNIE NUMÉRIQUE ET LA CLASSIFICATION DE PARADOXOSTOMATID OSTRACODA, Y COMPRIS UNE REDESCRIPTION DE *MACHAERINA TENUISSIMA* (NORMAN), 1869

RÉSUMÉ

En employant trente caractères de vingt-trois genres de paradoxostomatid Ostracoda, on a procédé à une étude phenetique comme un prélude à l'étude proposée numérique cladistique. On discute la méthode à employer dans l'étude numérique et on décrit encore une fois le *Machaerina tenuissima* (Norman).

INTRODUCTION

Undeniably, fossils are not "sports of the devil" as they were labelled in Renaissance times (Adams, 1938) but are the actual remains of once-living organisms. They have been preserved in a sequence that can often be determined by careful study, and in many instances they have living descendants that evolved from them. The evolutionary history of organisms is their phylogeny, an understanding of which is dependent on knowledge of cladistics, the branching sequences in evolution; phenetics, the overall similarity of organisms irrespective of their taxonomic affinities; and chronistics, the sequence of events in the evolution of the taxon (Sokal and Camin, 1965). Thus, considering phenetics, one would not ordinarily regard two taxa as closely related phylogenetically if they are highly dissimilar. Moreover, considering chronistics, one would not regard a Jurassic species as the ancestor of a Triassic one.

The most difficult aspect of phylogeny to determine is the branching sequence, the cladistics. One obtains phenetic information directly from the study of organisms, living or fossil, and chronistic information from the study of the fossil record and the biostratigraphic framework of the enclosing rocks. But cladistic information is not preserved, and parent-daughter relationships must be inferred, usually from phenetic information and chronistic relationships.

Much of numerical taxonomy has been directed toward the study of phenetic similarity, and some biologists have been led to discount the significance of the fossil record in determining phylogenetic relationships. One of them has even referred in general to phylogenies that are based on the available fossil record as a "phylogenetic fallacy" (Colless, 1967). Now it is true that one does not find cladistic information preserved in the fossil record, but the availability of chronistic information from the fossil record greatly improves the likelihood of reconstructing a phylogeny that is a close approximation to the parametric one. Naturally, paleontologists maintain that cladograms (family tree diagrams, often expressing the results of numerical analysis of branching sequences) should be reconstructed if necessary until they are consistent with evidence from the fossil record (Rowell, 1970).

For Ostracoda, this fossil record is exceptionally long-ranging and diverse. The group, which ranges from Cambrian to Recent and from marine to freshwater environments, comprises about 35,000 known species (H. V. Howe, personal communication) with many more new fossil than living forms being described each year (Table 1). For this group, therefore, and for other groups with good fossil records, *e.g.,* mollusks, bryozoans, pollen, Foraminifera, brachiopods, and trilobites, it is clear that fallacious evolutionary relationships are more likely to be established if the fossils are neglected than when they are incorporated into the study.

THE PROBLEM

Paradoxostomatid ostracodes range from Mesozoic to Recent. More than 20 genera containing some hundreds of species have been associated with the group. Their group systematic relationships have already been proposed (Orlov, 1960; Moore, 1961), and a suggested phylogeny of the genera has also been published (Text-figure 1, from McKenzie, 1969).

It is McKenzie's proposed phylogenetic tree that we shall test by the methods of numerical cladistics, modifying the result to be consistent with chronistic information. Few models such as McKenzie's exist in the ostracode literature, and the use of the numerical test also breaks relatively new ground in ostracode research. In addition to testing the proposed phylogeny, we shall also make a phenetic study of the genera and compare it both with McKenzie's proposed phylogeny and with the results of the numerical cladistic study.

This paper includes a brief discussion of the methods of numerical cladistics, the data matrix of characters from the paradoxostomatid genera, the results of the phenetic study, and a redescription of *Machaerina tenuissima* (Norman) (Norman, 1869). A complete presentation of the results of the numerical cladistic study and integration of the results with the phenetic and chronistic information will be presented in a later paper.

METHODS

Cladistic Methods

The various numerical methods for deriving phylogenies have been reviewed by Sneath and Sokal (1973). These methods yield either nondirected, nonrooted shortest connection networks or rooted, directed shortest connection

Table 1. Numbers of new species of Ostracoda described (to the nearest 25), subspecies and *nomina nova* not included. Data from the *Zoological Record,* 1958-1968.

	Approximate Numbers New Species Described	
Year	Fossil	Living
1958	450	50
1959	300	125
1960	450	50
1961	150	50
1962	900	75
1963	400	125
1964	1000	150
1965	625	100
1966	475	175
1967	400	100
1968	650	25

networks, called Wagner trees. When deriving the former, it is usual to use only the known OTU's, but in the Wagner method hypothetical intermediate taxonomic units (HTU's) may be determined by the computer and interpolated into the resultant cladogram.

An assumption that is common to all techniques is that of minimal evolution, *i.e.,* the familiar principal of parsimony. Since the minimum number of evolutionary steps required to achieve a particular character synthesis is assumed to be closest to reality, these networks are strictly maximum flow networks. The idea that evolution is parsimonious has been the subject of considerable discussion and some criticism, particularly by those who prefer to think of evolution as opportunistic. The two ideas are not incompatible, however. Although a particular evolutionary pathway may not have been parsimonious, nevertheless the only suitable *a priori* assumption *for the sake of modeling* is that a minimum number of evolutionary steps was involved in the real phylogeny. This is consistent with our general abhorrence of reversals of evolution, and hopefully any apparent reversals would be detected in time to allow for their coding as derived states.

Other assumptions regarding the data matrices used in such methods include the following: 1) the characters used can be expressed in discrete states which differ among the OTU's being studied; and 2) with most methods, the character states can be arranged in evolutionary order from primitive to derived before the cladogram is reconstructed. Further assumptions differ in the different methods. Thus, the Camin and Sokal (1965) method assumes that evolution is irreversible, but this assumption is not used in the Wagner method (*e.g.,* Kesling and Sigler, 1969).

In any variation of a Wagner method the choice of an ancestor is an important first step, and equally important is the coding of ancestral character states. Here the different methods can vary. For instance, Kluge and Farris (1969) coded all the ancestral character states as 0, whereas Kesling and Sigler (1969) coded both ancestral and descendant character states in accordance with criteria of primitiveness. It is essential to realize that for any well-defined group the ancestor may be a meld of specialized as well as of primitive characters. Therefore, the Kesling and Sigler rationale appears preferable.

In this study the following considerations served to establish an evolutionary order when coding the character states:

1. It was assumed that ancestral taxa had more segments in their several limbs than do their descendant taxa, *i.e.,* that evolution had proceeded by a reduction in the number of segments.
2. It was assumed that absences of entire limbs, organs, or setal groups represent adaptations rather than the primitive condition. In these cases the "normal" organization of the characters in question was considered to be primitive (coding 0).
3. Some character states were evidently special modifications to fit the habitat. For these characters the unmodified state was coded 0.
4. For some characters, their state in the genus belonging to the geologically oldest group was assumed to be primitive (the chorologic principle).
5. For some characters their state earlier in ontogeny was assumed to be primitive (the ontogenetic principle).

Phenetic Methods

The phenetic methods of cluster analysis and ordination have been discussed repeatedly in previous literature, and we will not cover that well-worn ground again here. The reader is referred to the textbook by Sokal and Sneath (1963), the pages of *Systematic Zoology* since about 1960, and articles by Kaesler (1967, 1969, 1970) and Rowell (1967, 1969, 1970).

Data Matrix

For the analyses of paradoxostomatid phylogeny, a relatively small data matrix was compiled, at first for 23 genera and 30 characters. The characters were expressed in either two or three states. Characters from the carapace as well as appendage characters were employed, but no measurements were used. When this matrix was completed, it was apparent that the characters chosen did not allow the genera *Luvula* and *Macrocytherina* to be satisfactorily differentiated either from each other or from the genus *Javanella*. As we were unable to study the types of the first two of these genera in the time available, they were omitted from the analysis. Thus, the final matrix consisted of 21 genera (OTU's) by 30 characters or 630 bits of information. For 53 bits we had no information, which represents about 8.4 percent of the matrix.

The character and their states, coded according to the criteria established earlier, are entered below. Primary data on the genera used are given in Table 2.

1. Strength of Carapace	0 = strong; 1 = moderately strong; 2 = fragile.
2. Anterior shape	0 = rounded; 1 = rounded in some species; subacuminate in others; 2 = subacuminate.
3. Surface ornament	0 = surface smooth; 1 = weak ornamentation such as striations, punctae; 2 = strong ornamentation such as reticulations, pits, costae.
4. Sulcus	0 = without a sulcus; 2 = with a sulcus.
5. Caudal process	0 = no cauda; 1 = cauda present in some species, absent in others; 2 = cauda in all species.

6. Inner lamella	0 = regular inner margin; 1 = some species with an irregular margin; 2 = irregular margin in most species.
7. Vestibules	0 = vestibulum continuous; 1 = broad anterior and elongate posterior vestibules; 2 = broad anterior and posterior vestibules.
8. Radial pore canals—type	0 = simple, grouped; 1 = simple, spaced; 2 = branched, especially anteriorly.
9. Radial pore canals—length	0 = short anteriorly; 2 = relatively long anteriorly.
10. Hingement	0 = adont; 1 = modified adont or lophodont; 2 = with terminal teeth, sometimes also with a crenulate median element.
11. Frontal muscle scar	0 = absent or weak; 2 = distinct.
12. Adductors	0 = five; 1 = four in some species, apparently five in others; 2 = four.
13. Antennule—segments	0 = seven; 1 = six; 2 = five.
14. Antennule—natatory setae	0 = present; 2 = absent.
15. Antennule—terminal sensory bristle	0 = normal; 2 = distinctly club-shaped.
16. Antenna—segments	0 = five; 2 = four.
17. Antenna—terminal claws	0 = three; 1 = two; 2 = one, usually with an accompanying bristle.
18. Mandible—coxale	0 = coxale with several powerful teeth; 1 = coxale with indistinct teeth or finely serrated cutting edge; 2 = coxale styliform.
19. Mandible—palp	0 = three or four segments; 1 = two segments; 2 = non-segmented.
20. Maxilla	0 = normal (palp and three lobes); 1 = palp and one or two lobes; 2 = palp absent.
21. Maxilla—epipod	0 = two or three downward — pointing Strahlen; 1 = one downward — pointing Strahlen; 2 = no downward — pointing Strahlen.
22. Fifth limb—protopod	0 = two dorsodistal bristles; 1 = one dorsodistal bristle; 2 = one coarse dorsodistal claw.
23. Fifth limb—protopod	0 = three proximoventral bristles; 1 = one proximoventral bristle; 2 = no proximoventral bristles.
24. Eye	0 = with eyes; 2 = blind.
25. Genital Hocker	0 = without Hocker; 2 = with Hocker.
26. Mouth parts	0 = without modification; 1 = modified (by lower lip serration, attenuation, terminal jaws) but not suctorially; 2 = with suctorial modification.
27. Color	0 = without specific color patterns; 1 = with uniform color; 2 = often with highly specific color banding (in black, green, red, brown, purple).
28. P III (seventh limb)	0 = without coarsely serrated distal spine on 2nd segment; 2 = with such a spine.
29. Normal pore canals	0 = simple; 2 = sieve-type.
30. P III (seventh limb)	0 = present; 2 = absent.

Table 2. Genera studied and character states for each character. Characters numbered as in text.

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Megacythere	0	0	2	0	0	0	1	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
Boldella	0	0	1	0	2	0	1	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
Paracytheroma	0	0	0	0	0	0	1	2	2	2	2	2	1	2	2	2	1	0	0	0	1	0	1	0	2	0	0	0	0	0
Pontocytheroma	1	2	0	0	0	0	1	1	0	1	2	2	1	2	2	2	1	0	0	0	1	0	1	0	0	0	0	0	0	0
Cytheroma	1	0	0	0	0	0	2	1	0	1	2	2	1	2	2	2	1	0	0	0	1	0	1	0	2	0	0	0	0	0
Microcythere	0	2	0	2	0	2	2	1	0	2	2	1	1	2	0	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0
Cobanocythere	0	2	0	0	0	0	1	1	0	2	2	2	1	2	0	2	2	0	0	0	2	0	1	0	0	0	0	0	0	0
Luvula	1	0	0	0	2	0	1	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
Macrocytherina	1	0	0	0	2	0	1	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
Javanella	1	0	0	0	2	0	1	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—
Pellucistoma	0	1	0	0	2	0	1	2	2	2	2	2	1	2	0	2	1	0	0	0	2	1	1	0	0	0	0	0	0	0
Sclerochilus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Cvtherois	1	2	0	0	0	1	1	1	0	2	2	2	1	2	0	0	2	1	1	0	0	1	2	0	0	2	2	0	0	0
Paracythere	1	0	0	0	0	0	1	1	0	0	0	2	1	2	0	2	1	0	0	2	0	1	1	0	0	0	0	0	2	0
Machaerina	1	2	0	0	1	0	1	1	0	1	0	1	1	2	0	0	2	2	0	1	0	2	2	0	0	2	2	2	0	0
Paracytherois	1	2	0	0	1	1	1	1	1	1	0	1	2	2	0	0	2	2	2	1	0	2	2	2	0	1	2	0	0	0
Paradoxostoma	1	1	0	0	1	0	1	1	0	1	0	2	1	2	0	0	2	2	1	1	0	2	2	0	0	2	2	0	0	0
Acetabulastoma	1	2	1	0	0	0	0	1	0	0	2	1	1	2	0	0	2	2	0	1	0	2	2	0	0	2	0	0	0	0
Redekea	2	0	1	0	0	0	1	1	0	0	0	1	1	2	0	0	2	0	2	0	2	1	0	0	0	2	0	0	2	0
Laocoonella	2	0	1	0	0	0	1	1	0	2	0	1	1	2	0	0	2	0	0	0	2	1	0	0	0	0	0	0	0	0
Aspidoconcha	2	2	1	0	0	0	0	1	0	0	2	1	2	2	0	2	1	0	0	0	1	1	1	2	0	0	0	0	2	0
Parvocythere	0	2	1	0	0	0	—	1	0	0	2	1	2	2	0	2	0	0	0	0	2	0	2	2	0	0	1	0	0	2
Pseudocythere	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0

EXPECTATIONS

As maximum flow networks, the cladograms at each branching or node associate groups (either OTU's or HTU's) with the greatest overall similarity, not in a phenetic sense but in the directional sense in which the data are coded from primitive to derived states. Under most circumstances, forms which show considerable overall resemblance to each other also satisfy the cladistic criterion of recency of common ancestry advocated by Bigelow and adopted by Hennig (1966), although there are several exceptions to this that are dealt with below. (Note that here *recency* carries no chronistic connotation but rather refers to the relative sequence of branching events.) The exceptions fall into two broad categories: 1) anhomeomorphic situations, in which overall resemblance separates OTU's which in biological reality are monophyletic, and 2) homeomorphic situations, in which overall resemblance associates forms which in biological reality are not monophyletic.

Anhomeomorphic Situations

Anhomeomorphy means morphologic dissimilarity and is a general term embracing the continuum of those dissimilarities which separate forms which in biological reality are monophyletic. Anhomeomorphy thus understood includes divergences, such as those expressed by closely-related forms which have adapted to different environments, and polymorphism. For example, in bisexual groups of animals, sexual dimorphic characters distinguish males from females. It can happen that in matrices which incorporate both male and female characters somes OTU's are included which have been described only from males or females. This is particularly the case where the matrices are partly based on data extracted from descriptions in the older literature. The expectation in this case is that males and females may line up along different branches of the resultant cladogram.

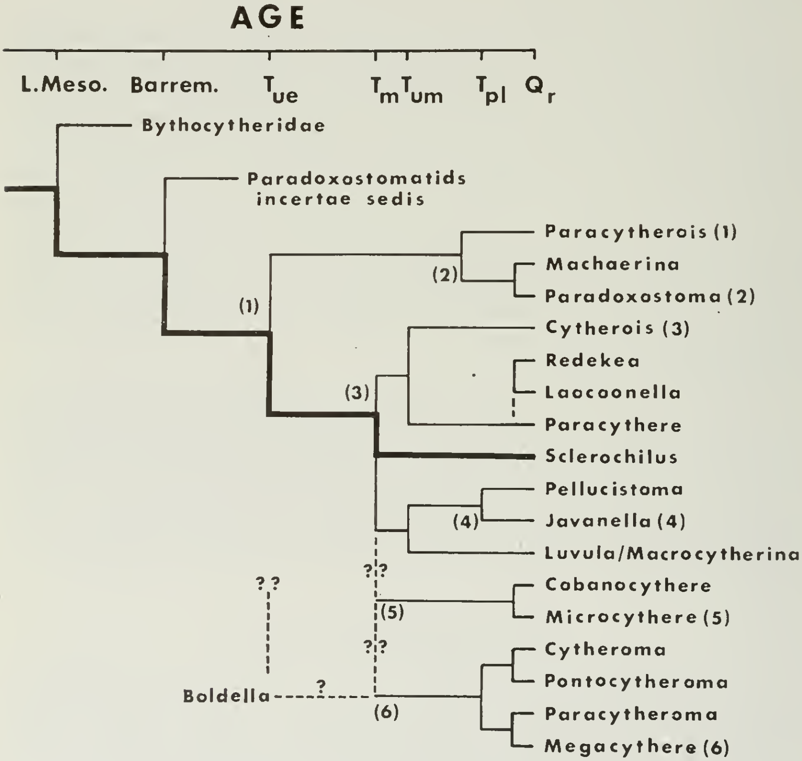
Homeomorphic Situations

Homeomorphy means morphological resemblance and is a general term embracing the continuum of those resemblances which associate forms which in biological reality are not monophyletic. Homeomorphy thus understood includes parallel development, convergence, and the various types of mimicry, the common adaptations which follow from a common habit of life. In cladograms, homeomorphs may be expected to cluster on adjacent branches whenever data matrices are based largely upon their homeomorphic characters.

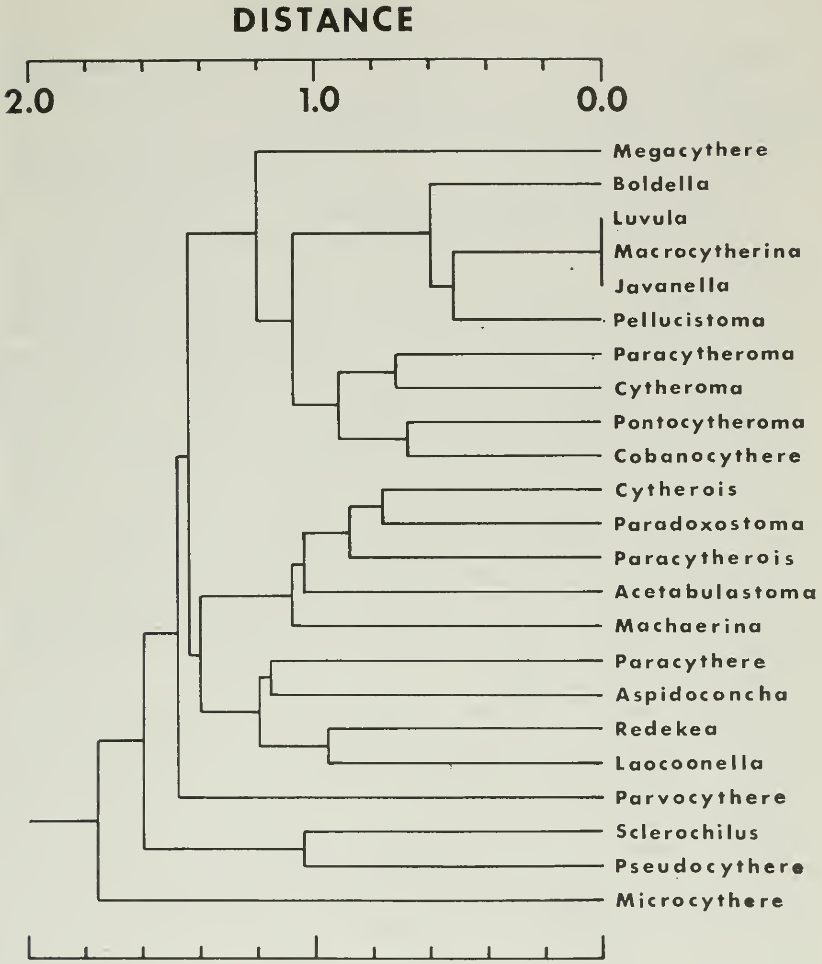
PRELIMINARY RESULTS

As was mentioned earlier, it has not been possible for us to complete the analysis of the results of the numerical cladistic study. Text-figure 2 shows the results of the phenetic study in which euclidean distances between genera were clustered by the unweighted pair-group method. The phenogram is in no sense a phylogenetic tree; instead it represents the phenetic distance between genera on the basis of the 30 characters on which the study was founded.

As would be expected, the phenogram displays many fundamental differences from the suggested phylogeny (Text-fig. 1) proposed by McKenzie (1969). Note, for example, the closeness of *Microcythere* and *Cobanocythere* in Text-figure 1 and their marked dissimilarity in Text-figure 2. Similarly, in the phenogram *Javanella* is not differentiated from *Luvula* and *Macrocytherina,* probably because of the lack of characters from the carapace, although *Javanella* is distinct in Text-figure 1. Assuming that the cladogram in Text-figure 1 represents the true phylogeny, the phenetic difference between *Microcythere* and *Cobanocythere* must be regarded as due to anhomeomorphy. Discrepancies between *Javanella* and *Luvula-Macrocytherina* are due simply to differences in weighting of information about the three genera. Nevertheless, many genera regarded by McKenzie (1969) as closely related phylogenetically are also closely similar phenetically.



Text-figure 1. — Proposed phylogeny of some paradoxostomatid Ostracoda (from McKenzie, 1969).



Text-figure 2. — Phenogram prepared by the unweighted pair-group method from a matrix of distance coefficients. Cophenetic correlation coefficient equals 0.836.

SYSTEMATIC SECTION

Machaerina tenuissima (Norman, 1869) Text-figs. 3-16

Bythocythere tenuissima Norman, 1869.
Xiphichilus tenuissimus (Norman), Brady, 1870.
Machaerina tenuissima (Norman), Brady and Norman, 1889. Refer to Howe (1962, pp. 138, 246)

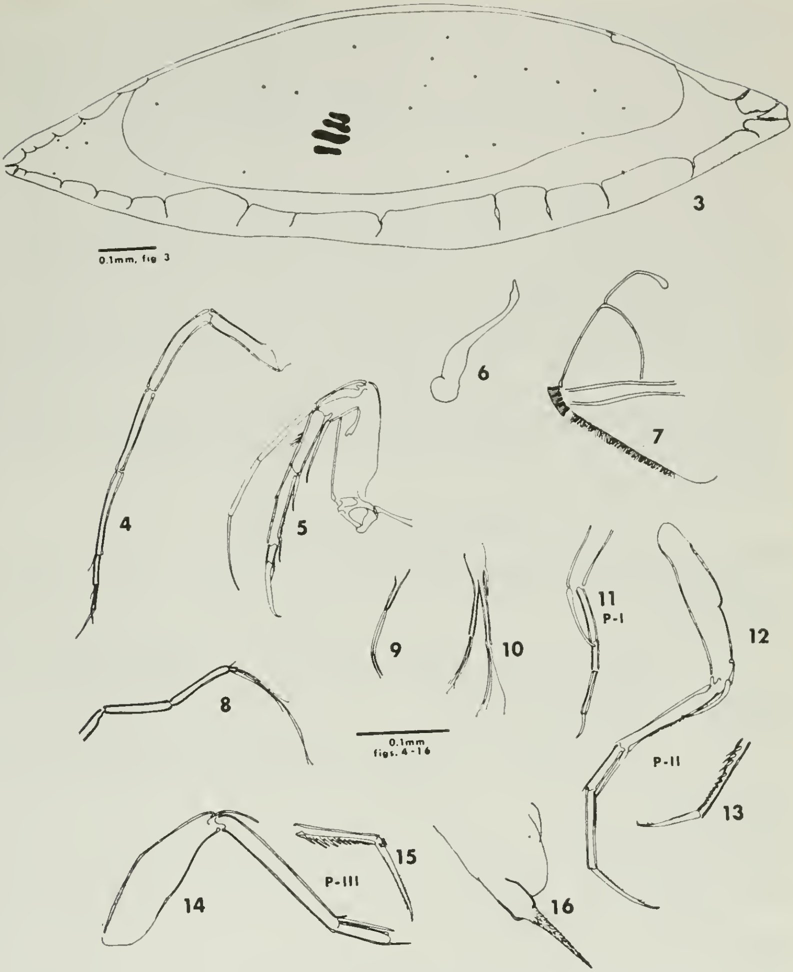
Type locality. — St. Magnus Bay, Shetland.

Location of types. — British Museum (Natural History), Norman Collection.

Redescription. — Carapace large (female about 1 mm); surface smooth; anterior narrowly subacuminate, posterior narrowly subtruncate; dorsum convex, slightly inflexed posterodorsally; venter also convex, slightly inflexed anteroventrally; general shape in lateral view subelliptical. In dorsal view subelliptical, compressed; ends acuminate; greatest breadth approximately medial. Internally, inner margin regular; line of concrescence inflexed anteroventrally almost reaching the inner margin; thus the vestibule is continuous (Text-fig. 3); radial pore canals number about 10 anteriorly, 6 ventrally, and 5 posteriorly, totaling 20 to 25; they are short anteriorly, longer elsewhere, and some are thickened medially; normal pore canals scattered, relatively few, simple; adductor muscle scar pattern consists of an oblique row of four large scars; frontal and mandibular scars apparently very indistinct since they were not observed in the specimen illustrated; hingement weakly lophodont, with terminal projections in the right valve and a corresponding accomodation in the left valve.

Antennule slender; 6-segmented; length ratio of the segments 16:20:19:-18:6:5; setation weak comprising a setule each on the 4th and 5th segments and two terminal setules (Text-fig. 4). Antennal endopod 4-segmented; length ratios 10:13:16:4; setation includes a relatively powerful terminal claw; exopod 3-jointed (Text-fig. 5); antennal gland lobate (Text-fig. 6). Oral cone subtriangular, modified suctorially (Text-fig. 7). Mandible coxa styliform; palp slender, 4-segmented, the terminal segment very small, setation all on the penultimate and terminal segments (Text-fig. 8). Maxillule elongate, slender; palp with two terminal setae; two slender lobes each with fine terminal setules and a third lobe reduced to a seta (Text-figs. 9, 10). Thoracic limbs pediform, 4-segmented; increasing in size from P I to P III; P I and P II with powerful dorsodistal claw-like setae on the protopods; P III with a single slender dorsodistal protopod seta; P II and P III each with a single powerful distal spine on the 2nd segment; 4th segment of the P II hirsute; 4th segment of the P III serrate; terminal claws of the P II and P III (at least) distinctly spinulose (Text-figs. 11-15). Posterior portion of the body produced into a single hirsute spine-like process (Text-fig. 16).

The above description is that of an adult female. A male could not be found in the material examined. All specimens examined were confined to species against the syntypic collection.



Text-figures 3-16. — Carapace of female. 4. Antennule. 5. Antennal endopod. 6. Antennal gland. 7. Oral cone. 8. Mandible palp. 9, 10. Maxillule palp. 11-15. Thoracic limbs. 16. Posterior portion of body.

Dimensions. — Adult female: length 1 mm; height 0.3 mm; breadth 0.2 mm; all approximate.

Localities. — Fairlie, Firth of Clyde; 5 fathoms; collected by A. M. Norman, F. R. S., in July, 1885. In the Norman Collection, B. M. (N. H.) 1911.11.8., M2769. Cumbrae; collected by G. S. Brady, F. R. S., and D. Robertson, 13 August 1888. In the Norman Collection, B. M. (N. H.) 1911.11.8., 36506-36510.

Discussion. — *Machaerina,* from this redescription, is evidently closer to *Paradoxostoma* than it is to *Paracytherois,* especially in the oral region. Further, the mandible palp in *Paracytherois* is usually described as non- or weakly segmented. In *Machaerina,* the segmentation is distinct. In shell characters the genus is distinguished by its two pointed ends and by the knife-edged venter, the latter feature accounting for the generic names by which it has been known. The arrangement of adductor muscle scars is closer to that in *Paracytherois* than it is to the *Paradoxostoma* pattern.

The genus probably ranges worldwide although it has been collected only infrequently. Its known range extends from Shetland through the Mediterranean to Australia.

REFERENCES CITED

Adams, F. D.

1938. *The birth and development of the geological sciences.* Williams and Wilkins Co., Baltimore, 506 pp.

Brady, G. S.

1870. *Notes on Entomostraca taken chiefly in the Northumberland and Durham district (1869).* Nat. Hist. Soc. Northumberland and Durham, Newcastle-upon-Tyne, Trans., vol. 3, pp. 361-373.

Brady, G. S., and Norman, A. M.

1889. *A monograph of the marine and fresh-water Ostracoda of the North Atlantic and of northwestern Europe. Section I. Podocopa.* Royal Dublin Soc., Sci. Trans., ser. 2, vol. 4, pp. 63-270.

Colless, D. H.

1967. *The phylogenetic fallacy.* Systematic Zoology, vol. 16, pp. 289-295.

Henning, Willi

1966. *Phylogenetic systematics.* Univ. Illinois Press, Urbana, 263 pp.

Howe, H. V.

1962. *Ostracod taxonomy.* Louisiana State University Press, Baton Rouge, 366 pp.

Kaesler, R. L.

1967. *Numerical taxonomy in invertebrate paleontology.* In *Essays in paleontology and stratigraphy* (Curt Teichert and E. L. Yochelson, eds.), Department Geology, Univ. Kansas, Spec. Pub. 2, pp. 63-81.

1969. *Numerical taxonomy of selected Recent British Ostracoda.* In *Taxonomy, Morphology, and Ecology of Recent Ostracoda* (J. W. Neale, ed.), Oliver and Boyd, London, pp. 21-47.

1970. *Numerical taxonomy in paleontology: classification, ordination, and reconstruction of phylogenies.* In *Computers in Paleontology* (E. L. Yochelson, ed.), North American Paleontological Convention, 1969, Symposium 5, pp. 84-100.

Kesling, R. V., and Sigler, J. P.

1969. *Cunctocrinus, a new middle Devonian calceocrinid crinoid from the Silica Shale of Ohio.* Museum Paleontology, Univ. Michigan, Contr., vol. 22, pp. 339-360.

Kluge, A. G., and Farris, J. S.
1969. *Quantitative phyletics and the evolution of anurans.* Systematic Zoology, vol. 18, pp. 1-32.

McKenzie, K. G.
1969. *Notes on the paradoxostomatids.* In *Taxonomy, morphology, and ecology of Recent Ostracoda* (J. W. Neale, ed.), Oliver and Boyd, London, pp. 48-56.

Moore, R. C., editor
1961. *Treatise on invertebrate paleontology. Part Q. Arthropoda 3, Crustacea, Ostracoda.* Geol. Soc. America and Univ. of Kansas Press, 442 pp.

Norman, A. M.
1869. *Shetland final dredging report. Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera.* British Assoc. Adv. Sci., pp. 247-336; suppl. pp. 341-342.

Orlov, Y. A.
1960. *Basic paleontology: Arthropoda-Trilobitomorpha and Crustaceamorpha.* Moscow (*in* Russian), 516 pp.

Rowell, A. J.
1967. *A numerical taxonomic study of the chonetacean brachiopods.* In *Essays in paleontology and stratigraphy* (Curt Teichert and E. L. Yochelson, eds.), Department of Geology, Univ. of Kansas, Spec. Pub. 2, pp. 113-140.
1969. *Numerical methods and phylogeny of the Calceocrinidae.* Jour. Int. Assoc. Mathematical Geology, vol. 1, pp. 229-234.
1970. *The contribution of numerical taxonomy to the genus concept.* In *The Genus: A basic concept in paleontology* (E. L. Yochelson, ed.), North American Paleontological Convention, 1969, Symposium 6, pp. 264-293.

Sneath, P. H. A., and Sokal, R. R.
1973. Numerical Taxonomy. W. H. Freeman and Company, San Francisco, 573 pp.

Sokal, R. R., and Camin, J. H.
1965. *The two taxonomies: areas of agreement and conflict.* Systematic Zoology, vol. 14, pp. 176-195.

Sokal, R. R., and Sneath, P. H. A.
1963. *Principles of numerical taxonomy.* W. H. Freeman and Co., San Francisco, 395 pp.

Kenneth G. McKenzie,
School of Applied Science
Riverina College
Box 588
Wagga Wagga N.S.W.
Australia 2650

Roger L. Kaesler,
Department of Geology,
University of Kansas,
Lawrence,
Kansas, 66045

DISCUSSION

Dr. J. Hazel: Did you try that last dendrogram with anything other than euclidian distances?

Dr. R. Kaesler: We also clustered correlation coefficients, and I think Ken may have used Manhattan distance.

Dr. Hazel: Did you like the correlation dendrogram?

Dr. R. Kaesler: It didn't bother me too much, but in general I don't like using correlation coefficients in this way.

Dr. Hazel: It has been my experience that with bioassociational data the clustering of correlation coefficient (r) matrices or Cos Θ matrices results in more meaningful dendrograms than does the clustering of distance matrices.

Dr. Kaesler: I brought the correlation dendrogram with me if you would like to look at it.

Dr. Hazel: I have spoken with other workers who have got the results and also can't seem to explain it.

Dr. P. A. Sandberg: I was wondering what influence on clustering is produced by forms for which you have carapace only?

Dr. Kaesler: In the case of the phenetic clustering it is quite dramatic when you compare *Machaerina* with *Pellucistoma.*

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

AUTHORS

INDEX

GENERA AND SPECIES

Note: Light face type refers to page numbers. Bold face type refers to illustrations.

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES

INDEX

GENERA AND SPECIES