

Jim M. Benson

*Richard H. Benson*

The *Bradleya*  
Problem, With  
Descriptions of  
Two New  
Psychrospheric  
Ostracode Genera,  
*Agrenocythere* and  
*Poseidonamicus*  
(Ostracoda:  
Crustacea)

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*Richard H. Benson* The *Bradleya* Problem,  
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## ABSTRACT

Benson, Richard H. The *Bradleya* Problem, with Descriptions of Two New Psychrospheric Ostracode Genera, *Agrenocythere* and *Poseidonamicus* (Ostracoda: Crustacea). *Smithsonian Contributions to Paleobiology*, number 12, 138 pages, 67 figures, 14 plates, 4 table. 1972.—The “*Bradleya* problem” is concerned with the discovery and definition of a group of fossil and Recent reticulate ostracodes, several of which are common to Cenozoic deep-sea sediments in many parts of the world ocean floor. These species have often been misunderstood and taxonomically confused with genera characteristic of the study of shallow-water forms. The present study attempts to resolve some of these misunderstandings by designation of several important type-specimens, description of new evidence and the proposal of a new classification based on the concept of the evolution of a reticulum in response to environmental change. A method of pattern analysis is used to define elements of the reticulum subject to evolutionary change.

Over 40 reticulate species, which would have at one time been regarded as *Bradleya*, were examined; only 14 of these are assigned and belong to *Bradleya*. Two new genera, *Agrenocythere* and *Poseidonamicus*, are described for the reception of the others, and these are placed in the new subfamily, Bradleyinae, and placed with Thaerocytherinae Hazel in a new family (Thaerocytheridae Hazel). Twenty-seven of these species are described, including *Bradleya arata* (Brady), *B. dictyon* (Brady), *B. normani* (Brady), *Agrenocythere radula* (Brady), *A. pliocenica* (Sequenza), and *A. hazelae* (van den Bold). The diagnostic characteristics of the related genera *Cletocythereis*, *Oertliella*, *Jugosocythereis*, and *Hermanites* are discussed and illustrated.

It is concluded that the psychrospheric species *Agrenocythere pliocenica*, which has been reported from outcrops in Italy and a long core from the Tyrrhenian Sea floor, is most closely related to *A. hazelae*, which became geographically widespread during the Miocene. *Bradleya*, *Jugosocythereis*, *Agrenocythere*, and *Cletocythereis*, now genera in separate families, are all thought to have been derived from a common stock of Cretaceous age.

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**Introduction**

During the study of fossil and living ostracodes of the deep-sea (psychrosphere), I have been particularly impressed with the reticulate form that Brady (1880) originally described from Indonesia as *Cythere radula*. This species, which he easily differentiated (on one specimen, in fact) from the deep-sea form *Cythere dictyon* Brady, is similar to a Neogene species originally described from Italy as *Cythereis pliocenica* by Sequenza (actually the same year, 1880, as the publication of the *Challenger* Report). Several workers, including Ruggieri (1962) and van den Bold (1968b), have puzzled over the relationships of these three species and a fourth, *Cythereis hazelae*, originally described by van den Bold (1946) from "deep-water sediments" of the upper Paleogene and lower Neogene of the Caribbean region. The generic concept of *Bradleya* (conceived by Hornibrook in 1952 for *Cythere arata* Brady (1880) and several other species, including *C. dictyon*) has been considered for these four species and several more. Confusion from several sources has resulted in what van den Bold

(1968b) termed the "*Bradleya* problem." Unraveling the complex relationships of these four species (and twenty more new ones) and the study of patterns in the reticulate carapace ornament and the muscle scars are the subjects of this report.

During the course of the present study, it was noted that basic reticular patterns are common to several genera and that modifications in these patterns can be traced to determine phyletic relationships. Among these genera, the trachyleberids *Oertliella* (Pokorný 1964a), *Cletocythereis* (Swain 1963), and a new genus *Agrenocythere*, can be shown to have a common origin. Another group, including the thaerocytherids *Bradleya* (Hornibrook 1952) and *Jugosocythereis* (Puri 1957), has yet another pattern. A third group, of which I have only studied part, includes *Hermanites* (Puri 1954), *Hornibrookella* (Moos 1965), and *Limburgina* (Deroo 1966) and has some of the characteristics of both preceding groups. *Cletocythereis*, whose V-shaped frontal scar (as seen in the type-specimen) is slightly divided, is seen as an example of the tendency of the frontal scar to divide in separate phyletic lines. The lack of a developmental theory including the evolution of the reticulum as well as muscle-scar patterns, has led to confusion about generic assignment of several important species. I

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Richard H. Benson, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

hope the following discussion will shed some light on these problems and also contribute to the formulation of such a theory.

In 1960, Ruggieri identified "*Hermanites?*" *hazelae* (previously "*Cythereis*," also "*Trachyleberis*," and later "*Bradleya*" *hazelae*) from the Miocene of Sicily. For several years the full significance of this discovery was only appreciated by Ruggieri, who in several places (unfortunately for some of us, in Italian) was pointing out the possible deep-sea aspect of several Italian ostracodes. The properties of ornateness and large size are characteristic attributes of "deep-sea" ostracodes, and Ruggieri was quick to recognize that these species (*hazelae* and *pliocenica*) were different from most of the other forms found in southern Europe. It was not until Ascoli (1969) called attention to the presence of "*Bradleya hazelae*" (now called *Agrenocythere antiquata* Benson, new species) in the Paleocene and Eocene of northern Italy that one possible link in the solution to the relationship of *Cythere radula* and *Cythereis pliocenica* appeared. Another link comes from the study of Recent and fossil deep-sea species in the Atlantic, including specimens from the Tertiary of the Caribbean (supplied to me by W. A. van den Bold) and those from the cores of the Deep Sea Drilling Project.

Coincidentally with the discovery by Ascoli and my examination of deep-sea (psychrospheric) species, I was fortunate to examine and photograph that part of Brady's Challenger collection repositied in the British Museum. With the help of J. P. Harding and H.S. Puri, I was able to establish the identity of those specimens that are most likely to have been considered by Brady as representative of some of his original species concepts (herein designated as lectotypes). These include the types of *Bradleya arata* and *Cleto-cythereis rastromarginata*, as well as *Bradleya dictyon* and *Agrenocythere radula*.

In pursuit of an explanation of both the taxonomic and biogeographic relationships of the two genera *Bradleya* and *Agrenocythere*, new genus, I discovered a third genus *Poseidonamicus*, whose form was obscured in Brady's species concepts. This new genus will be described, and some of its species introduced, as they seem relevant to the general discussion.

Implicit in the study of the relationships among the species of these genera is the establishment of the likelihood of genetic continuity across the shortest geographic distance possible; a coincidence of taxon-

omic and paleobiogeographic distance. Such is not easily obtained considering the scale of the distribution of the evidence I had available, and the tectonic changes that must have occurred during the tenure of the taxa involved. Because of the importance of *Agrenocythere pliocenica* (Sequenza) as a prominent member of the fossil psychrospheric ostracode fauna in the Mediterranean, special attention is given to this form. Demonstration of its relationship to Atlantic deep-sea predecessors has a great bearing on the tectonic and hydrographic evolution of the Mediterranean from Tethys (Benson and Sylvester-Bradley 1971; Benson, n.d.b.). Unfortunately, not all of the pieces of this evolutionary puzzle are available, calling for a careful study of present evidence.

### The *Bradleya* Problem

There have evolved, one from the other, two "problems" concerning the developmental explanation and classification of several of the important reticulate, deep-water ostracode species. One of these is the "*Bradleya* problem" (referred to first by van den Bold 1968b: 67). The other is related to finding the best of possible explanations of genetic continuity among species of the genus *Agrenocythere*, now separated by fragments of continents and hydrographic barriers.

Briefly, the "*Bradleya* problem" is concerned and originated with Brady's study (1880) of several very unusual reticulate ostracode species from the Challenger collection. Some of these species are now known to be restricted to the psychrosphere, rarely to be seen as fossils on the continents, and others simply were from remote parts of the world. Some had remains whose detailed morphology has not been easy to examine. A few of the psychrospheric species, such as *Cythere dictyon*, have been reported from widely separate parts of the world. Yet their description has been vague and their taxonomy subsequently confused.

In the case of *Cythere dictyon*, almost every identification of classification has been appended by remarks questioning its proper status. In 1952, Hornibrook established the genus *Bradleya* to receive two of Brady's species, including *Cythere dictyon* and using *Cythere arata* Brady as the type. The genus was conceived using morphologic criteria that were advanced for that time; yet the concept of *Bradleya* became

almost as vague in application as that of *Cythere dictyon*. Also, because of the lack of other available genera or generic concepts for related or at least morphologically similar forms, I, as well as others, enlarged Hornibrook's original concept to the point of meaninglessness.

It is necessary, therefore, to return to a very conservative position in the analysis of this genus, and with more data than has been available in the past, to attempt to follow the gradual morphological changes that have occurred among the originally described and closely related species. It soon becomes evident that "*Bradleya*" is a much different, and even larger genus, from what was previously suggested. It is one with considerable variation in form among its constituent species. Also, as others have suspected, some species that have been assigned to "*Bradleya*" are not *Bradleya*. Some in fact belong to another family-level taxon.

Concerning the problem of distribution (the "*Agrenocythere* problem") we have stressed (Benson and Sylvester-Bradley 1971; Benson, n.d.b.) that the presence of psychrospheric ostracodes in the fossil record of southern Europe, presently far removed from the deep sea, requires some radical alterations in theories regarding the nature of the barriers that were once supposed to separate Tethys from the rest of the world ocean. "*Bradleya pliocenica* (Seguenza) (the combination first used by Ruggieri 1962) found in the Pliocene of Italy and in the floor of the Tyrrhenian Sea, was considered to be among the Tethyan psychrospheric ostracodes that occupy this "displaced" geographic position. Its similarity to "*Cythere radula*" seems evident, however remote geographically. The regularity of reticular pattern and V-shaped muscle scar are the same or very similar in each. Yet there are subtle differences. The sculpture around the muscle scar node, the castrum, is not the same. At the time of the original study other candidates of possible close relationship from the nearby open Atlantic were missing. I will show in the present report that the species *pliocenica* or *radula* are not *Bradleya*, but are related, although not closely, and belong to another important psychrospheric ostracode genus, and that *pliocenica*, now found more than 1000 miles from the ocean, is related to an important Atlantic Neogene species.

The reticulate genus *Bradleya* was first described in 1952 by Hornibrook to accept nine species of Ceno-

zoic and Recent ostracodes from New Zealand. Principal among these were *Cythere arata* (designated type-species) and *C. dictyon*, both species described originally by Brady (1880). Brady reported *Cythere arata* from the Recent of the Tasman Sea. *C. dictyon* was found in many regions of the world ocean floor. The other species treated by Hornibrook were local fossil forms that were in general similar to *Bradleya arata*, but which also included the Paleogene species, *B. semivera* Hornibrook. This later species is more tapered, even caudate, and less rectangular in shape with a reticular pattern like that of *Cythere radula* Brady, 1880, and differs in other respects from *Bradleya arata*. In particular it has a V-shaped frontal scar compared to the simple paired frontal scars of the *Bradleya arata*-*Bradleya dictyon* complex. The original breadth of generic concept by Hornibrook, which included such different species as *B. semivera*, has caused others (Ruggieri 1960, Hazel 1967) to have concern about the significance of the difference in muscle-scar pattern in preference to the overall similarity of size and reticulation shared by this group. This problem was further clouded by the fact that Brady had included several related, yet dissimilar forms in *C. dictyon*, the second most important species of Hornibrook's new genus. Brady readily conceded that he had included several varieties of form within this species; however, he seems convinced (by his discussion) that differences in surface ornament can be explained by simple "exaggeration of characters" due to the effects of "senility." As will be shown later, the specimens, whose assignment to *C. dictyon* Brady did doubt, are probably closely related to *C. normani* (which he described from the North Atlantic in 1865, but which I believe he misidentified at least once, Plate 26: figure 4a, b in the *Challenger* report), and to *C. viminea*, also described in the *Challenger* report.

Brady (1880:101) remarked on the general similarity of *Cythere dictyon* to *Cythere arata*, which he suggested differs in the "style of ornament." The latter species is relatively smooth and devoid of apparent reticulation, which is characteristic of the former species. I hope to demonstrate that through examination of the finer surface features of both forms, and through the development of a concept about progression in a morphotypic series within the pattern of the reticulum, that these differences are not of primary importance on the generic level. *Cythere dictyon*

(that is, those forms conspecific with the lectoholotype) and *C. arata* (type-species of *Bradleya* Hornibrook, 1952) are indeed both species of *Bradleya*. That van Morkhoven (1963) questioned the assignment of *C. dictyon* to *Bradleya* is based on his assumption that Hornibrook had selected the correct form as being *C. dictyon*. This, as we will see, was not a valid assumption. Hornibrook's misidentification of *Cythere dictyon* was not without just cause. Matters were complicated by the long delay in selecting a lectoholotype from among Brady's specimens to represent *C. dictyon*. He was more fortunate in the identification of *C. arata*. The specimen (BM 80.38.52a) of *Bradleya arata* (Brady) in the British Museum seems to me without doubt assignable to the description and illustration of Hornibrook (1952, pl. 6: fig. 80), and to the same population from which a specimen was taken for illustration in this report (Plate 11: figures 16, 17).

In summary, I hope to present evidence that *Bradleya* is a thaerocytherid genus, with morphologic aspects characteristic of a large group of species and genera (constituted as a new subfamily, the Bradleyinae); and that *Bradleya dictyon* is in general restricted to deeper waters. Although quite variable, *Bradleya* does not contain reticulate forms like *C. viminea* Brady (included in the new genus *Poseidonamicus*, even though they were mistaken by Brady for *C. dictyon*) or *C. radula* Brady, or a host of others that have been suggested including those trachyleberid forms such as "*Bradleya*" *semivera*, herein assigned, at least provisionally, to *Agrenocythere*. Also in the present work, I will present evidence that *Cythereis hazelae* and *Cythereis pliocenica* do in fact differ from those species properly assigned to *Bradleya* in "essential nature" (van den Bold, 1968:66) rather than "degree." The subdued subcentral tubercle of *Bradleya* is joined to the anterior margin by a reticular bridge (typical of other bradleyines as well). The subcentral tubercle of *Bradleya* is not developed as a castrum as in *Agrenocythere*, the new genus to which these species are assigned (see p. 58). The reticular, fossal, and pore conuli patterns of *Bradleya* are different than that of either new genera, *Agrenocythere* or *Poseidonamicus*. Above all, the frontal muscle scar of *C. hazelae* and *C. pliocenica* is decidedly trachyleberid and not thaerocytherid. No matter which specimen was chosen from among those logically available as type-specimen of *Bradleya dictyon*, none would be

similar in these respects to *Bradleya* (now *Agrenocythere*) *hazelae*. Removing *Agrenocythere hazelae* along with "*Bradleya*" *semivera* from *Bradleya* begins to substantially reshape the problem around the definition or a morphotypic series including *Bradleya arata* and *B. dictyon*. Twelve other species are added to this (or these) series.

## Methods

ILLUSTRATION.—Some aspects of methodology regarding the collection and illustration of deep-sea ostracodes were mentioned in a previous report on *Abyssocythere* (Benson 1971) and will not be discussed again here. The usefulness of the stereo-pairs of Scanning Electron Microscope photographs is by now self-evident. It would be difficult indeed to analyze the distribution of pore conuli, so important for the analyses of *Agrenocythere*, new genus, in this report, without this instrument. (This comment is in rebuttal to one made earlier by me in Neale 1969: 238.) The light photographs were made with the aid of a back-lighting technique, which allows the silver nitrate stained specimens to be shown darker than is often customary, bringing out more depth to the shape. The several drawings of carapace morphology attempt to portray the concept of form and in most instances are not intended to represent a particular specimen.

PATTERN ANALYSIS.—One of the principal methods of morphological analysis used in this study is the creation of a series of progressively more abstract models of carapace form. By this method, it is possible to demonstrate the contrast in form that exists among different but related species. The presence of conservative patterns of the reticulum and pore conuli distribution (and to a lesser extent the pattern formed by the fossae; the fossal pattern) can be shown and compared with the general changes in shape, size, and robustness of the rest of the carapace. This process of analytical reductionism also includes identification and naming of homologous features, and characterizing their patterns of distribution in as simplified a way as possible, in some cases by structural analogy and in others by graphic substitution.

The first portion of the reductionist process in part follows the method first described and used by Pokorný (1969a, b) on specimens from samples in my collection from the Galapagos Islands, and also later employed by Liebau (1969; his "Koordina-

tensystems"; see also Anderson 1967). By this method, particular fossae and pore conuli were to be identified (fossal and pore conular patterns) using an arbitrary system of codification developed principally by Liebau for his study of *Oertliella*. In general this method, which identifies aligned fossae in parallel series, was found to be satisfactory, except that the enumerative code of specific features can be difficult to remember, and comparison of the reticular patterns (using the letter-number combinations) among many different forms can be confusing. In particular, I find that this method tends to focus on the wrong aspect of reticulation; that is the fossae rather than the ridges or muri. In the diagrams of both Pokorný and Liebau, it is what is not present in the reticulum that is emphasized.

I have named some of the more important architectural features of the reticulum, using the mnemonic device of architectural or structural analogs, in the case of *Agrenocythere*, new genus, analogs from medieval fortifications. Mapping the distributions of pore conuli over the reticular field represents a separate problem. This nomenclatural system is defined and explained on pages 6, 7 and under the sections devoted to the general morphology of *Bradleya* and the new genus *Agrenocythere*. In the analyses of *Bradleya* and *Poseidonamicus*, new genus, whose reticular patterns are simpler, the individual fossae are not identified for purposes of this study, but they are zoned for comparison. In comparing many forms related to *Agrenocythere*, a color code system was used for the patterns of fossae which was superimposed on reticular silhouettes (Plates 5 and 6). A constellar framework system shown on the acetate overlays represents the distribution of pore conuli. As can be seen, superposition and comparison of these patterns exaggerates the differences between the various forms. Inspection of the constellar patterns by themselves emphasizes the similarity of the same forms. The effectiveness of this method can be demonstrated by comparing the degrees of allometric distortion shown by the male relative to the female of *Agrenocythere pilocenica*, and with the interspecific variation among the other examples of female left valves.

Reticular silhouettes represent a first order reduction of the pattern of the reticulum. In mapping the muri some information about the form is lost (especially the vertical relief of the muri, which must be brought out through other means), but the original

form of the species is still identifiable. Identification of homologous fossae (through study of fossal patterns) among various different forms is facilitated by the silhouettes (reticular patterns), which emphasize the overall pattern of reticulation and decrease differences in overall shape (but not outline). Recognition of combinations of mutually adjacent sides among contiguous fossae helps to resolve difficulties in identification of the same fossae within the more rapidly changing portions of the fossal patterns taken in series. The greatest difficulty may come as some fossae merge or are excluded by other fossae. This problem apparently gave Liebau (1969) difficulty in his "Koordinatensystem," as is reflected in the break in alphabetic sequence of his code with contiguous placement of the fossae. The logic of the present method does not entirely resolve this problem, but it does at least recognize it. Fortunately, many intermediate forms exist that have partially formed muri indicating fossal division, or combination, in progress. These can be seen clearly in *Bradleya* and *Poseidonamicus*, new genus. Their presence gives some insight into the course of pattern change as fossae merge and lose their individual identity.

One would assume that eventual conversion of this reduced information to computer schemes could account for the tendency of disappearance or multiplication of the fossae in certain sectors of the fossal patterns. This leads to the next order of mathematical abstraction (permutation, from enumeration) and might be used to show degrees of difference or similarity among species in a quantitative manner. This has only been done by inspection with the present display of patterns. I suggest that this present system, which is primarily graphic and in part geometric, is a necessary step in transformation toward a proper quantitative analysis (of which the most difficult part is deciding which changes are important). I would suspect that an information function might be appropriate to describe the association between fossae and their repetitive order within the patterns. Yet, as mentioned earlier, I am concerned that attention given only to the several series of fossae removes from analysis the actual subject on which selection operated.

CAUSES OF PATTERNS.—The interpretation of the cause of the reticular patterns is germane to the present study insofar that it is assumed, here at least, that its development among different species is genetically

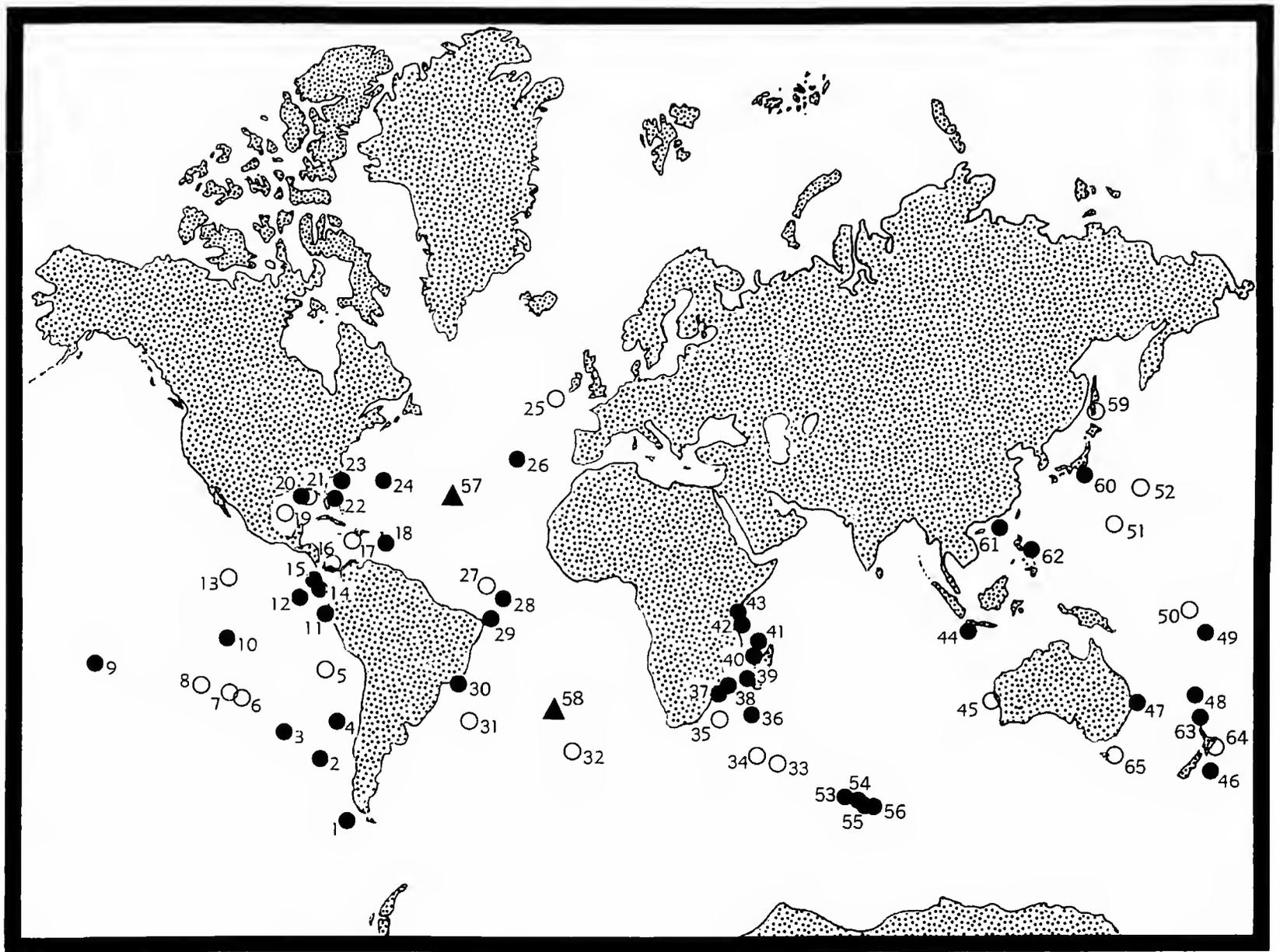


FIGURE 1.—Sample localities where specimens of *Bradleya* were found. Dots indicate Recent localities; circles indicate fossil localities; and solid triangles indicate DSDP Hole locations. Data for the locations are given in Table 1.

controlled. That is to say, natural selection is dominantly responsible for the change in emphasis of the muri between forms within a more conservative framework responsible for the fossal pattern. This change is not simply some kind of somatic adjustment in the distribution of strengthening elements of the shell structure. An alternate argument might claim that the similarity among various reticular or fossal patterns is caused by convergence arising from ecological pressure on individuals within their own life span. Mechanical compensation among carapace forming cells to adjust for overall changes in shape might also be given as the cause for the arrangement or rearrangement of the patterns. Both genetic and nongenetic causes are possible, I suppose. Yet the consistency of the patterns in a given sample is striking, and

the conservatism, even among different genera derived through other analyses, is most impressive. Presently I doubt that ecophenotypic variation within a single reproducing population is a significant factor in deep-sea species.

**PORE CONULI DISTRIBUTION.**—The value of recognizing the individual pore conuli lies in their status as fixed reference points on the carapace. They seem to be more conservative in number and distribution than even the elements of the reticular or fossal patterns. The importance of having reference points among a complex array of elements composing the surface ornament can be readily appreciated. Consistency of relative position among reference points is required for accurate estimation of changes in phyletic allometry within a taxal series. The production of a grid

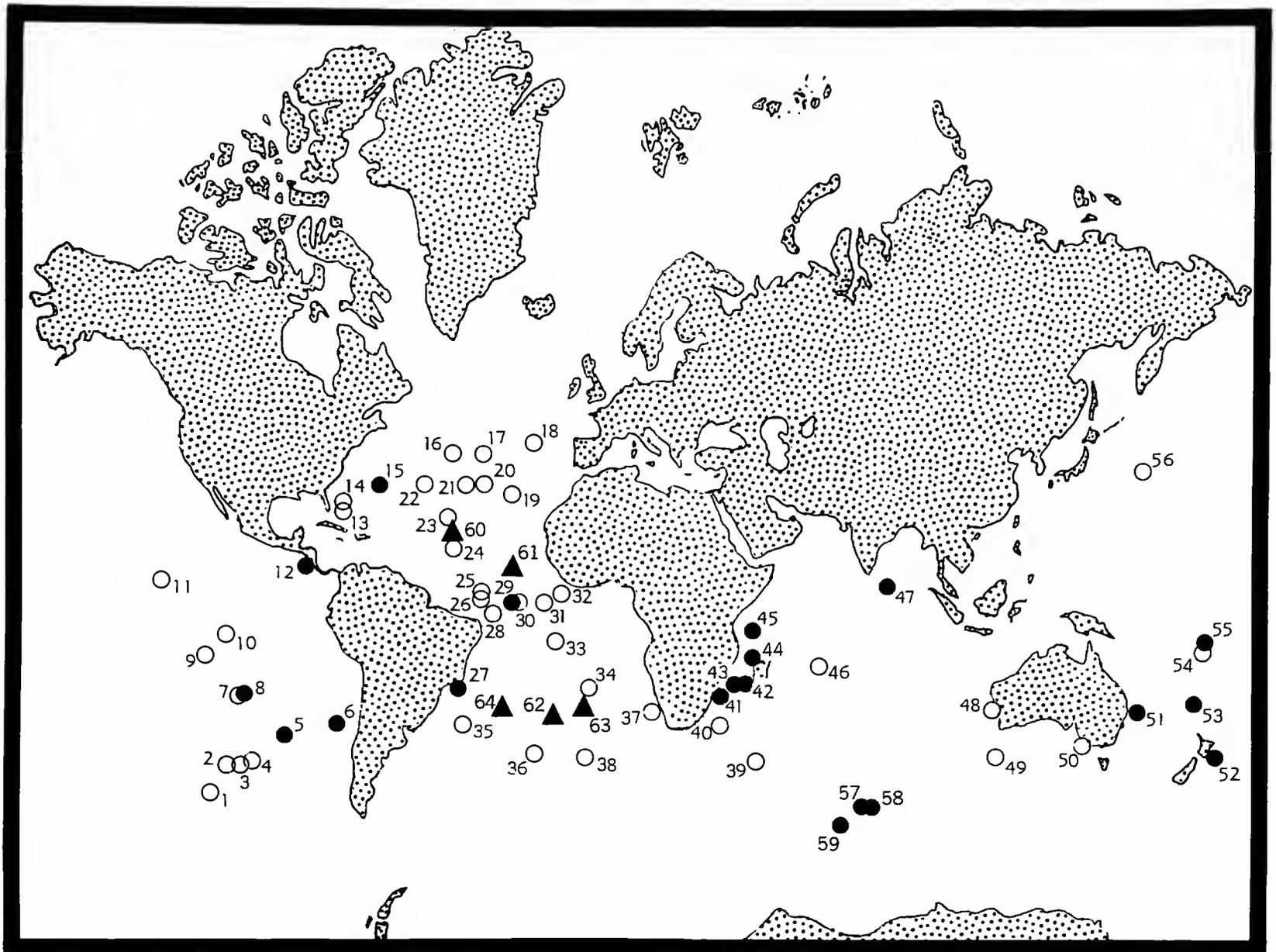


FIGURE 2.—Sample localities where specimens of *Poseidonamicus*, new genus, were found. Dots indicate Recent localities; circles indicate fossil localities; solid triangles indicate DSDP Hole locations. Data for the locations are given in Table 2.

composed of lines drawn between these points (the purest geometric form of the reductionist abstraction) allows comparison of the distortion of form that results from dimorphism or phyletic adjustments of different adaptive modes. For example, it now can be shown that a basic difference in shape exists between *Cythereis* (Plate 5: figure 2), whose reticulum in the central lateral regions of the carapace is compressed relative to enlarged marginal areas, and *Oertliella* (Plate 5: figures 5, 6), whose shape is formed by a more equitable distribution of many of the same carapace elements.

**ARCHITECTURAL FORM.**—With the Scanning Electron Microscope it is possible to magnify portions of the complex carapace with great clarity, and even in three dimensions. It is this last aspect of the instru-

ment's ability that impresses the observer with the intricate and integrated architecture of carapace form. I have discussed this subject elsewhere (Benson, n.d.a). It is soon obvious that carapace architecture, or the actual form solution of the problems of metabolistic limits in shell formation and strength, is of paramount importance in the success of some kinds of ostracode shapes over others. To acknowledge this fact, I have tried to emphasize the architectural forms, through identification and analogy, in the discussions of the carapace morphology of the various species diagnosed in this report. This, at least in the beginning, supplements the various pattern analyses and, to some extent, compensates for the loss of the three dimensional aspect (vividly shown in photographs) that is lost in diagrams of patterns.

THE MEANING OF CHARACTERS.—Lastly, in consideration of the classification of an evolving taxon into discrete categories, it is necessary to recognize that the character group used for their definition must be of sufficient complexity and flexibility (present or absent in prograding groups) to accurately reflect this evolution. This multistage aspect allows for the characterization of evolution by shifting matrices of attributes and is best derived from integrated groups of characters and not reliance on single characters (polythetic versus monothetic classification). I believe this is one of the strongest arguments for pattern analysis as is attempted in the present work.

### Material Studied

Psychrospheric ostracodes, like many deep-sea animals, are relatively rare compared to those living on the shelf. I have attempted in every sample studied to obtain 300 specimens. Many times this was not possible. Often obtaining 300 specimens required washing several, even tens of liters of mud sample. Even so, in a given sample a single species may only be represented by a few specimens.

Ninety-nine samples yielded specimens of the various species of *Bradleya*, and 116 samples yielded specimens of species of *Poseidonamicus*, new genus.

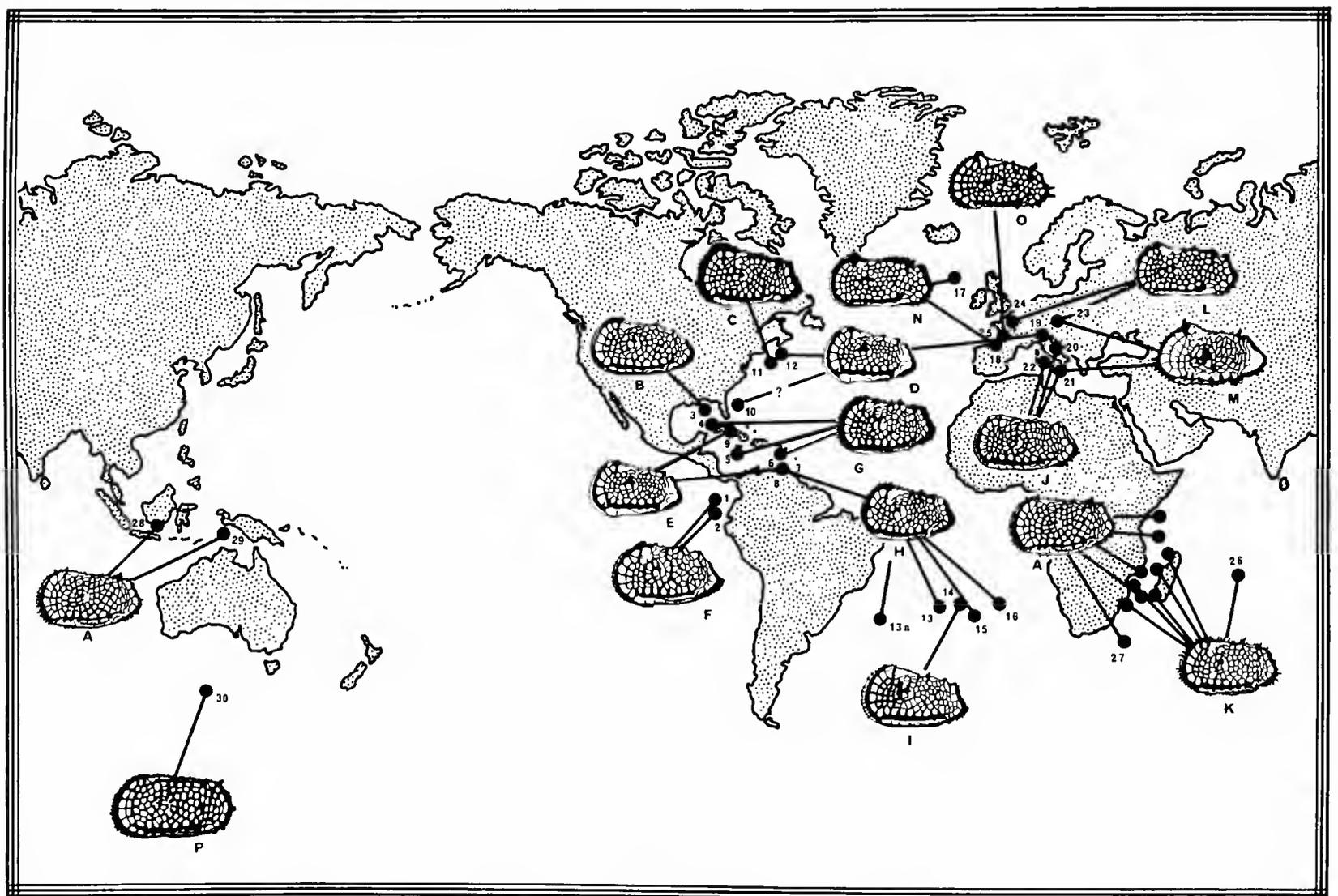


FIGURE 3.—Sample localities where specimens of *Agrenocythere*, new genus, were found. The numbers correspond to those given as map designations in Table 3. The species (designated by letters) are as follows: (A) *Agrenocythere radula* (Brady, 1880); (B) *A. americana*, new species; (C) *A. gosnoldia*, new species; (D) *A. antiquata*, new species; (E, F, G, H, I) geographical and temporal variants of *A. hazelae* (van den Bold, 1946); (J) *A. pliocenica* (Sanguenza, 1880); (K) *A. spinosa*, new species; (L) *Oertliella reticulata* (Kafka, 1886); (M) *Cythereis ornatissima* Reuss, 1846; (N) *Oertliella ducassae*, new species; (O) *Oertliella aculeata* (Bosquet, 1852); (P) *Agrenocythere? cadoti*, new species. A more detailed map of the distribution of sampling localities in the Mozambique Channel area is given in Figure 30.

These are listed with their locations in Tables 1 and 2 and in Figures 1 and 2. The specimens of these taxa were much more abundant than those of *Agrenocythere*, new genus. I have not counted them for the present study, but I would judge their number to exceed several thousand. Because the variation within the groups of forms assigned to *Bradleya*, sensu stricto, and *Poseidonamicus* is very considerable I have deferred its study until later. Nonetheless I have distinguished 14 species of *Bradleya*, of which 10 are new, and 4 (all new) species of *Poseidonamicus*.

Of the 75 samples examined, which yielded specimens of *Agrenocythere*, new genus, more than one-third had only one specimen, although three had over 100 each. Approximately 1000 specimens in all were examined. Their distribution both geographically (Figure 3) and stratigraphically (Figure 12) is presented in Table 3. These occurrences of *Agrenocythere* represent successful attempts to find specimens among some 500 samples of deep-water sediments examined. Seven species were found of which four are new.

I did not consider the limited number of adult female left valves (males were even rarer) found for any given species, of those accounted for above, to be sufficient to warrant a critical population study. Therefore, I turned to the study of changes in form between what seemed to be morphological isolates. In prior discussion of this study with others, some concern was expressed that there was insufficient information about variation within species to warrant division among species. This could be true in those cases where only a few specimens from a few samples were found, if the described new species were distinguished only by minor differences in morphology. I have tried to avoid such problems and have named new forms on a few specimens only where I felt it was necessary to focus on evidence for morphologic transition. Yet with the exceptions of the two new larger species of *Poseidonamicus* (*P. major* and *P. minor*) and *Agrenocythere hazelae*, which could conceivably be more than single species, most of those described herein are morphologically distinctive and are thought to be consistently so within a suspected biogeographical province.

In the several samples where 50 or 100 or more specimens were found, the variation in individual morphology is negligible compared to the differences used to define species. Those instances, where changes

do occur, are discussed in the pages that follow. It must be concluded for this stage in the understanding of deep-sea ostracodes that the consistency of morphological form among samples of populations of approximately the same geological age is as equally impressive as are the gaps between them. It is expected that this separation will decrease as more samples of older Tertiary forms are found.

### Acknowledgments

For samples and specimens, appreciation is expressed to W. A. van den Bold of Louisiana State University (Trinidad samples), D. B. Erickson and Goesta Wolin of Lamont-Doherty Oceanographic Laboratory (Vema core samples), H. M. Cadot of the University of Kansas (Southern Ocean sample), Francis Parker of Scripps Institution of Oceanography (cores from the Pacific), H. L. Sanders (Atlantis II samples) and W. A. Berggren of Woods Hole Oceanographic Institution (DSDP 117, 117A samples), A. H. Cheetham of the Smithsonian Institution (French samples), N. de B. Hornibrook of the New Zealand Geological Survey and W. M. Briggs of Victoria University, Wellington (New Zealand samples), Piero Ascoli of Milan, Italy (Italian Miocene and Eocene samples), P. A. Sandberg, University of Illinois (Austrian Miocene sample), J. E. Hazel, U.S. Geological Survey (Atlantic, Eocene sample).

The samples of the International Indian Ocean Expedition were collected by me in 1964 and those from France, with help of Jean Moyes and Odette Ducasse and others, in 1969. Jesse Merida of the Smithsonian Institution collected the samples from the Kerguelen-Gaussberg Ridge (Eltanin Cruise 47) in 1971.

I have used the illustrations of V. Pokorný, E. Herzig, and H. J. Oertli as bases for identification or morphological drawings as indicated. I would especially like to credit Alexander Liebau of Berlin with whom I had some brief, but spirited, discussions of the problem of conservatism in fossil patterns. I borrowed liberally from his ideas and those of Professor Pokorný, who spent much of 1967 at the Smithsonian, and subsequently extended them into areas that they may seek to challenge.

Thanks is expressed to J. E. Hazel, P. C. Sylvester-Bradley, and J. P. Harding for their critical reviews of the manuscript and to Ruth Lerner-Seggev for her

assistance in preparation of some of the material for this study and many intervening discussions. Laurie Jennings helped prepare most of the samples and also helped with the illustrations. Donna Copeland aided in construction of the tables and typing of the manuscript. The drawings were constructed by myself with some aid on the stippled drawings from Manuela Farfante (Figure 26 by Larry Isham).

Sediment samples from the Albatross collection and the A. R. Loeblich collection were available in the National Museum of Natural History, Smithsonian Institution. Samples from the *Glomar Challenger* cores were supplied to me through the curator, W. R. Riedel, of the Deep Sea Drilling Project.

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After this report had been submitted to the editors for publication I received from Alexander Liebau a printed copy of his dissertation (Liebau 1971) for the Doktor der Naturwissenschaften of the Technischen Universität Berlin. In this thoughtful work Liebau discusses in more detail the basis of his analytical procedure for pattern analysis ("Koordinatensystems") and gives examples of several more genera than were published in his earlier brief description (Liebau 1969) of this study. Of special interest are his analyses of several species of *Limburgina* Deroo, 1966, *Oerthliella* Pokorný, 1964, and *Quadracythere* Hornibrook, 1952, which bear upon remarks made in the present report.

### Conceptual Development of the Genus *Bradleya*

A more formal description of *Bradleya* will be included in the section on Systematics; however, one can hardly begin to discuss the proper division of a taxon as important as this one without some understanding of the evolution of the concepts behind its many past usages, and the background of taxonomic theory that influenced its development. A critical review of this evolution is attempted here.

CONCEPTUAL BACKGROUND.—Until 1952, when Hornibrook introduced *Bradleya* as a new genus and new generic concept, the Trachyleberididae had no general taxon specifically for the acceptance of the strongly reticulate forms. There was no particular reason that this group of ostracodes should be recognized

separately. There was no theory providing for an explanation of the function or development of reticulation.

The concept of *Cythereis*, invented by Jones (1849) a hundred years earlier (as a subgenus of *Cythere*), was intended for the recognition and inclusion of the very ornate fossil marine ostracodes (spinose and/or reticulate). Later it was much used for almost any post-Jurassic ostracode with a complex carapace morphology. It had just begun to be conservatively applied to the type-species (Triebel 1940) in the 1950s (see Sylvester-Bradley 1948, and Pokorný 1963). Among Recent ostracodes (since Sars 1866), the concept of *Cythereis* was largely applied to species like *Pterygocythereis jonesi* (Baird 1850) partly on the assumption that grossly ornate cytheracean ostracodes also shared more complicate or more primitive appendages as compared with the simpler (both in carapace and appendages) *Cythere*-like forms. The introduction of the subgenus *Hemicythere* by Sars (1925) as morphologically half-way between *Cythereis* and *Cythere* is relevant in this regard. However, as Müller (1894) pointed out, the differences among the soft parts of this family, then called the Cytheridae (now several families), are slight compared to those found in other living ostracode genera.

What Müller failed to appreciate (the number of described fossil forms was much less than now) is that adaptation and the evolution of this group has been primarily within the carapace and not in the soft parts. [It must be remembered that Brady (1865) could not bring himself to accept *Cythereis* after his first very limited usage. His would be an extreme and unworkable taxonomic position, even forty or fifty years ago. Yet surely even Brady must have become concerned about the growing lists of species (totaling approximately 175 in number, of the 580 described by him and his close associates), all of which he ascribed to the genus *Cythere*.]

Skogsberg's (1928) attempt at a classification of *Cythereis*, to include a broad spectrum of types of appendage morphology, unfortunately neglected the carapace. With the advent and influence of more modern paleontological studies, especially during the 1930s, it soon became apparent that this wealth of morphologic diversity could not be contained in the available zoological taxonomic concepts. If for no other reason, many new genera were needed just to accept the increased multitude of *Cythere* species.

THE SEARCH FOR PROGRESSIVE CHARACTER DEVELOPMENT.—As new species continued to be discovered, the problem of Brady remained. Among the many species for the few genera described, there was no theory of carapace development. Differences in carapace ornament were described, but very few phyletic sequences were noted. It was hoped that with the discovery that the ostracode hinge had developed in a progressive evolutionary sequence (Sylvester-Bradley 1948, Triebel 1940), that a taxonomic character with morphological conservatism somewhere between the outer carapace and the appendages had been found. A. W. Sweyer, in 1949, as translated in Pokorný (1957:14), thought that because the carapace hinge was generally protected “against the influence of the environment and immediately adjacent to the organism” that it should furnish a significant morphologic indication of generic relationships. He suggested that every ostracode genus would have a distinctive, if not unique, hinge structure (and this is still stated in modern papers).

It wasn't until after Hornibrook's description of *Bradleya* (1952) that a progressive hinge classification (apart from the old one based on molluscan hinges) was advanced by Sylvester-Bradley (1956). Its absolute value was quickly questioned by Pokorný (1957). Pokorný feared oversplitting by paleontologists and urged a return to respect for the taxonomic value of the soft part anatomy in the classical zoological sense, that of Sars and Müller. Meanwhile, discoveries regarding the stability of muscle-scar patterns were being made (some by Pokorný) and many new species were being described—but this begins to anticipate the consequences of Hornibrook's work which was just beginning to be received and considered.

There have been few places in the fossil record where ostracodes characteristic of the deep sea were found. Therefore, an important part of the evolution of this animal group was unavailable for consideration, while general morphologic and taxonomic concepts about shallow water ostracodes continued to form. Brady's (1880) *Challenger* report, while interesting as a catalog of forms to be studied, is not in itself a very useful instrument for the study of ostracode morphology. It was with Hornibrook's work that the first modern examination of some of the deeper water forms (especially the reticulate species) began. While Hornibrook, himself, did not have deep-sea species, he began to recognize similarities between the

fossil and living ostracode faunas of New Zealand and those described by Brady in 1880.

THE CONCEPT OF BRADLEYA.—Confronted by the absence of suitable taxa to receive his reticulate species with amphidont hinges (Hornibrook still recognized *Cythereis* as a Tertiary and modern spinose genus, along with Brady's (1898) resurrected genus *Trachyleberis*), he constituted the two new genera *Bradleya* and *Quadracythere*. Both of these generic concepts included reticulation (differences in pattern not considered, only the presence of a reticulum), prominent ventral and dorsal carina, two anterior muscle (frontal) scars, and rectangular to subquadrate lateral outlines.

A notice of major difference seemed to be placed on the conformation of the hinge, especially the posterior tooth (no doubt influenced by the work of Sylvester-Bradley 1948). *Bradleya* has a “sometimes distinctly denticulate, often obscurely denticulate or lobed [terminal posterior tooth],” whereas *Quadracythere* has “a stout, smooth posterior tooth, obscurely lobed” (Hornibrook 1952:38, 43). As Pokorný feared (1957), and others have also subsequently learned, the subtle differences in tooth crenulation, while important to note, are not that consistent as diagnostic features (among the more ornate cytherid genera). Or if they are used as such, there is a likelihood that relationships among species, with different mechanical requirements for valve closure, may well be overlooked. A specific example of this oversight may exist in the genus *Cythere* itself, which has almost become monotypic.

Hornibrook's concern for the importance of the hinge and its relationship to *Cythereis* and *Trachyleberis* is evident, although at the same time he calls attention to the difference in the smooth posterior hinge tooth of *B. dictyon* and the denticulate tooth of the type-species, *B. arata*. *Bradleya semivera* was described as having a smooth lobate posterior tooth, which may be important in the development of *Agrenocythere radula*, but has little to do with *Bradleya dictyon* or *B. arata*.

OVEREMPHASIS OF THE HINGE AND RETICULATION.—Consequently, within these several years of concentration on the importance of the ostracode hinge, many workers (including myself, Benson 1959) were quick to find species of *Bradleya* on the basis of what now seems rather doubtful criteria. The name *Bradleya* began to appear frequently as part of the binomen

of subquadrate or subrectangular reticulate trachyleberid species. Puri's concepts of *Hermanites* (1954, 1955) and *Jugosocythereis* (1957) were not well understood although the former was also widely employed. By the early 1960s many other new generic concepts began to appear, and critical examination of muscle-scar patterns increased.

**MUSCLE SCARS.**—Although Hornibrook included *Bradleya semivera* (Plate 1: figure 5 as close as I could get to a form like Hornibrook's 1952, pl. 8: fig. 103) in his new genus, he fails to discuss the fact that it has a different muscle scare (V-shaped, as noted later by both Ruggieri 1962 and Hazel 1967) than the kind required by his generic diagnosis (two frontal scars). Even so, he both questions the inclusion of the form, and suggests that the significance of the muscle-scar pattern, as a guide to the evolution of the Trachyleberidinae, had not been sufficiently realized.

In the section on the Family Trachyleberididae, (in Moore 1961), Sylvester-Bradley made no group distinctions among the member genera (though generally subfamilies were not recognized in this work). He comments on the importance of the caudal process, the subcentral tubercle, and the lack of division of the adductor muscle scars. At this time there was no special significance applied to the differences in frontal scars ("antennal scars") in this family. Subsequently I described *Australicythere* (Benson 1964), which had both divided adductor scars and a subcentral tubercle, and I have subsequently seen several trachyleberid deep-sea species with the typical V-shaped frontal scar and a divided adductor scar. Transitions between conventional V-shaped and divided frontal scars and adductors have been amply noted by Moos (1965), Deroo (1966), and Bassiouni (1969).

Hazel (1967) discusses at length the problems involved in resolving the relationships among the muscle-scar patterns, and these arguments need not be repeated here. He touches briefly on the "*Bradleya* problem," and with *Hermanites*, *Jugosocythereis*, *Quadracythere*, and some other genera, considers their carapace to be intermediate between those typical of the families Trachyleberididae and Hemicytheridae. It is notable that van Morkhoven (1963) has considered the divided frontal scar (included by Sylvester-Bradley, in Moore 1961, as diagnostic of the trachyleberids) as typically hemicytherid. Also, as stated before, Ruggieri (1962) expressed concern over

the difference in muscle scars included within *Bradleya* in attempting to place *Cythereis pliocenica*, which he had previously identified as *Bradleya dictyon pliocenica* (Seguenza) (Ruggieri 1959), and recognized its similarity (by implication) with *Bradleya semivera* Hornibrook.

**TRACING CHANGES IN SEVERAL CHARACTERS.**—It soon becomes evident that monothetic definitions (those that have both "necessary and sufficient" criteria) of this complex group will not suffice. Comparison of *Bradleya* and *Carinocythereis-Cistacythereis* species groups provide an interesting exercise of this point. *Bradleya* and *Carinocythereis-Cistacythereis* have muted muscle-scar nodes, both groups lack caudal processes, both have species with marginal and median carina (see Sissingh 1971 compared to illustrations in this report), both have species that tend to become "naked" (smooth with the loss of the reticulum), and both have hemiamphidont to holamphidont hinges. Yet the frontal scars and details of the reticular patterns (from what I can observe of the patterns shown in Uliczny 1969) are different. Through careful tracing of the development of these forms, it has been shown (Sissingh 1971) that *Falunia* is ancestral to *Cistacythereis* and *Carinocythereis*, and I believe that probably one of the forms described by Deroo (1966) as *Limburgina* (without divided adductors) is ancestral to *Bradleya*.

I believe that examination of the above evidence and the history of the study of this ostracode group shows how reliance on any one criteria can at best be provisional in the quest for the actual phyletic lineage in ostracodes.

**SUMMARY.**—From what may seem like increasing confusion with continued consideration of *Bradleya* comes the following observations of this history, added to the results of my own experience.

First, the assumption of relationship, based on similarity or differences of details in hinge structure (stressed heavily in the beginning, by Hornibrook) among ornate ostracodes with different shapes or muscle-scar patterns, can be misleading. The conclusion of Schweyer (in Pokorný 1957) that the hinge is immune to external selective environmental and convergent influences is not likely to be true.

The ornate cytheracean ostracodes, while having striking conservatism in soft parts, have a variable and complex external carapace morphology. This morphology, as presented in the past, does not lend

itself to classifications relying on the importance of a few characters. A polythetic analytical method (requiring analyses of variations in patterns, including those of hinge structure) is required for their understanding, and this will likely require many attempts at clustering (by inspection and numerical) similar species to form higher taxa rather than placing too much faith in one or two "important" characters to distinguish groups among a complex array of species.

Complexes of characters, such as muscle-scar patterns, have elements that are relatively simple and their changing state can be recognized. Although the arrangement of attachment of the adductor muscles are concerned with exerting mechanical advantage to the closure of the valves, they are still internal and may receive the same protection enjoyed by the soft parts. By the same token, the cells that are responsible for the formation of the carapace may be less subjected to change in relative position than is their activity toward the formation of stronger or weaker architectural shell elements. Tracing of their pattern, through mapping of their consequent patterns of reticulation, may result in simpler yet somewhat more conservative patterns than do the observations of the coming and going of keels, carinae, costae, ridges, etc.

Even more conservative may be the presence and distribution over the carapace of certain normal pores, whose canals transmit sensory responses from functional setae or possibly contribute to the balance of body metabolism. These pores are often associated with external surface conuli that may even be observed in reticulate ostracodes. It is possible to trace the patterns of their distribution from reticulate, smooth, and even to spinose or conulate forms. (For other remarks on this subject the reader is referred to van Morkhoven 1962, Hazel 1968, Plusquellec and Sandberg 1969, and Hanai 1970.)

There has been no general theory of development of the carapace to explain how its architectural modes (e.g., ribbed, reticulate, carinate) have become adapted to their habitats or how the carapace shape or ornament shape (which often are convergent in form) has served as a solution to existence. Without such a workable theory we must continue to be victim of every nuance of form, without a synthesis, in much the same way that Brady was. Certainly in consideration of the evolution of a genus we must allow for a history of invasion of different habitats of quite different substrate stability or temperatures. Also there may

be more than one solution to existence in a single habitat.

To resolve the status of *Bradleya* is to accept the primary nomenclatural importance of the type-species *Cythere arata* and begin again, only this time with a working theory of carapace form evolution. A new generic concept of *Bradleya* must be developed. *Bradleya* is a genus with considerable differences among species in the emphasis of the reticulum, from smooth to extremely robust. These differences are expressed as grades in emphasis of certain muri in several very important species in the deep sea, and those species restricted to the shelf regions of the western and southwestern Pacific.

*Bradleya dictyon* (Brady, 1880) is a distinctive psychrospheric species, which can be traced over much of the world ocean floor. How closely is it related to *Bradleya arata*? I will furnish evidence of the fact that it is closely related, by showing how the general shape and reticular pattern fits into the scope of the variation of form in the genus. The slight differences in hinge are no more than to be expected in different yet related species living in different habitats which have different strength requirements for closure of the carapace.

What is to be done with "*Bradleya*" *semivera*, whose trachyleberine frontal scar has been the concern of several authors? I will demonstrate that those characteristics that define "*B.*" *semivera* are similar to those of *Cythere radula*, *Cythereis pliocenica*, and *Cythereis hazelae*. These latter species together with several new species constitute a new genus (which may include *B. semivera* or is closely related to one that does) with a closer relationship to trachyleberid genera than to thaerocytherid genera, of which *Bradleya* is a member.

Lastly, in the systematic section I will present evidence that some of the forms identified in the past as *Bradleya dictyon* are species in their own right and one represents another new genus, which I have called *Poseidonamicus*. I will attempt to deal with some of the other misidentifications of *Bradleya* and to describe the ten new species that are in my collections.

### Morphologic Trends in *Bradleya* and *Poseidonamicus*

There are too many missing pieces of the puzzle to

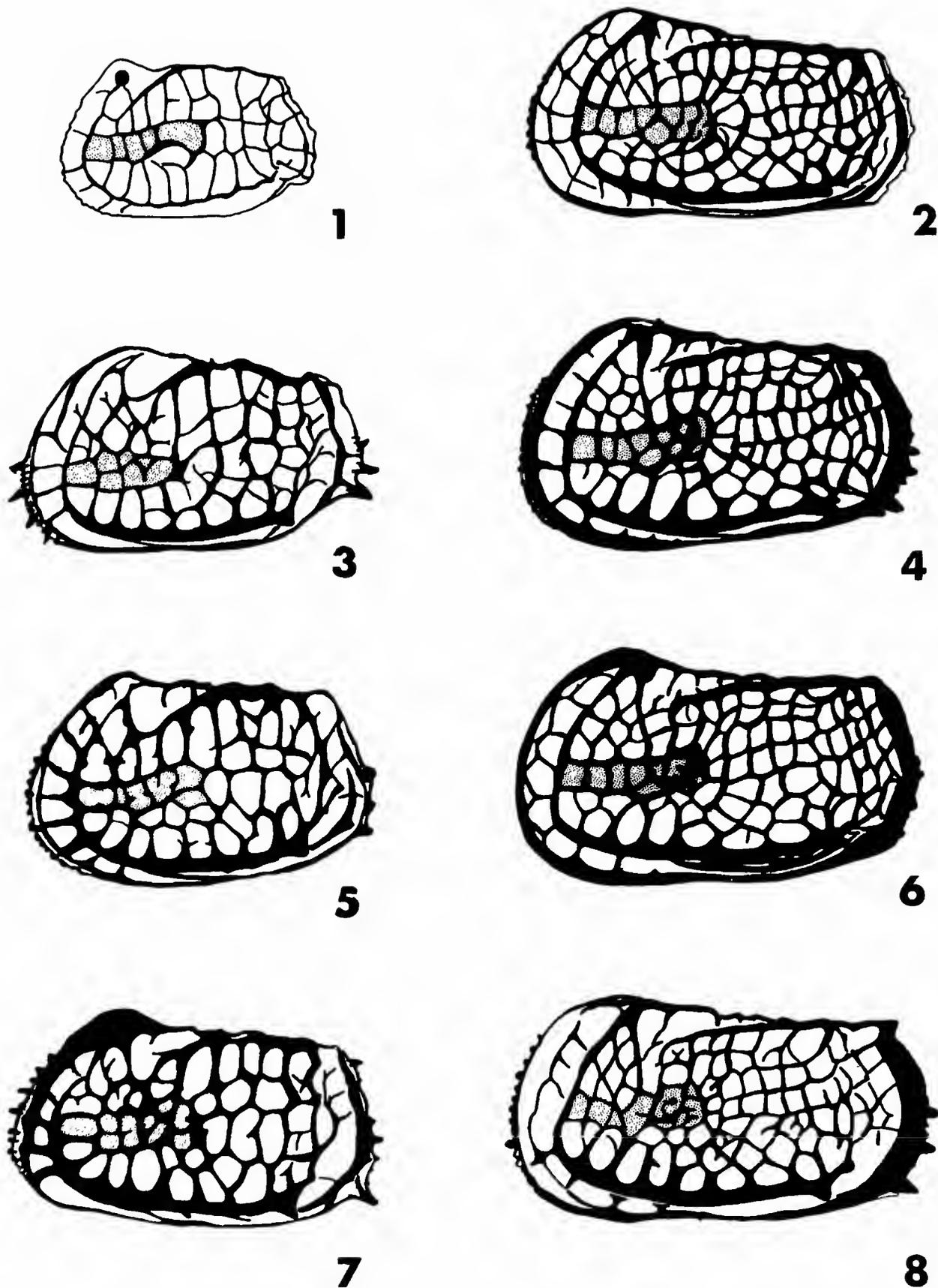
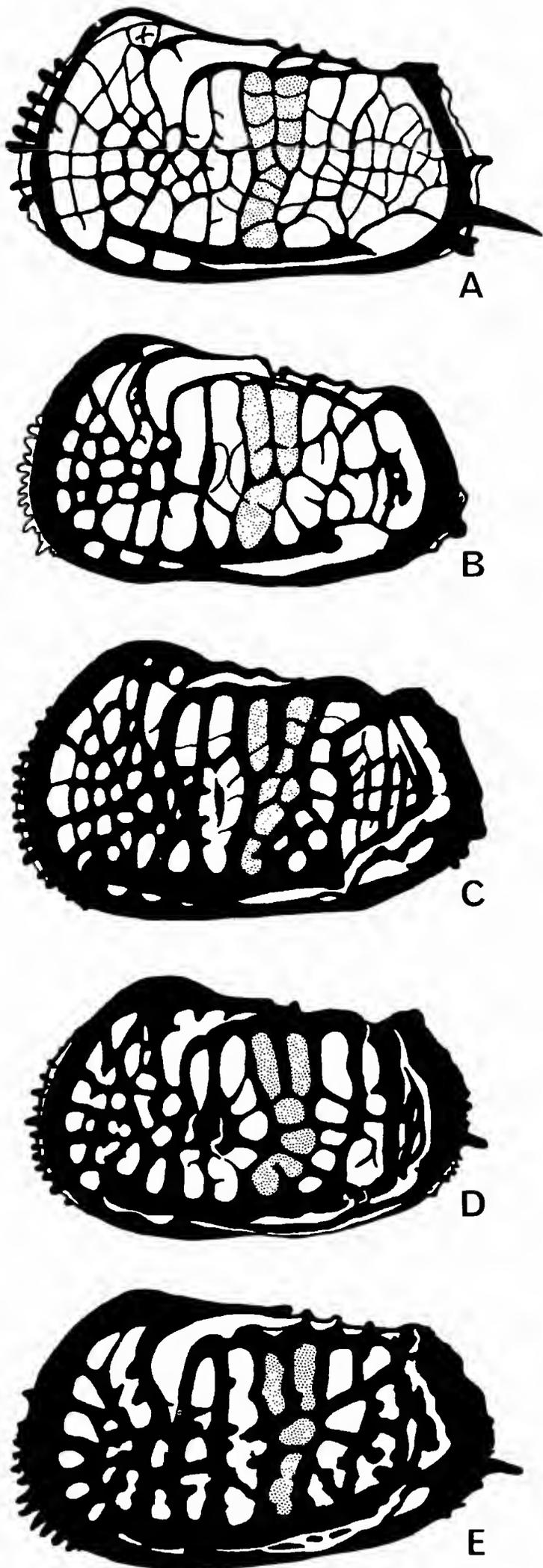


FIGURE 4. —Reticular silhouettes of various modern forms of *Bradleya* showing the consistency in the pattern of the reticulum and tracing the bridge structure (stippled area) from the small, coarsely reticulate species of *B. andamanae*, new species (Figure 4:1) through intermediate expressions of *B. normani* (Figures 4:3, 4:5) to larger forms of *Bradleya dictyon* with relatively thinner muri and with more fossae added. Specimens from the following station localities 1, OSS-01-255G, Andaman Sea; 2, IIOE 380C, Mozambique Channel; 3, *Anton Bruun* 766C, Peru-Chile trench slope; 4, ALB 2751, Caribbean Sea; 5, IIOE 374, Mozambique Channel; 6, ALB 3376, Gulf of Panama; 7, ALB 2817, Galapagos Island; 8, OSS 01-170L, Tasman Sea.



speculate on an evolutionary model for either of the genera *Bradleya* or *Poseidonamicus*, new genus, at this time, as I have later with *Agrenocythere*, new genus. These former genera represent both very widely distributed and very diverse groups. Eighteen species belonging to these genera (eight more in *Agrenocythere*) are discussed in this report (at least three more forms might have been considered, but I did not feel confident about their spatial or morphological relationships. It is possible to note some morphological trends suggested by the ones that are better known and which contribute to a theory of development for these groups of species.

First, although there are several exceptions, the species that have large individuals seem to occur in deeper waters and the smaller ones are found in shallower waters. This grade in size from larger to smaller with decreasing depth, and perhaps increasing mechanical agitation of the bottom, is often accompanied by an increase in shell robustness. An example of such a series would include *Bradleya dictyon* as a representative of the deep sea, *B. normani*, which ranges much more often into shallower slope habitats, and species such as *B. mckenziei*, new species, and particularly *B. andamanae*, new species, which are common to shallower shelf environments. One can imagine *B.?* *telisaensis*, if truly a *Bradleya*, to represent the ultimate in this sequence toward small strong adaptations.

The details of morphological change in this morphotypic series, which in the present discussion only correlates with an ecologic gradient (presumably also evidence of adaptive invasion), include the deletion or addition of mural elements from the reticulum, a change in the relative mass of the remaining muri, and consequently a change in general architectural

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FIGURE 5.—A series of reticular silhouettes of different forms of *Poseidonamicus*, new genus, including examples from the Recent of (A) Mozambique Channel (IIOE 366A), (B) the southeastern Pacific (ALB 4693), (C) the Tasman Sea (OSS-01-17OL), (D) the Pleistocene of the south Pacific (DWBG 74); and (E) South Atlantic (RC-8-91). The stippled portion refers to a homologous region in each form. This region is designated as a convenient reference but has no special morphological significance. The series shows a general increase in massiveness of the muri and the tendency of particular muri to be displaced. These particular species are not formally described in this report. This diagram is to show one direction of change among several possible in this group.

mode of the carapace. This process might be termed "mural accommodation" as the ridges seem to "trade off" responsibility in carrying the work load. A particularly interesting species to examine in this regard, and which represents an important link in the chain or series, is *Bradleya normani*. Two morphological variants of this species are shown on Plate 7: figure 8 and Plate 8: figure 6. Both forms are found in depths less than 500 meters. They come from very separate regions (Galapagos Islands and Straits of Magellan) where temperatures and exposure to water motion are quite different. It is not known why one form is more or less robust than the other. However, there is a difference in robustness and this fact alone suggests that adaptive change is occurring within this species. Notice how the fine muri of one form are absent in the other. In the second form the principal muri are much heavier than in the first. It is through such a shift that it is thought (Benson 1970) that the stress load is being shifted from one architectural solution in design to another.

Of course, it would be desirable to see this change in mural accommodation occurring along a single gradient in depth and bottom stability, but unfortunately such examples are hard to find with a morphologic series present. I have attempted a composite of grading forms of *Bradleya* taken from many parts of the world ocean and shown their reticular patterns in Figure 4. This series is composed primarily of *B. dictyon* (the deepest), *B. normani* (intermediate depths), and *B. andamanae*, new species (the shallowest). One can also see the changes in architecture much better in comparisons between species. The shift of emphasis from the major tricarinate design to a more parsimonious celate design (with fewer structural elements) is noticeable within the *Bradleya* (*Quasibradleya*) complex, a new subgenus (including four new species, *B. dictyonites*, *B. Prodictyonites*, *B. pliocarinata*, and *B. paradictyonites*). Although somewhat different in final result, the loss or gain of reticular structural elements that takes place between the almost totally smooth *Bradleya* species and coarsely reticulate forms constitutes a major replacement in architectural design.

A similar change in *Poseidonamicus*, new genus, from delicate to robust, as a consequence of mural displacement and enlargement (accommodation) is shown in the reticular patterns and silhouettes in Figure 5, and in the species of Plate 10. The progression

shown in the patterns generally represents adaptation to shallower or perhaps warmer waters. Notice the parallelism in development, that is mural accommodation, of the two new smooth species, one in *Poseidonamicus* and the other in *Bradleya* (*B. nuda* and *P. nudus*) in Plates 7 and 11.

The loss of eye tubercles with invasion of deeper waters is another morphologic trend. Eye tubercles are present in robust species, but seldom in the less coarsely reticulate forms.

It should be noted that celation (Sylvester-Bradley and Benson 1971), or the process of addition of a second, distally removed, outer layer to the shell, is an important development observed in many genera. *Bradleya arata* seems to be an extreme example of this process. The addition of a second floor, architecturally speaking, forms a sandwich shell structure in which the strength of the shell wall is carried through two lateral surfaces ("skins"), with increasing distance from the neutral axis of the carapace design. It is a lightweight solution to the problem of transference of strength. In an ostracode, whose decreasing rate of metabolism limits the amount of skeletal material being secreted in deeper or colder water (as with the change of number or position of major mural struts), this design also represents an efficient use of material. The concept of parsimony in design is very important here.

Lastly, notice the occurrence of the structure on the anterior lateral surface of *Bradleya* (referred to as the anterior reticular field), which I have called the bridge (Figure 9). This structure, common not only to *Bradleya* but particularly emphasized in *Jugosocythereis*, is composed of two parallel, elevated, sometimes ponticulate muri, with cross-member elements forming a truss that extends forward of the muscle-scar node. I believe that it acts as a major transferer of stress through resistance to compression (note that its elements are often columnar in cross-section) to distribute strength forward over an ever broadening surface or stress field. However, it is but one solution to the problem of stress in the overall anterior design. Another would be to simply add more mass to the carapace wall or a third might be to form a celate sandwich, or the outer shell just mentioned.

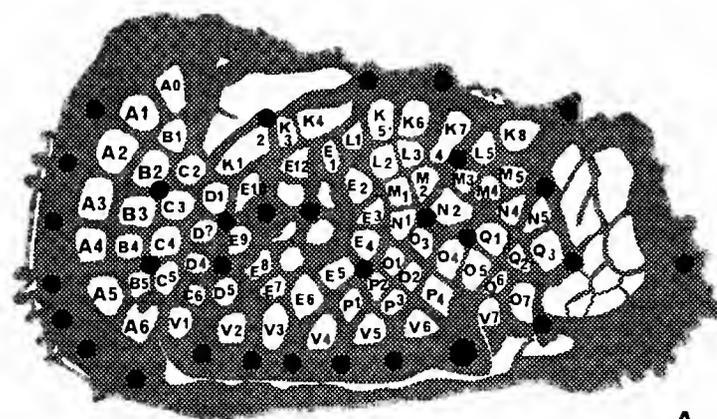
It is the consideration of these forms as structural alternatives which I believe allows us to explain how and why so many quite different shapes can occur in one genus or the same forms repeated among several

genera. Such theoretical consideration and examples of evidence set in a proper time frame will allow for eventual evolutionary model construction.

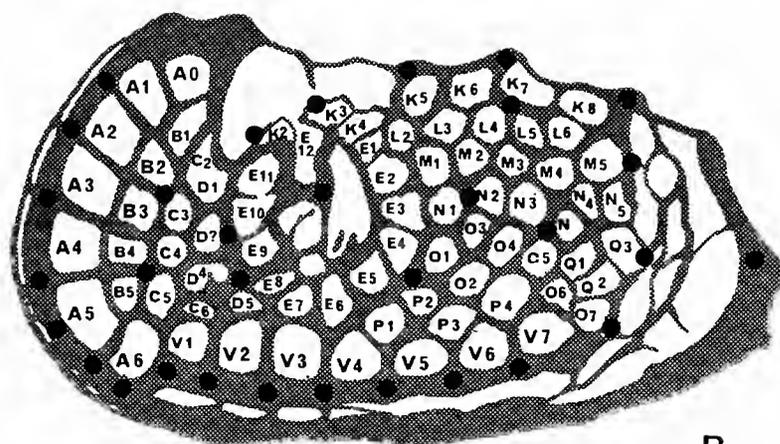
### Origins of *Agrenocythere*, *Bradleya*, and *Poseidonamicus*

The discoveries by Moos (1965) and Deroo (1966) of late Cretaceous and Paleogene species with frontal-scar patterns intermediate between those typical of thero-cytherids and trachyleberids, suggest that some genera of both families could have originated from the same stock in the Cretaceous. Similarities in reticular patterns can be seen between such diverse species as those frequently identified as "*Hermanites*", for example, "*H.* *haidingerii* (Reuss), *Limburgina* Deroo, *Trachyleberidea*, those of *Agrenocythere*, new genus, and *Oertliella aculeata* (Bosquet) (as shown in Figures 6 and 7) and even the form called *Cythereis zygopleura expressa* by Herrig (1969). The analysis of muscle-scar development, especially the frontal scar, as well as that of tracing similarities in the reticular pattern between modern and Cretaceous forms suggests continuity in both of these sets of features over a very long time (also see Liebau 1969 for comparisons of fossal patterns).

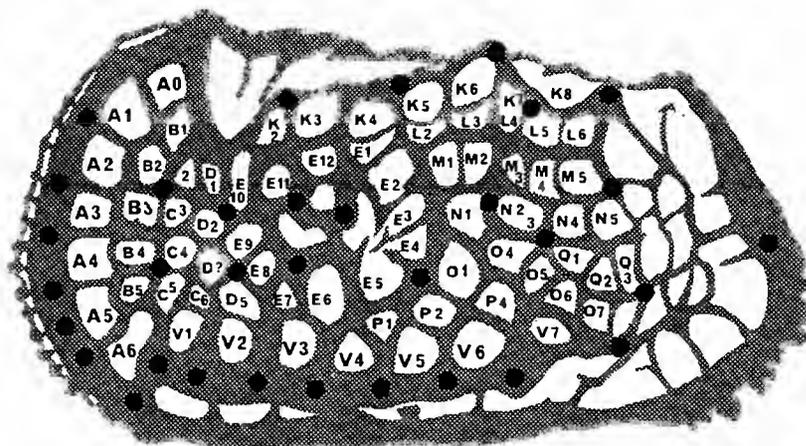
Evidence for the earliest appearance of *Agrenocythere* consists of specimens found in the Eocene of Italy, Trinidad, and from outcrops in submarine canyons along the Atlantic margin of the United States. The first two were first noted by van den Bold (1946) and Ascoli (1969) as "*Cythereis*" or "*Bradleya*" *hazellae* (now called *A. antiquata*) and the last by myself in this report. They are not typical of the deep sea in that they are smaller and more robust, suggesting that they may have come from upper bathyal in contrast to abyssal habitats. I have not found *Agrenocythere* in the fossil record of the deep sea floor in rocks older than Oligocene (Rockall Plateau, DSDP XIII, 117;



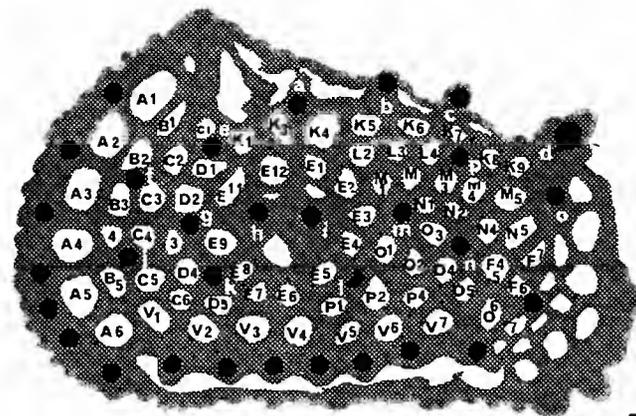
A



B



C



D

FIGURE 6.—Reticular silhouettes of (A) *Agrenocythere gosnoldia*, new species; (B) *A. americana*, new species; (C) *A. pliocenica* (Seguenza, 1880) female; and (D) *Oertliella aculeata* (Bosquet, 1852). The fossae (and the pore conuli of D) are coded according to Liebau's (1969) scheme, after which the latter form was constructed. Specimens from Hazel 2621C, ALB 2383 and ARL 446. These silhouettes were selected to show the consistency in pattern of the reticulum between geographic and possibly phyletically distant, yet related forms.

the problem of *Oertliella aculeata* (Bosquet) from the Eocene of Europe and its intermediate relationship is discussed later). Miocene specimens of *Agrenocythere* are relatively common, as are younger species.

*Agrenocythere* seems to be most similar to *Oertliella* which was first described by Pokorný (1964a) based upon a species (*Cythere reticulata* Kafka) from the upper Turonian of Czechoslovakia. (These similarities are discussed in detail on page 60.) The genera are sufficiently close to cause difficulty in assignment of some species, whose castrum (Figure 8) or dorsal ridge (bullar series) may be obscure or transitional. An example is *O. aculeata* (Bosquet) (Figures 61 and 62) whose reticular pattern is analyzed and compared with several of the *Agrenocythere* species using Liebau's method (Figures 6 and 7).

I have found a Paleocene (Thanetian) specimen of the new genus *Poseidonamicus* (an unnamed species from the South Atlantic; DSDP III, 21A) and one of *Bradleya* from the Upper Cretaceous (an unnamed species of the same area; DSDP III, 21; a single specimen with possible doubt about its original stratigraphic position). Neither of these specimens yields information suggesting the origins of their genera beyond what is known from younger and better preserved specimens. Both genera, known from the Oligocene of the South Atlantic and common to Miocene deep-sea samples and shallower species of *Bradleya*, are well represented from Eocene onwards in the Australian and New Zealand region.

In his description of the Upper Cretaceous (Turonian) form *Oertliella*, Pokorný (1964a) gives a brief passing remark about its resemblance to *Hermanites* Puri (not known by me to be older than Eocene), even though he did not know that the two had dissimilar frontal muscle scars (divided J-shaped in *Hermanites*, and V-shaped in *Oertliella*). The type-species of *Hermanites* (*Hermania reticulata* Puri; from the Miocene, Alum Bluff Stage, Chipola formation of Florida) has been poorly understood and is illustrated herein (Plate 1: figure 10) with a closely related older and better preserved form also shown (Plate 1: figures 11, 12). This predominantly Cenozoic genus may in fact be congeneric with, or include, the subgenus *Hornibrookella* Moos (1965) whose reticular pattern is similar. Its relationship to *Cletocythereis*, sensu stricto (see type-specimen of type-species on Plate 1: figures 1-4), is close, and represents a particularly interesting problem, which is discussed

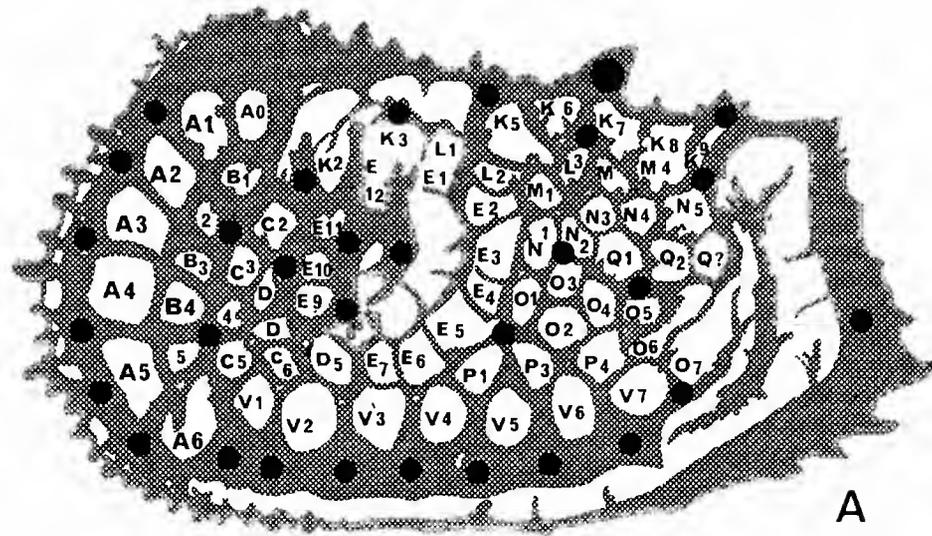
on page 22.

The problem of discrimination between these taxa results in part from the possible effects of shallow water (as suggested by Moos 1965) on not only modification of the muri, and consequently the number of elements of the reticular pattern, but also the possible division of elements within the muscle-scar pattern. Both Moos (1965) and Deroo (1966) clearly show fission of the frontal scar (as well as the uppermost adductor scar) forming a single upper and a U-shaped lower scar, leaving a residual V-shaped scar. This change takes place in *Limburgina* in the Upper Cretaceous (Maestrichtian) and is still evident in the lower Oligocene. Nevertheless, the fact of the change suggests that *Cletocythereis* (with a partially divided V-shaped frontal scar) could have evolved from *Oertliella* (V-shaped frontal scar) retaining the basic reticular pattern to become particularly adapted to shelf depth waters. *Hermanites* on the other hand may not be in the direct line of descent of *Cletocythereis*. It may instead represent a series of local shallow-water species whose development through *Hermanites* (*Hornibrookella*) *macropora* (Bosquet, 1852) may have produced other thaerocytherid genera. These would include *Thaerocythere* itself or a group of even more costate and smoother species, which are sometimes also identified as *Hermanites*.

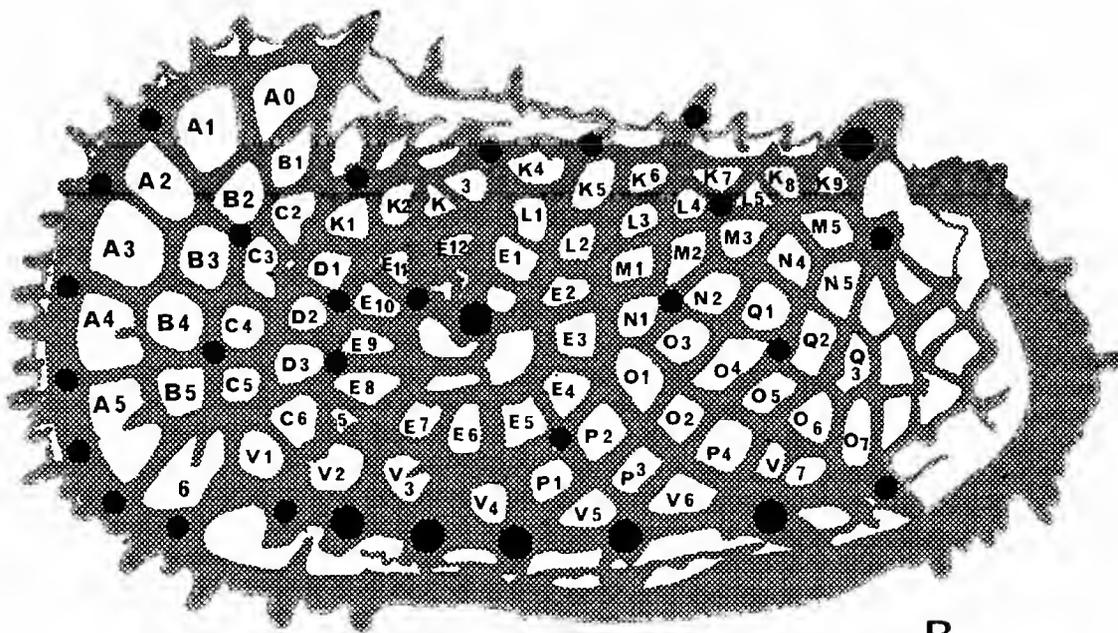
The place of *Bradleya* in this speculation is not clear (Figure 9). Some Maestrichtian species of *Limburgina* (as illustrated by Deroo (1966), such as *L. ornata* (Bosquet)) have a posterodorsal loop (shown better in Deroo 1966, pl. 23; fig. 719, than in Liebau 1969, pl. 2: fig. 1), an ocular ridge, and the general reticular pattern of earlier species of *Bradleya*; however, the subcentral tubercle of these earlier species is massive. The reticulum forms a castrum. There is no bridge (although Liebau 1969 has suggested one; it is less clear in Deroo's illustration). The similarity of some of Deroo's species (for example the Montian

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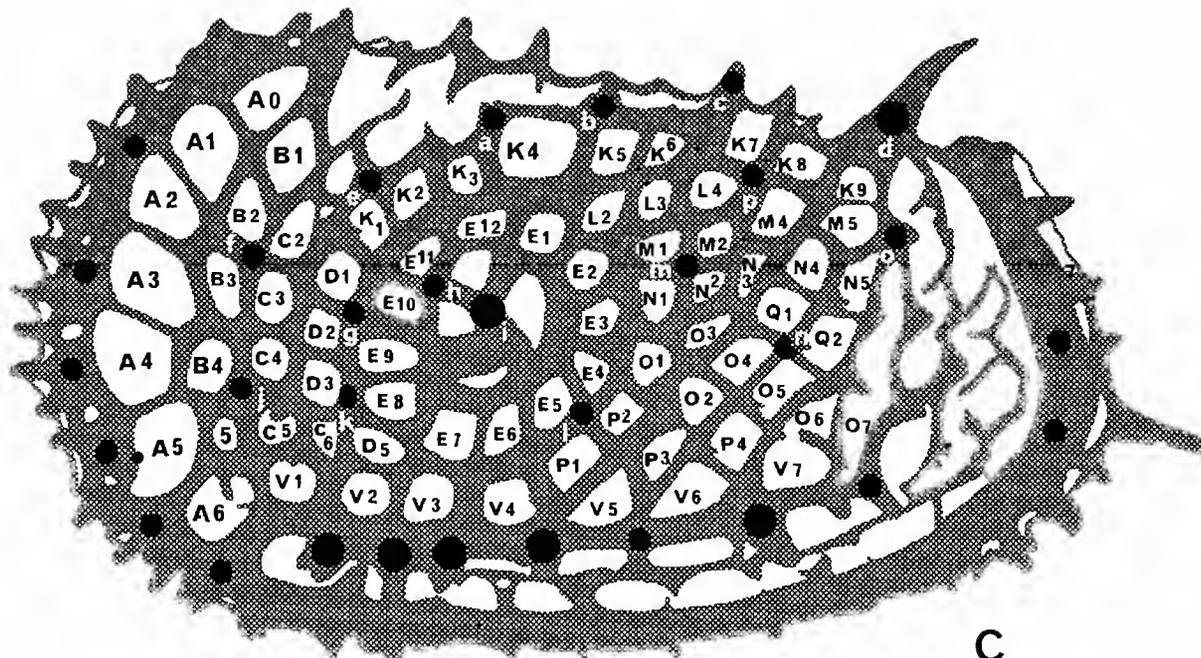
FIGURE 7.—(A) Reticular silhouettes of *Agrenocythere hazelae* (van den Bold, 1946) and (B) male and (C) female of *A. radula* (Brady, 1880). The fossae (and the pore conuli of C) are coded according to the scheme of Liebau (1969). Specimens from samples ALB 2751, IIOE 409A, and IIOE 363, respectively. These two species would appear to be the principals in the two lines of descent of *Agrenocythere*, new genus. Whereas their shapes and sizes differ considerably (even dimorphically) the patterns of the reticulum remain (except for minor differences) remarkably constant.



A



B



C

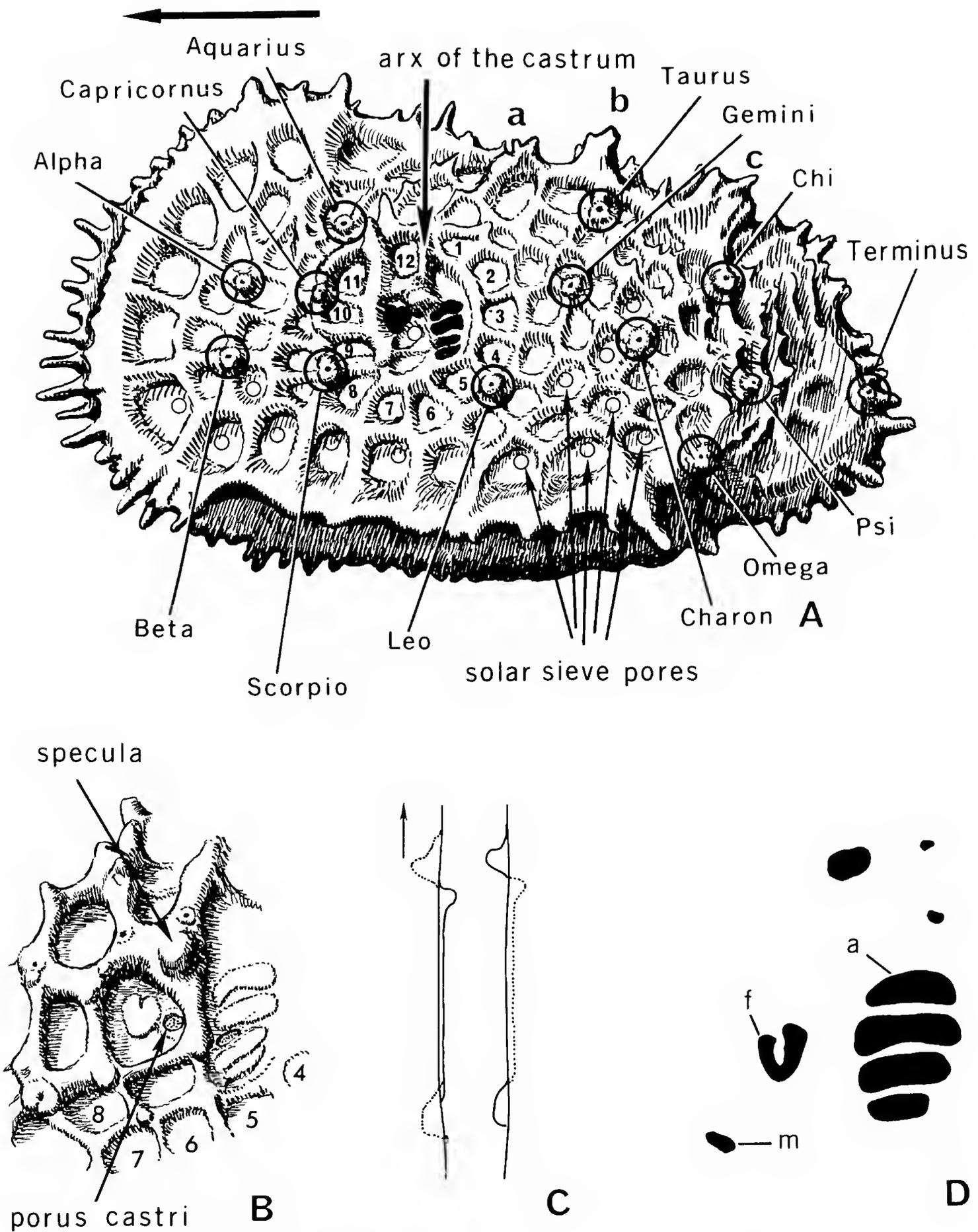


FIGURE 8.—Morphology of *Agrenocythere*, new genus: (A) The left valve of the carapace (arrow indicates anterior) showing reticulum (numbers indicating the order of ballial fossae within the castrum (1–12); see discussion on carapace morphology, p. 58). The principal pore conuli (indicated by zodiacal and Greek names), some of the solar sieve pores, and the dorsal bullar series (*a*, *b* and *c*). (B) The arx of the castrum (with part of the ballial series) showing the specula, the porus castri and the muscle-scar pattern (not arrowed). (C) A dorsal schematic drawing of the hinge (anterior arrowed). (D) The muscle-scar pattern with the mandibular (*m*), frontal (*f*), and adductor-scar group (*a*) indicated.

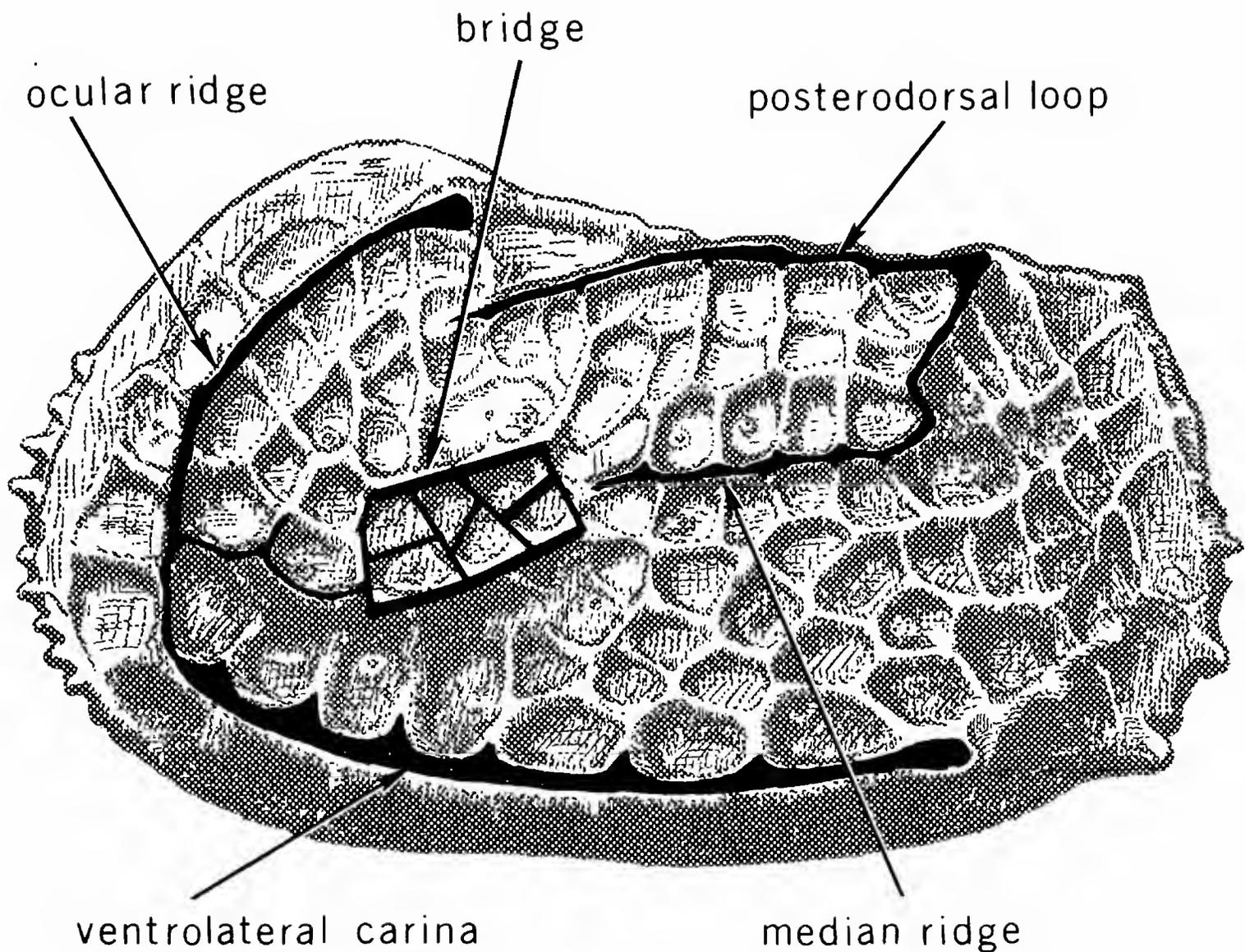


FIGURE 9.—The general morphology of the reticulum of *Bradleya*, showing its major elements, including the penecircumferential ocular ridge and ventrolateral carina, the bridge structure joining the muscle-scar node with the anterior reticular field, and the posterodorsal loop composed of the median ridge joined with the dorsal carina.

species *L. mauritsi* (Marliere)) to *Jugosocythereis* (common from the upper Eocene and Oligocene onward) is also apparent. The bridge as well as the eared posterodorsal loop is suggested in its reticulum. Certainly very little modification of any of those *Limburgina*-like forms or their immediate predecessors could have produced *Bradleya* in deeper waters, or for that matter as *Hermanites* in shallower waters. It is too early to trace this lineage with the specimens I have at hand. Liebau (1969) has proposed to do so, and his results should prove valuable.

*Poseidonamicus* is a very special case of reticular development. Its reticulum (Figure 10) has elements vertically aligned in the posterior with a massive anterior reticular field, no ocular ridge, and wide but suppressed dorsal and ventrolateral carinae. In some

species the reticulum is formed with a somewhat circular pattern of fossae around the region of the muscle-scar node, suggesting the relic of a castrum. I suspect that the ancestry of this genus reaches far back into the Cretaceous, perhaps even farther than that of *Bradleya* to its pre-*Limburgina* stock. Potential ancestors of *Poseidonamicus* from continental strata are unknown to me at this time.

In an even broader overview, I have suggested that *Cythereis* has a reticulum with elements and patterns similar to those of *Agrenocythere*. One can carry these comparisons to *Trachyleberidea* and *Limburgina* as Liebau (1969) has done. It soon becomes obvious that the solution to the problem of origins is to be found in the understanding of Cretaceous ostracode evolution. It may be demonstrated by identification of

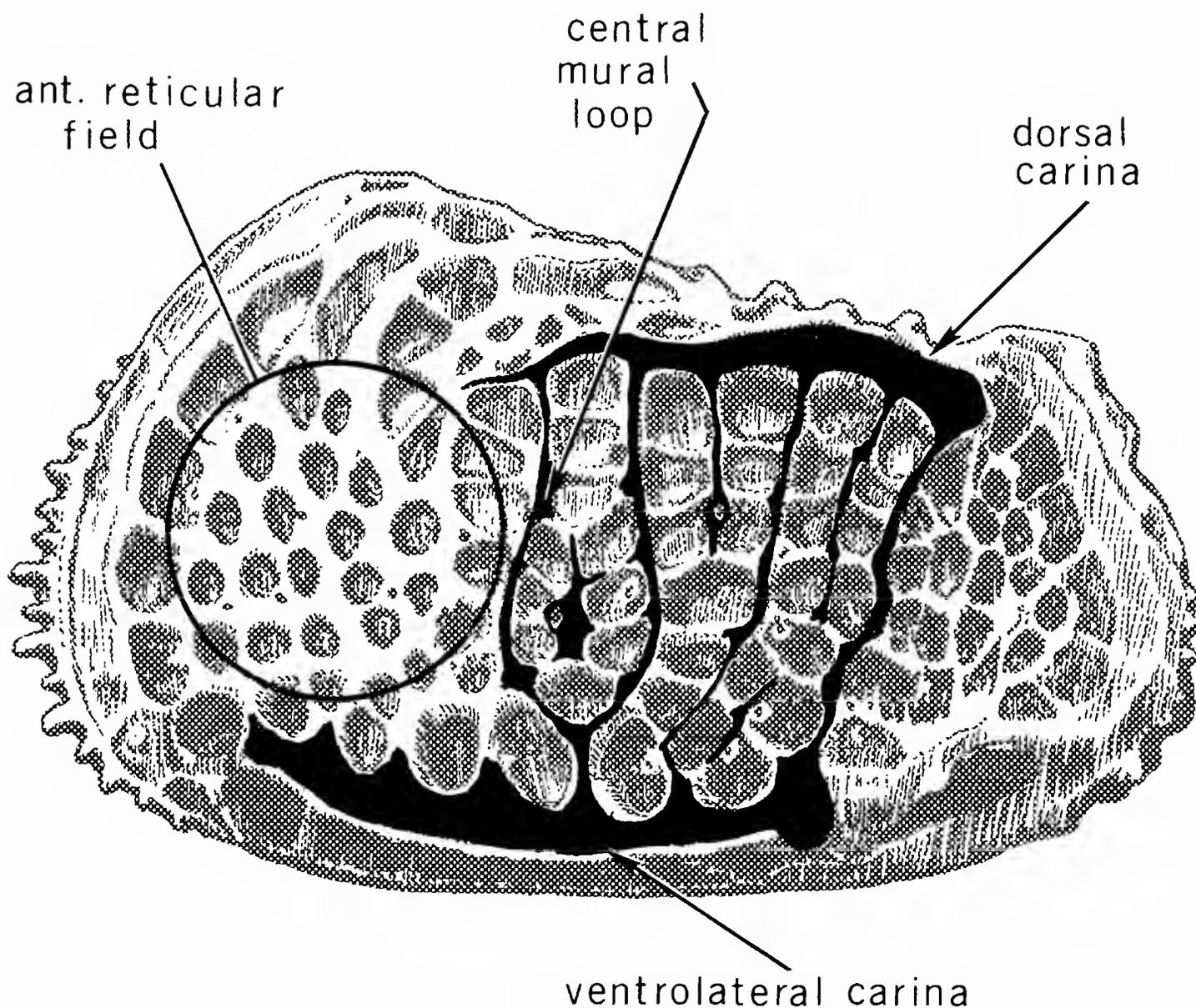


FIGURE 10.—The general morphology of the reticulum of *Poseidonamicus*, new genus, showing its major elements, including the massive punctate anterior (ant.) reticular field, and the vertical alignment of the muri and fossae of the central mural loop and the posterior reticular field between the dorsal and ventrolateral carina.

conservative reticular elements in carapace morphology among the many semireticulate species of this time interval. In summary there seems to be a convergence in both reticular patterns and muscle-scar patterns of *Bradleya* and *Agrenocythere* toward the reticulate ostracode complex of Late Cretaceous age that includes the genera *Limburgina*, *Oertliella*, *sensu stricto*, and *Cythereis*. One cannot help but wonder if some of the family level distinctions, which show up so clearly in Recent ostracode taxa, have validity or relevance as the taxa merge in the Cretaceous. Could not this stock group of forms represent a distinct taxon of higher rank?

An interesting problem, which quickly tends to get beyond the scope of the present paper, is the origin and the phyletic relationship of Swain's (1963) genus *Cletocythereis*. I have reillustrated one of Brady's several specimens of *Cythere rastromarginata* (the designated type-species; Plate 1: figures 1-4) from the *Challenger* report that were obtained from the reefs off Honolulu. I have included remarks about its description in several places herein and designated a lectoholotype (indicated by catalog number in the plate explanation and identified by its photograph). This genus is clearly not what Swain intended (Hazel 1967: 34), yet *Cletocythereis* is a genus in its own right. Of considerable interest is the fact that *Cythere*

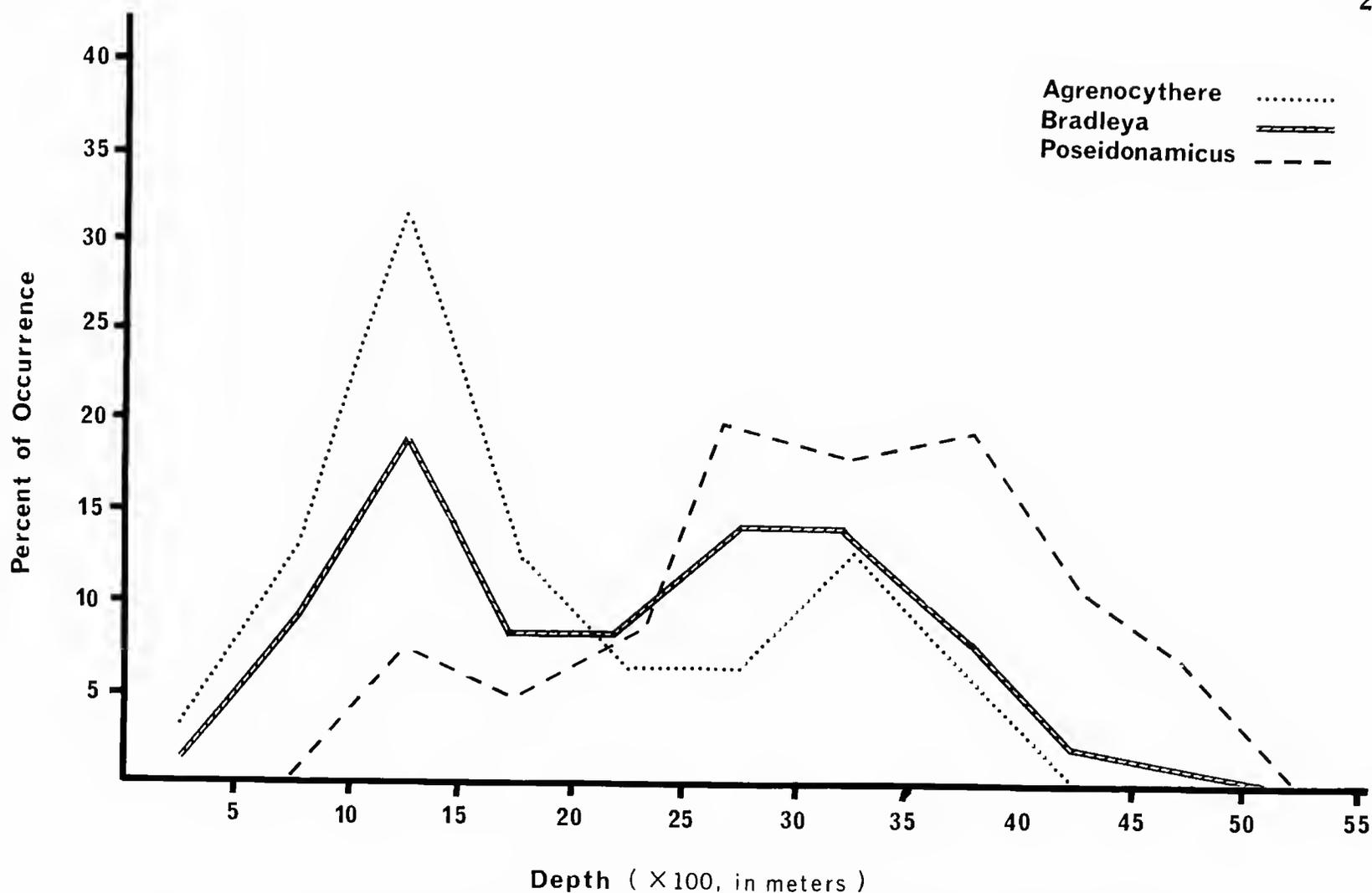


FIGURE 11.—Observed depth distribution of all Recent species of *Agrenocythere*, new genus, plotted as the likelihood of occurrence (relative percent) of samples found at a given depth interval (500 meters) extending from sea level to 4500 meters depth (based on 31 Recent samples), compared with the distributions of *Bradleya* (including only the species *B. dictyon* and *B. normani*, based on 80 samples) and *Poseidonamicus*, new genus (based on 85 samples).

(now *Cletocythereis*) *rastromarginata* has a fossal pattern very similar to that of *Oerthella reticulata* (Kafka); its reticular pattern differs by the very massive development of the dorsal and ventrolateral carinae and the absence of any noticeable ornament within the castral region. Especially important is the partly severed V-shaped frontal muscle scar (Plate 1: figure 4), which indicates the closeness of this genus to the trachyleberid line of development. This relationship is also suggested by its caudate posterior. (I have also included illustrations—Plates 1 and 2, of three other specimens of species not all named—of the genus *Cletocythereis* from around the world, including a topotype of *Cythereis haidingerii* Reuss to illustrate how widespread this morphological form has become.) Dr. Hazel has shown me *Cletocythereis*-like species from the Maestrichtian of Jamaica suggesting that this genus, like the others discussed herein, is very

long ranging. It could possibly be antecedant to *Hermanites*.

As stated in the introduction, the study of *Agrenocythere* has included a special problem of distribution as well as the description of the evolution of its species. These two subjects will be treated together in the following section.

#### Distribution and Evolution of *Agrenocythere*

Recent species of the new genus *Agrenocythere* described in this report have not been difficult to distinguish from other reticulate ostracodes. The conformation of the castrum seems particularly convenient for the discrimination among different species. With the exception of a few stations where both *Agrenocythere radula* and *A. spinosa*, new species, occurred together, no two species were ever found in the same sample. Recognition of relatively consistent forms of *A. pli-*

*ocenica* in Mediterranean Pliocene sediments has not been difficult compared to the difficulties often encountered in determining the variable ornate taxa of shallower habitats in the same region. It was this seeming distinctiveness and its apparent consistency that first attracted my interest. A form whose environmental distribution (for depth distribution compared with deep-sea species of *Bradleya* and *Poseidonamicus* see Figure 11) was well defined could provide a useful indicator of past changes in depth of considerable magnitude (Benson, n.d.c.), or the flooding of tectonically isolated basins by the psychrosphere (Benson and Sylvester-Bradley 1971; Benson, n.d.b.).

Therefore, it was disquieting, if not surprising, that this distinctiveness should become blurred in an attempt to find the origins of *Agrenocythere*. The characters that are used to distinguish among Neogene species are less distinctive among Paleogene forms. These same characters may be absent or confused in possible Cretaceous ancestors. In Figure 12 I have attempted to construct a possible model of the evolution of *Agrenocythere*. The model becomes increasingly problematic as the Mesozoic-Cenozoic boundary is approached. I have found that there may be several possible explanations depending on the weight of importance ascribed to changes in particular parts of the reticulum and on the increasing scarcity of evidence.

Only a few species of *Agrenocythere* are living today. They seem to be confined to two very separate geographic regions, the eastern Pacific and Caribbean-Gulf of Mexico region (referred to sometimes as the American Tropical Province), and the Indian Ocean (my sampling is poor in the Pacific). With one exception the species were neither indigenous nor unique to any one physiographic basin. *Agrenocythere hazelae*, extant since the Oligocene, now occupies parts of both the Atlantic (Caribbean Sea) and the Pacific oceans (near the Gulf of Panama); and the two species, *A. radula* and *A. spinosa*, new species, are found living concurrently in Mozambique Channel. *A. hazelae*, which seems to have become extinct in the Atlantic during the late Neogene (at least no Pleistocene or Recent specimens have been found), had its climax during the Miocene. It is found in Miocene sediments in the Caribbean, the Mediterranean, and the South Atlantic.

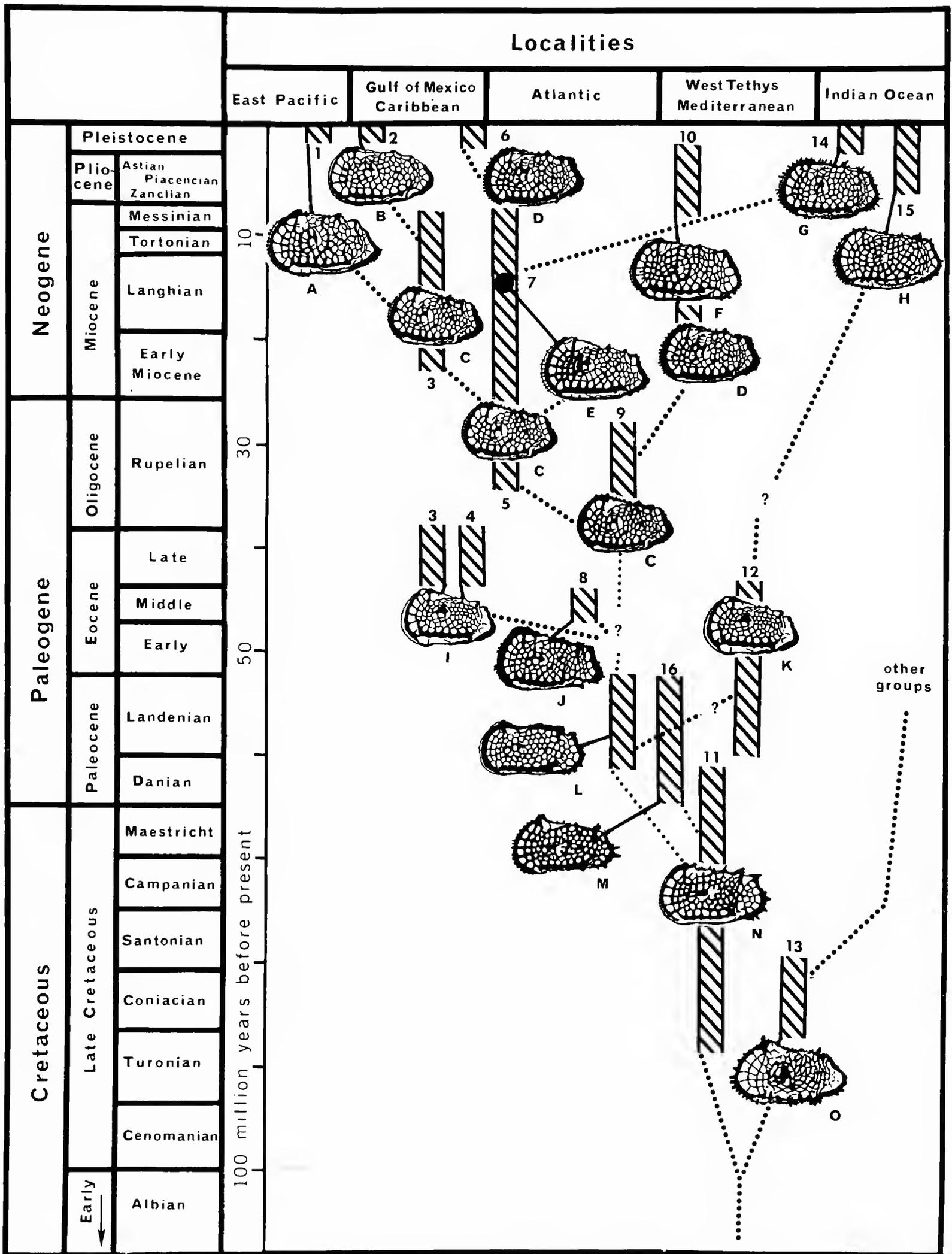
Through tracing of the several variations in the morphology of the castrum, it seems likely that *A. spinosa*, new species, evolved from *A. hazelae* as a

portion of this latter species invaded the Indian Ocean around the southern tip of Africa (probably during the late Miocene). The reticulum became more spinose or tuberculate, the arx more confined, and the reticulum less massive. Surprisingly, the part of *A. hazelae* that invaded the Pacific, ostensibly through a deep opening in the Panamanian or Columbian region, did not alter significantly from its parent form (except for an increase in size). I could not find sufficient morphologic justification for recognition of this Pacific variant as a separate species.

The relationship of *Agrenocythere pliocenica* to *A. hazelae* is not an easy one to postulate. Because the arx of *A. pliocenica* is divided on either side of the perval fossa and encompasses the fossa arcis and because of the formation of a parapectus near the Leopore conulus, I judge it to be more closely allied to *A. hazelae* and its derivatives than to *A. radula*. It is distinguished by its produced posterior, lack of accentuated dorsal bullae and general lack of definitive pore conuli. The illustration of a Miocene representative of *A. hazelae* by Ruggieri (1960, pl. 1: fig. 8) from Ragusano, southeast Sicily, shows a much greater similarity to the Atlantic form. (The specimens I have from the lower Miocene of Ancona, Italy—sent to me by Ascoli—are identifiable as *Agreno-*

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FIGURE 12.—Stratigraphic distribution and evolution of *Agrenocythere*, new genus, and related forms. Species (designated by letters) are as follows: (A) *Agrenocythere hazelae* (van den Bold, 1946) in the Pacific; (B) *A. americana*, new species; (C, D, E) Caribbean, Atlantic and Mediterranean geographic and temporal variants of *A. hazelae* (van den Bold, 1946); (F) *A. pliocenica* (Seguenza, 1880); (G) *A. spinosa*, new species; (H) *A. radula* (Brady, 1880) (I, K) *A. antiquata*, new species; (J) *A. gosnoldia*, new species; (L) *Oertliella ducassae*, new species; (M) *Oertliella aculeata* (Bosquet, 1852); (N) *O. reticulata* (Kafka, 1886); (O) *Cythereis ornatissima* Reuss, 1846. More precise locality information is given in Figure 3 and in Table 3 in the Appendix. For quick reference locality regions (designated by numbers) are as follows: 1, Malpelo Rize, eastern Pacific; 2, North continental slope, Gulf of Mexico; 3, Trinidad; 4, Cuba; 5, DSDP cores, South Atlantic; 6, Caribbean Sea; 7, Singular occurrence of an extreme form of *Agrenocythere hazelae* in the Miocene of the South Atlantic; 8, Submarine canyon outcrops in the continental shelf of eastern North America; 9, Rockall Plateau, North Atlantic; 10, Central Mediterranean (including the Ragusano, Sicily section); 11, Central and western Europe; 12, northern Italy; 13, Sicily and central Europe; 14, Mozambique Channel; 15, Western Indian Ocean and Indonesia. The dotted lines are suggested lines of descent.



*cythere*, but their preservation is poor.) The castrum of the Ragusano specimen is not clearly defined, but the dorsal bullar series is pronounced (suppressed in *A. pliocenica*), the posterior is acuminate and small (enlarged in *A. pliocenica*), and the reticulum is coarse (more like *A. hazelae*).

The Miocene *Agrenocythere* species in the Mediterranean is a very important link in the sequence of history of this region. As I have stated elsewhere (Benson, n.d.b.), the Pliocene psychrospheric ostracode fauna occurs directly above the evaporite series of the Messinian in the sea floor of the Tyrrhenian Basin. It is assumed therefore, that the Messinian represents a critical time in the evolution of Mediterranean psychrospheric faunas (which actually became extinct with the onset of the Pleistocene). From the present evidence, yet very incomplete, it would seem that open access to the Atlantic from the central Mediterranean existed during the early and middle Miocene. Whether or not the *Agrenocythere* survived the Messinian evaporite "crisis" in the Mediterranean, or reinvaded, remains a mystery. Because of the lack of evidence of gradual change from *A. hazelae* (known from Miocene sediments in the South Atlantic) to *A. pliocenica* it could be postulated that this considerable morphologic difference resulted from the severe adjustment required of the species to survive the Messinian crisis. This conclusion, however, is speculative until the psychrospheric fauna immediately below the evaporite sequence can be examined and described. Unfortunately, as yet, no specimens of *Agrenocythere* have been found in sediments of Miocene or Pliocene age from the North Atlantic to confirm or compare the nature of this contemporary fauna with that in the Mediterranean.

After having discovered that *Cletocythereis* has a nearly V-shaped frontal muscle scar, and realizing that its fossal pattern and that of *A. pliocenica* were very similar, I became aware of the possibility that *A. pliocenica* might be an extreme variant of the same lineage as *Cletocythereis haidingerii* or even from some unknown link with *Oertliella*. Enlarged and particularly accentuated forms of *Costa edwardsii* (Roemer, 1838) and *Chrysocythere* are known from the Mediterranean Neogene, and *A. pliocenica* could simply be a freak form with indigenous roots and without a connection with an Atlantic ancestry. My defense against these alternate hypotheses depends upon homologies in two features, the castral arx and

the dorsal bullar series. *A. pliocenica* has a well-defined, though centrally confined, arx with elements homologous with those of *A. hazelae*, and weak but definite indications of a dorsal bullar series. These features are absent in the other possible ancestral forms. Also these species have posterodorsal crests or massive ventral and dorsal ridges, which do not appear in *A. pliocenica*.

Although I examined many samples from the Pleistocene and several from the Pliocene of the central and northern Atlantic, I found no representatives of *Agrenocythere*. I do not consider this negative evidence conclusive, but implicit in this lack of discovery is the possibility that *Agrenocythere* may have become extinct in this region at the time of which the rate of fall in temperature was greatest. It may have survived only as species caught in confined and warmed basins, or in more open circulatory ocean systems with shallow rises or warmer currents such as the South Atlantic, Indian, and Pacific ocean areas. *Agrenocythere* survives in a very narrow temperature range (approximately 4° to 8° C).

The predecessors of *Agrenocythere hazelae* (probably going back to *A. antiquata*, new species) had less well-developed castral elements. The arx was more confined to the region of the specula and the pore conuli were pronounced (but not developed into parapecti along the circular rampart muri). A form intermediate between *A. antiquata* and *A. hazelae* of Oligocene age from Rockall Plateau (northeastern Atlantic) is shown in Figure 57. *A. gosnoldia*, new species, from the middle Eocene of the Atlantic slope of North America is small and massive with wide marginal rims and carinae. It is known only from one area and is quite distinct from *A. antiquata*, which ranges from the Caribbean and western Antilles region to the Mediterranean.

The castrum of *Agrenocythere radula*, so far known only from the Neogene of the Indian Ocean (including southern Indonesia), has the primitive aspect found in the ancestors of the *A. hazelae* group. I believe that it is a more primitive form and probably descended from the same ancestral stock as *A. semivera* (Hornibrook 1952, pl. 8: fig. 103; also see Plate 1: figure 5 of this report), the Paleogene, New Zealand species. *A. semivera* lived in shallow water and retained its eye tubercles. *A. ? cadoti*, new species, has many traits in common with *A. semivera* and may also be related.

In probing backwards toward the ancestors of *Agrenocythere* the characters that are used to define the younger species are lost or diminished. Those of other genera become paramount. Those of *Oertliella* or of the Cretaceous *Cletocythereis*-like forms or *Limburgina* become dominant. The patterns of the reticulation are retained, but the relationships are not clear. One of the characteristics of the younger forms is that they are all blind, presumably having invaded the darker waters of the deep sea and lost the need of sight. Their ancestors were not necessarily blind. They must have come from shallower waters, or at least had shallow water relatives which later evolved into forms to be quite different than the large ornate psychrospheric forms. Such "near antecedents" may be "*Oertliella*" *ducassae*, which I have described for the first time in this report (Figures 63–66), and *O. aculeata* also illustrated herein (Figures 61, 62).

### Systematics

The following hierarchic classification is used in this report:

- Subclass OSTRACODA Latrielle, 1806
  - Order PODOCOPIDA Pokorný, 1953
    - Suborder PODOCOPINA Sars, 1866
      - Superfamily CYTHERACEA Baird, 1850
        - Family THAEROCYTHERIDAE Hazel, 1967

### Family THAEROCYTHERIDAE Hazel, 1967

In 1967, Hazel proposed the subfamily Thaerocytherinae to receive his new genus *Thaerocythere* (using *T. crenulata* (Sars, 1866) as a type-species) and the genera *Jugosocythereis*, *Hermanites*, *Verrucocythereis*, *Quadracythere*, *Puriana*, *Aquitaniella*, and *Bradleya*. All of these genera contain species with strong hinges, four single adductor muscle scars (dorsomedian scar sometimes divided), and two discrete frontal scars. The first antennae have five podomeres, and the exopodites of the second antennae are well developed. He expressed the conviction that *Bradleya* together with the other genera, when dissections would be made, would anatomically be hemicytherid. In 1968, Hazel removed *Verrucocythereis* and questioned the inclusion of *Aquitaniella*, but he added Swain's genus *Cletocythereis* (which I would place elsewhere), and *Hornibrookella* Moos, 1965. To these latter genera I would also add *Procythereis* Skogsberg, 1928. I have

seen no specimens of *Martinicythere* Bassiouni, 1969, and can make no judgment about its inclusion.

I have elevated Hazel's taxon to have status equivalent to that of the families Trachyleberididae and Hemicytheridae in the belief that (1) the soft-parts are only in part similar to those of the Hemicytheridae (there are almost as many trachyleberid characters present as hemicytherid), and (2) because of a considerable number of genera with quite long geologic ranges, whose separate evolution is obscured under the old classification. Some groups within the thaerocytherids need to be recognized for their special attributes. One of these is given subfamily rank below. This elevation in rank of the thaerocytherines does not do special violence to Hazel's phylogenetic model; it only allows more room for recognition of relationships for which he had relatively few forms for comparison at the time it was suggested. Another consideration must also be mentioned. The phyletic lines of development are inseparable in the ancestral stock, which is early Paleogene and Cretaceous in age. This group could in fact be recognized as a fourth family, depending on the practical recognition of a horizontal versus a vertical classification. In either case the lines of descent seem sufficiently discrete to now warrant equal hierarchic rank.

Many of the generic characteristics present in the morphology of the carapace sculpture of deep-water ostracodes are adaptively modified in shallow-water marine species. This often obscures their phyletic and therefore their family or subfamily relationships. An example is found in the relation that is characteristic of the species *Bradleya arata* (Brady, 1880) the type-species of *Bradleya*. It is so strongly celate that the basic pattern, shown in the more murate relatives, is barely visible. Other examples in which carapace morphology is strongly and convergently modified are found in the two very important species (not thaerocytherid), *Hemicythere villosa* (Sars, 1866) and *Cythere lutea* (Müller, 1776). These species are both very heavily calcified, smoothed, and simplified. Their shells are highly adapted (strengthened and streamlined) to agitated sedimentary regimens and consequently their taxonomic relationships to other forms are obscured by the heavy calcification.

I see no reason to believe that fusion between the fourth and fifth antennal segments or the development of secondary reinforcement at the thoracic leg knee could not also be adaptive, like that of carapace

architecture. The increased cross-section of appendages of shallow-water marine species is characteristic of many shallow-water inhabitants. Some degree of caution should be exercised in the use of appendage morphology for family level taxonomic characters, especially when these strength modifications are involved.

I cannot help but suspect that the use of so many of Sars' or Brady's species as types of new genera and higher taxa is done out of an undeserved respect of the importance of soft-part morphology, or in the case of Brady, for the precedence of his work. In either case, there is not a sufficient appreciation for the significance of function and the selective pressures responsible for the special forms inherent in shallow-water ostracodes (not to mention the uncertain status of the carapace morphology of many of these species). Because the work of both Brady and Sars encompasses more than one hundred thaerocytherid species, the priority of the names they gave must be honored, but as will be shown in some of the subsequent discussion, the longevity of the name is not an indication of validity of the species concepts they label. The problems developed by the selections of *Cythere arata* Brady and *Cythere rastromarginata* Brady as type-species are cases in point.

I have added *Procythereis* Skogsberg to the Thaerocytheridae on the basis that species of this genus, i.e., *P. torquata* Skogsberg and *P. igandersoni* Skogsberg, both from Tierra del Fuego, have two frontal scars, reticulate to punctate carapaces, amphidont hinges with smooth to lobed posterior teeth, fused podomeres (iv and v) in the first antennae, and with complicate epipodites. I believe that the subquadrate shape of the carapace may in part result from adaptation to shallow high-energy habitats and that the patterns of their reticulate sculpture are also significant. I have studied topotype material of this genus and hope to report more fully on the description of this important Southern Ocean shallow-water genus at a later time.

### Subfamily BRADLEYINAE, new subfamily

TYPE-GENUS.—*Bradleya* Hornibrook, 1952: 38.

DESCRIPTION.—Thaerocytherid ostracodes with amphidont hinges, four single adductor muscle scars, perhaps with the uppermost divided, with two frontal scars, appendage intermediate between those of the Hemicytheridae and the Trachyleberididae, with

strong ventrolateral and dorsal carinae, a strong characteristic reticulum or its traces, and a blunt, noncaudate posterior. Cretaceous to Recent.

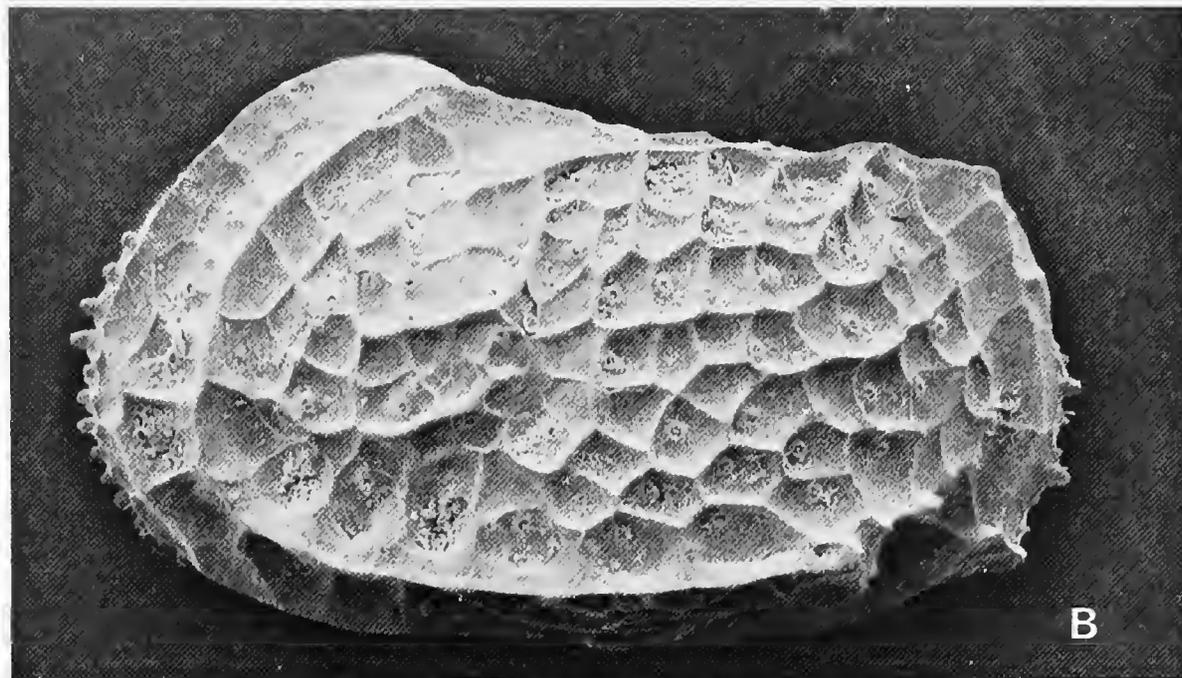
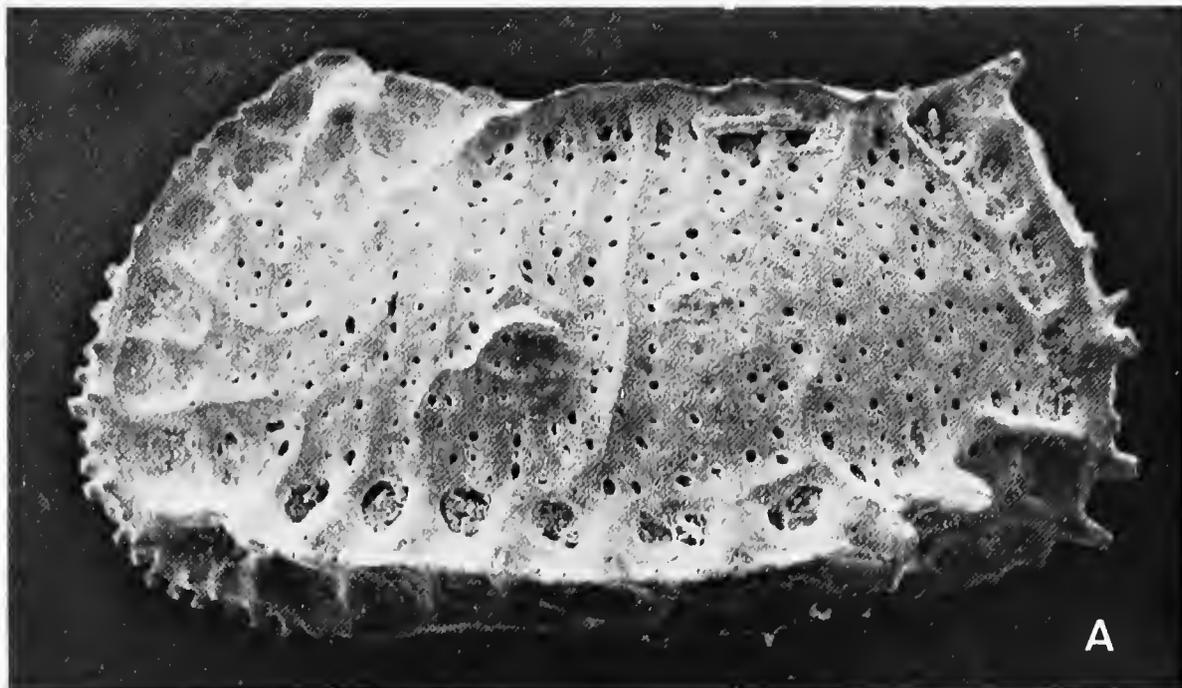
REMARKS.—At present this subfamily is intended to include the genera *Bradleya*, *Jugosocythereis*, *Quadracythere*, *Poseidonamicus*, new genus, and *Limburgina* Deroo, 1966, and the new subgenus *Quasi-bradleya*. The relationship of this subfamily to the rest of the taxa of the Family Thaerocytheridae, especially *Hermanites*, *Hornibrookella* (with divided dorsal adductor scars) and possibly *Curfsina* (Deroo 1966), is not certain at this time. However, I am reasonably confident that the five genera above share characteristics in common and their relationships warrant recognition. Of the questionable genera, *Hermanites*, sensu stricto, and *Hornibrookella* may be synonymous. The muscle scars of the types of *Hermanites reticulata* (Puri) are obscured by bad preservation. The frontal scar is divided with a U-shaped lower part, but I am less certain about division in the upper adductor scar. The reticular pattern is similar to that of *Hornibrookella*. I have shown *Cletocythereis haidingerii* (Reuss) to demonstrate their close similarity with the type-species *C. rastromarginata* (Brady). *Cletocythereis* would not, in my opinion, belong to this subfamily. I would add to the Bradleyinae a new yet undescribed genus, which would include "*Bradleya*" *oertlii* Ducasse (1964) from the Eocene of France.

### Genus *Bradleya* Hornibrook, 1952

*Bradleya* Hornibrook, 1952:38.—Keij 1957:97.—Benson 1959:63.—Reyment, in Moore 1961:Q336.—Morkoven 1963:158.—Ruggieri 1962:21.—Benson and Maddocks 1964:35.—Hartmann 1964:103.—Hazel and Paulson 1964:1057.—van den Bold 1968:67.—Russo 1968:23[19].

TYPE-SPECIES.—*Cythere arata* Brady, 1880: 101, pl. 24; fig. 2a-c. Originally described from the Tasman

FIGURE 13.—Three important previously described species of *Bradleya*: (A) *Bradleya arata* (Brady, 1880), from Recent near North Cape, New Zealand, USNM 174336; x115; (B) *Bradleya dictyon* Brady, 1880), from off northern Chile, see Plate 8: figures 7, 8 x100; (C) *Bradleya normani* (Brady, 1865), from off Peru, Eltanin station 48, lat. 14°11', long. 77°08'; 4000 meters; x115. These species exhibit special cases of development within the reticulum. *B. arata* is so grossly celate that only small openings or pores to the underlying fossae remain (also seen are foveolae). *B. dictyon*, generally the largest species, has thin delicate muri. *B. normani* with bold nonexcavate, caperate muri, has secondary, as well as primary, reticulation. (Compare also with Figure 14.)



Sea, lat. 39°32'S, long. 171°48'E, depth 150 fathoms (*Challenger* Station 167). Lectoholotype designated herein, specimen (British Museum, BM 154:9.4.1) is not figured in the present report (see discussion on page 33).

**DIAGNOSIS.**—Carapace subrectangular to subquadrate with broadly rounded anterior margin and squared posterior margin without noticeable caudal process; dorsal and ventrolateral carinae. Surface smooth to grossly reticulate with celate overgrowth (in the type-species); the reticular pattern is grid like rather than radiate and consistent within species, with variation due to increased coarseness of some muri and loss of others. Most species have traces of a bridge or box-girder construction (Figure 9) within the pattern of the anterior field of the reticulum, extending from the region of the suppressed muscle-scar node (absent in smooth forms) to the ocular ridge, which extends from the position of the eye tubercle (absent in blind species) to join with the ventrolateral ridge. In some species a median ridge, postjacent to muscle-scar node, is formed from emphasis of one set of longitudinal muri and may be joined with the dorsal carina at the posterior to form a posterodorsal loop. This feature becomes well developed as the lower element of the bridge decreases in size. Several species having this feature are considered together as the new subgenus *Quasibradleya*. Hinge hemi- to holamphidont commonly with a lobed posterior tooth; vestibule absent, duplicate broad. Muscle-scar pattern thaerocytherid with two frontal scars. First antennae with five segments (iv and v fused), epipodite with five "fingers," knee apparatus in thorassic legs, exopodite large in second antennae (Figures 15 and 16).

**AGE.**—Paleocene? Eocene to Recent. This genus was very important in the Neogene, especially in the deep sea. Although it is known to be common in the Paleogene fossil record of New Zealand, it is less common in Europe and very rare in the Paleogene of the western hemisphere. It has been reported in the past as ranging from Cretaceous to Recent (originally in Hornibrook 1952), but evidence of this older record has not been cited. "*Bradleya*" *semivera* Hornibrook, found commonly in the Paleogene of New Zealand, is not *Bradleya*. It is assigned herein to *Agrenocythere*, new genus, in a different family. The Paleogene species identified as *B. dictyon* by Hornibrook (1952) is not that species, but is given a new name *Bradleya* (*Quasibradleya*) *dictyonites*, new species, in the pres-

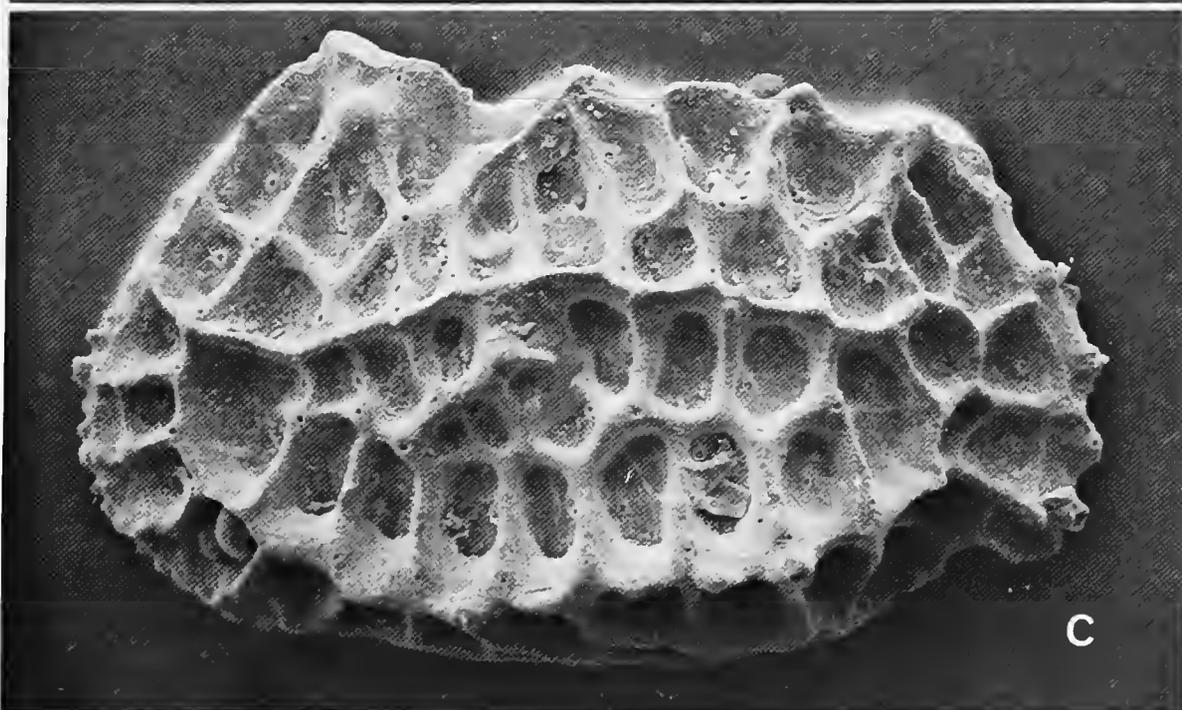
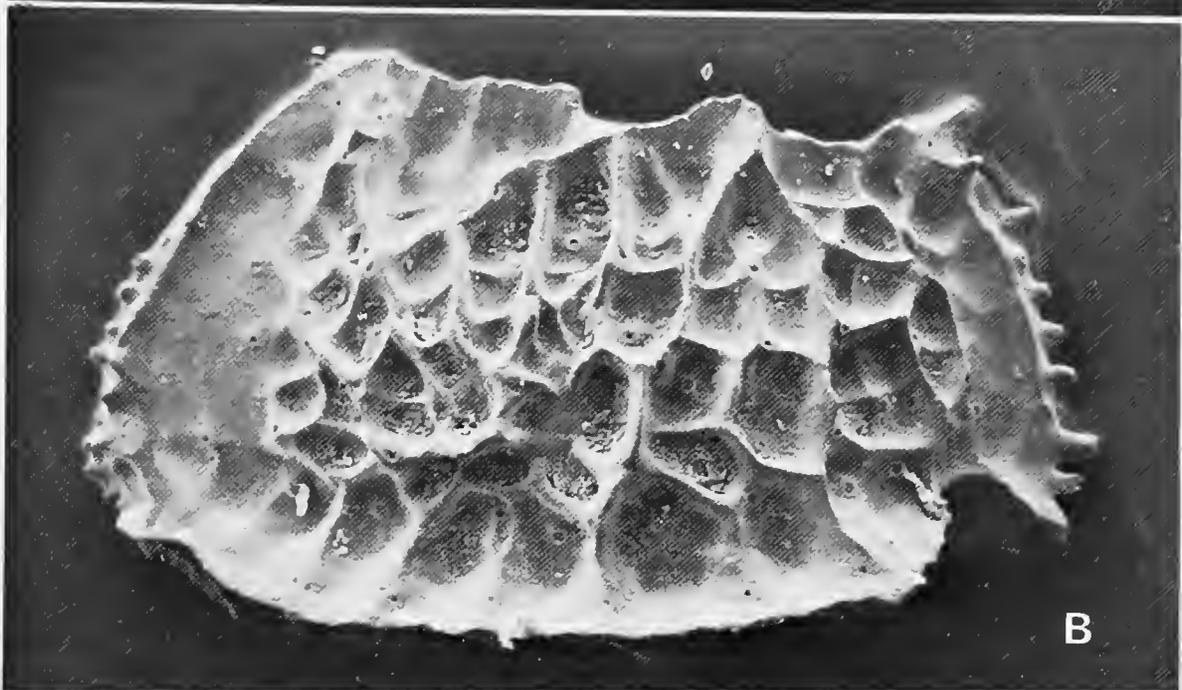
ent report. Depending on the significance of the evolution of the median ridge, several species related to this taxon are identified. This group is considered as the oldest known. The Eocene species called *Bradleya kaiata* by Hornibrook (1952) seems questionable and is excluded. Among those Paleogene species identified by Keij (1957) only *B. kaasschieteri* may belong to *Bradleya*. Van den Bold (1957) stated that *B. dictyon* had a worldwide range from Oligocene to Recent, but I can validate a range of Upper Oligocene (Chat-tian) to Recent in the deep-sea cores [DSDP III 22 (4, 2)] examined to date. A possible Paleocene *Bradleya* species (or possibly transitional between *Bradleya* and *Limburgina*) from New Zealand (sent to me by W. Briggs; Plate 1: figure 9) is given herein.

**REMARKS.**—As stated in the earlier sections devoted to discussion of the "*Bradleya* problem" and to the evolution of the concept of *Bradleya*, I prefer to restrict the concept to the type-species and those other species with characters traceable to the type (the alternative being to use the growing concept of *Bradleya* arising from usage). This includes *Bradleya dictyon* (restricted in the present work from Brady's broad inclusion of several species under one, and excluding Hornibrook misidentification, which actually includes several new species). Added to these two species are at least twelve more which include variations of carapace architecture that are derived from the more common and perhaps basic form of *Bradleya*.

The type-species *Bradleya arata* (Brady) is, as Brady suggested, unusual in surface ornament (Figure 13). Few ostracodes have the overgrowth of celate muri so extremely developed as does this form. What appeared to van Morkhoven as sieve-pore canals are actually the remains of the fossae that are otherwise closed by celation. In this form the patterns of the reticulum are masked, but the positions of the muri are still evident (as suggested in the drawings of Hornibrook). The reticular pattern becomes more obvious

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FIGURE 14.—(A) *Bradleya nuda*, new species, from the upper Pliocene of Japan; (B) *Bradleya japonica*, new species, from the Recent of Japan; and (C) *Bradleya andamanae*, new species from the Recent of northeast Indian Ocean (see Plate 7: figures 5, 3, 4, respectively, for locality and specimen data). These three enlarged photographs show homologous fine structures such as pore conuli that are traceable through a series of increasingly rugose ornamentation occurring in ever smaller specimens (magnifications x110, x130, x160).



in other species of *Bradleya* (Figures 13 and 14), and is very conspicuous in some of the small coarsely reticulate forms (Figure 14c). In others it diminishes as these species become truly without a reticulum except for a few mural traces. This is shown in the development of Japanese and Philippine Neogene new species, *B. nuda* and *B. paranuda* (Figure 14A; Plate 7: figures 5, 7) or possibly in Hornibrook's species *Bradleya proarata* (a questionable species from the evidence I have examined). In one species (*B. japonica*, new species) the reticulum is diminished in the anterior marginal region, while remaining robust, but confused, in the central lateral region (Figure 14B). Other variations of the reticulation are found in deep-sea forms, which become larger and more delicate. Some of these illustrated in Plates 7 and 8 are to be compared with the reticular patterns of Figure 4, especially the extremely small but robust form of *B. andamanae*, new species (Figure 14c).

Through examination of the variation of the reticulum, a range of expression becomes evident. This same range of from smooth to finely reticulate, to robust, celate, masked, and massive, is found in the carapaces of several other ostracode species groups besides *Bradleya*. For the present the decision of when or at what point a particular expression of reticular robustness becomes of generic value, is likely to be controlled by the accident of sampling or the absence of intermediate material for examination.

Hartmann (1964) included a new species, *B. reticulata*, in *Bradleya*. His specimens had soft parts, and his study served as a basis for the first attempt at diagnosis of this aspect of *Bradleya* morphology. Unfortunately, this species is not *Bradleya*, nor even thaerocytherid, but it is probably a shallow reticulate echinocytherid. A six-segment first antennae as well as his descriptions of the mandible are not applicable to *Bradleya*. The actual soft-parts of *Bradleya* are more severely modified and closer to those more typical of the hemicytherid end of the appendage morphotypic series found in cytheraceans. The appendages of *Bradleya dictyon* are described below (Figure 15 and 16).

Van Morkhoven (1963) doubted whether "*Cythere*" *dictyon* Brady, 1880, should be included in *Bradleya* because it displays a prominent third (median) lateral ridge and a more pronounced subcentral tubercule than is found in *Bradleya arata*, new species. I can only guess that he had the form of Hornibrook

(1952) erroneously identified as *B. dictyon* in mind (Plate 1: figure 8 or Plate 8: figure 4), and not those described or illustrated by Brady (1880) in the *Challenger* study. Only one of the Brady forms (similar to Figure 14c) could be construed as having a third ridge and this was questioned even by Brady, although perhaps for other reasons. The form chosen as the type for *B. dictyon* (lectoholotype designated herein; Plate 11: figure 18), from among the several options of Brady's included variations in form, is demonstrably part of the *Bradleya* carapace morphologic series.

COMPARISONS.—Of the presently described thaerocytherid genera of Oligocene and younger age, *Bradleya*, as now constituted, is most closely allied to *Jugosocythereis*. As the series of photographs of specimens in Plate 8 reveal, there are similarities in general shape and ridge configuration, as well as muscle-scar patterns. As suggested elsewhere, species such as "*Bradleya*" *oertlii* Ducasse and "*B.*" *kaasschierti* Kiej (Tertiary of western Europe) may constitute yet undescribed genera closely related to *Bradleya*. *Limburgina* of Late Cretaceous (Maestrichtian) age has species similar to some of the older *Bradleya* (*Quasibradleya*) species.

The relationship of *Bradleya* to *Quadracythere* is still vague to me, although the two genera have shape and muscle-scar characteristics in common. I have not studied the reticular patterns sufficiently well at this time to make a judgment.

*Bradleya* is related (but how closely is not sure) to the new genus *Poseidonamicus*, described for the first time in the present study. Both groups are subrectangular with rounded terminal margins and have carinae along the dorsal margins and the ventrolateral regions. Both are thaerocytherid with amphidont hinges. The principal ridges of the reticular patterns differ. The anterior region of the reticulum of *Poseidonamicus* is uniformly punctate (muri widened to the exclusion of the rounded fossae) without the bridge structure or the ocular ridge of either *Bradleya* or *Jugosocythereis*, and the fossae and muri of the posterior of *Poseidonamicus* are aligned vertically whereas those of *Bradleya* are more randomly, if not longitudinally, arranged. The muri of any given species of *Poseidonamicus* usually are uniform in height, although its species can range from very coarse to absolutely smooth (with only the ghosts of the pattern showing) as in *Bradleya*. This same kind of variation

in the strength of the reticulum, which is thus far notable in several genera, both emphasizes the need to trace its basic patterns as well as to form genera on the basis of coarseness or smoothness with utmost caution.

The new subgenus *Quasibradleya* consists of those species of *Bradleya* that have tended to replace the bridge structure of the reticulum with a stronger upper mural element (at the sacrifice of the lower) and have developed the median ridge of the posterior. This gives these forms a tricarinate appearance.

**SPECIES NOT BRADLEYA.**—These species have been incorrectly classified as *Bradleya* and should be assigned to other genera (not a complete listing).

"*Bradleya*" *saitoi* Ishizaki, 1963; possibly *Thaerocythere*.  
*Cythereis aurita* Skogsberg, 1928; a species of *Radimella*.  
*Cythereis pennata* Le Roy, 1943; *Jugosocythereis*?, probably a new genus.

*Cythereis diegoensis* Le Roy, 1943; *Ambostracon*.  
*Bradleya* sp. cf. *B. schencki* (Le Roy), in Benson, 1959; genus unknown.

*Bradleya kaiata* Hornibrook, 1952; genus unknown.  
*Bradleya reticlava* Hornibrook, 1952; possibly *Agrenocythere*, new genus.

*Bradleya semivera* Hornibrook, 1952; *Agrenocythere*.  
*Cythereis hazelae* van den Bold, 1946; *Agrenocythere*.  
*Cythereis pliocenica* Seguenza, 1880; *Agrenocythere*.  
*Cythere approximata* Bosquet, 1852; *Hermanites*.

*Cythere bosquetiana* Jones and Sherborn, 1889; genus unknown.

*Cythere cornueliana* Bosquet, 1852; genus unknown.  
"Bradleya" *oertlii* Ducasse, 1964; I have examined this unusual form and suggest that it, with "Bradleya" *kaasschierti* Keij, may be a new genus, possibly related to *Bradleya*.

"Bradleya" *kaasschierti* Keij, 1957; see above species.  
"Bradleya" *crassicarinata* Hazel and Paulson, 1964; genus unknown, with U-shaped frontal scar, possibly ancestral; Taylor Group, Campanian, Texas.

*Cythereis plummeri* Israelski, 1929; genus uncertain.  
*Cythereis hazardi* Israelski, 1929; genus uncertain.  
*Cythereis rugosissima* Alexander, 1929; genus uncertain.

**PROBABLE OR QUESTIONABLE SPECIES OF BRADLEYA.**—Because I have not seen specimens of the following species or found their characters to be different than originally described, these assignments could not be confirmed. In the case of *B. proarata* I have found only immature forms to be nude. What the adult form is like is still to be determined.

*Bradleya sendaiensis* Ishizaki, 1966; Miocene of Japan.  
*B. semiarata* Hornibrook, 1952; Miocene of New Zealand.  
*B. proarata* Hornibrook, 1952; Paleogene of New Zealand.

**SPECIES INCLUDED IN BRADLEYA.**—The following species are considered to be properly assigned to the genus *Bradleya*. These include three previously described species, of which one is the type and another whose type-specimen may be in doubt (*B. normani* (Brady)), and nine new species (one of which was previously described, but misidentified).

*Bradleya arata* (Brady, 1880); New Zealand and surrounding seas; Pliocene to Recent.

*B. dictyon* (Brady, 1880); deep-sea, cosmopolitan; Miocene to Recent.

*B. normani* (Brady, 1865); deep-sea of the Atlantic, southern and east Pacific Oceans; Neogene to Recent.

*B. albatrossia*, new species; China Sea; Recent.

*B. japonica*, new species; western Pacific, Japan; Recent.

*B. andamanae*, new species; eastern Indian Ocean; Recent.

*B. nuda*, new species; Japan; Neogene.

*B. paranuda*, new species; Philippines, western Pacific; Recent.

*B. mckenziei*, new species; Australian sector, Southern Ocean; Recent.

*B.?* *telisaensis* (Le Roy, 1939); Indonesia; Miocene.

*B. (Quasibradleya) prodictyonites*, new species; New Zealand; lower Oligocene.

*B. (Q.) dictyonites*, new species (for *B. dictyon* of Hornibrook); New Zealand; Oligocene.

*B. (Q.) paradictyonites*, new species; Tasmania; Oligocene-Miocene.

*B. (Q.) plicocarinata*, new species; South Australia; Miocene? to Recent.

**DIAGNOSES OF BRADLEYA SPECIES.**—For the present report, a brief summary of distinguishing characteristics is given for each of the species included in *Bradleya* with comparisons. The distributions and analysis of variation within the species are left for a future study.

### *Bradleya arata* (Brady, 1880)

#### FIGURE 13A

*Cythere arata* Brady, 1880:101, pl. 24: fig. 2a-c.

*Bradleya arata* (Brady).—Hornibrook 1952:39, pl. 6: figs. 80, 83, 86.

**TYPE-SPECIMEN.**—Brady failed to designate type-specimens, therefore a lectoholotype has been chosen and is hereby designated from among the few valves studied by Brady and one repositied with the British Museum. This specimen, BM 154:9.4.1, was originally separated from the rest of Brady's specimens in 1954 but was never established as the lectoholotype. In my opinion it is conspecific with recent specimens identified by Hornibrook from North Cape, New Zealand.

A specimen from Hornibrook's locality is illustrated here (Figure 13A) for comparison with a photograph of a lectoparatype (BM80.38.52) shown in this report as Plate 11: figures 16, 17.

TYPE-LOCALITY.—The species was described from only one locality by Brady, *Challenger* Station 167, in the Tasman Sea; lat. 39°32'S and long. 171°48'E, depth 150 fathoms.

AGE.—Pliocene (fide Hornibrook 1952) to Recent of Tasman Sea, New Zealand.

DIAGNOSIS.—Distinguished from other species of *Bradleya* by its strongly celate reticulum in which the muri have extended their uppermost or distal limits laterally to join and seal the fossae (except for multiple openings that resemble normal pores). The primary pattern of the reticulum remains evident, however. Traces of its extent are visible as smooth lines in between densely scattered foveolae that cover the outer tegmental layer; with eye tubercles and living on the outer shelf.

COMPARISONS.—*Bradleya arata* is unique among *Bradleya* species, in the extent of merger of its celate muri. On superficial inspection it could be mistaken for *Bradleya nuda*, new species, *B. paranuda*, new species, or *B. proarata*, species with almost smooth surfaces. *B. arata* has a short longitudinal ridge over the region of the muscle-scar node. This ridge is all that remains of the upper element of the bridge. Hornibrook described *B. proarata* and *B. semiarata* from the Paleogene of New Zealand which he considered as closely allied to *B. arata*. These are described as smooth with numerous pores. They both have eye tubercles as does *B. arata*. The Eocene specimens of *B. proarata* I have for examination are immature instars and not well preserved. It is not possible to determine whether they are celate or simply smooth with solid carapace walls like *B. nuda*. I believe this distinction is important and the apparent smoothness of *B. arata* is convergent with that formed by the disappearance of muri as shown in *B. japonica*, new species, and in *B. nuda*.

### *Bradleya dictyon* (Brady, 1880)

FIGURE 13B, PLATE 9.

*Cythere dictyon* Brady, 1880:99, pl. 24: fig. lh-i, l, o, p, s, t, u [not a-g, j, k, m, n, q, r, v-y].—Brady and Norman 1889:152, 244.

?*Cythere dictyon* Brady.—Chapman 1906:109; 1910:433;

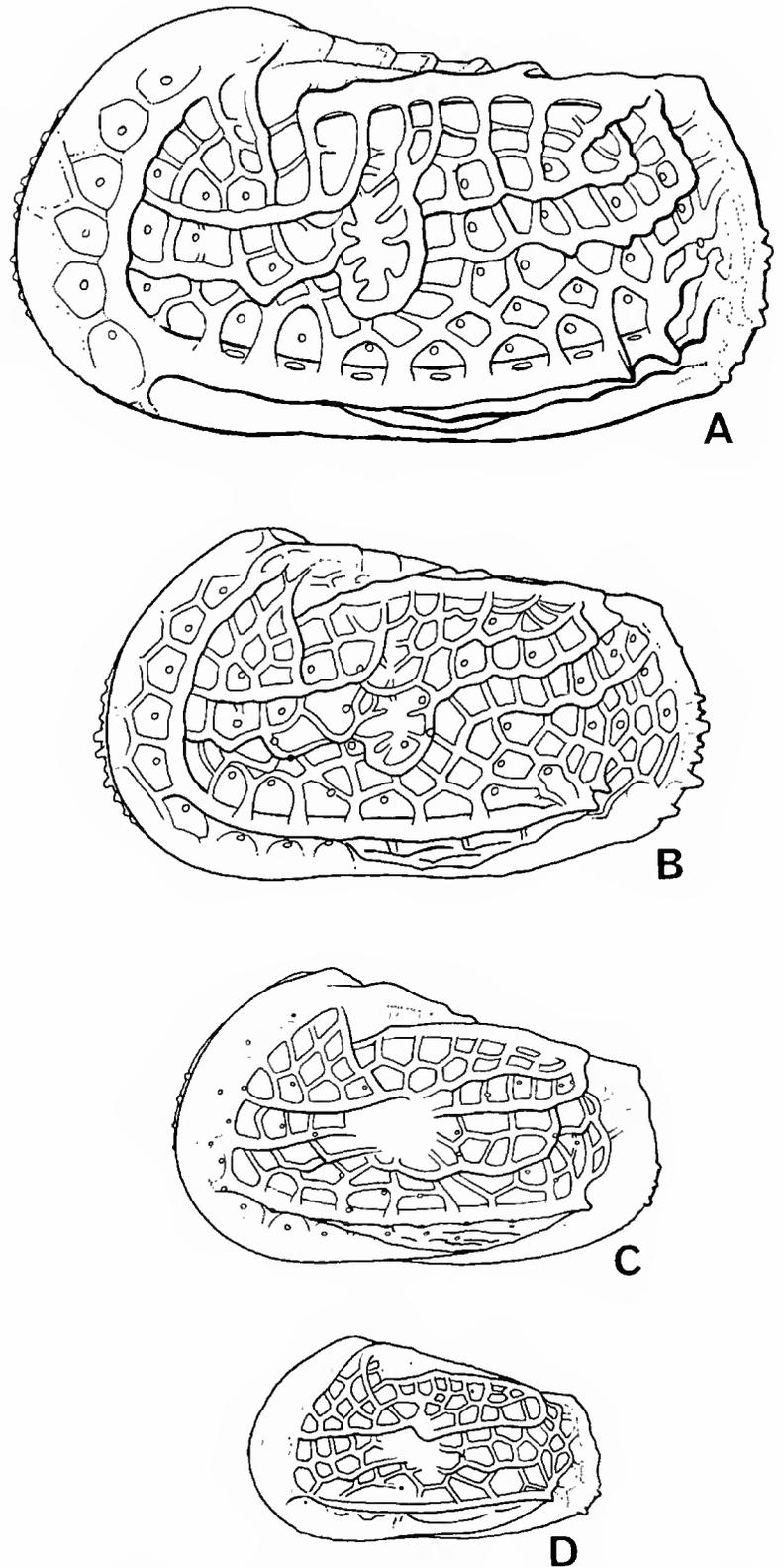


FIGURE 15.—A series of four instars of *Bradleya dictyon* (Brady, 1880) showing changes in emphasis of some of the muri in the reticulum with maturity: (A-C). The larger three stages including the adult stage; (D) The smallest is judged to be about the fourth stage before maturity. Comparison shows the disappearance of a posteromedian ridge and posterodorsal loop (B and C) the perpetuation of parts of the bridge structure, and the appearance of the ocular ridge (B) to join the anterior of the ventrolateral ridge. Specimens from the eastern Pacific near Panama, *Albatross* station ALB 3376; USNM 174378.



FIGURE 16.—*Bradleya dictyon* (Brady, 1880), dissection of a male: (A) the second antenna with a long exopodite (ex); (B) the first antenna with fused segments v and vi; (C) the copulatory apparatus, and (D) the maxilla. Same specimen as Figure 17, USNM 174382, 174383. From Eltanin station 63 off the Chilean coast, lat.  $25^{\circ}44'S$  and long.  $70^{\circ}58'W$ ; depth about 1900 meters.

- 1914:34, pl. 7: figs. 12, 13; 1915:41; 1919:25.—van den Bold 1957:241.—Tressler 1954:435.—Egger 1901:442, pl. 6: figs. 41, 42.—Guppy 1921:128.  
 Not *Cythere dictyon* Brady.—Chapman 1926:101, pl. 21: fig. 7.  
 Not *Trachyleberis dictyon* (Brady).—Keij 1954:222, pl. 4: fig. 9.  
*Cythereis* species.—Tressler 1941:101, pl. 19: figs. 18, 19.  
 Not *Cythereis dictyon* (Brady).—van den Bold 1946 [fide]: 90, pl. 10: fig. 13.—Kingma 1948:80, pl. 9: fig. 8.  
 Not *Cythereis dictyon* (Brady) *pliocenica* (Seguenza).—Ruggieri 1953:78, pl. 2: figs. 10, 11.  
 Not *Bradleya dictyon* (Brady).—Hornibrook 1952:39, pl. 6: figs. 81, 82, 84, 85.—van Morkhoven 1963:160.  
 Not *Bradleya dictyon* (Brady) *pliocenica* (Seguenza).—Ruggieri 1959:176; 1960:4, pl. 1: fig. 5.  
 Not *Cythereis* (*Pterygocythereis*?) *telisaensis* Le Roy 1939: 275, pl. 11: figs. 9–16.

TYPE-SPECIMEN.—A lectoholotype; an adult, left valve, is selected and designated herein. Brady (1880) chose no type-specimen, nor have subsequent workers. The specimen in the British Museum *Challenger* material (BM 1961.12.4.32a) is illustrated in this report in Plate 11: figure 18.

TYPE-LOCALITY.—North Atlantic in the vicinity of *Challenger* Station 78 (lat. 37°24'N and long. 25°13'W, 1000 fathoms).

AGE.—Lower Miocene to Recent; southern hemisphere and central Atlantic.

DIAGNOSIS.—Distinguished from other species of *Bradleya* by its large size and delicate to only moderately robust, generally foveolate reticulum. The dorsal carina is poorly developed; two prominent muri extend from the region of the obscured muscle-scar node toward the ocular ridge forming a bridge. Often with large celate solar sieve pore canals. Blind and confined to the psychrosphere.

COMPARISON.—Often in the past this species has been confused with others. As presently conceived, *Bradleya dictyon* is a very common and widespread deep-sea ostracode species. I have had few occasions on which recognition of Neogene specimens was a problem. It is larger, more delicate and more elongate than *B. normani*. The bridge is well formed but not of great relief. The longitudinal ridges or upper and lower elements of this girder-like structure are almost always apparent. It is more reticulate than *B. arata*, *B. nuda*, new species, or *B. paranuda*, new species, whose solar pore canals are obscured. It lacks the median ridge characteristic of *B. andamanae*, new species, or the subgeneric *Quasibradleya* group of new species *B. prodictyonites*, *B. paradictyonites*, *B. dic-*

*tyonites*, or *B. pliocarinata*. It retains the mural elements of the basic reticular pattern which is simplified in *B. mckenziei*, new species, *B. japonica*, new species, or *B. normani*.

DIMENSIONS.—The smaller lower Miocene specimen (Plate 8: figure 7) is length 1.02 mm; height 0.65 mm; the larger Recent specimen (Plate 8: figure 8) is length 1.41 mm; height 0.86 mm.

REMARKS.—Brady in the original study (1880) of *Cythere dictyon* confused at least three species of two genera in his identifications. Because he did not designate types for any of the *Challenger* ostracode species, there is no way to know which of these several forms he considered paramount in importance for the formation of his original species concept. Later authors were unsure of Brady's intentions, and because his illustrations are wanting in detail and specimens such as he described have been rarely found since, misunderstanding of the taxon increased. Now with the acquisition of abundant samples of deep-sea species, it becomes necessary to begin again to sort out the different forms of his very diverse group.

As indicated in the synonymy I have accepted very few of the many identifications of *Bradleya dictyon* made by others. A case might have been made for selecting a type to conform to a majority usage of the term *dictyon* if in fact such a usage had existed, but it has not. The major advantage of the present decision of strict usage is (1) it agrees with an important one of Brady's several possible forms, (2) it includes most of the misidentified forms in the same genus, and (3) it represents a very widespread and abundant deep-sea ostracode population.

If Chapman (1906–1941) correctly identified *Bradleya dictyon* in his many reported finds (for which few illustrations were given), there is no evidence of this fact short of restudying his collections. I have not done this as I did not believe that this data, considering the accuracy of its collection, would add significantly to my own about the knowledge of the distribution of this species.

Kingma (1948) stated that his specimens, together with those of van den Bold (1946) from the Oligocene of Cuba and Seran and those of Le Roy (1939) from the Tertiary of central Sumatra (called *Cythereis* (*Ptergocythereis*?) *telisaensis*), are all identical. If so, then his is not *Bradleya dictyon*. Le Roy's species, valid in its own right, is discussed and illustrated elsewhere in this report.

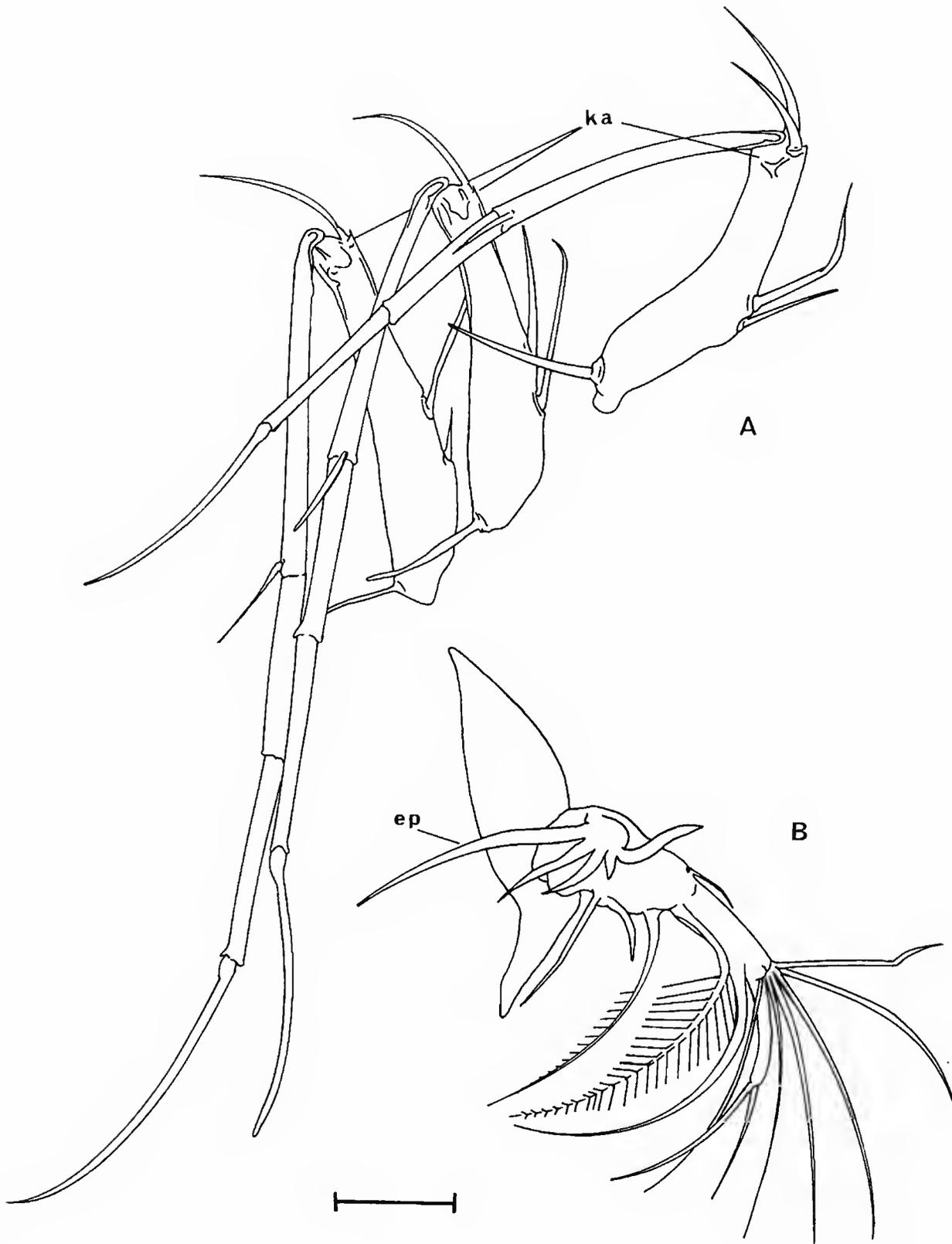


FIGURE 17.—(A) The thoracic legs showing the knee apparatus (ka), and (B) the mandible showing the five-“fingered” epipodite (ep) of *Bradleya dictyon*. Same specimen as in Figure 16.

The subject of Ruggieri's (1953, 1962) concern, Seguenza's species *Cythereis pliocenica*, which he thought could be *Bradleya dictyon*, is shown elsewhere to be of a different species of a different genus and family. Similarly, Hornibrook's (1952) form is shown to be representative of a species complex (constituted as a subgenus of *Bradleya*, i.e., *Quasibradleya*) characterized by a strong median ridge (now called *B. (Q.) dictyonites*, new species) having a distinctive tricarinate aspect.

I am less certain of the correct identification of van den Bold's (1957) forms, but I suspect that the coarse reticulate species he has considered *dictyon* is *normani* or a Caribbean antecedent.

Tressler (1941 pl. 19: figs. 18, 19, same specimen; USNM 153811) was one of the few workers to actually find *B. dictyon*; however he classified this North Atlantic specimen in open nomenclature as *Cythereis* species.

Many of the specimens illustrated by Brady (1880) as *Cythere dictyon* are actually more closely allied, if not identical, with his own species of *C. viminea*. This is the same form that Ruggieri (1962) thought was most similar to *Cythereis pliocenica* Seguenza (at the same time recognizing species differences). I have included this group of Brady's specimens in a new genus *Poseidonamicus* under two new species (*C. viminea* is considered nomen dubium). I have referred Seguenza's species to a third new genus, *Agrenocythere*.

It is of interest to note that confusion about the identification of *Bradleya dictyon* in large part stems from a misconception of morphologic change that takes place during maturation. Brady assumed that the *dictyon* carapace becomes more coarsely reticulate with age, toward senility, as he called it. I have examined the allometric changes taking place in a series of instars of the true *Bradleya dictyon*. As can be seen in Figure 15 the reticulation continues to develop toward the margins with increasing maturity, but the robustness remains much the same. It should also be noted that the posterodorsal loop is present in the earliest instars. This feature is characteristic of some mature thaerocytherids, especially *Jugosocythereis*.

The relationship between *Bradleya dictyon* and *Bradleya arata* has been mentioned in several contexts earlier. I would reassert that the reticular patterns are very similar (as shown in Figure 13A, B) and that the major features are of the same basic form although of different parts of the morphologic range of the genus.

Older adult specimens (Miocene) are usually smaller (about 1.0 mm long) than Recent specimens (about 1.4 mm long).

APPENDAGES.—The appendages of a male specimen of *Bradleya dictyon* are illustrated in Figures 16 and 17. It is noted that segments v and vi of the first antennae are fused, the epipodite of the mandible has five "fingers," the exopodite of the second antenna is well developed, and the knee of the thoracic appendages have slightly developed reinforcement. These characteristics are typically thaerocytherid.

### *Bradleya normani* (Brady, 1865)

FIGURE 13C, PLATE 1: FIGURE 7, PLATE 7: FIGURE 8.

*Cythere normani* Brady, 1865:379, pl. 61: fig. 5a-d; 1880: 101, pl. 17: fig. 3a-d [not pl. 26: fig. 4a, b].  
Not *Cythere normani* Brady.—Chapman 1916:50, 73, pl. 6: fig. 2 [= *Australicythere polylyca* (Müller, 1908)].

TYPE-SPECIMEN.—In the original description of *Cythere normani*, Brady (1865) mentions that several specimens were examined; however, none is indicated in such a way as to be considered the type.

The specimens later identified by him (Brady 1880) as *C. normani*, from the Challenger collection (BM 1961 12.4.27), include some that are questionable. Until a lectoholotype can be designated (I have not seen his original material), the concept of the species and the present identifications will have to be considered on the strength of his illustrations (Brady 1865, pl. 61: fig 5a-d). Although somewhat crude they incorporate many of the attributes of the species as described here.

TYPE-LOCALITY.—Described originally from Abrolhos Bank, which lies off Caravelas, Baia, Brazil between 17° and 18° south latitude. Brady (1880) later identified specimens from between Heard and Kerguelen Islands in the Southern Ocean in 150 fathoms and also from off the west coast of South America (1825 fathoms). Specimens illustrated in the present report are from near Kerguelen Island (Plate 1: figure 7) in the vicinity of Brady's collecting locality, from the west coast of South America (Figure 13c) and from the Straits of Magellan (Plate 7: figure 8).

AGE.—Stratigraphic range uncertain. Known from Pliocene to Recent deep-sea sediments, but older specimens identified by van den Bold (1957, 1968b) as *Bradleya dictyon* could possibly be this species.

DIAGNOSIS.—Carapace large, but foreshortened, with coarse heavy muri (primary reticulation) together with various stages of their loss as the fossae become fused. The elimination of mural elements leads to a more simplified reticular pattern. The fossae in the posterolateral region are usually large and evenly spaced compared to those more crowded in the anterior. The ocular ridge is weak. A median ridge is absent in the posterior. In its place is a box-like arrangement of a line of reticular cells similar to the bridge structure of the anterior (whose pattern is apparent, but whose mass is reduced). The dorsal carina is not as strong as the ventrolateral carina. Marginal teeth are concentrated along the ventral portions of the anterior and the posterior. Deep-sea (primarily a slope species) and blind.

COMPARISONS.—*Bradleya normani* is the most robust of the deep-sea *Bradleya* species. Yet it is much less murate than the smaller shallow-water species, such as *B. andamanae*, new species, which is also differentiated by a pronounced longitudinal ridge (believed to be of a different origin than that of the *Quasi-bradleya* species). Its reticulum is characterized by the development of a few heavy muri at the expense of other muri, which become fainter with decreasing size (and depth of water). However, *B. mckenziei*, new species, which has notably strong carinae (also an ocular ridge), also has primary reticulation with secondary divisions (secondary reticulation, like foveolation, does occur but is not the same as the suppression of muri mentioned here). *B. normani* is not easily confused with *B. dictyon* (although Brady did possibly mix the two species), as there seems to be little gradation between the robust, abrupt subquadrate form of the former and the elongate, more delicate form of the latter. Undoubtedly, there will be samples where these two merge, but they are not yet known. *B. normani* bears a close resemblance also to *B. japonica*, new species, which is coarser with very high and even peaked muri with only a few traces of diminishing (relic) muri.

DISTRIBUTION.—Eastern Pacific, Atlantic, Southern Ocean; generally in upper bathyal depths.

DIMENSIONS.—Adults range in length, 0.95 to 1.25 mm; in height, 0.65 to 0.71 mm.

REMARKS.—This species has been seldom identified since the two original studies of Brady (1865, 1880). Chapman (1916, see synonymy) misidentified *Australicythere polylyca* (Müller, 1908) from elevated

marine muds from the Ross Sea and the Ross Sea itself as *Cythere normani*. Van den Bold (1968b: 67) suggests that “a fair amount of the specimens attributed to *Bradleya? dictyon* in the Western Hemisphere belong in reality to *Bradleya? normani* (Brady).” This is probable as *B. normani* is known by me to be distributed around the whole of South America, except for the Caribbean, where my data are comparatively sparse (especially in the fossil record). It is also equally likely that indigenous species ultimately will be described from this area, which will parallel the development of a coarse reticulum in a way similar to those of the western Pacific. I would speculate that *B. normani* has a transitory and intermediate architectural form that would not remain stable in a tectonically active region.

It is noteworthy that in Brady's (1865) own remarks, he compares *Cythere normani* with *Cythere arachnoidea* (Bosquet, 1852), which is probably more closely related to the new genus *Agrenocythere*. One striking difference in the surface ornament between the two forms is the presence of conjunctive spines (probably pore conuli) on the coarse reticulum of *C. arachnoidea*, which are totally absent on the carapace of *Bradleya normani*.

### *Bradleya albatrossia*, new species

PLATE 7: FIGURES 1, 2

ETYMOLOGY.—Named for the United States Fisheries Steamer *Albatross*, which worked in the western Pacific in 1900 and again in 1908.

TYPE-SPECIMEN.—The holotype (USNM 174318) is an adult female (?) left valve, from the Recent of the China Sea (Plate 7: figure 1). Paratype, USNM 174319.

TYPE-LOCALITY.—China Sea off Hong Kong in the vicinity of *Albatross* station 5301, lat. 20°37'N and long. 115°43'E, 208 fathoms depth.

AGE.—Recent of western Pacific; no specimens with soft parts found.

DIAGNOSIS.—Distinguished from other known species of *Bradleya* by its bold, high, yet nonexcavate muri; the lack of a conspicuous discrete bridge structure or median ridge complex; its sharp, angled reticulum in the region of the dorsal carina, which fails to form a continuous ridge; the presence of relic mural struts crossing enlarged fossae; and the absence of a prominent ocular ridge or an eye tubercle.

COMPARISONS.—The reticulum of *Bradleya albatrossia* has been formed into a bold, box-work frame similar to that of *B. andamanae*, new species, yet it lacks any of the major structural members, such as the median ridge complex or the dorsal carina, found in other species of *Bradleya*. This species maintains a strong reticulum by forming high mural webs at right angles to the main carapace wall whereas other species may accomplish the same function through the formation of massive muri, celate muri, reduction in relative size, forming major reticular members of increasing the thickness of the carapace wall.

*Bradleya albatrossia* is very similar in many respects to the larger form *B. japonica*, new species, in the development of high muri, at least in the central and posterior regions. *B. japonica*, however, is devoid of reticular development in the anterior and posterior regions, and both the dorsal and ventrolateral carinae are much more evident.

*Bradleya normani* is generally larger but also differs from *B. albatrossia* in the degree of reticular development. These two species may represent parts of a morphological series of which *B. japonica* and *B. nuda*, new species, could also be components. More discussion of these relationships is given elsewhere.

This species was found in two localities including the type-locality and in the North Fiji Basin (Alexa-Penguin Bank, lat. 11°5'S, long. 175°10'E; 2560 meters). It is probable that this species is widely distributed over the western Pacific at the present time.

DIMENSIONS.—Length of holotype 0.82 mm; height 0.57 mm.

DISTRIBUTION.—Western Pacific, from China Sea to Fiji Basin, 200 to 2500 meters.

### *Bradleya japonica*, new species

PLATE 7: FIGURE 3

TYPE-SPECIMEN.—The holotype (USNM 174320) is an adult left valve, from the Recent of the Pacific side of Japan (Plate 7: figure 3).

TYPE-LOCALITY.—This species is known only from the Recent of Japan in the vicinity of *Albatross* station 3708, off Honshu Island (bearing S. 55° W. distance 2.25 miles off Ose Zaki) in 60–70 fathoms.

AGE.—Recent; no specimens with soft parts found.

DIAGNOSIS.—Distinguished from other species of *Bradleya* by the incomplete development of the reticulum in the anterior and posterior regions near the

margin, the confused pattern of the reticulum in the anterior, its broad ventrolateral carina, and its fore-shortened and peaked dorsal carina.

COMPARISONS.—This species is the only one known which is nude or smooth in the terminal regions on the carapace, and in the same adult stage has coarse reticular elements over the rest of the carapace. This difference in development in the reticulum is known in early instars of *Poseidonamicus*, new genus (whose fossae are filled in), but not observed to such an extreme degree before in *Bradleya*. The earlier instars of *Bradleya dictyon* (Figure 15) have the reticulum somewhat incompletely developed near the anterior margin, suggesting that *B. japonica*, new species, may be neotonous.

The pattern of the reticulum is irregular, especially anterior to the muscle-scar region. The species appears to be transitional in form between the boldly reticular species *Bradleya albatrossia*, new species, and the smooth *B. nuda*, new species. All three of these species are common to the western Pacific. Attention is called to a murus that extends downward and slightly toward the anterior from the high peak of the dorsal carina. This same murus, one of the more prominent on the central carapace of *B. japonica* is clearly identifiable on *B. nuda*. Both species also have a posteriorly directed process on the posterior cardinal angle, as also does *B. paranuda*, new species.

DIMENSIONS.—Length of holotype 1.07 mm; height 0.58 mm.

DISTRIBUTION.—So far found only at type-locality off Japan.

### *Bradleya andamanae*, new species

FIGURE 14c, PLATE 7: FIGURE 4

ETYMOLOGY.—Named for the Andaman Sea, around whose waters this species was found.

TYPE-SPECIMEN.—The holotype (USNM 174322) is the left valve of an adult, from the Andaman Sea in the northeastern Indian Ocean; Figure 14c.

TYPE-LOCALITY.—The Andaman Sea in the vicinity of *Oceanographer* station OSS-01,260G (lat. 06°39.4'N, long. 98°52.0'E; 78 meters). Also found commonly in the Bay of Bengal.

AGE.—Recent; no specimens with soft parts found.

DIAGNOSIS.—Carapace small in size with very coarse reticulation. Distinguished from other species of *Bradleya* by its reduced size and deep fossae; how-

ever, the pattern of the major reticular elements includes a median ridge extending end to end with only a partial ventral element of the bridge present. An eye tubercle is present.

COMPARISONS.—This species represents an end member in a morphological series that includes a form with a reduced size, reduced number of mural elements of the reticulum, and yet maintains a structure of considerable strength potential. Similar to the much larger form *Bradleya albatrossia*, new species (1.1 mm compared to 0.7 mm length) in coarseness, it has more recognizable principal reticular structures such as the dorsal carina (even though irregular) and the median ridge. It is also similar to the much larger (1.1 mm length) *B. (Q.) dictyonites*, new species, but it can be easily distinguished from this species just on the basis of relative proportions of the reticulum to overall size. It also bears some resemblance to *B. mckenziei*, new species, in the anterior region, but the muri become excavate and the fossae angular in this latter species whose dorsal carina and margin is straight and even. The average length of this species is about 40 percent of that of the modern deep-sea species *B. dictyon*.

The origin of this species is uncertain. It has a median ridge as does the several species of *Quasi-bradleya*. The general pattern of the reticulum and its high webbed muri, however, suggest that the median ridge may be the product of simple alignment of the muri in a longitudinal direction, and the median ridge is only analogous to that of *B. (Q.) dictyonites*. With the reduction of mural struts or reticular elements, it seems inescapable that convergence in pattern would result.

DIMENSIONS.—Length of holotype 0.68 mm; height 0.44 mm.

DISTRIBUTION.—Northeastern Indian Ocean, depth range generally from 60–70 meters to 500 meters (limits uncertain at present).

### *Bradleya nuda*, new species

FIGURE 14A, PLATE 7: FIGURE 5

TYPE-SPECIMEN.—The holotype (USNM 174323) is a left valve adult, from the Pliocene of Japan (Plate 7: figure 5).

TYPE-LOCALITY.—Upper Pliocene section, near Okuwa, Kaga Province, Japan (Ozawa locality F25510).

Diagnosis.—Distinguished from other species of *Bradleya* by its smooth, nonfoveolate carapace, devoid of a reticulum except for faint traces in the postero-central region. A posteriorly directed process surmounts the posterior cardinal angle, and a sharp ridge runs from the posterior end of the bold and smooth ventrolateral carina around to a major spine on the postero-ventral margin. No eye tubercle is visible.

COMPARISONS.—Most similar to *Bradleya paranuda*, new species, a smooth, reticulum-free Recent species from the Philippines, except for a more indrawn anterior margin and different and more abundant traces of the reticulum (compare Plate 7: figures 5 and 7) in *B. nuda*. Also very close in appearance to *B. proarata* Hornibrook, which is about the same size (from the Paleogene of New Zealand). This older species, however, is sighted (eye tubercles present). The two forms are undoubtedly very similar, and the difference of sight and also the cause of the smoothness of the carapace are significant factors in suggesting their taxonomic separation. It is not yet known (but inferred by Hornibrook) if the smoothness of *B. proarata* is caused by loss of muri or infilling of fossae by celation (the only specimens of *B. proarata* I have seen are immature instars and not celate). The resultant appearance could be much the same. As mentioned in the comparative statements of the description of *B. japonica*, new species, these two species have similar elements of the reticular pattern in common, although there are far fewer in *B. nuda*. It is noteworthy that the pores along the anterior portion of the ventrolateral carina are in pairs rather than singular, as in the case in the posterior portion. These same paired pores can be found in *B. japonica* and even in *B. arata*.

*Bradleya arata* is similar to *B. nuda* in outline and in the tendency to become smooth. However, no signs of celation can be observed in *B. nuda*. Either the developmental process has continued to completely fill in the reticulum of the ancestors of *B. nuda*, or, on the other hand, the reticulum has simply been absorbed into the development of a thicker shell as suggested by the intermediate morphological series stage represented by *B. japonica*. The existence of *B. japonica* is very strong evidence to suggest that the nudity of *B. nuda* is the result of mural loss, and not the paving over of the outer surface by a secondary tegmen as occurs in the process of celation. The tendency toward the removal of the reticulum is success-

fully compensated for by an increase in the mass or the thickness (including celation) of the shell, as well as by a flaring of the ventrolateral ridge to produce a more triangular (and theoretically stronger) cross-section.

**DIMENSIONS.**—Length of holotype 1.12 mm; height 0.62 mm.

**DISTRIBUTION.**—Known only from the type-locality at present.

### *Bradleya paranuda*, new species

PLATE 7: FIGURE 7

**TYPE-SPECIMEN.**—The holotype (USNM 174325) is an adult left valve from the Recent of the Philippine Islands (Plate 7: figure 7).

**TYPE-LOCALITY.**—The Gulf of Davao, in the Philippine Islands in the vicinity of *Albatross* station 5250; lat. 7°05'07"N, long. 125°39'45"E; 23 fathoms

**AGE.**—Recent; no specimens with soft parts found.

**DIAGNOSIS.**—Like the smooth form *Bradleya nuda*, new species, this species is almost devoid of any traces of the reticulum. Except for *B. nuda* and possibly *B. proarata*, it can be distinguished from all other species of *Bradleya* by this characteristic. The anterior margin is very well rounded and exceptionally produced. Traces of the reticulum are confined to a murus joining the posteriors of the dorsal and ventrolateral carinae. No eye tubercle is visible and although the species was found in shallow water (23 fathoms); it is presumed to be blind.

**COMPARISONS.**—This species is like *Bradleya nuda* except for its produced anterior margin (neither species has a discrete rim) and different and fewer traces of the reticulum. Reinforcing mural struts are visible next to the ventrolateral carina. A single mural trace connects the posterior of the ventrolateral ridge with the dorsal carina. So far as can be determined the pore systems of the two nude species are the same. The species are smooth and are not foveolate or celate as in *B. arata*, which also has a small horizontal ridge in the region of the muscle-scar node. The ridge joining the posteroventer with the posterior of the ventrolateral ridge (described for *B. nuda*) is also present in *B. paranuda*.

**DIMENSIONS.**—Length of holotype 0.98 mm; height 0.57 mm.

**DISTRIBUTION.**—Known at present only from the type-locality.

### *Bradleya mckenziei*, new species

PLATE 7: FIGURE 6

**ETYMOLOGY.**—Named for K. G. McKenzie who kindly furnished the samples (February 1967) in which this species was found.

**TYPE-SPECIMEN.**—The holotype (USNM 174324) is an adult left valve from Recent sediments of Bass Strait, between Australia and Tasmania.

**TYPE-LOCALITY.**—Bass Strait south of Australia between Tasmania and Flinders Island in the vicinity of McKenzie station M290; lat. 39°58.7'S, long. 147°02.9'E; depth uncertain, less than 100 fathoms.

**DIAGNOSIS.**—Distinguished from other species of *Bradleya* by its overall box-like shape caused by the unusually straight and even, dorsal and ventrolateral carinae that are joined by fairly evenly spaced mural elements (slightly celate muri) of the reticulum. The fossae are angular and the muri excavate. The ocular ridge is not well developed, although the eye tubercle is well formed. No median ridge complex is present; however, traces of the bridge can be seen in the reticular pattern. The fossae are enlarged by resorption or exculsion of some of the muri. A posterodorsal spine is present at the margin.

**COMPARISONS.**—Somewhat similar to *Bradleya normani* in lateral outline, but the carinae are much more conspicuous. Many homologous aspects of the reticular patterns are noticeable among *B. mckenziei*, *B. normani* and *B. andamanae*, new species (compare Plate 7: figures 4, 6, 8). Differs from *B. albatrossia*, new species, in the lesser strength and regularity of the muri, as well as the evenness of the carinae.

**DIMENSIONS.**—Length of holotype 0.96 mm; height 0.65 mm.

**DISTRIBUTION.**—On the southern continental shelf of Australia.

### *Bradleya? telisaensis* (Le Roy, 1939)

PLATE 2: FIGURE 9

*Cythereis* (*Pterygocythereis*?) *telisaensis* Le Roy, 1939:275, pl. 11: figs. 9–16.

*Cythereis dictyon* (Brady).—Kingma 1948: 80, pl. 9: fig. 8.

**TYPE-SPECIMENS.**—The holotype described by Le Roy is repositied in the Government Geological Museum at Bandoeng, Java (P.S. 1096a), where it was subsequently examined by Kingma (see synonymy) who considered it synonymous with Brady's species

*Cythere dictyon*. Le Roy also repositated paratypes in the U. S. National Museum and one of these (USNM 56147) is illustrated here (Plate 2: figure 9).

TYPE-LOCALITY.—Described originally from the Telisa formation, Miocene in age, from the Rokan-Tapanoeli area of Central Sumatra (locality Ho-1512; Tapoeng Kiri area near Aliantan).

AGE.—Miocene.

DESCRIPTION.—After Le Roy (1939: 275) "Carapace rather strong and thick, subquadrate in side view, roughly quadrangular in cross-section, highest anteriorly, thickest posterior to the middle, left valve slightly larger than the right, best shown near the anterodorsal angle. Dorsal margin straight to slightly curved, sometimes shown an upward curve near anterodorsal angle. Ventral margin slightly convex downward. Ventral margin rather broad and flat due to presence of moderately extended lateral processes at the ventrolateral edge of the two valves. In some specimens a short heavy spine projects backward from this edge. Anterior end broadly rounded, oblique, slightly compressed around the marginal border, somewhat denticulate near anteroventral angle. Posterior end bluntly angled, somewhat truncate. Surface coarsely and irregularly reticulate. Two rather strongly developed longitudinal ridges are situated along the median line and the other near the ventrolateral edge. Connecting these are numerous ridges. The areas between the ridges are very irregular in shape and form. Hinge margins well developed and are typical of the genus. Marginal radial pore canals straight and numerous. Line of concrescence coincides with the inner margin throughout. Muscle scar poorly defined, appears to be represented by a single depressed area approximately along the median line in the anterior half. Dimensions of the holotype, length 0.70 mm; height 0.40 mm; thickness 0.40 mm."

DIMENSIONS.—Length of paratype (USNM 56147), 0.68 mm; height 0.41 mm.

DISTRIBUTION.—Miocene of Indonesia.

DISCUSSION.—From examination of paratypes (Plate 2: figure 9) it is apparent that Le Roy's species is not conspecific with *Cythereis dictyon* (Brady) as Kingma (1948) stated. So far as I can determine, it was correctly designated originally by Le Roy, and it is hereby reinstated.

Its generic status is another problem. Le Roy guessed that it might be a pterygocytherid, which is

incorrect, and assigned it to the genus *Cythereis*, which is also improper as now defined. It appears to me to be closely related to *Bradleya* (which is implied by Kingma's identification), but I believe that this may be extending the concept of *Bradleya* too far without stronger phyletic evidence. Therefore I place it in this genus with some doubt.

*Bradleya? telisaensis* (Le Roy) has the following aspects in common with other *Bradleya* species: It has a rounded, noncaudate posterior, well-developed dorsal and ventrolateral carina (however massive and blunted), a median ridge complex with the suggestion of a ventral bridge member similar to the subgenus *Quasibradleya* species group. The ocular ridge is diminished like several *Bradleya* species as is the high anterodorsal marginal area.

It is unlike *Bradleya* in that the marginal rims are blunted or even absent (a variation perhaps typical of a very shallow water form). The reticulum is disorganized with many "unexpected" muri present. It is obvious that the existence of this form indicates there is still much more to learn about this group and this genus.

#### Subgenus *Quasibradleya*, new subgenus

TYPE-SPECIES.—*Bradleya (Quasibradleya) dictyonites*, new species.

DIAGNOSIS.—A group of species of the genus *Bradleya* characterized by the development of a median ridge complex formed from the upper element of the *Bradleya* bridge, which is emphasized at the sacrifice of the lower one, and a longitudinal median ridge postjacent to the muscle-scar node, sometimes joining the dorsal carina in the posterior to form a loop. This subgenus, which is comprised predominantly of shelf-dwelling species, is thought to be indigenous to the Australia-New Zealand region.

COMPARISONS.—One can see indications of the subgeneric characters expressed in the smaller Miocene form of *Bradleya (Bradleya) dictyon* (Plate 8; figure 7), or possibly in *B. (B.) andamanae*, new species. I believe that this subgenus is part of a larger continuum characteristic of the genus *Bradleya* and can see no value in raising it to the rank of genus. This would, in my opinion, obscure the concept of the overall development of *Bradleya* of which we can only see in detail the changes of form in a small part. For this reason the enumeration of these species continues

from those of *Bradleya*, which have been unassigned to other subgenera.

**OTHER POSSIBLE SUBGENERA.**—For the present I do not consider that evidence warrants the erection of other subgenera within *Bradleya*. In my opinion adaptive change to increase the strength in the carapace has been accomplished by several different paths. Convergent solutions to increased strength (easily classified as subgenera) could be misunderstood at present. I see no reason to group the remaining species at this time, before having the chance to explore the developmental theory farther. To make further subgeneric divisions without more phyletic evidence would just obscure the actual relationships. A case in point is the problem of the origin of smooth *Bradleya* species. These could have formed independently by celation and by fossal infilling or by simple removal of muri. Until links can be found or relic structures recognized in surface detail, the end results would appear to be the same. Another possible subgenus might include those species similar to *B. normani*, which would have muri of strength and number intermediate between *Bradleya (B.) dictyon* and *B. (B.) andamanae*. Again, I believe that present evidence of the correlation between depth changes and the reconstitution of the reticular pattern is insufficient to rule out the strong possibility that simplification and strengthening of the pattern does not occur numerous times in the fossil record.

### ***Bradleya (Quasibradleya) dictyonites*, new species**

PLATE 8: FIGURE 4

*Bradleya dictyon* (Brady).—Hornibrook 1952 [part]:39, pl. 6: figs. 81, 82, 84.

**TYPE-SPECIMEN.**—The holotype (USNM 174328) is an adult male(?) left valve from the upper Oligocene of New Zealand (Plate 8; figure 4).

**TYPE-LOCALITY.**—The holotype was chosen from Hornibrook's sample locality F6487, the Old Rifle Butts Section, at Oamaru S.D., New Zealand; upper Oligocene (Awamoan). Sample supplied to me by Dr. Hornibrook in 1960.

**AGE.**—Upper Oligocene.

**DIAGNOSIS.**—A coarsely reticulate species of *Bradleya* with a conspicuous median ridge in the posterior, which joins with the upper element of the anterior bridge structure (the lower element is proportionally

diminished to become almost nonexistent in the anterior). The upper structural member of the bridge is securely connected to the ocular ridge and not joined at the posterior end to median ridge. The median ridge is separate from the dorsal carinae (joined in *B. (Q.) prodictyonites*, new species). The overall aspect of these ridges together with the well-developed dorsal and ventrolateral carinae give the carapace a tricarinate appearance more strongly produced in this species than in any other known in *Bradleya*. The eye tubercle is not strong but present. The flange forming the posterior marginal rim is wide and produced in the posterodorsal cardinal region. This species is believed to be sighted and probably lived in the outer shelf region.

**COMPARISONS.**—*Bradleya (Quasibradleya) dictyonites* is the most tricarinate of all of the named *Bradleya* species (or of the subgenus; another similar and closely related unnamed Recent species is shown on Plate 1: figure 8). It has sharp conspicuous ridges dividing the carapace reticulum longitudinally into an upper and lower section. This feature also is found in *B. (Q.) prodictyonites* in which the median ridge complex (including the upper member of the bridge) is disjunct (joined in *B. (Q.) plicocarinata*, new species) from the ocular ridge and joined posteriorly to the dorsal carina to form a loop. The Tasmanian species *B. (Q.) paradictyonites*, new species, of similar mid-Cenozoic age is much coarser in appearance with celate muri. It has a different reticular pattern resulting from fusion of particular mural struts. *B. dictyonites* is much more robust, and its tricarinate appearance and eye tubercle easily distinguishes it from *B. dictyon* with which it was identified earlier by Hornibrook (1952).

**DIMENSIONS.**—Length of holotype 1.18 mm; height 0.65 mm.

**DISTRIBUTION.**—New Zealand, Paleogene.

**REMARKS.**—This form, now designated as a species (and the type-species of a new subgenus), was first noticed by Hornibrook (1952) but misidentified as *Bradleya dictyon*, presumably because of the vague status of this species at that time. His illustration of a left valve (Hornibrook 1952, pl. 6: fig. 81) is Recent (off North Cape, Station 27) in age (see Plate 1: figure 8 of this report), is almost identical to the upper Oligocene specimen illustrated herein (Plate 8: figure 4). This Recent form is different from the

older one, herein described as a new species, in the boldness of its reticulation and a difference in the pattern in the posterior field. Nevertheless the general conservatism in form for a considerable portion of the Cenozoic is exceptional for an ostracode with eye tubercles, and living in a shallow (shelf 28 fathoms) environment. The evolution of *B. (Q.) dictyonites* from *B. prodictyonites*, to the Recent species (being studied by W. M. Briggs, Jr., and tentatively named *Bradleya zealandica* (now nomen nudum), should prove to be an interesting sequence. Hornibrook placed some emphasis on the importance of the marginal spines. So far I can find little of species-level significance about these features as taxonomic characters, although further work may suggest otherwise.

Hornibrook (1952, pl. 6: fig. 85) illustrates an Eocene form, which he also identified as *B. dictyon*. I do not know what species this is, but it is not *B. dictyon*. The age range of *B. (Q.) dictyonites* as considered here is only a small part (Oligocene) of that suggested for *B. dictyon* by Hornibrook (Eocene to Recent).

***Bradleya (Quasibradleya) prodictyonites*,  
new species**

PLATE 8: FIGURE 2

TYPE-SPECIMEN.—The holotype (USNM 174327) is an adult female (?) left valve from the lower Oligocene of New Zealand (Plate 8: figure 2).

TYPE-LOCALITY.—The specimens considered in the description of *B. (Q.) prodictyonites* were from Hornibrook's (1952) sample locality F5052 (Dunroonian; lower Oligocene) from near Chatton S.D., New Zealand. Sample supplied to me by Dr. Hornibrook in 1960.

AGE.—Lower Oligocene.

DIAGNOSIS.—A robust species of *Bradleya* distinguished by its conspicuous ocular ridge (with eye tubercle), prominent dorsal and ventrolateral carinae, and particularly a median ridge in the posterior central region that curves upward to join the posterior end of the dorsal carina (also seen in *B. (Q.) plicocarinata*, new species). The bridge structure reaches forward from the muscle-scar node region toward the broad ocular ridge, but does not join it, nor does it join the median ridge to the posterior. The lower segment of the bridge is short but strong with a knot-

like protuberance over the muscle-scar region (less well developed in *B. dictyonites*, new species). The posterodorsal carina area is truncate. The species is sighted.

COMPARISONS.—*B. (Q.) prodictyonites* is most closely related to *B. (Q.) dictyonites*, but is more quadrate. The ocular ridge of *B. prodictyonites* is disjunct from the bridge, and the posterior median is joined much more conspicuously with the dorsal carina. Other comparisons are mentioned above.

Plate 8: figure 2 illustrates the holotype of *Bradleya prodictyonites* and Plate 8: figure 1, a Recent species of *Jugosocythereis* from the western Indian Ocean. Notice the similarity in the posterodorsal loop, the ocular ridges, and the bridge structures of *Jugosocythereis* with those of *B. (Q.) prodictyonites*. The caudal process of *Jugosocythereis* is obviously more produced and I am not convinced that one can trace homologous fossae from one form to the other. Nonetheless the general structures of the reticulum are quite similar suggesting strong analogical convergence in general architecture.

REMARKS.—I had only a few valves of this species available for study. It could be an ecophenotypic variant of *B. (Q.) dictyonites*, but evidence other than the morphologic difference noted here will be required to support this theory.

DIMENSIONS.—Length of holotype 1.08 mm; height 0.64 mm.

DISTRIBUTION.—Paleogene of New Zealand.

***Bradleya (Quasibradleya) paradictyonites*,  
new species**

PLATE 8: FIGURE 3

TYPE-SPECIMEN.—The holotype (USNM 174328) is an adult male (?) left valve from the Oligo-Miocene of northern Tasmania (Plate 8: figure 3).

TYPE-LOCALITY.—The sample from which this species is described was collected by N. G. Lane in about 1957 from the Fossil Bluff locality (Oligo-Miocene) near Wynyard Beach on the north coast of Tasmania.

AGE.—The precise age is unknown, but the Fossil Bluff locality has been described as Oligo-Miocene. A more accurate determination is required, but the means to do this were not at my disposal.

DIAGNOSIS.—The massive reticulum of this species of *Bradleya* has strongly excavate muri and many of

the fossae have merged by removal of the mural struts separating the principal members. The dorsal carina is well formed as are the ventrolateral carina and the median ridge complex. As in *B. (Q.) dictyonites*, new species, this latter feature is joined to the ocular ridge. It is disjunct over the muscle-scar node region and continues over the posterior region to merge with the rest of the reticulum at about half way from the node to the posterior margin. The lower element of the bridge is almost absent except for a knot-like configuration over the muscle-scar node proper. The marginal rim in the anterodorsal cardinal region is wide and is strongly accentuated in the posterodorsal region. The eye tubercle is large and conspicuous indicating that this species, like the others of the *B. (Q.) dictyonites* group, is a shelf dweller.

COMPARISONS.—*Bradleya (Q.) paradictyonites* is most similar to *B. (Q.) dictyonites*, a larger contemporary species, from which it can be distinguished by its more celate, excavate, and simplified massive reticulum. Also, the median ridge complex does not proceed as far toward the posterior as that of *B. dictyonites*. None of the other species of *Bradleya* seems to be very close in morphology to this species, which, while not well understood as yet, in large part justifies its taxonomic notice here.

DIMENSIONS.—Length of holotype 0.86 mm; height 0.59 mm.

DISTRIBUTION.—Known only from the type-locality in Tasmania. It is considered an inner shelf inhabitant judged on the basis of its massive morphology and somewhat smaller size. Other ostracode faunal elements in the sample tend to confirm this observation.

### *Bradleya (Quasibradleya) plicocarinata*, new species

FIGURES 18, 19

TYPE-SPECIMENS.—The holotype (USNM 174334) is an adult male left valve from the Recent of the Great Australian Bight (Figure 18).

TYPE-LOCALITY.—The Great Australian Bight in the vicinity of *Oceanographer* station OSS-01,60K (lat. 33°10.0'S and long. 130°54.5'E; 100 meters).

AGE.—Miocene(?) to Recent.

DIAGNOSIS.—This species of *Bradleya (Quasibradleya)* is distinguished by its moderate size, elongate shape, and unique formation of tricarinate ridges, with the median ridge joined with the dorsal carina forming a posterodorsal loop. The median ridge ex-

tends anteriorly to join a complex of muri over the muscle-scar region, which is characterized by the prominent development of the central longitudinal member (Figure 19). The dorsal element of the bridge, which unites with the bold ocular ridge, passes over this complex to join the median ridge. The lower bridge element is prominent only in the posterior portion. In general, the muri are foveolate, nonexcavate and noncelate. The posterior cardinal angle is not produced; however, the posterior margin is generally enlarged toward the posteroventer. Species is sighted with an eye tubercle.

COMPARISONS.—This species is similar to *Bradleya (Quasibradleya) dictyonites*, new species, in that the median ridge has continuity and reaches forward to join the ocular ridge. *B. (Q.) dictyonites* has no loop formed by the ridge and its more flared dorsal carina, and the reticulum covers the muscle-scar node in a more knotlike fashion, rather than the prominent ridges of *B. (Q.) plicocarinata*. *B. (Q.) prodictyonites*, new species, has the posterodorsal loop, but its posterior margin is foreshortened as the whole lateral appearance is considerably more quadrate. The much bolder appearance and lack of a loop separates *B. (Q.) paradictyonites*, new species, from the present species.

I have noted yet another species, or a variant of the present species which is very similar to *B. (Q.) plicocarinata* from the Miocene Mannum formation on the River Marne about 50 miles west of Adelaide, Australia. Some years back Mary Wade sent this material to me, but I do not trust my locality data sufficiently to describe this new form. It is characterized by a very elongate shape in the male with a very flared extension in the ventrolateral ridge causing the posterior to seem bent downward. This flaring of the posteroventer in the male is common to a number of species in quite separate genera. Examples are "*Cythere*" *dunelmensis* Brady, *Cletocythereis rastromarginata* (Brady), and *Agrenocythere pliocenica* (Seguenza).

DIMENSIONS.—Length of holotype 0.88 mm; height 0.46 mm.

DISTRIBUTION.—Mid-shelf south of Australia. Miocene(?) to Recent.

### Genus *Poseidonamicus*, new genus

ETYMOLOGY.—Latin and Greek combination, friend of Poseidon, god of the sea.

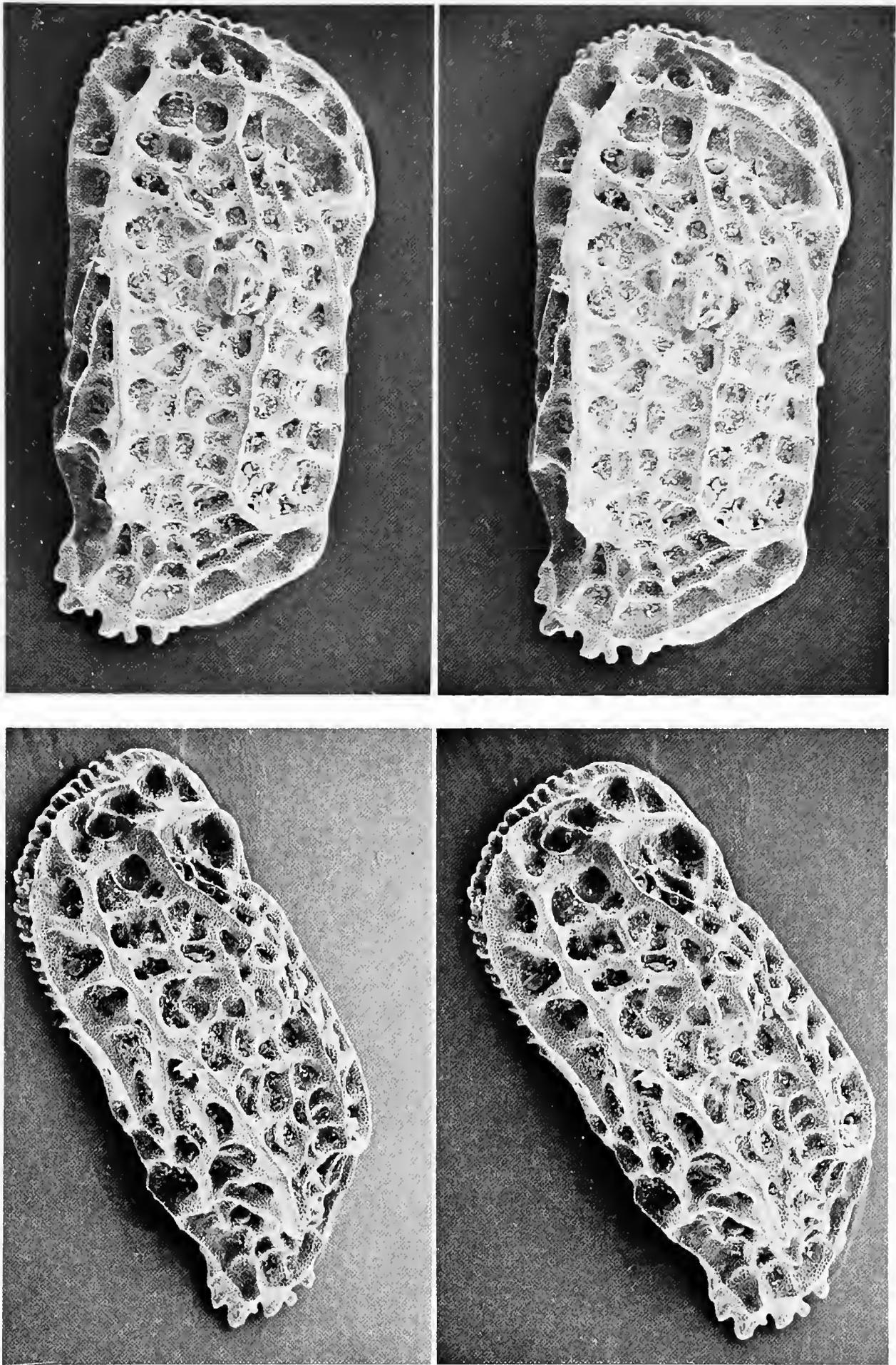


FIGURE 18.—*Bradleya* (*Quasibradleya*) *plicocarinata*, new species, stereomicrographs of the exterior of the holotype, an adult male, left valve, USNM 174334, from the Recent of the Great Australian Bight, *Oceanographer* station, OSS-01, 60K (x90).

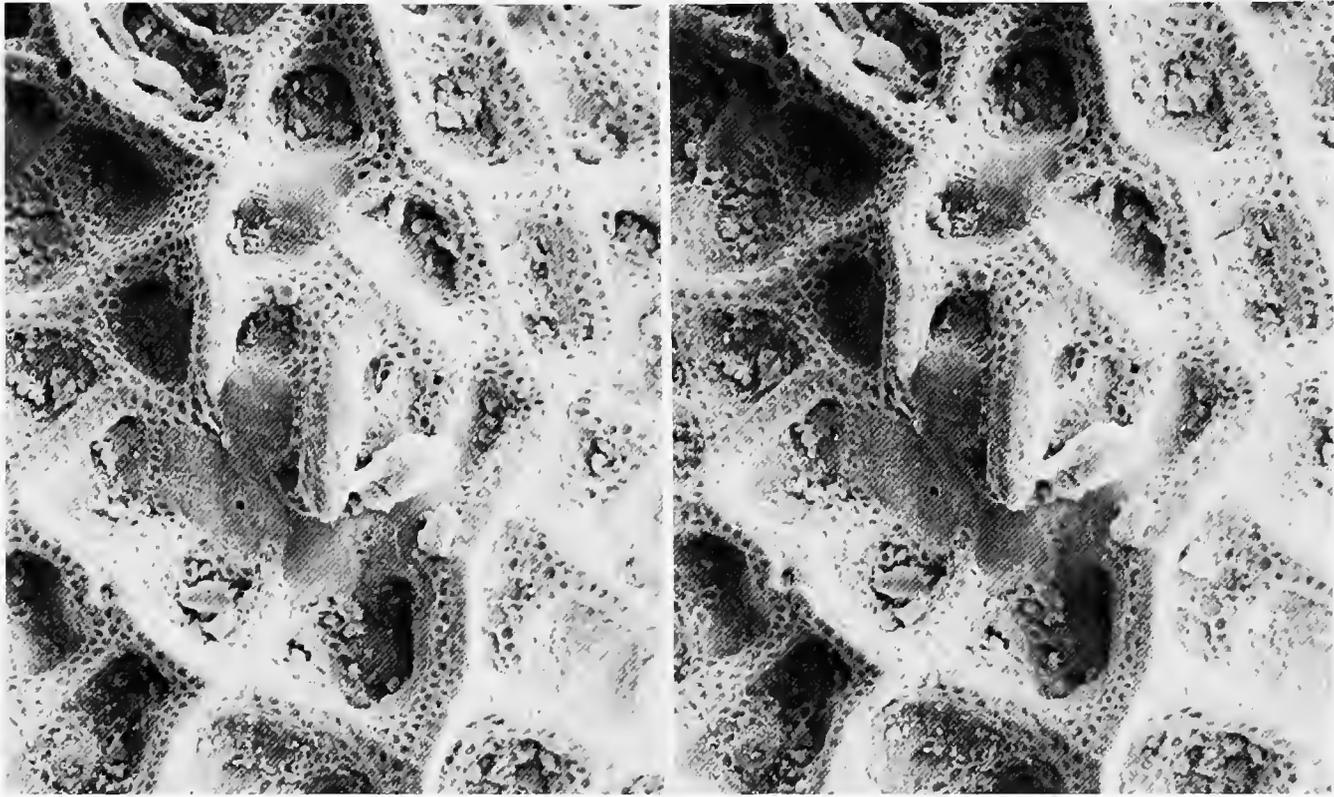


FIGURE 19.—The region of the muscle-scar node in *Bradleya* (*Quasibradleya*) *plicocarinata*, new species (same specimen as in Figure 18), showing the juncture of the partly formed bridge with the median ridge and the muscle scars (x200).

TYPE-SPECIES.—*Poseidonamicus major*, new species.

DIAGNOSIS.—Distinguished from other reticulate, holamphidont thaerocytherid genera, principally by its suppressed but wide dorsal carina, the lack of an ocular ridge, the regular, vertically aligned fossae and muri (in reticulate species, or indicated in the pattern of fine structure within the carapace wall of nude forms) of the posteromedian portion of the reticulum, the semipunctate to reticulate aspect of its anterior region, and a characteristic, vertically oriented central mural loop that occurs between these two regions in the area of the muscle-scar pattern. Often there is a conspicuous vertical ridge that joins the posterior of the dorsal carina with the posterior of the ventrolateral carina. Muri and solae are usually featureless except for celate pores, both sieve and murate; few spines other than marginal spines are present. Smooth or nude forms with underlying reticular “ghosts.”

AGE.—Cretaceous?, Paleocene to Recent of the deep-sea.

OUTER CARAPACE MORPHOLOGY.—The carapace of *Poseidonamicus* as viewed externally from the side (Figures 10, 19) is bounded by moderately well-formed rims and has a conspicuous ventrolateral ridge and a less obvious or suppressed dorsal carina. These

latter features are usually joined at their posterior ends by a third ridge, which is one of the emphasized vertically oriented muri of the reticulum. The anterior field of the reticulum, which can be defined as that region in front of the muscle-scar node above the large fossae of the ventrolateral ridge and anteroventral of the well-formed angular fossae of the central field, is composed of rounded almost puncta-size fossae. No ocular ridge is present as in *Bradleya* and there are no relief features such as the “levatum” as is present in *Abyssocythere* (Benson, 1971). The fossae of the anterior reticular field are almost never angularly shaped as in *Bradleya* and are without secondary conuli or spines giving this region a smooth and massive aspect.

The posteromedian or “central” field of the reticulum, which extends from the anterior field to the three main ridges, is composed of open, well-formed fossae with primary muri running vertically and with smaller secondary mural struts crossing laterally. These give the appearance of the net ladders formed of the main shrouds in old sailing ships. This pattern is very strongly emphasized in the more robust species and becomes lost in the nude species. One segment of this pattern, the one over the region of the muscle

scars (there is no pronounced node), is composed of a centered or axial muri (over the adductor scars; the "forum" region of *Agrenocythere*, new genus) that extends secondary mural struts to join a vertical loop, formed by the bordering muri of the anterior field and the one in the central field (the one passing through the position of conulus Leo; see p. 58). The posterior field (from the vertical muri to the posterior marginal rim) is less regular and undistinguished as now understood.

At least one species (*Poseidonamicus nudus*, new species), whose distribution is disjunct between two geographically distant regions, is devoid of muri; however, the pattern of the reticulum is still apparent if the carapace is viewed in transmitted light (Plate 11: figures 1-11). Although the pattern of vertical continuity of the principal muri of the central field is not as well ordered as in coarsely reticulate forms, the basic elements are nevertheless apparent.

The pore patterns of *Poseidonamicus* are not yet well understood. There are, however, some pores that seem homologous with those of other genera such as *Bradleya* or even *Agrenocythere*. By close inspection of Figure 20 it can be judged that pores (without the conuli) Leo, Charon, Scorpio, Capricornus, Alpha, Beta, Taurus, and Chi are present (see p. 58 for terminology). The absence of conuli and the presence of celate solar pores that may be absorbed into the widening of muri may cause difficulty in identifying some of these principal pores.

In many of the carapaces of the early instars, the anterior field is completely filled in as though snow were obscuring the basic reticulum topography. It was noticed also that pore conuli were present in some areas at this stage in development. This observation suggests that morphological similarities among higher taxa may exist in the instars and become obscured in

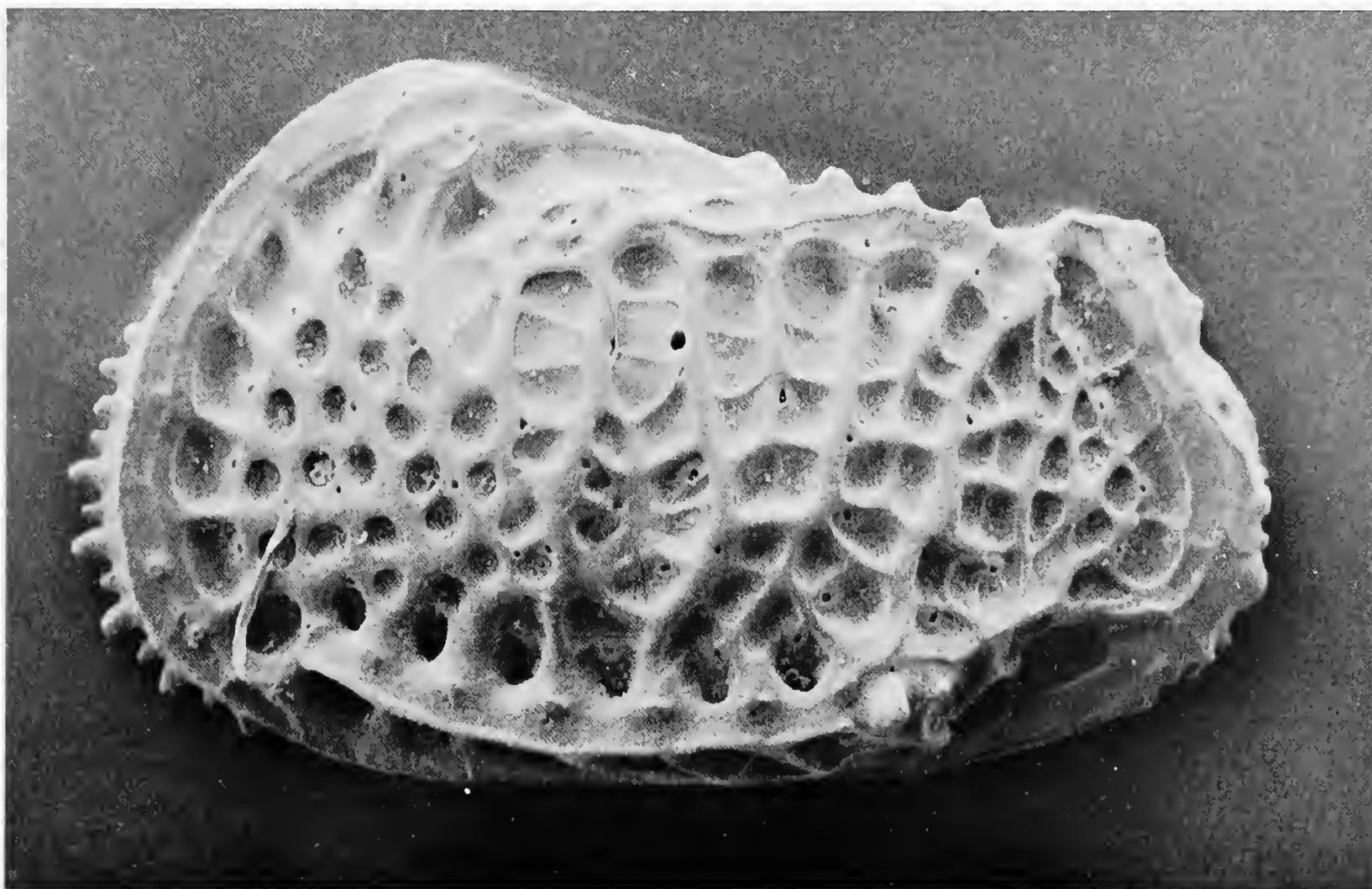


FIGURE 20.—*Poseidonamicus major*, new species, a micrograph of the exterior of the holotype, a left valve, USNM 174335, from the Mozambique Channel, Indian Ocean, IIOE Station 368C (x150), showing the pattern of the reticulum and pore systems for comparison with those of *Bradleya* and *Agrenocythere*, new genus.

the adults. The form is blind and without an eye tubercle.

INTERIOR CARAPACE MORPHOLOGY.—The following features are noted.

Hinge: Holamphidont with only slight indications of lobation in the underside of the posterior tooth. The anterior tooth of the right valve is often massive and stepped. Otherwise the hinge is undistinguished.

Duplicature: Without a vestibule. The simple radial-pore canals with slight intermediate swelling number between 14 and 16 in the anterior and a few less in the posterior.

Muscle-scar Pattern: Consists of four undivided adductors and two frontal scars.

APPENDAGE MORPHOLOGY.—This diagnosis of the soft part anatomy of *Poseidonamicus* is based on the dissection of a female specimen of an undescribed form of *Poseidonamicus* (Figure 21) from Mozambique Channel (IIOE 416A, dissection 124; USNM 174379-80). This specimen unquestionably is *Poseidonamicus*; however it is not *P. major*. Live specimens with soft parts are rare and this one was the best available at this time.

The first antennae are divided into five segments with podomeres v and vi (following scheme of Müller 1894) fused. The second antennae are moderately robust with a long well-formed exopodite. The mandible has a "two-fingered" epipodite and only one major brushlike setae was observed. The thoracic appendages have poorly developed knee apparatus and a very small proximal carrot-like bristle was seen.

The appendages seem typical of several outer-shelf hemicytherid species that I have examined, yet the carapace characteristics suggest that these aspects are not by themselves reliable for taxonomic determination on the family or generic levels. The antennae are very similar to those of *Bradleya* as are the thoracic legs and maxillae. The epipodite of the mandible is simpler however, with only two "fingers" observed in that of *Poseidonamicus* compared to five in *Bradleya*. The significance of this difference is not fully understood, but it was also noticed that the carrot-like setae of the basal podomere of the legs and the mandible is also smaller. In general the differences in appendage anatomy that exist between the two genera are minor as compared with those of *Agrenocythere*, new genus, described on pages 60-62.

COMPARISONS WITH OTHER GENERA.—For the present no other genus seems closely related to *Poseidon-*

*amicus*. It is a deep inhabitant of the psychrosphere and seems to have changed little since the early Cenozoic (Paleocene). The older forms have been found only in deep-sea cores (DSDP III) and then only a few specimens. In the present report only the younger species are described.

*Poseidonamicus* is believed to be related to *Bradleya* on the basis of similarity in lateral outline in which both forms are broadly rounded anteriorly and have very blunt caudal extensions. The patterns of the reticulum are also similar, although the formation of prominent ridges from the muri between the dorsal and ventrolateral carinae is different. The anterior of *Bradleya* has a bridge structure, as does *Jugosocythereis*, and a median ridge in the posterior area is often present; whereas the anterior of *Poseidonamicus* is devoid of ridges of any kind and seems to maintain strength through a general increase of mass within the reticular field. The pattern of the reticulum in the posterior of *Poseidonamicus* is dominantly vertical, whereas that of *Bradleya* is either horizontal, uniform, or irregular. This genus is thought to have been confined to the deep-sea during the Cenozoic. Comparisons with older fossil forms known from shallow water are not obvious to me at present.

INCLUDED SPECIES.—For the purposes of this report I have not made a detailed study of all of the possible species of *Poseidonamicus* that I believe may be represented in the Recent and fossil record of the psychrosphere. Five possible species are discussed here, of which four are included as valid and diagnosed, and the fifth is included, but its usability as an identifiable taxon is questioned. The stratigraphic ranges cited below are tentative. Those given as Recent probably are much longer lived than now known.

*Poseidonamicus major*, new species, deep Indian, South Atlantic and Southern Oceans; Oligocene?, Miocene to Recent; designated as type-species.

*P. minor*, new species, eastern Pacific; Pleistocene to Recent.

*P. nudus*, new species, western Indian Ocean and south-eastern Pacific; Recent.

*P. pintoii*, new species, continental slope, western South Atlantic Ocean; Recent.

*P. viminea* (Brady), 1880: 94, pl. 18: fig. 3a-c.

Brady, in the *Challenger* report, described a single specimen now in the British Museum (BM 81.5.33; holotype by virtue of monotypy) from station 146, Southern Ocean between Prince Edward and Crozet Islands (lat. 46°46'S and long. 45°31'E; 1375 fathoms) as *Cythere viminea*. From this specimen, its

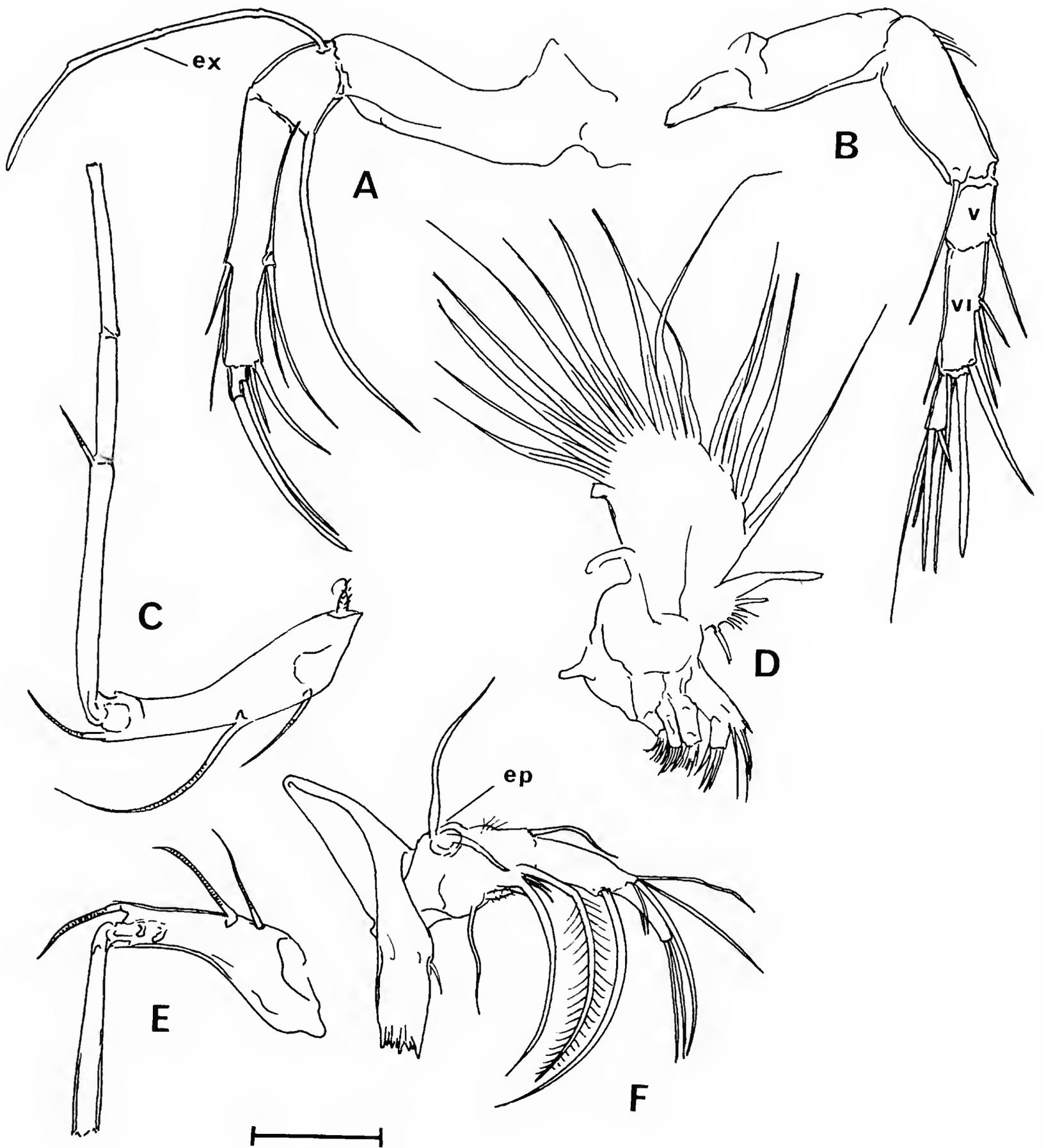


FIGURE 21.—The appendages of a female specimen *Poseidonamicus* species from Mozambique Channel (locality IIOE 416, see Table 2; dissection 124, USNM 174379, 174380), the same specimen (USNM 174381) whose carapace is shown in Plate 11: figure 13. (A) The second antennae has a long exopodite (ex); (B) the first antennae has segments v and vi fused; (C, E) the knees of the thoracic legs have some additional reinforcement; (D) maxilla; and (F) a two-“fingered” epipodite (ep) in the mandible.

surface worn and now broken (see Plate 11: figure 15), he deduced the following reticulum description, which he must have considered diagnostic. "Shell sculptured with closely set polygonal fossae and produced round the margins so as to form a stout encircling flange" His illustration and the type-specimen show this "flange" to be the anterior and posterior marginal rim, which unfortunately is a feature common to many ostracode species and genera. Further evidence of Brady's lack of understanding of this taxon is the fact that he identified and illustrated (Brady 1880, pl. 24: fig. 1e-g) another specimen of this form as *Cythere dictyon* which he suggested was a male of *C. dictyon*. Apparently the artist failed to see the features in common between these specimens, as the vertical muri on the type-specimen of *C. viminea* that are characteristic of *Poseidonamicus* are not shown in his drawing. This species was only identified once (Chapman 1910: 433) since Brady's original description almost one hundred years ago. Because of the condition of the type-specimen (the only specimen considered by Brady in this species), the confusion of identification of this taxon by Brady, and the failure to define adequate criteria for its identification (both in description and illustration), I suggest that the species is not identifiable (except to generic assignment) and therefore the trivial name *viminea* be considered nomen dubium.

Although four of several possible species are first described here, the purpose of this report is not to analyze the whole morphological range of *Poseidonamicus* (a very common, diverse and widely distributed psychrospheric genus), but to show some of the morphological trends that resemble those of *Bradleya*. This relationship was confused by Brady in his original description of *Cythere dictyon* (now *Bradleya dictyon*) and his failure to consistently identify *C. viminea*. Unlike *Agrenocythere*, new genus, which has also been previously identified as *Bradleya*, and which I have described in detail on pages 58-62, species that I would class with *Poseidonamicus* have never been recorded to my knowledge under any name during previous studies of living or fossil deep-water marine ostracodes. Considering its abundance in deep-sea samples and the very wide distribution of this particular ostracode, this lack of discovery is somewhat of a mystery. Brief diagnoses of the new species follow.

*Poseidonamicus major*, new species

FIGURES 20, 22; PLATE 8: FIGURE 5; PLATE 10: FIGURES 1-6

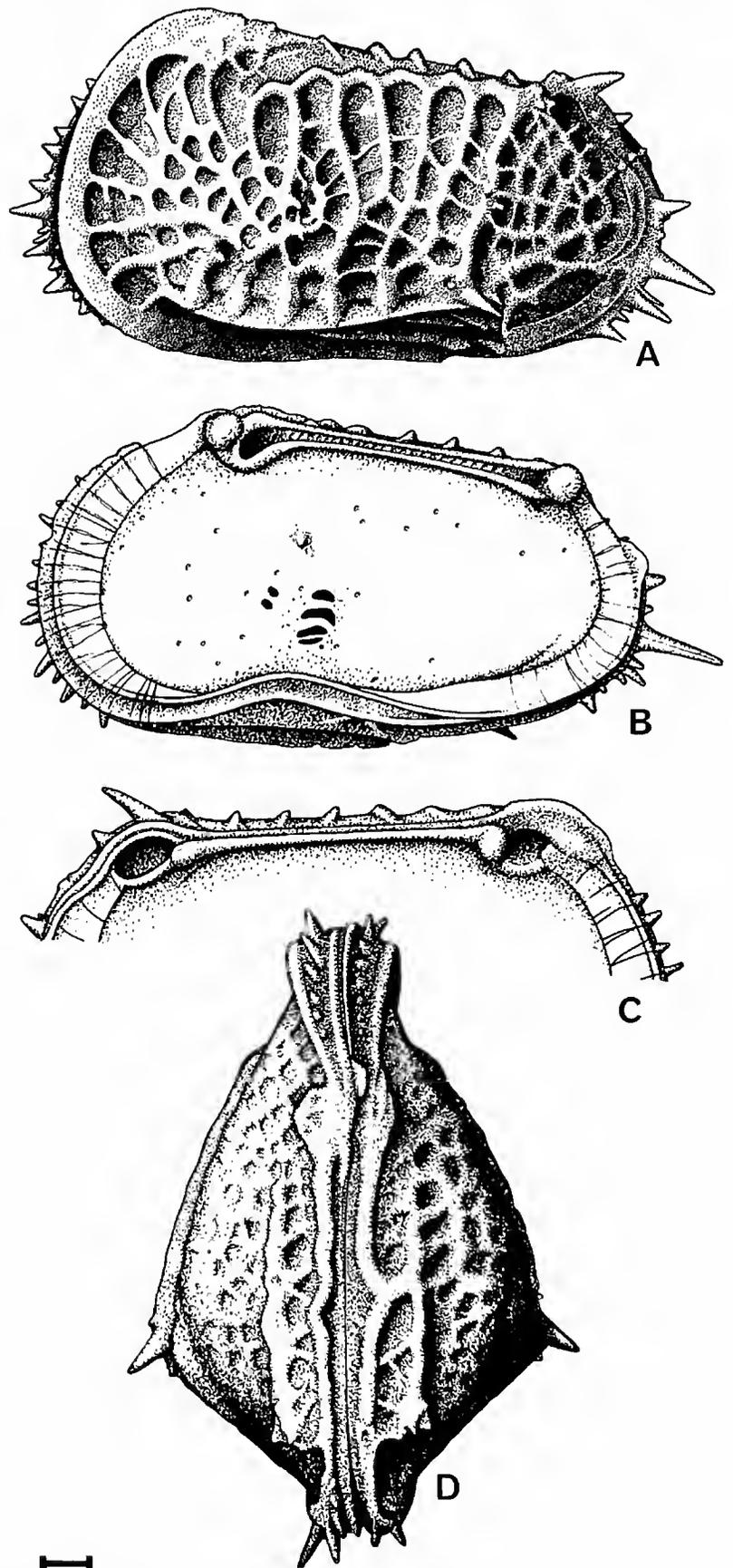


FIGURE 22.—Drawings of the carapace *Poseidonamicus major*, new species, from Mozambique Channel (IIOE 363B) showing (A) the general aspect of the surface sculpture, (B) the fused duplicature and thaerocytherid muscular pattern, (C) the holamphidont hinge elements, and (D) a dorsal view of a whole specimen. Scale = 100 microns.

**HOLOTYPE.**—Left valve, adult female from the Recent of Mozambique Channel; Figure 20 (USNM 174335); paratypes (USNM 174354).

**TYPE-LOCALITY.**—Indian Ocean, Mozambique Channel southwest of Europa Island in the vicinity of IIOE station 368c; lat. 23°00'S and long. 38°37'E; 2995 meters depth; bottom temp. 1.6° C.

**AGE.**—Oligocene?, Miocene to Recent, on the basis of present data. Live specimens found.

**DIAGNOSIS.**—A moderately reticulate species of the genus *Poseidonamicus* (see pp. 46-52) with strong principal muri in the central field and broad punta in the anterior field. The shape in lateral view is elongate subrectangular. Species is blind.

**COMPARISON.**—Among the various forms of *Poseidonamicus* observed, *P. major* is somewhere near the mean of the distribution of robustness within the possible development of the reticulum. A nude form (*Poseidonamicus nudus*, new species), one with only traces of reticulation, is described here along with *P. minor*, new species, a very strongly reticulate form (in which the secondary horizontal muri in the central field tend to disappear). *Poseidonamicus pintoii*, new species, is higher, relative to length, with a less conspicuous ocular region and anterodorsal flange.

**DIMENSIONS.**—Length of holotype 1.09 mm, height 0.67 mm; length of lower Miocene specimen (USNM 174329) 0.85 mm, height 0.52 mm.

**DISTRIBUTION.**—Neogene of the southern Atlantic and Indian Oceans. Oligocene in the northern Atlantic (DSDP XII, 117).

### *Poseidonamicus minor*, new species

PLATE 10: FIGURES 13, 14, 16, 17

**HOLOTYPE.**—Left valve, adult female (?), Plate 10: figure 13 (USNM 174357); paratypes USNM 174358, 174359.

**TYPE-LOCALITY.**—Southeastern Pacific near (south of) the Chile Rise in the vicinity of Downwind Expedition station DWBG 74; lat. 28°43'S and long. 107°36'W, 3137 meters depth; bottom temperature uncertain.

**AGE.**—Pleistocene to Recent; no specimens with appendages were found.

**DIAGNOSIS.**—A coarsely reticulate species of *Poseidonamicus* with excavate muri in which the massive

development of the reticulum, in particular the muri running vertically over the carapace in the central reticular field and the anterior (usually punctate) field, has become preeminent to the exclusion of many of the weaker longitudinal muri seen in other species. The dorsal ridge is strong and a vertical ridge, not seen in other species, is formed postjacent to the vertical ridge joining the posterior ends of the dorsal and ventrolateral ridges. Species is blind.

**COMPARISON.**—This species is the most robust of those of *Poseidonamicus* known. The increase in the development of some muri apparently relieves the need of a reticulum with more mural strut members (mural accommodation) as is characteristic of *P. major*, new species, a slightly larger form. This species is analogous in architecture to *Bradleya andamanae*, new species, although not so small relative to others of its genus and paradoxically (at least for the moment) not typical of shallower water. It is premature to define the range of morphology of this species. I am not convinced that the simple factor of increased robustness is sufficient to define *P. minor*. I have observed a robust older form in cores from the South Atlantic, but whose increase in mass within the muri is arranged differently. Further study of these differences in reticular pattern should yield profitable results.

**DIMENSIONS.**—Length of holotype 0.98 mm, height 0.60 mm.

**DISTRIBUTION.**—Southeastern Pacific, deep ocean floor (depth range not yet determined).

### *Poseidonamicus pintoii*, new species

FIGURE 23, PLATE 10: FIGURES 7-12

**ETYMOLOGY.**—Named in honor of Professor Iraja D. Pinto of the University of Rio Grande do Sul in Brazil.

**HOLOTYPE.**—Left valve of adult male, Plate 10: figure 11 (USNM 174355); paratypes USNM 174356.

**TYPE-LOCALITY.**—Continental slope off Brazil near Rio de Janeiro in the vicinity of *Albatross* station 2763; lat. 24°17'S and long. 42°48'30"W, 671 fathoms depth; bottom temperature 37.9° F.

**AGE.**—Recent of the central Atlantic.

**DIAGNOSIS.**—Distinguished from other species of *Poseidonamicus* by its more quadrate outline; a nar-

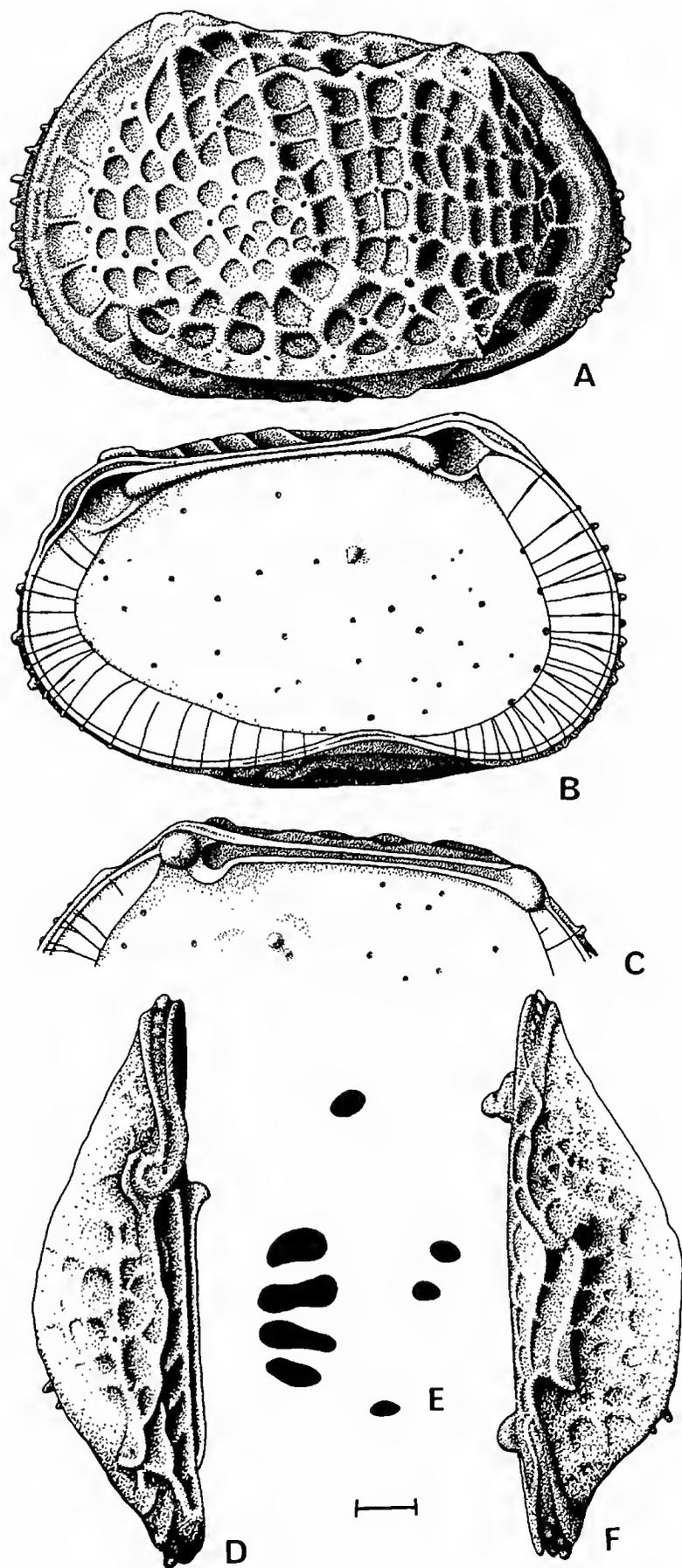


FIGURE 23.—*Poseidonamicus pintoï*, new species, adult female (?): (A) exterior of the left valve (USNM 174355) showing the pattern of the reticulum; (B) interior of the same valve showing the hinge end and the duplicature; (C) the hinge of the right valve; (D, F) dorsal views of both valves; and (E) the muscle-scar pattern. Scale = 100 microns.

rower anterior and posterior marginal flange, especially in the ocular region; an even distribution of the reticulation without specific differences in the emphasis of certain muri (such as the vertical muri in the posterior), but still with the generic pattern.

COMPARISON.—This species is as heavily reticulate, but relatively shorter than *Poseidonamicus major*, new species. It lacks the emphasis of vertical muri in the central field of that species. It is near the shape of *P. minor*, new species, but with many more reticular elements. Those present are much less massive and excavate.

DIMENSIONS.—Length of holotype 0.82 mm, height 0.56 mm.

DISTRIBUTION.—Central Atlantic Ocean, continental slope regions.

#### *Poseidonamicus nudus*, new species

FIGURE 24, PLATE 11: FIGURES 1–11

HOLOTYPE.—Left valve, adult; Plate 11: figure 5 (USNM 174351); paratypes, Plate 11: figures 1, 4 (USNM 174352).

TYPE-LOCALITY.—Mozambique Channel, western Indian Ocean, in the vicinity of IIOE station 367G, lat. 22°42'S and 39°19'E, 3140 meters depth; bottom temperature 1.85° C.

AGE.—Pleistocene to Recent; no specimens with soft parts were found.

DIAGNOSIS.—A species of the genus *Poseidonamicus* with only faint mural traces. The pattern of the reticulum can be seen within the carapace wall by light transmitted through the shell from below. The ventrolateral carinae is present, though not pronounced. The dorsal carinae is only faintly suggested by a small-angled ridge in the posterodorsal region. Species is blind.

COMPARISON.—This species is easily distinguished because of its lack of expressed reticulation; however, the late instars of samples found in the eastern Pacific did have a subdued yet positive reticulum formed. It is quite possible that the formation of a smooth carapace may represent convergence. For the present, however, all nude forms are considered as the same species. The form is slightly smaller than *P. major*, new species, and more elongate than *P. minor*, new species, or *P. pintoï*, new species. The wall structure

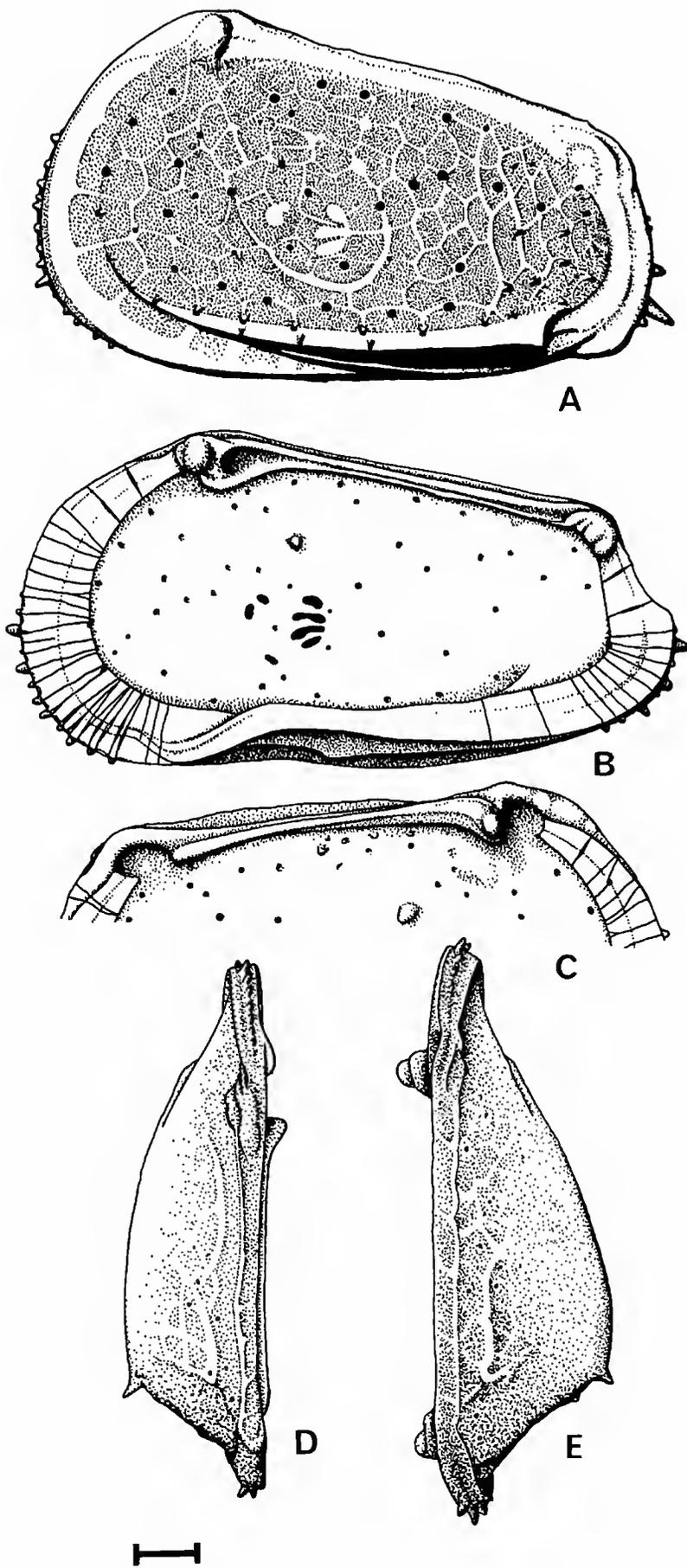


FIGURE 24.—*Poseidonamicus nudus*, new species; adult male (?): (A) exterior of the left valve with the pattern of the reticulum, as seen in transmitted light, reconstructed on its surface; (B) interior view of the right valve showing the amphidont hinge, the thacrocycytherid muscle-scar pattern and the wide duplicature; (C) hinge of the left valve; dorsal views of both valves. Scale = 100 microns.

of the valves has not yet been studied to determine the cause of the loss of the reticulum.

**DIMENSIONS.**—Length of holotype 1.03 mm, height 0.60 mm.

**DISTRIBUTION.**—Identified from the Indian Ocean (type-locality) and the southeastern Pacific (near Easter Island).

**Family TRACHYLEBERIDIDAE** Sylvester-Bradley, 1948

**Subfamily TRACHYLEBERIDINAE** Sylvester-Bradley, 1948

In 1967, Hazel proposed a division between the families Trachyleberididae and Hemicytheridae on the bases of differences in soft part anatomy and muscle-scar morphology. He disagreed with Pokorný (1964b), who considered the divided frontal muscle-scar to have doubtful reliability as a taxonomic indicator. Hazel (1967: 7) suggested instead that "the great majority of hemicytherids have two or more frontal (muscle) scars, whereas most of the Trachyleberididae have a single frontal scar." He recognized divisions within the Hemicytheridae (Hemicytherinae, Thaerocytherinae, and Campylocytherinae) containing various stages of frontal and adductor scar division. In the Trachyleberididae he included the pterygocytherines, the butoniines, and the cytherettines. All of these forms have four undivided adductor scars and a V-shaped frontal scar. He also included the Mauritsiinae and the Brachycytherinae with divided adductor scars. The echinocytherines, which have a trachyleberid anatomy (except for the so-called knee-joint apparatus) and thaerocytherine (sometimes single) frontal scars, were included as a new subfamily in Trachyleberididae. These latter forms were considered to have characteristics convergent with the hemicytherids rather than being transitional.

Hazel cites 24 genera to be assigned to the nominal subfamily of Trachyleberidinae suggesting some hesitation to recognize as many subfamilies in this taxon as he had in the Hemicytheridae. This reflects his earlier assertion that the divisions among the Hemicytheridae appear to be more "natural" than those of the Trachyleberididae. One can also see this imbalance reflected in the number of genera of the various branches of his phylogenetic tree (five paired branches have 2, 3, 5, 6, and 8, respectively) two individual branches have 9 and 10, respectively) as

compared with the trachyleberine trunk (which has 24 genera).

Hazel's work is reviewed here to demonstrate an important point—the absence, in the past, of appropriate criteria to discriminate among subgroups within the very large group of ornate trachyleberine genera. The 24 genera, mentioned by Hazel, in fact contain a proportionally large group of poorly understood species, whose generic assignments are at best insecure. Liebau's (1969) attempt to recognize species groups on the basis of fossal patterns and pore conuli is an important step in defining some of the necessary criteria. Some of my observations (which include study of about 50 patterns) agree with those of Liebau. They were made independently of his study. Therefore, our results do not necessarily agree.

The reticulate patterns are generally consistent within the Trachyleberinae (where they can be observed). I was skeptical that the same pattern would be found within the Thaerocytheridae. I believe that *Cletocythereis rastromarginata* (Brady) and *C. haidingerii* (Reuss) (which have divided V-shaped frontal scars) actually are only slightly modified trachyleberids. The Cretaceous genus *Limburgina* Deroo, which has a divided frontal scar (the lower part U-shaped), has a reticulum that is trachyleberine and yet has mural ridges like that of the bradleyines. This group may represent, or be closely related to, the ancestral stock of both families.

The individual pore conuli can be identified in many nonreticulate trachyleberids (such as smooth forms of *Veenia*). The pore conulus of Pokorný ("porenkegal" of Triebel 1940) is only one of these. Although the conulus itself may not always be evident, many of the associated pores, which are distinct from other normal and sieve pores in their positions and relationship to the muri, are also recognizable in nontrachyleberids *Poseidonamicus* (less so in *Bradleya*) and *Jugosocythereis* (thaerocytherid), and *Patagonacythere* (hemicytherid).

The positions of (and patterns formed by) the pore conuli are subject to minor changes, but on the whole they change less than do the patterns of the reticulum and less than aspects of general shape or carapace robustness. Those distal to the central region appear to change in position or presence (among different species) more than those closer to the central lateral region of the carapace. These differences are thought to reflect allometric change (change in proportion

due to ontogeny, dimorphism, adaptive modification) in the general shape of the carapace. Comparisons between the allometric changes, as reflected in pore conuli pattern differences, and those of modifications of the reticulum emphasize the role of mural compensation (accommodation) in the general architecture of the various forms.

Within the individual fossae often can be seen finer muri (mural struts as well as secondary reticulation), which can be observed to increase in intensity or add fossae within a species. Liebau (1969) suggested that the primary fossae can be recognized as homologous sets containing the secondary reticulate subsets. It is also true that some fossae seem to be excluded or new ones appear between sets (perhaps depending on what is defined as a set).

As the muri become thicker and consequently the carapace becomes more robust, the number of muri and fossae decreases. This is usually correlated with a decrease in overall carapace size or changes in shape in a particular sector of the carapace.

The median ridge ("mitte rippe" of Triebel 1940), associated spines or tubercles, and other such major topographic features of the carapace seem to arise independently of either the pattern of the reticulum or the pore conuli. Often the pore conuli are displaced to the side of the median ridge, rather than remaining on the crest. The reticulum seems to respond to the form of these features, giving them strength.

The muscle scars appear to "interfere" with the continuity of the pattern of the reticulum. Muri can be observed either to stop (forum) or bridge (ponticulus) the region of the muscle-scar pattern, often in quite different ways in different species or genera. Those secondary architectural features must arise from the original reticular pattern and are thereby limited in the kinds of such structures that can form.

As the reticulum passes over the muscle scar node the muri change in mass and structural form to accommodate for the stress requirements imposed by differences in shape and the "load" of this special region of the carapace. In the Bradleyinae this accommodation is often expressed as a bridge. In *Agrenocythere*, new genus, and related forms it is expressed as a radial structure called the castrum. The stresses are transferred from the location of the scars to the reticular fields by means of a truss system (the bridge) or a reinforced radial grid (the castrum and

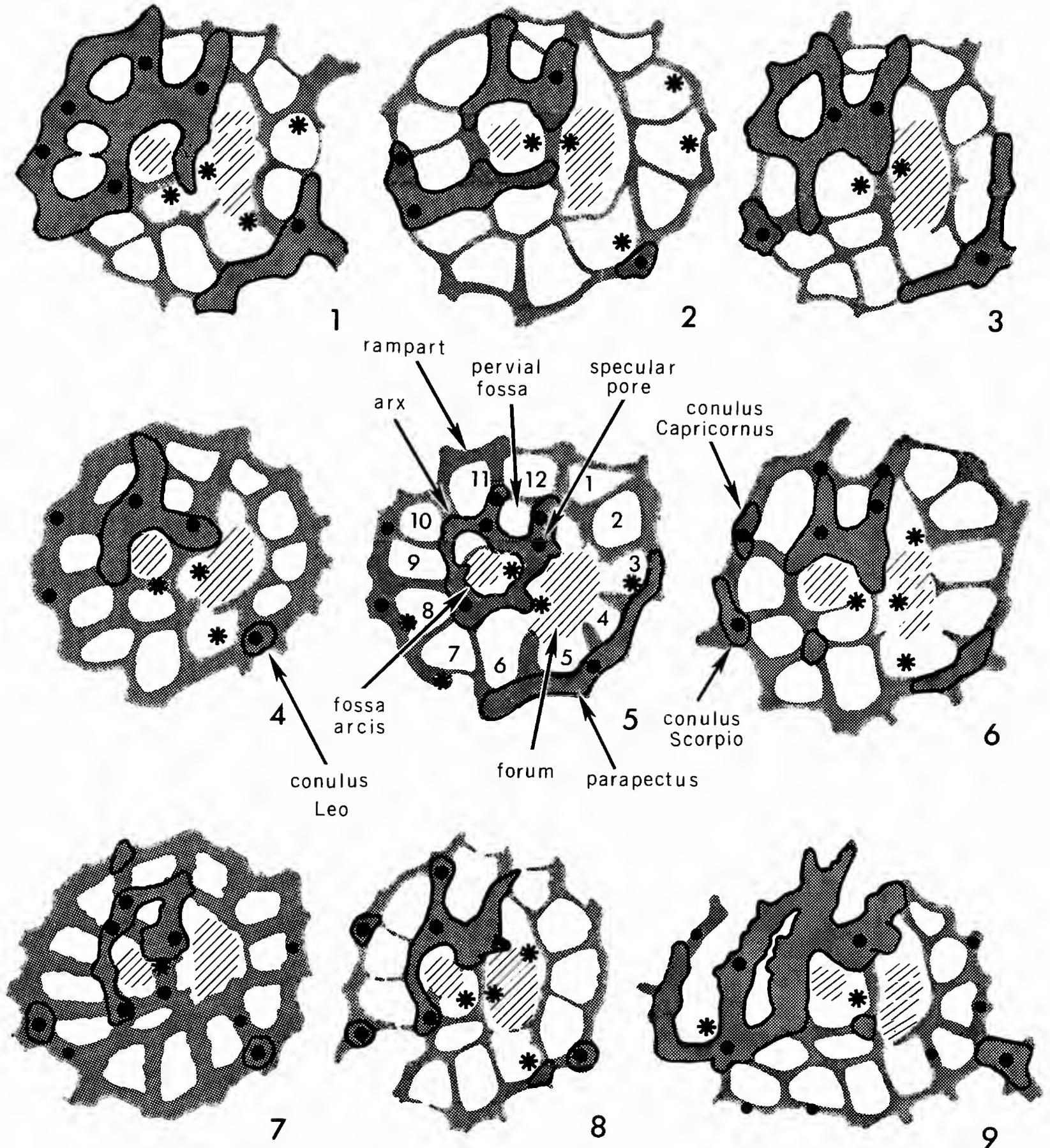


FIGURE 25.—Variation within the castrum among species of *Agrenocythere*, new genus. These include (1) *A. hazelae* (van den Bold, 1946), Recent, Caribbean; (2) *A. americana*, new species, Recent, Gulf of Mexico; (3) *A. hazelae* (van den Bold, 1946), Miocene, Trinidad; (4) *A. gosnoldia*, new species; (5) *A. pliocenica* (Seguenza, 1880), with morphological terms, Pliocene, Italy; (6) *A. hazelae* (van den Bold, 1946), Recent, eastern Pacific; (7) *A. radula* (Brady, 1880), Recent, Indian Ocean; (8) *A. spinosa*, new species, Recent, Indian Ocean; (9) *A. hazelae* (van den Bold, 1946), Miocene, South Atlantic. Note the consistency in the basic pattern of the muri, yet how the arx becomes strongly developed, especially in the variations of *A. hazelae* in different regions in different ages.

arx). From a utilitarian standpoint, it is fortunate that because the carapace usually breaks around this structure (responding to its increased strength), fragments containing the castrum can be used for species identification (with difference in castral architecture). Since specimens are rare in deep-sea samples, this aspect of *Agrenocythere* morphology proves to be especially advantageous.

A bold enlargement of the muri over the muscle-scar node at the center of the castrum is often the most conspicuous feature of the castrum, sometimes extending from its central part in the region of a large spine (specula) to its outer mural ring (rampart) and in one case (Miocene, South Atlantic *A. hazelae*) even to the mural series beyond this ring. The architecture of the castrum does not always include a parapectus (raised outer murus; see pages 58, 59). Often pore conuli surmount the castral rampart without an enlargement. In Figure 25 nine variations of castral architecture are shown that occur among some of the various species of *Agrenocythere*. The descriptions and significance of these changes will be given in more detail in the discussion in the next section.

### Genus *Agrenocythere*, new genus

ETYMOLOGY.—Greek *agrenon*, net.

TYPE-SPECIES.—*Agrenocythere spinosa*, new species.

DIAGNOSIS.—Distinguished from other reticulate, holamphidont trachyleberine genera by its large size, its usually produced and upturned posterior, the absence of an eye tubercle and the development of a circular and radial complex (castrum) in the design of the reticulum over the muscle-scar node reinforced by mural thickening near the center (the arx) or around its outmost ring (the parapectus). The posterodorsal region is marked by a dorsal bullar series, which distinguishes this genus from those with long dorsal carinae. The system of intramural pore conuli includes one emphasized in the posteromedian region (Charon), another in the position of the "porenkegal" (Leo) and a third on the posterior margin (Terminus). The appendages are attenuate.

GENERAL OUTER CARAPACE MORPHOLOGY.—The reticulum can be divided (Figure 8) into character complexes and reticular fields. The character complexes include (1) the marginal rims, (2) the ventrolateral carina, (3) the dorsal bullar series, and (4) the castrum. Between these complexes lie the reticular

fields, which are simply designated by location or region of the carapace. *Agrenocythere* and several other genera are characterized by that part of the reticulum that surrounds and surmounts the muscle-scar node, the radial structure called the castrum.

The **castrum** (Latin, fort) consists primarily of an outer mural ring (rampart) that defines the outer boundaries of twelve fossae (numbered clockwise, one through twelve) of the **ballium**. Often portions of the rampart murus are enlarged or raised to form a **parapectus**, which usually includes one of the principal pore conuli. There may be several parapecti. If the muri of the inner castrum (inside the ballium) are raised, they form a conspicuous, often **H-shaped** structure called the **arx** (inner or principle fort). The arx is usually surmounted by a prominent spine (the **specula**; watchtower), approximately at the center of the castrum. The arx may be confined to the center of the castrum and surrounded by a relatively open mural ballium and rampart system. There may be parapecti, or some of the parapecti (usually in the region of ballial fossae 9–12) may be joined to the arx enlarging its extent (thereby being considered an integral part of it). Within the center of the arx is a fossa termed the **fossa arcis**, containing a characteristic sieve pore, the **porus castris**. Just dorsal to the fossa arcis is another fossa, the **pervial fossa**, which is often open and exposed to the dorsal reticular field. To the posterior of the arx and just beneath the specula lies the **forum**, which is a smooth region formed by interference of the adductor muscle scars (the crystal prisms are frequently visible from the exterior) with the reticulate pattern of the castrum. The terms delineating these important features were chosen because of the similarity in form of the overall structure to an ancient fortification (especially impressive in stereo-SEM view), and to make them easy to remember. This terminology also seems appropriate as this structural system seems to lend strength to the central lateral part of the carapace.

The remainder of the reticulum, or the reticular field, extending from the rampart of the castrum outward toward the margins of the valve is intermittently punctuated with pore conuli. These features are formed by a series of normal, usually conjunctive, intramural pores. Each individual egress of a pore from the carapace is marked by a raised rim forming a volcano-like pore conulus. In the absence of a conulus, the murus is notably raised and widened to ac-

commodate the pore, which is almost always there if preservation of the carapace is adequate. Of the few specimens examined that still had setae attached to the carapace, none were observed by me to have these emerging from the pore conuli. I cannot state with assurance that they had none when the animals were alive. It is noteworthy that the pore conuli are located on the muri between fossae. Many of the fossa contain solar sieve pores. These may indicate a relationship of the fossa to cells deeper within the soft tissue, dermal layers underlying the carapace. There may be a direct correlation between the pattern of the carapace secreting the sensory epithelium, and the pattern of the reticulum and distribution of solar sieve pores. As noted by Liebau (1969), the locations of the pore conuli appear to be constant within a yet unknown but significant range of different genera and species (Plates 3 and 4).

I do not find the numerical system of fossal or pore conulus identification suggested by Liebau to be as useful as I would like. These descriptors are not sufficiently neutral. Although the terms are serial, their placement is not. There is a lack of consistency of the serial alignment between some species. Perhaps at a later time a system of enumeration, consistent with development can be devised, but until that time I find proper names or zone coding (color or nomenclatural) easier to use and remember.

The terminological scheme for the pore conuli I have used here is based on reference of the position of the individual conulus relative to the castrum (on the left valve). The ballium is usually divided into 12 parts of fossae and can be consistently enumerated in a clockwise direction or in the manner of a circular calendar. The pore conuli closest to the ballium can be identified relative to its closest ballial fossa (Figures 8, 25). I have indicated them by use of signs of the zodiac, which are at least known *en passant* by most. Farther away from the castrum short names of Greek origin (proper names of letters or mythological characters) are used and chosen to suggest relationship to the anterior and posterior margin. These terms will be used in the following discussion. They are open in the sense that more can be added or some subtracted without prejudicing the rest.

The marginal rim is best developed on the broadly rounded anterior and the caudate posterior of the carapace. It is present along the ventral margin but less conspicuous. It is best developed in *Agrenocythere*

*gosnoldia*, new species, and least developed in the Caribbean forms of *A. antiquata*, new species. The emphasis with which it is expressed is also reflected in the massiveness of the ventrolateral ridge, and the dorsal bullar series. The massiveness of these features influence the general outline of the animal. They are relatively narrow or confined in *Agrenocythere radula*, become broader and sharpened in *A. hazelae*, to blunted and somewhat massive in *A. americana*, new species, narrow in *A. pliocenica*, and exaggerated (broad) in *A. gosnoldia*.

The dorsal bullar series, which consists of two or three dorsally produced portions of the reticulum, may be a series of nodes as in *A. americana*, or tuberculate complexes as in *A. hazelae*, or form a punctuated, crested ridge as in *A. gosnoldia*, or be diminished as in *A. radula*.

The ventrolateral ridge is a very prominent feature in all species of *Agrenocythere*. It is often ponticulate with fenestra joining the ventral and lateral regions of the carapace. There are pores at the junctions of the ridge and their supporting struts, and often there are also conjunctive spines and a large terminal spine. The extension of this ridge as a skidlike support is reflected in the increase in mass of the muri that join this feature to the rest of the reticulum.

Both the mass and the spinosity of the reticulum differs among species. Whereas none of the forms described could be considered delicate, the muri of *Agrenocythere radula* and *A. pliocenica* are not as massive or not as high in relief relative to the solar width in contrast to the considerable relief of *A. hazelae*. The regularity of pattern of the reticulum varies also, perhaps related to the massiveness of the rest of the carapace (Plates 5 and 6). The junctions of the muri forming the reticulum of some *Agrenocythere* species are surmounted with small spines (conjunctive spines), however only a few of these are pore conuli. Spines, some with pores, line the marginal rims and ventrolateral ridge with some variation in number and size among species. Celate spines are seen in some specimens of *A. radula* and *A. gosnoldia*, especially in the anterior (in the B fossal series). Celation of the muri in the anterior may be related to the development of the formation of additional intrasolar muri within the anterior fossae of forms such as *A. radula* and *A. pliocenica*.

INTERIOR CARAPACE MORPHOLOGY.—In general the

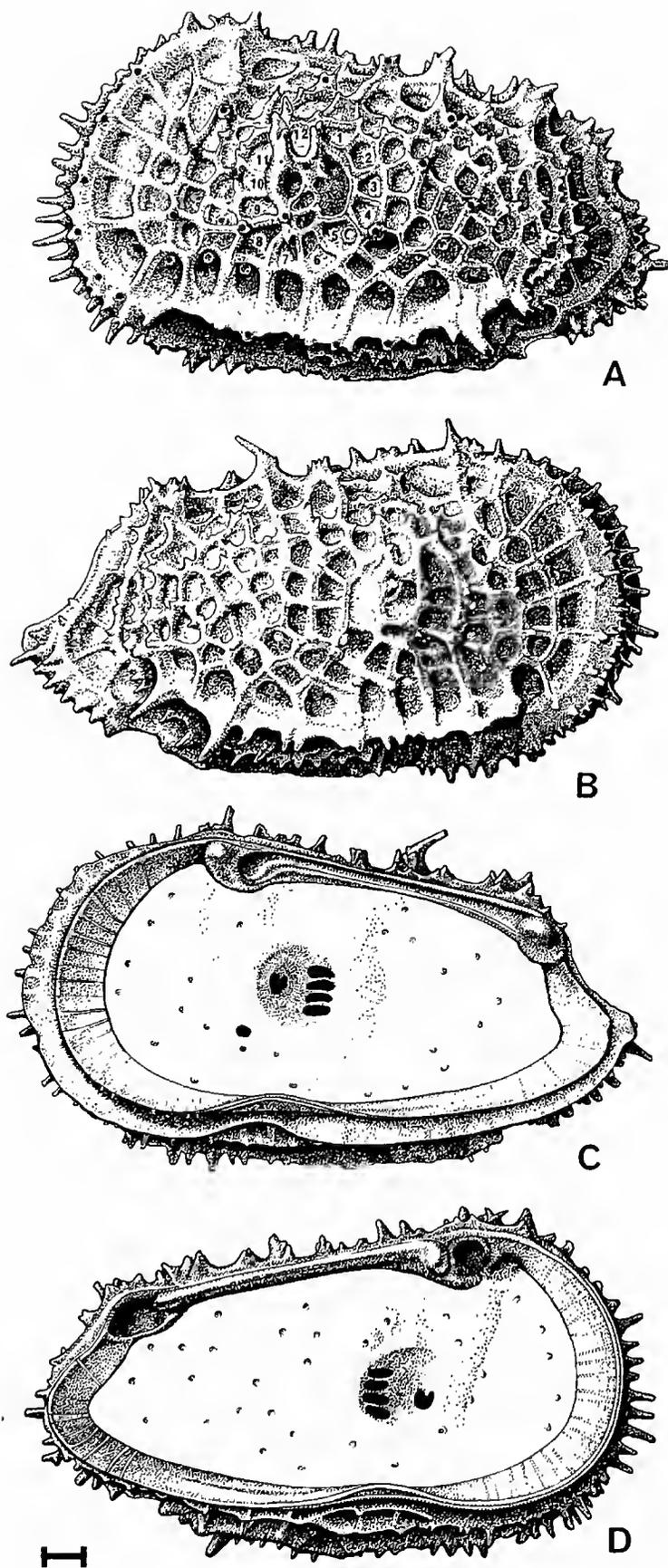


FIGURE 26.—*Agrenocythere spinosa*, new species; the designated type-species; adult, female (USNM 174366): (A) exterior of the left valve with the order of the fossae in the ballium and the locations of the pore conuli indicated; (B) the exterior of the right valve; (C) the interior of the right valve showing the terminal tooth elements of the holamphidont hinge, the features of the duplicature, and the trachyleberid muscle-scar pattern; (D) the interior of the left valve. Scale = 100 microns.

interior of the carapace is typical of others found in trachyleberine genera (Figure 26).

Hinge: Holamphidont (Figures 8c, 26c, d).

Muscle-scar Pattern: Four undivided adductor scars, simple mandibular scar, V-shaped frontal scar, prominent dorsal scar (Figure 8d).

Duplicature: Wide, "welded," no vestibule.

Radial-pore Canals: Simple, approximately 20 in the anterior, 10 in the posterior.

APPENDAGE MORPHOLOGY.—The following description of the soft part anatomy of *Agrenocythere* is based on the dissection of a female specimen of *A. radula* (Brady), USNM 174384-5; from Mozambique Channel (IIOE 407A, dissection 382, Figure 27).

The first antennae are divided into six segments with podomeres v and vi (following the scheme of Müller 1894) being unfused. The second antennae are long and narrow with an abbreviated exopodite. The mandible has a "five-fingered" epipodite (trachyleberid characteristic) and two brushlike major setae. The thoracic appendages are serially similar without modification of the first legs. They are long and reinforced ("knee apparatus"; considered a hemicytherid characteristic) at the knee; a basal proximal carrot-like bristle is present on the anterior two prodopodites.

The appendages of *Agrenocythere* like many other deep-sea ostracodes have attenuated and cirrose aspects. To what extent these are primarily phyletic or adaptive is not yet understood (see pages 30-31). It is possible, however, that primitive divisions of appendages are perpetuated in a low mechanical energy environment. The stronger adaptive forms of shallower water (greater cross-sections relative to length, fewer segmental divisions) is a recent specialized development peculiar to more agitated waters, coarse and unstable bottoms.

COMPARISONS WITH OTHER GENERA.—Of the reticulate trachyleberine genera thus far described *Oertliella* and *Cletocythereis* are most similar to *Agrenocythere*. Comparison between the type-species of *Oertliella* (*O. reticulata*; Plate 5: figures 5, 6) and *Oertliella aculeata* (Figure 6d) can be made with the species of *Agrenocythere* given here (Figures 6, 7; figures on Plate 6). The patterns of the reticulum and of the pore conuli are substantially the same. The castral regions of *Oertliella* (see examples at the end of this report) are without an arx even though a specula and adjacent spine are present. *Oertliella* has

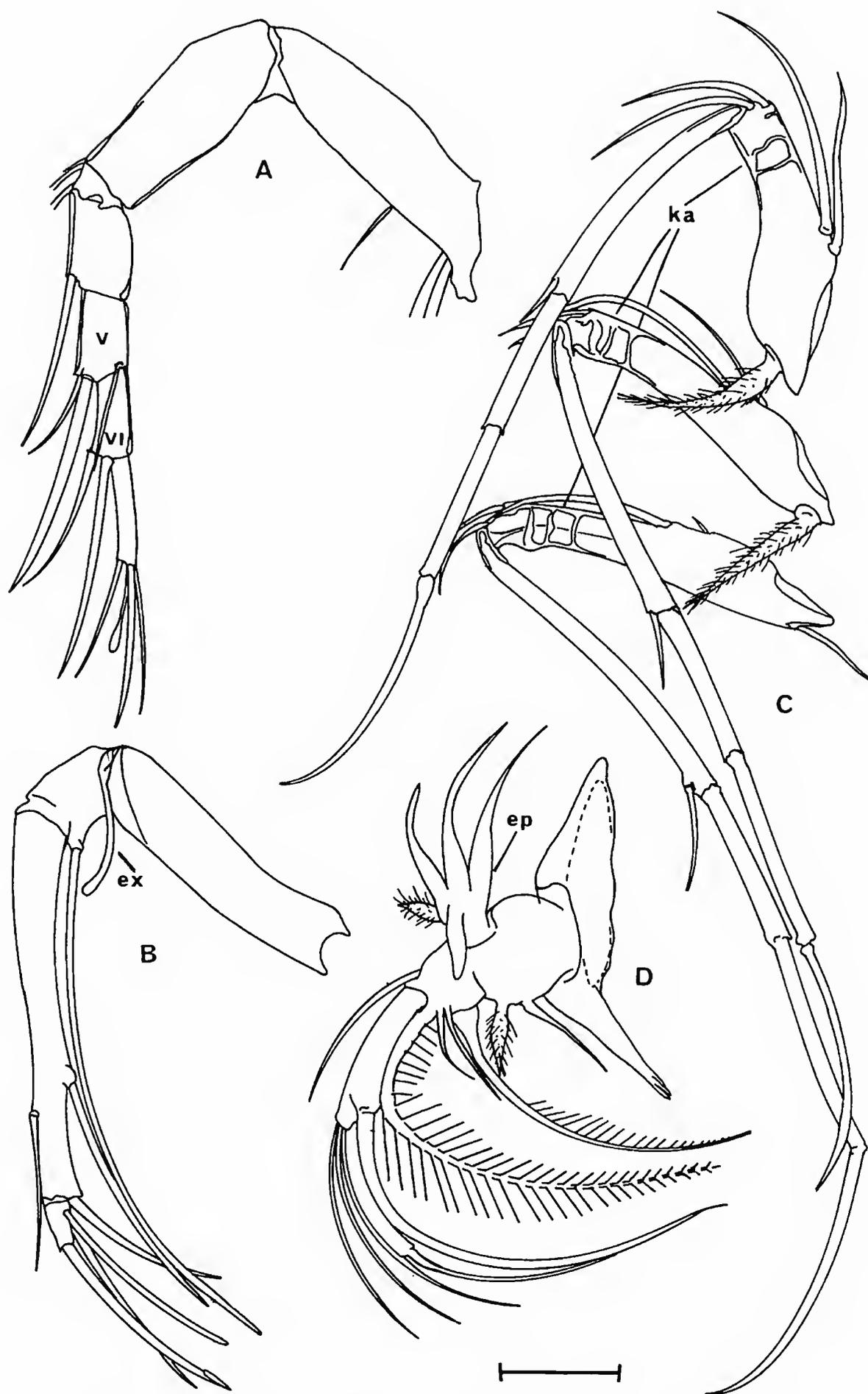


FIGURE 27.—Appendages of female specimen (USNM 174384, 174385) of *Agrenocythere radula* (Brady, 1880) from Mozambique Channel (IIOE 407A; dissection 382): (A) the first antennae; (B) the second antennae; (C) the thoracic appendages; and (D) the mandible. Scale = 100 microns; roman numerals refer to the segmentation system of Müller, 1894, ka = knee apparatus, ex = exopodite, ep = epipodite.

a prominent eye tubercle which *Agrenocythere* does not. The specimens of *Oertliella ducassae* that I have described from the Bartonian of the Biarritz section have a long, accentuated, dorsal crest similar to the male (?) of *O. reticulata*. The distinction between the two groups may lie in the adaptive differences in morphology that became stabilized during the Paleogene with *Oertliella* remaining smaller and robust with eye tubercles and a long dorsal ridge, while *Agrenocythere* became larger, more embellished with detail along the dorsum and in the castral region, and blind. *Oertliella aculeata* represents a problem in this classification as it has characteristics of both *Oertliella* and *Agrenocythere*. It is compressed in size with exaggerated pore conuli, dorsal bullae, and ventrolateral ridge, compared to *O. horridula* or any of the *Agrenocythere* species. It has no castral arx and has an eye tubercle.

*Trachyleberidea* and *Hazellina* also have aspects of general resemblance to *Agrenocythere* although they are much smaller, often more attenuated (especially toward the posterior) and have developed more massive posterodorsal ridges or partial median ridges. Their castral regions are not well developed and although the reticular pattern remains the same, there is no arx or other such features. The reticulum of these genera is frequently celate, which rarely is seen in *Agrenocythere*. Many of the pore conuli are present in all three genera, but more study is required to examine how stable this latter system is in *Trachyleberidea*.

Liebau (1969) has illustrated similarities in fossal patterns between *Oertliella aculeata*, *Cythereis longaeva longaeva*, and *Limburgina ornata*. He identified *O. aculeata* as the subspecies *horridula* including Bosquet's species in *aculeata*. I believe this is an error, and that *horridula* is not only a separate species but much closer to *O. ducassae* and therefore a truer *Oertliella*. He refers to the more or less primitive type of "limburginotypes ornament" in which he would include the type of *Oertliella* (*O. reticulata* (Kafka)), *O. gr. horridula aculeata* (Maestrichtian-Paleogene) and several other species. I am sure he would have included *Agrenocythere* species also, had they been available. In my opinion this grouping has merit in that it does recognize the similarities in fossal pattern, but I believe that it also overlooks important differences in the pattern of the reticulum itself. As discussed elsewhere *Limburgina* also has a strong re-

semblance to older *Bradleya* species. The divided frontal scar, which may simply be a breakup of the V-shaped scar, shows the morphological instability of this complex of forms near the Mesozoic-Cenozoic boundary.

Many features of the reticular pattern of *Agrenocythere* can be traced to reticulate variants of *Cythereis ornatissima* Reuss. Comparison of the similarity in pattern can be made by inspection of figures 1 to 8 of Plates 3-6, especially figures 2 of Plates 3 and 5. *Cythereis ornatissima* is quite variable even within a given population; however, the major differences between this form and that of most *Agrenocythere* species is the proximal compression and distal distention of the pattern of the reticulum and spinose marginal features of the former. The median ridge ("mitte rippe") often considered typical of *Cythereis* and *Cythereis*-like forms (Triebel 1940) is not always present within a single *Cythereis* species population. There is often a retention of only the pore conulus Charon as is also characteristic of some species of *Agrenocythere*.

It is still premature to offer comparisons between other reticulate trachyleberine genera such as *Costa*, *Reticulocythereis*, or *Chrysocythere* as these genera, especially the former as it is known in the western hemisphere, are in a confused state.

*Cletocythereis* also has reticular and pore conuli patterns like *Agrenocythere*. Its castrum is relatively unadorned with reticular structures, such as a specula or arx. The ventrolateral and dorsal carina are massive and elongate. The caudal process may become exaggerated in the male as in some species of *Agrenocythere*. The frontal muscle scar is V-shaped; however, it is becoming divided. This division is sometimes complete and apparently is a parallel trend to that division occurring in the Thaerocytheridae.

#### INCLUDED SPECIES

- Agrenocythere spinosa*, new species; Mozambique Channel, Recent, designated type-species.  
*A. radula* (Brady, 1880); Indian Ocean; Pliocene to Recent.  
*A. hazelae* (van den Bold, 1946); Caribbean, Atlantic, and Mediterranean; Oligocene to Recent.  
*A. americana*, new species; Gulf of Mexico; Recent.  
*A. pliocenica* (Seguenza, 1880); Mediterranean, Pliocene-Early Pleistocene.  
*A. gosnoldia*, new species; western North Atlantic; Eocene.  
*A. ? cadoti*, new species; Southern Ocean off Australia.  
*A. antiquata*, new species; Europe, Caribbean; Paleogene.

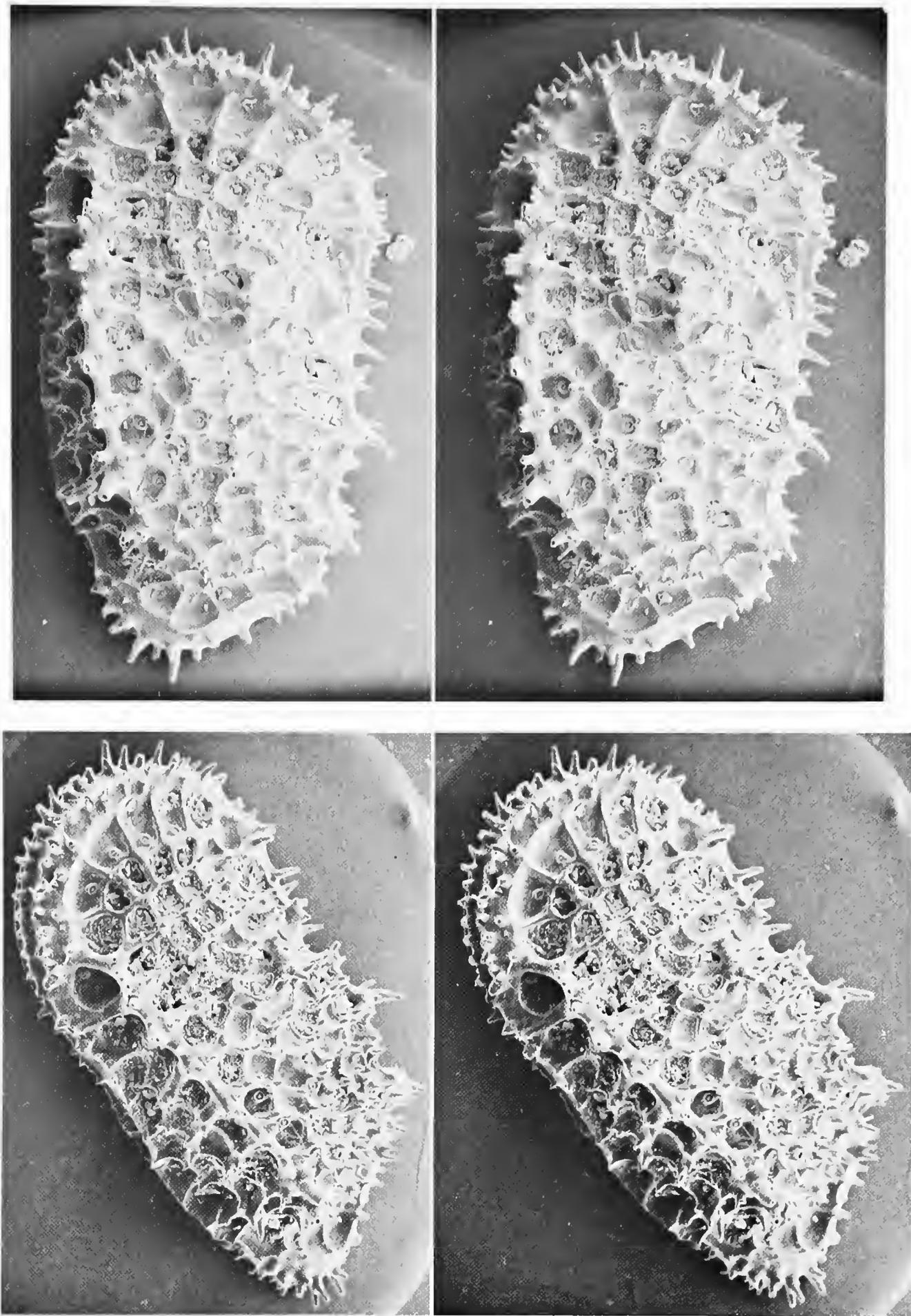


FIGURE 28.—Stereophotomicrographs of the holotype (USNM 174339) of *Agrenocythere spinosa*, new species, the type-species, from the Recent of Mozambique Channel (IIOE 407D) as seen from left lateral, and left anteroventral oblique views (x50). Also see Figure 26 for drawings of other views.

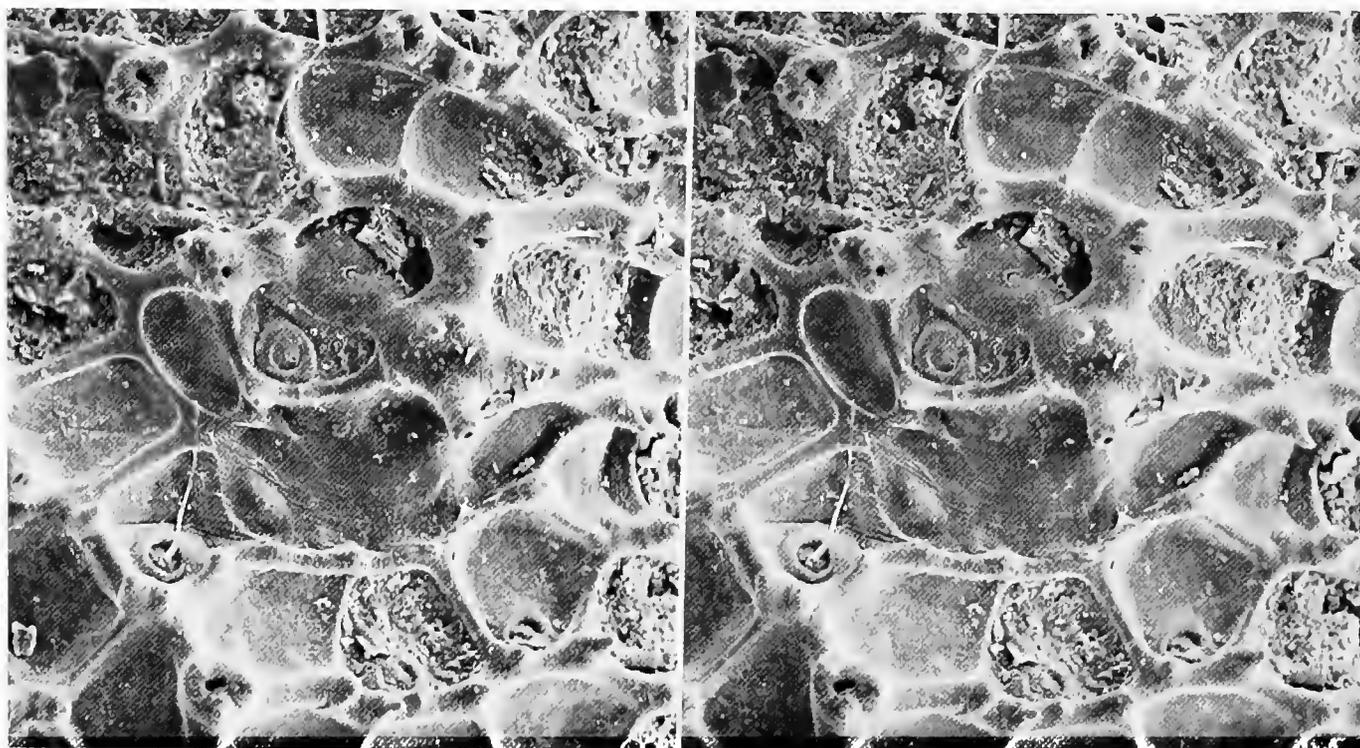


FIGURE 29.—Stereophotomicrographs of the castrum of the holotype of *Agrenocythere spinosa*, new species (x200).

### *Agrenocythere spinosa*, new species

FIGURES 26, 28, 29; PLATE 3: FIGURE 7; PLATE 5: FIGURE 7; PLATE 12; PLATE 14: FIGURE 5.

HOLOTYPE.—Left valve, adult female; Figures 28, 29 USNM 174339; paratypes USNM 174336, 174365, 174366.

TYPE-LOCALITY.—Indian Ocean, Mozambique Channel off western Madagascar in the vicinity of IIOE Station 407D; lat. 17°32'S, long. 43°15'E, 1360 meters depth; bottom temperature 4.5° C.

AGE.—Recent; no specimens containing appendages were found.

DIAGNOSIS.—Distinguished from other species of *Agrenocythere*, new genus, by a prevalence of elongate and often complicate conjunctive and marginal spines, a narrow and ponticulate ventrolateral ridge, conspicuous rimmed solar sieve pore canals and simple and delicate muri. The arx of the castrum is well defined toward the dorsal rampart only, with the fossa arcis remaining open toward the pore conulus Leo. The pore conuli Capricornus, Scorpio, and Leo surmount the castral rampart without extension of a parapectus. The second bulla (b) of the dorsal bullar series is attenuated by a large hollow spine.

COMPARISONS.—Some remarks of comparison of the type-species with others of the genus is also given in the general section on comparative morphology of

the genus. The castral arx is not massive and confined to the central part of the castrum, being weak in the ventral part compared to that of *A. hazelae*. It lacks the connecting muri to parapectal elements on the rampart. It lacks the uniformity of reticular pattern in the posterior characteristic of *A. radula*. Its spinosity is greater than any of the other species.

DIMENSIONS.—Length of the holotype 1.32 mm, height 0.77 mm.

DISTRIBUTION.—Western Indian Ocean. The stations where both *Agrenocythere spinosa* and *A. radula* were found are shown in Figure 30. It is notable that *A. spinosa* is consistently found closer to shore and in shallower water than *A. radula*. Of the 24 stations from which specimens were obtained, the 11 with *A. spinosa* were predominantly from waters from 400 to 1600 meters and 13 with *A. radula* were predominantly from 1000 to more than 3000 meters depth. Both species seem to be concentrated in greatest number of specimens at depths of from 1200 to 1600 meters.

### *Agrenocythere hazelae* (van den Bold, 1946)

FIGURES 31–38

*Cythereis hazeli* van den Bold, 1946:92, pl. 10: fig. 4a–c.  
*Trachyleberis? hazelae* (van den Bold).—van den Bold 1957:241, pl. 1: fig. 11; 1960:165.

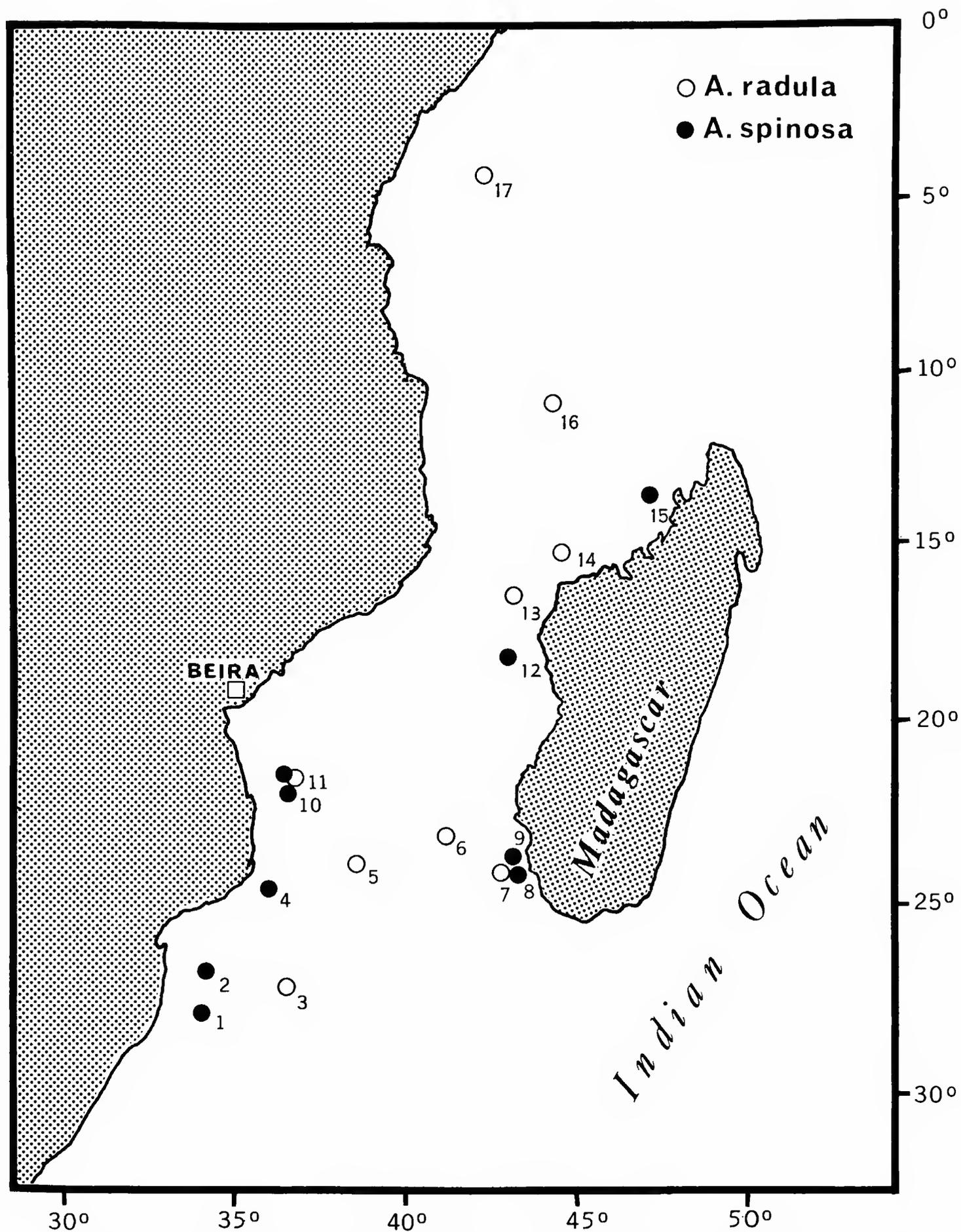


FIGURE 30.—Localities in the region of the Mozambique Channel (separating Madagascar and mainland Africa) in which *Agrenocythere radula* (Brady, 1880) (circles) and *A. spinosa*, new species, (dots), were found. *A. radula* was generally found to occur in the deeper regions away from the slope areas frequented by *A. spinosa* (see p. 64).

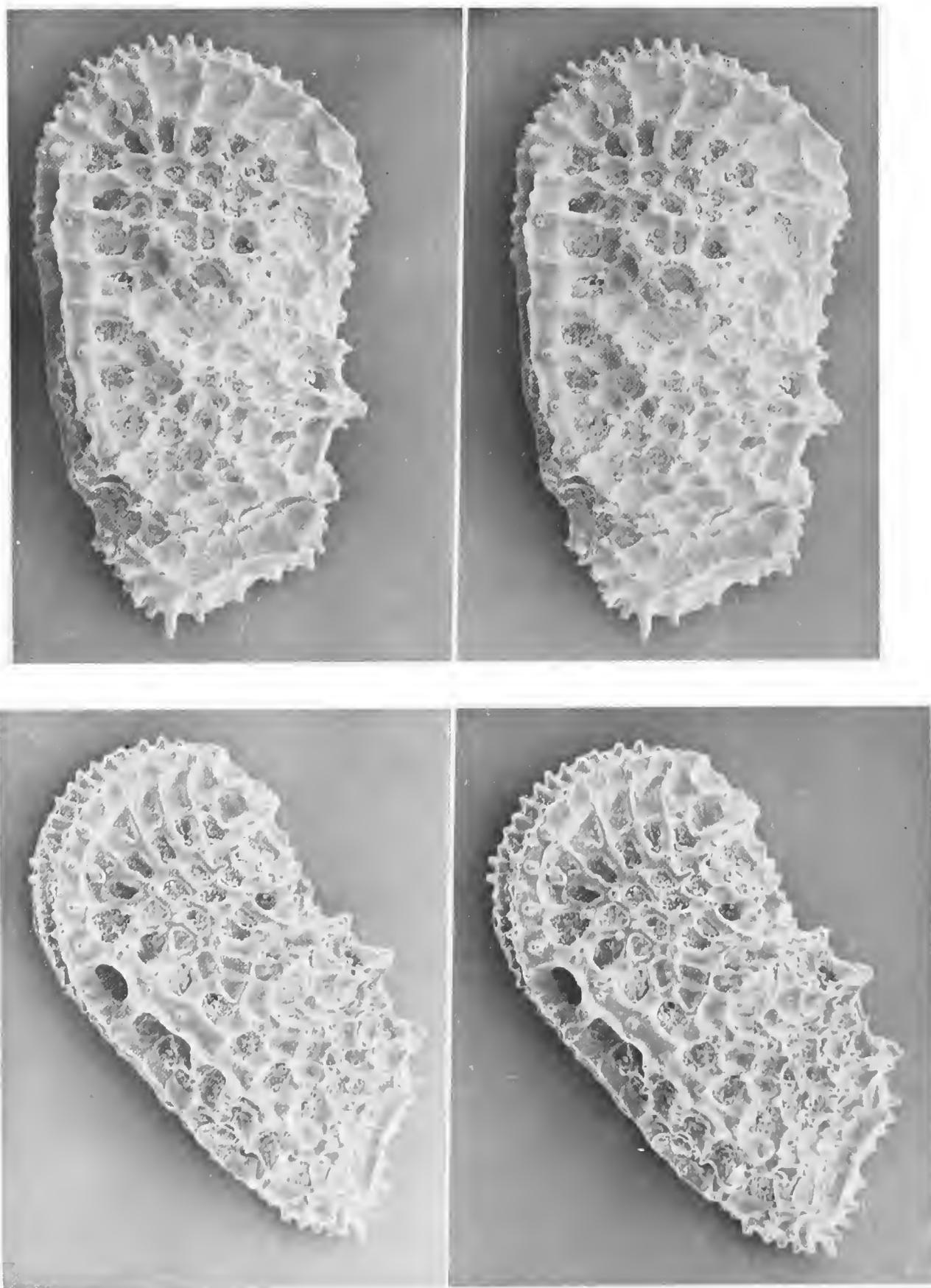


FIGURE 31.—Stereophotomicrographs of a hypotype (USNM 174345), an adult, female left valve, of *Agrenocythere hazelae* (van den Bold, 1946), from the Recent of the eastern Caribbean Sea (ALB 2751), as seen from left lateral, and left anteroventral oblique views (x 50).

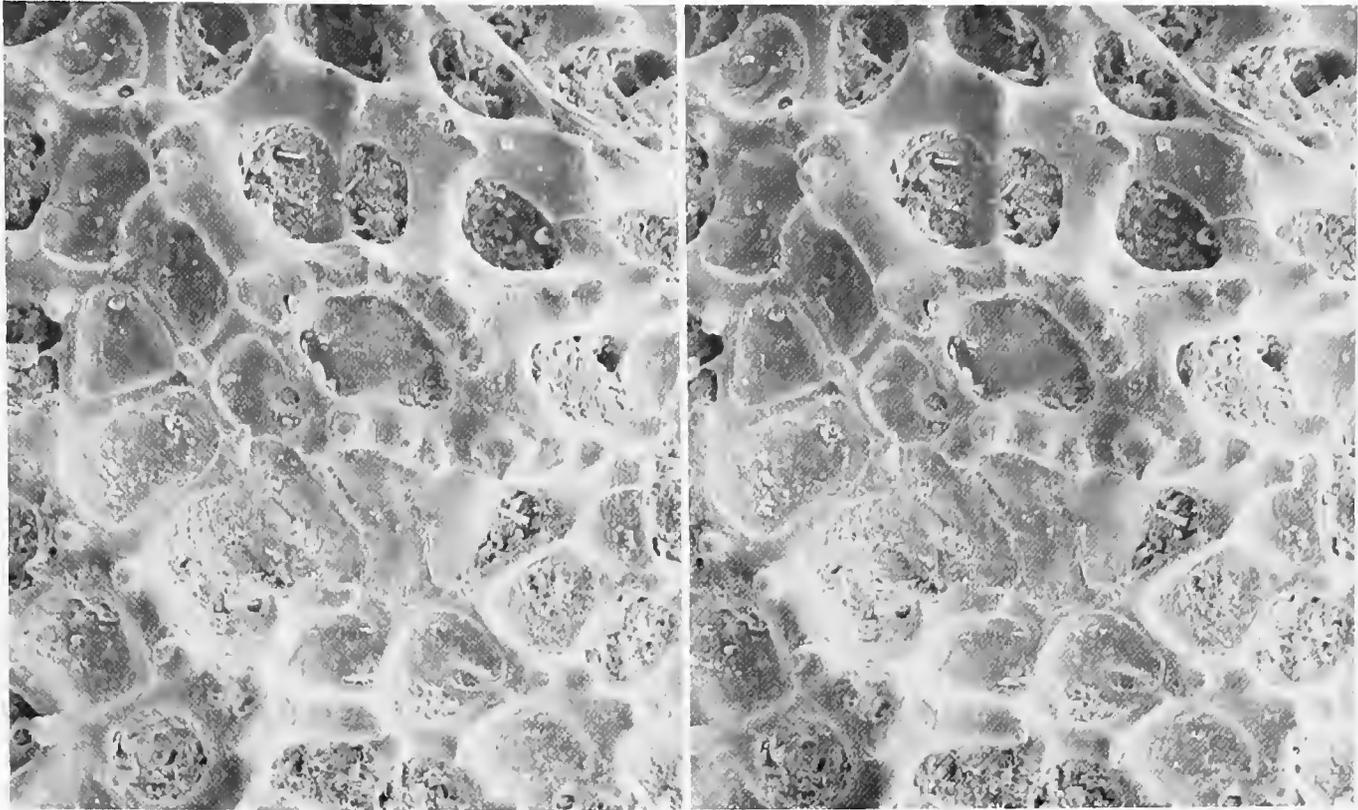


FIGURE 32.—Stereophotomicrographs of the castrum of a hypotype of *Agrenocythere hazelae* (van den Bold, 1946) (same specimen as Figure 31, x200).

*Hermanites*(?) *hazelae* (van den Bold).—Ruggieri 1960:3, pl. 1: fig. 8.  
 “*Bradleya*” *hazelae* (van den Bold).—van den Bold 1968b: 66, pl. 3: fig. 6.  
 Not *Bradleya hazelae* (van den Bold).—Ascoli 1969:54.  
 ?*Trachyleberis reticulospinosa* (van den Bold).—van den Bold 1957:241, pl. 1: fig. 10 [instar?].  
 Not *Trachyleberis reticulospinosa* (van den Bold).—van den Bold 1946:100, pl. 6: fig. 18.

ETYMOLOGY.—Named for Hazel van den Bold (*hazelae*), but gender originally in error (*hazeli* in van den Bold 1946).

HOLOTYPE.—A right valve from the lower Miocene of Cuba (Tchopp locality 1479 in van den Bold 1946; table 1); repositied in the Mineralogist-Geologisch Instituut of the State University of Utrecht (Cat. No. S13015); originally described and illustrated in 1946 (van den Bold, page 92: pl. 10: fig. 4), later designated by van den Bold (1968: 66) as holotype. Length of holotype 1.15 mm, height 0.61 mm (van den Bold 1946: 92).

TYPE-LOCALITY.—Lower Miocene of Cuba, East Oriente Province, Tchopp locality 1479; age originally given as Oligocene now considered lower Miocene by van den Bold (personal communication).

DIAGNOSIS.—*Agrenocythere hazelae* (van den Bold) is distinguished from other species of the genus

by its more rugose appearance, which includes the accentuation of the castrum to form a strong arx that extends to include the parapectus of the 9 through 12 ballial fossae; the ventrolateral ridge is prominent, the dorsal bullae are accentuated and robust, and the fossae in the posterior median region are not as well ordered as they are in other species. The species is blind.

COMPARISONS.—*Agrenocythere hazelae* has more subdued marginal rims and is generally larger (geologically younger populations) than *A. gosnoldia*, new species. Its reticulum is considerably less ordered than *A. radula* whose muri may also be celate with spines, whereas *A. hazelae* has only been observed to be celate with flanges (forming strongly excavate muri). The marginal and conjunctive mural spines of *A. hazelae* are absent, diminished, or knobby compared to the more complicate spines of *A. spinosa*, new species. *A. americana*, new species, is much more massive with greater reticular regularity by comparison. *A. pliocenica* is often larger with finer, simpler muri and lacks the rugose aspect. *A. hazelae* is larger and its reticulum more developed (muri better defined and higher) than *A. antiquata*, from which it may have evolved. It also developed the castral arx which is blunted in *A. antiquata*, new species.



FIGURE 33.—Castral region of right valve (same specimen as shown in Figure 34) of *Agrenocythere hazelae* (van den Bold, 1946) from the eastern Pacific (x150).

DISCUSSION.—The generic assignment of *Cythereis hazelae* (né *hazeli*) has been troublesome from the beginning of its description, as is reflected in the above synonymy. The assignment of this species to a new genus was first proposed by Ruggieri in 1960, and later by van den Bold in 1968(b). It was for a different reason, however, that the present new genus *Agrenocythere* was first considered. The concurrence of morphologic similarity between newly discovered specimens of the Recent species *Cythere radula* Brady and the new species *A. spinosa* with "*Bradleya*" *pliocenica* Seguenza prompted a search for Atlantic relatives which led to examination of "*Cythereis*" *hazelae*. Fortunately, the discrimination between *Bradleya dictyon* (Brady, 1880) and *Agrenocythere radula* (Brady, 1880) is pronounced in deep-sea forms and this problem which concerned previous authors, was avoided. The problem not avoided unfortunately, as discussed by Ruggieri (1960), is the relationship of the "*hazelae* form groups" with other genera in the Trachyleberidiidae. This subject is discussed elsewhere.

Specimens of *Agrenocythere antiquata*, new species, from the lower and middle Eocene of Europe and America, are typically of medium size (often slightly more than 1000–1100 microns in length) with suppressed detailed features but enlarged feature complexes. One notes these aspects in the two specimens

of similar but not identical age (middle and late Eocene) from Trinidad (Figure 55) and Italy (Figure 54). In both forms the castral, bullar, and ventrolateral ridge regions are produced as is the pore conulus Charon. The rest of the muri are subdued and the carapace is in general spineless. The arx later becomes developed in the anterodorsal sector of the castrum and is typical of the younger descendant species *A. hazelae*, but the specular region of *A. antiquata* is most prominent and projects as a massive bosslike tubercle.

During the Oligocene and early Miocene, the size of the carapace of *Agrenocythere antiquata-hazelae* species complex increases slightly and the reticulum begins to be more robust throughout the extent of the muri. Details of the castrum become sharper and in some cases by middle Miocene may become exaggerated (Figures 35 and 36) while in others (Figure 25) may simply become enlarged. The dorsal bullae are produced and no longer butte-like. Conjunctive and marginal spines are developed in younger forms.

Comparison between Recent forms (Figures 31, 32) of *A. hazelae* from the Caribbean with the Recent forms from the Pacific (Figures 33, 34, Plate 13; figures 7–11) shows much less change has occurred between these forms than in the Atlantic alone. It is not known when the Pacific form emigrated from the Caribbean region, but it does not share the distally enlarged arx as a common feature with the eastern forms, especially those of the South Atlantic. It is similar in almost every other respect, however, and is less extreme in morphologic departure from the stock forms than are some of those which had geographic and chronistic continuity. The one aspect in which it does differ is in size with the Pacific specimens being 25 percent longer (1.4 mm versus 1.1 mm) than the Caribbean and Atlantic specimens. With the few specimens available it seems inadvisable to erect a new species on such minor morphological grounds even though genetic continuity may have been broken some time ago.

The evolutionary change that may have taken place in Europe between Miocene remnants of *Agrenocythere hazelae* and the developing *A. pliocenica* is still a matter of conjecture. Ruggieri (1960) reported Sicilian Miocene representatives of *A. hazelae*, and I have Miocene specimens collected near Ancona, Italy, and sent to me by Ascoli. Also, I have post-Messinian specimens of *A. pliocenica*. Yet the

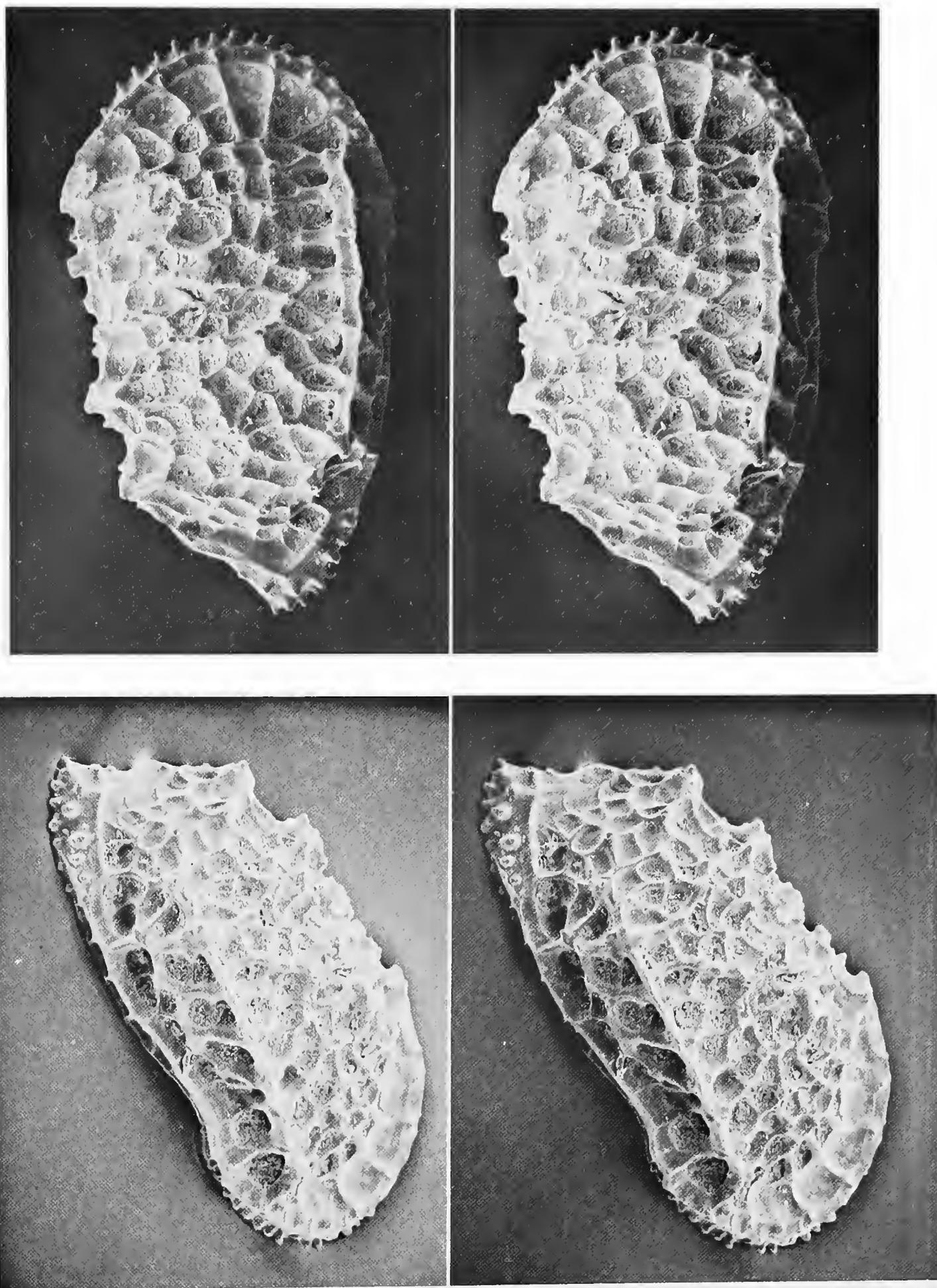


FIGURE 34.—Stereophotomicrographs of an eastern Pacific hypotype (USNM 174347), an adult, female right valve, of *Agrenocythere hazelae* (van den Bold, 1946), from the Recent of the eastern Pacific (Malpelo Rise; ALB 3375) as seen from left lateral, and left anteroventral oblique views (x50). For other illustrations of other specimens see Figure 33, Plate 13: figures 7–11, and Plate 14: figures 7–9.

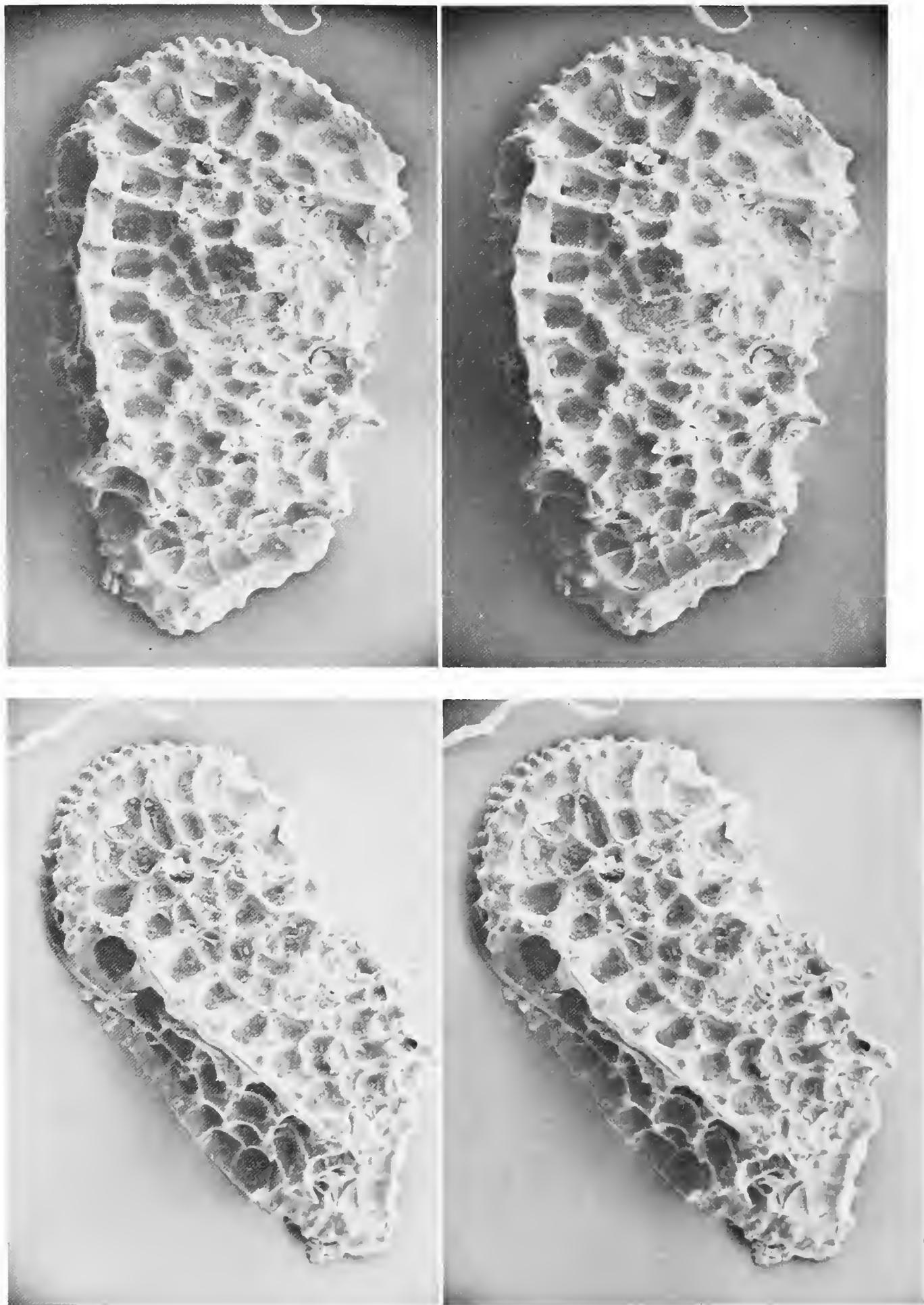


FIGURE 35.—Stereophotomicrographs of a hypotype (USNM 174337), an adult, female left valve of *Agrenocythere hazelae* (van den Bold, 1946) from the Cipero formation (middle Miocene) of Trinidad (RM 15715) as seen from the left lateral, and left anteroventral oblique views (x70).

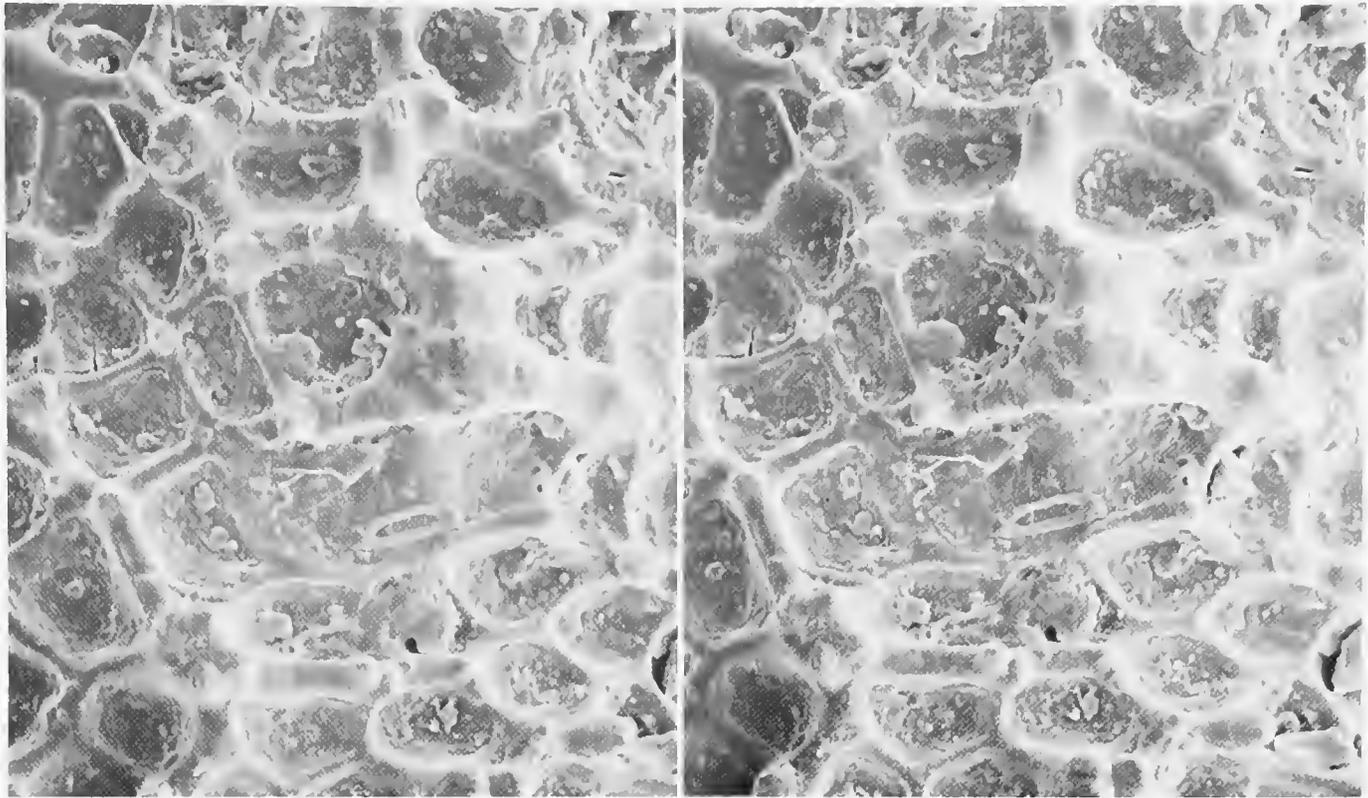


FIGURE 36.—Stereophotomicrographs of the castrum of a Miocene hypotype from Trinidad (same specimen as in Figure 5) of *Agrenocythere hazelae* (van den Bold, 1946) (x200).

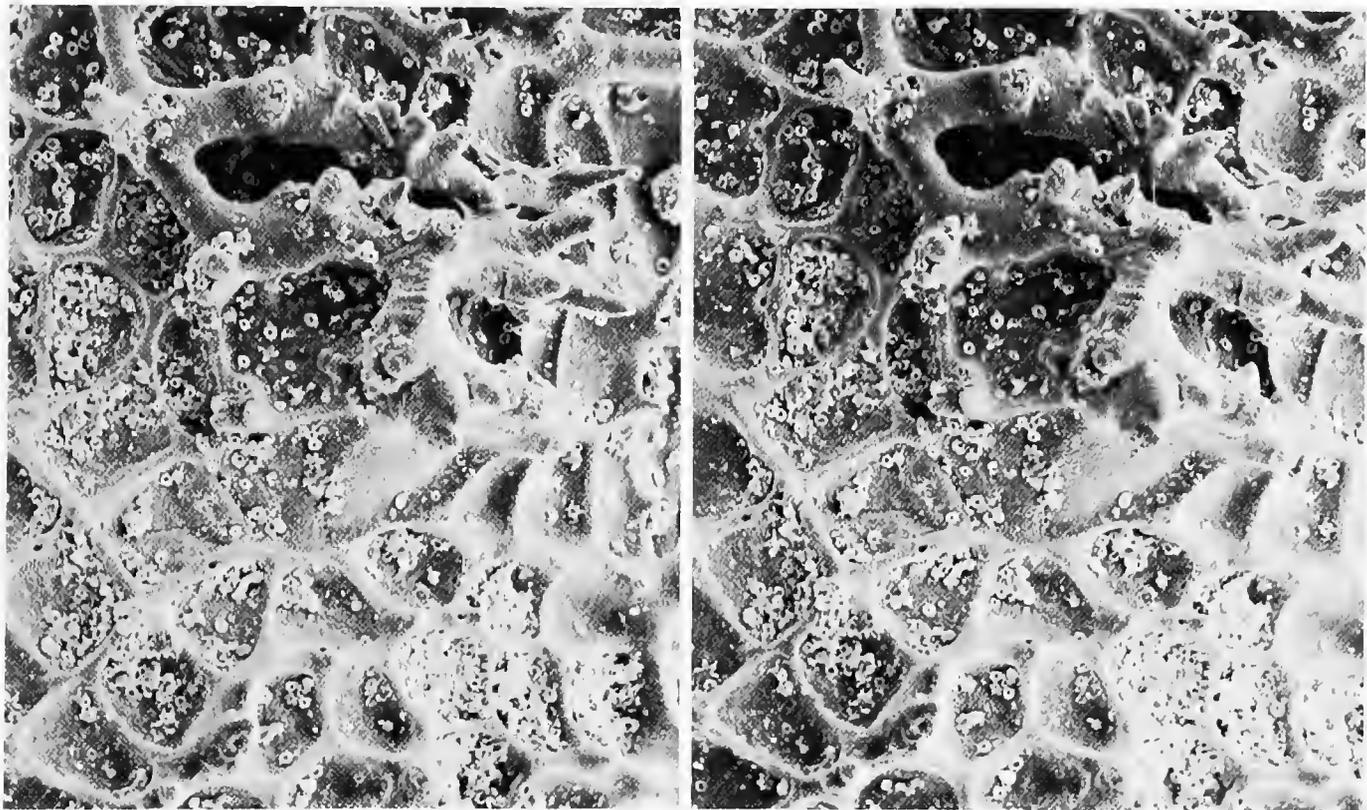


FIGURE 37.—Stereophotomicrographs of the castrum of a Miocene hypotype (same specimen as in Figure 38) of *Agrenocythere hazelae* (van den Bold, 1946) (x200).

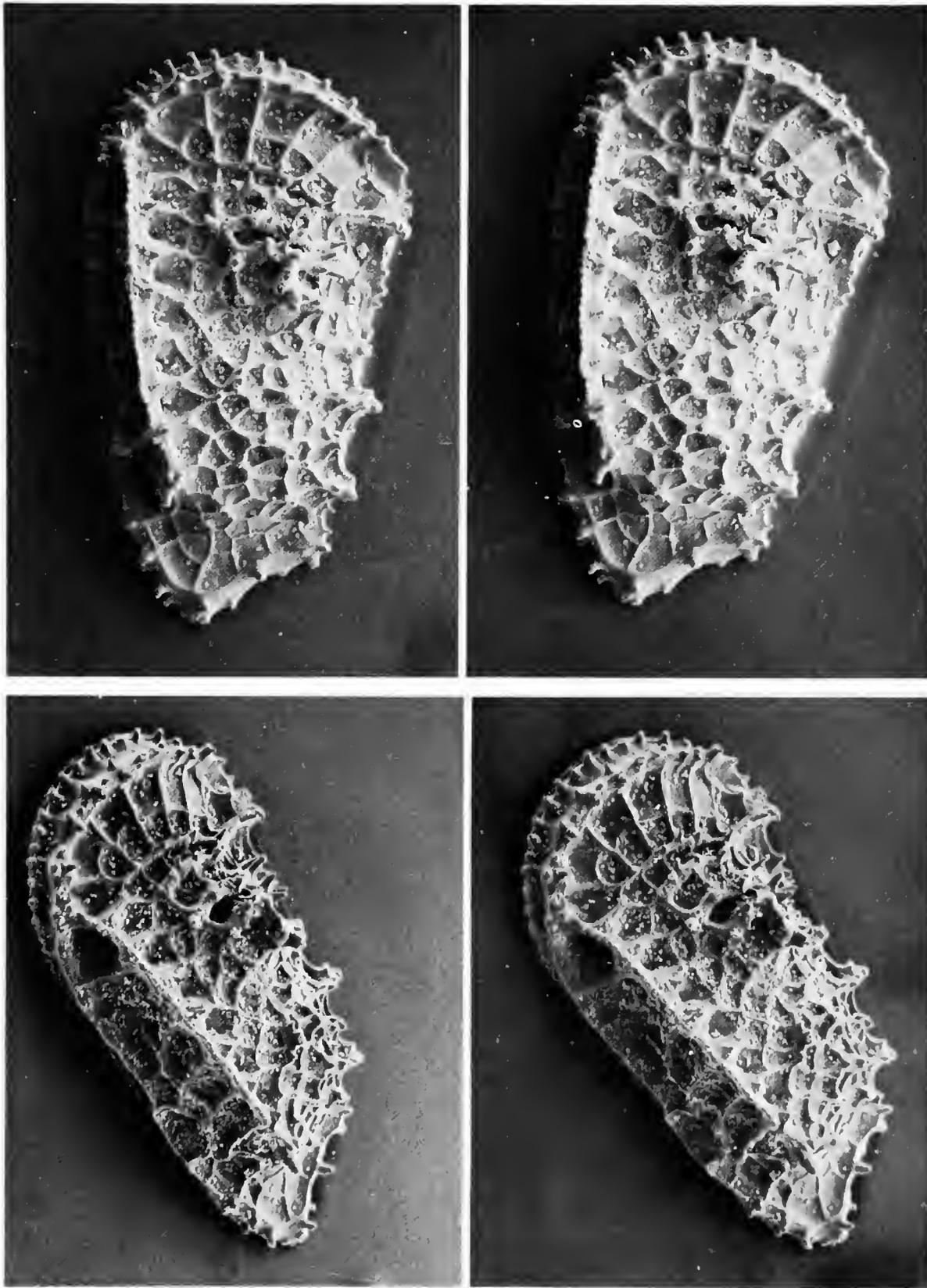


FIGURE 38.—Stereophotomicrographs of a hypotype (USNM 174344), an adult, female left valve, of *Agrenocythere hazelae* (van den Bold, 1946) from the Miocene of the South Atlantic (DSDP III 14, core 1a, section 3) as seen from the left lateral, and left anteroventral oblique views (x75); showing the anterior development of the castrum into the anterior field.

nature of the transition between the species, if indeed one existed, is not clear. More material of late Miocene age is required before the solution of this problem is reached. Further discussion of this problem is given in the section on *A. pliocenica* and has been mentioned in the introductory section on evolution of this group.

**DISTRIBUTION.**—*Agrenocythere hazelae* is the most widely distributed, stratigraphically long ranging, and the most variable of the known *Agrenocythere* species. It is probably the central stock from which most, if not all, Neogene species in the Atlantic and Mediterranean have been derived. First described by van den Bold in 1946 from the lower Miocene (first considered Oligocene) of Cuba, it has been widely reported by him from other regions in the Caribbean (although his identifications of Paleogene specimens would have included the new species now called *A. antiquata*). It was reported from Europe by Ruggieri in 1960 from the Miocene (Ragusano section) of Sicily (reported later erroneously by Ascoli (1969) from the Eocene of northeastern Italy). It is now reported from the south Atlantic near the Tristan da Cunha Islands, and from the middle and late Tertiary from the Caribbean region. No Pleistocene or younger specimens have been reported from the open Atlantic; however, it has been found in Recent sediments in the Caribbean and in the eastern Pacific. Its presence in the eastern Pacific poses a problem in the explanation of how it got there. As a typically deep-water form it is supposed that a deep-water passage across or around the Isthmus of Panama region was required. Its comparative lack of similarity with South Atlantic species suggests that it did not immigrate into the Pacific from this area.

#### *Agrenocythere americana*, new species

FIGURES 39–41; PLATE 14: FIGURES 6, 10–15; PLATE 4: FIGURE 7; PLATE 6: FIGURE 7

**HOLOTYPE.**—Left valve, adult male, Figures 40, 41; USNM 174348.

**TYPE-LOCALITY.**—Gulf of Mexico, southeast of the Mississippi River Delta in the vicinity of U.S. Fisheries R/V *Albatross* station 2383; lat. 28°32'N and long. 88°06'W; depth 2160 meters; bottom temperature 4.3° C.

**AGE.**—Recent; no living specimens were found.

**DIAGNOSIS.**—Distinguished from other species of

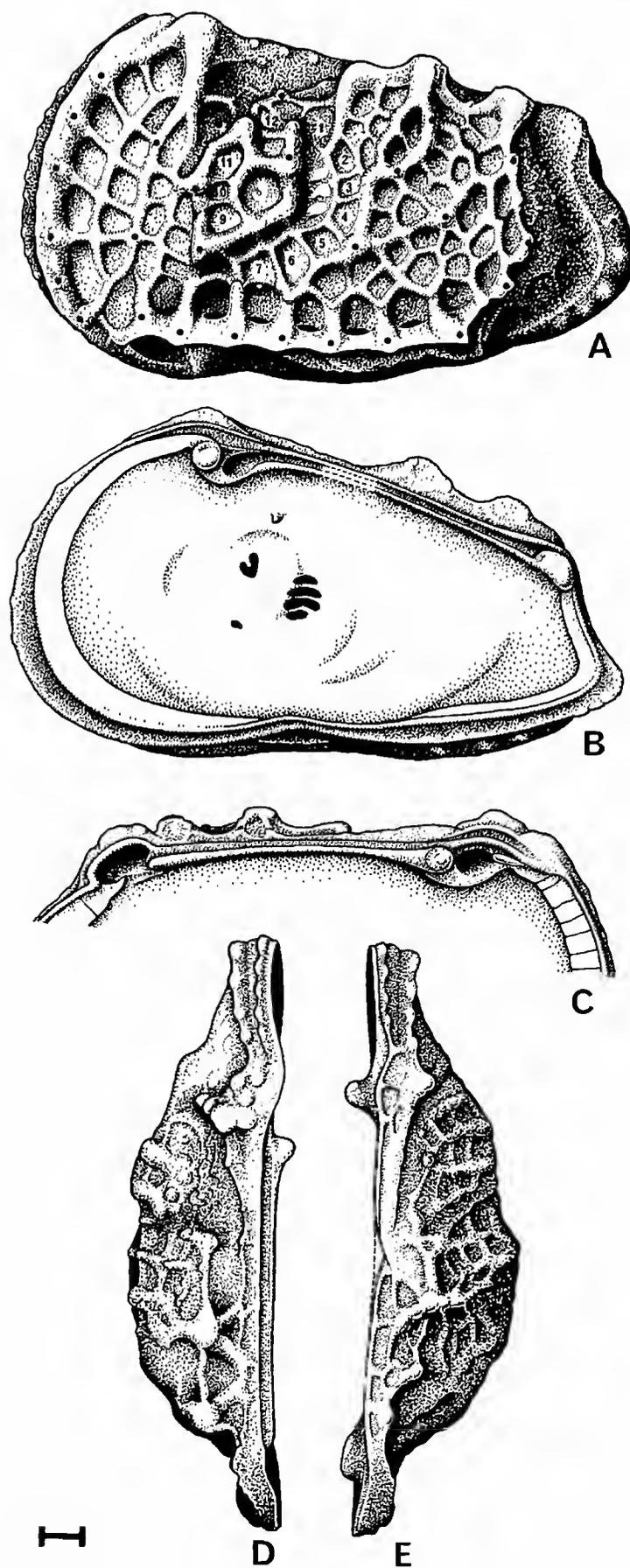


FIGURE 39.—*Agrenocythere americana*, new species, adult, female (USNM 168381): (A) exterior of left valve with the order of the fossae in the ballium and the locations of the pore conuli indicated; (B) the interior of the right valve showing the muscle-scar pattern and the holamphidont hinge elements; (C) the hinge elements of the left valve; (D, E) the right and left valves as seen from dorsal view. Scale = 100 microns.

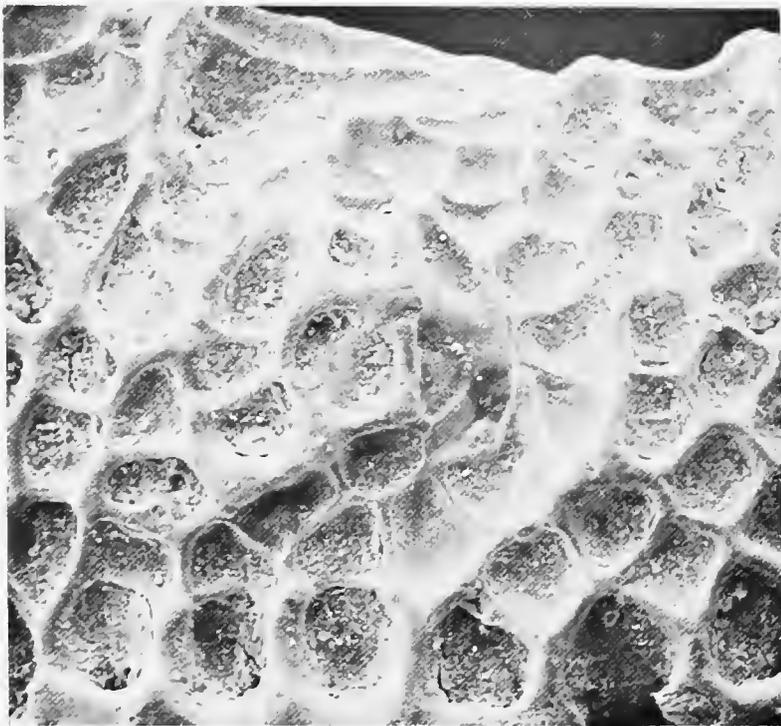


FIGURE 40.—The castral region of the holotype of *Agrenocythere americana*, new species (same specimen as shown in Figure 41; x150).

*Agrenocythere*, new genus; by the general absence of marginal and reticular spines, a massive ventrolateral ridge, simple massive (often distally enlarged) muri and a rounded to tapered posterior. The arx of the castrum has been noted to be divided into an H-shaped upper portion lying between the perval fossa and the fossa arcis (containing the specula) and a lower part underlying the fossa arcis and extending to form a parapectus between pore conuli Scorpio and Capricornus. The rampart extending from pore conulus Leo may be developed into a parapectus but as the muri in this area are generally massive, definition of this particular feature is difficult. The second bulla (b) and third bulla (c) of the dorsal bullar series are both massive and butte-like as is the ocular node.

COMPARISONS.—The general aspect of *Agrenocythere americana* is one of greater massiveness in the reticulum than with the other species. It is closest to *A. antiquata*, new species, in this respect; however, this latter species has prominent character complexes, whereas they are more subdued into a generally regular, even slightly celate (in the anterior) reticulum of *A. americana*. The ventrolateral carina is ponticulate with the suspended segments rounded to blade-like, somewhere between the angled blade of *A. hazelae* and the columns of *A. spinosa*, new species. The dorsal bullar series is massive but not prominent. The posterior marginal rim is more bluntly rounded than

the other species which may be produced to attenuated. The castral arx bipillar is in the form of an "H" rather than radiate. It is simple like the more conservative forms of *A. hazelae* or like *A. pliocenica*. There is a general overall similarity with some specimens of *A. pliocenica* (especially from the Trubi formation of Sicily) except in the posterior, which is more tapered in *A. americana* due to the absence of the posterodorsal angle of *A. pliocenica*.

DIMENSIONS.—Length of holotype, male, 1.32 mm, height 0.73 mm; length of paratype, female, 1.25 mm, height 0.73 mm.

DISTRIBUTION.—Recent of Gulf of Mexico.

### *Agrenocythere radula* (Brady, 1880)

FIGURES 42, 43; PLATE 13: FIGURES 1–6; PLATE 14: FIGURES 1–4, 16–18

*Cythere radula* Brady, 1880: 102, pl. 19: fig. 4a, b.

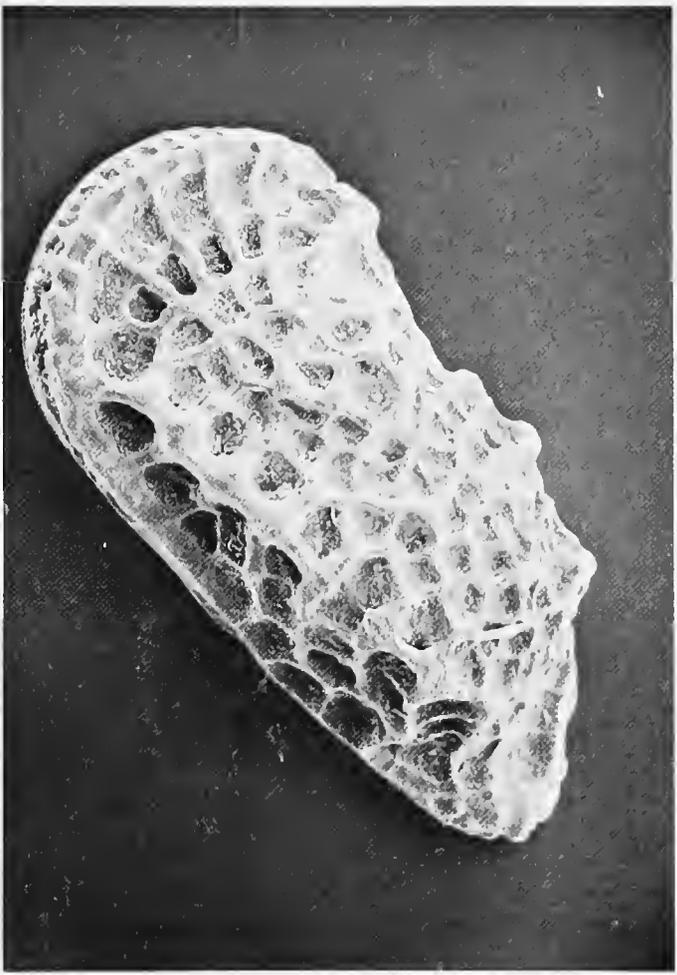
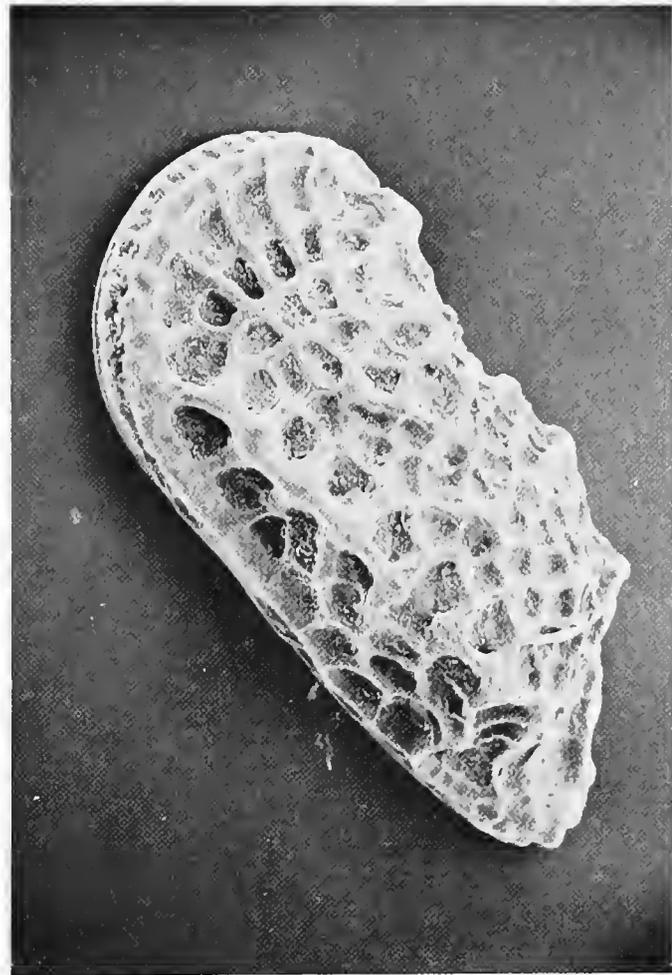
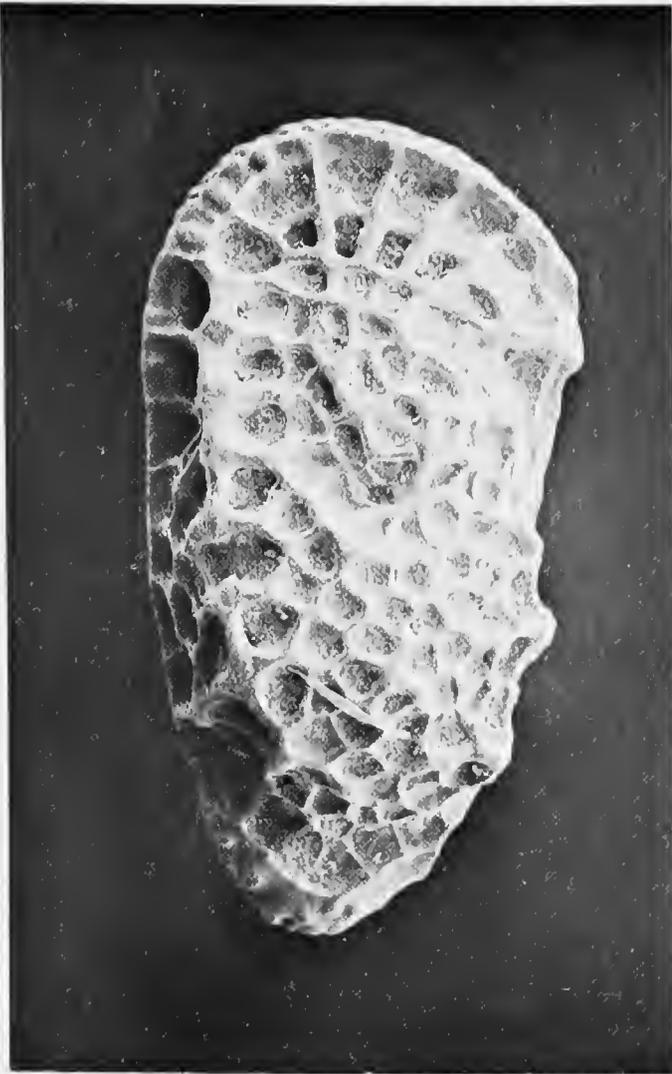
LECTOHOLOTYPE.—Designated herein, British Museum specimen (BM 81.5.28), collected from *Challenger* station 191A (Plate 14; figures 16–18).

TYPE-LOCALITY.—Vicinity of Ki Islands, southern Indonesia; lat. 5°26'S, long. 133°19'E; 580 fathoms depth; bottom temperature 4.9° C.

AGE.—Pliocene to Recent.

DIAGNOSIS.—Brady (1880) originally was struck by the sculptural pattern of *Cythere radula* which he compared to that of *C. arachnoidea* Bosquet [now *Oertliella aculeata* (Bosquet)]. We find now that in fact *Agrenocythere radula* (Brady) has a very regular reticular pattern (more so than *O. aculeata* although admittedly very similar), which distinguishes it from all of the other *Agrenocythere* species. The muri in the posterior region are aligned into opposed crossed systems. The intersections of the muri are often marked with conjunctive spines or conspicuous pore conuli. The muri are often celate. The ventrolateral ridge is not conspicuous except for the serially arranged spines. The dorsal bullar series is subdued except for a prominent posterior spine (c). The castrum is open and regular with a prominent specula. The

FIGURE 41.—Stereophotomicrographs of the holotype (USNM 174348), an adult, male left valve, of *Agrenocythere americana*, new species, from the Recent of the Gulf of Mexico (ALB 2383), as seen from left lateral, and left anter-ventral oblique views (x50). For light photographs of other specimens see Plate 14: figures 6, 10–15.



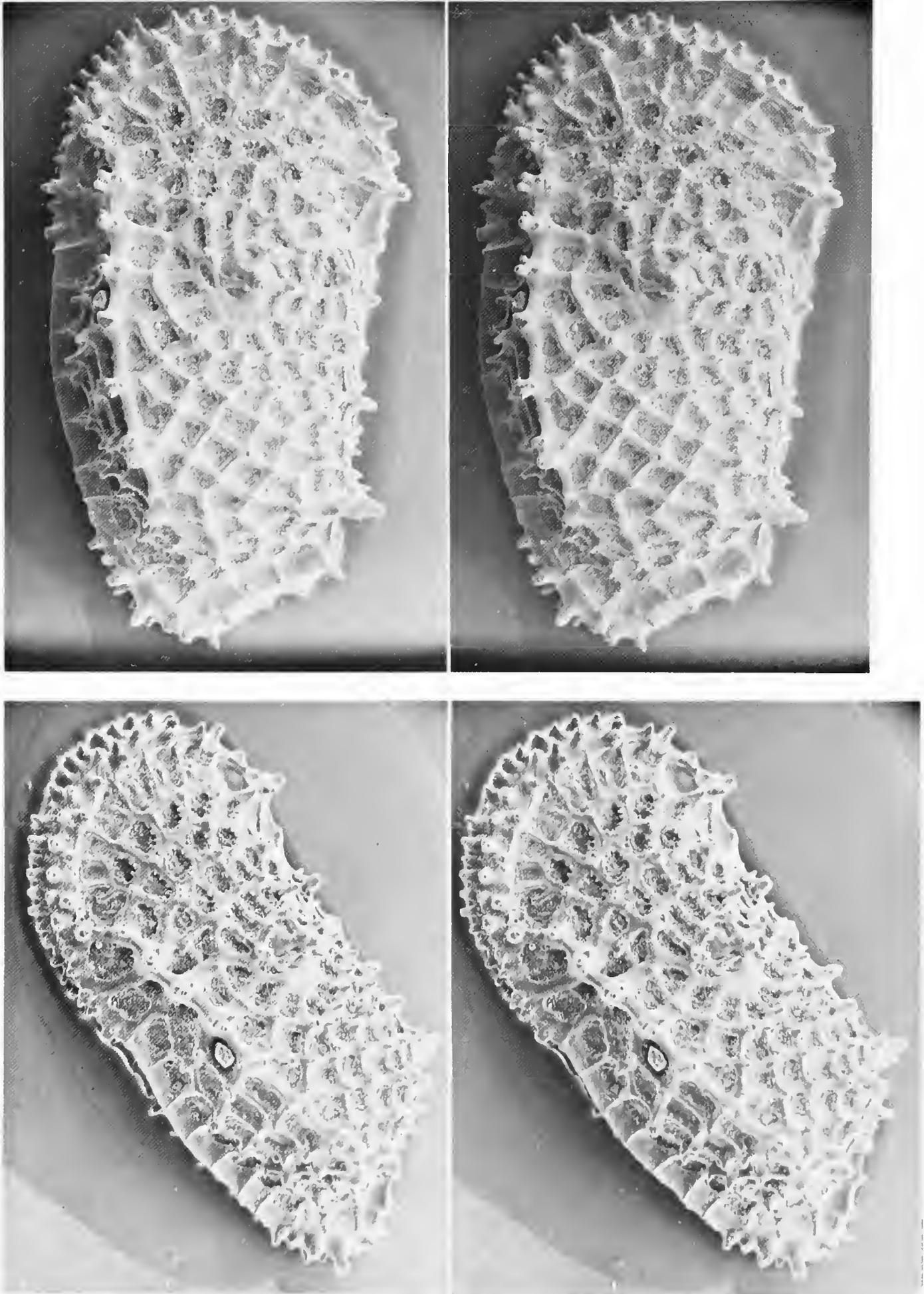


FIGURE 42.—Stereophotomicrographs of a hypotype (USNM 174362) of *Agrenocythere radula* (Brady, 1880), from the Recent of Mozambique Channel (IIOE 407D) as seen from the left lateral, and left anteroventral oblique views (x50).

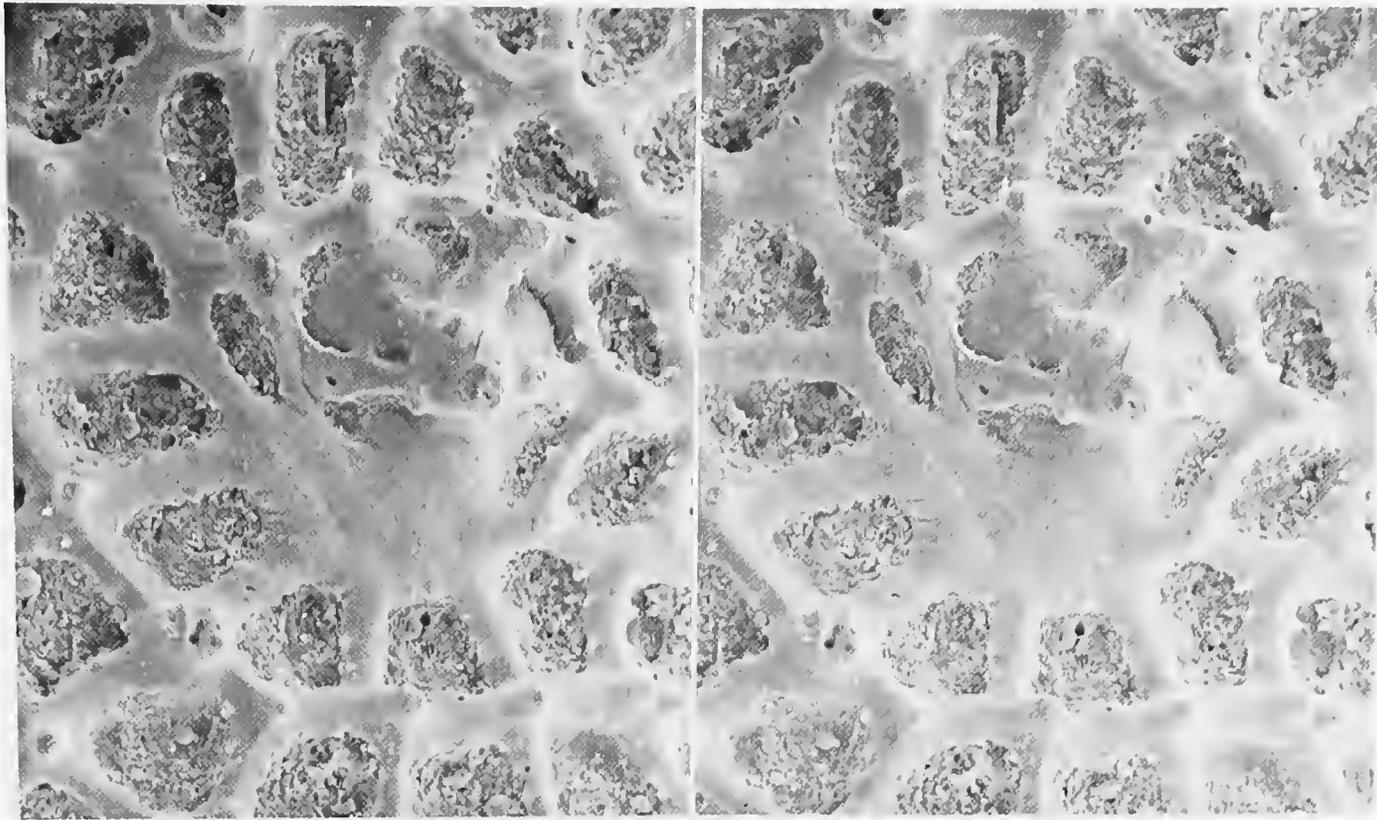


FIGURE 43.—Stereophotomicrographs of the castrum of *Agrenocythere radula* (Brady, 1880) (x200), same specimen as in Figure 42).

arx is subdued and one must look hard to imagine parts of it to be present at all. Because Brady's species was founded on one specimen, a late instar, this represents the first diagnosis that includes consideration of variation and also comparison with related forms.

COMPARISONS.—This is one of the more extreme member species of the genus. The regularity of the reticular and fossal patterns is pronounced in the alignment of its elements, in columns in the posterior and radially in the anterior. The castrum is also radiate from the specula with the arx (characteristic of the Atlantic derived forms) diminished to almost absent. The dorsal bullar series is produced as spines, rather than strong bullae, and bulla B is enlarged or attenuated, often oriented toward the posterior. This same feature (the "cocked" B dorsal bulla) is also found in *A. spinosa* and in some variants of *A. hazelae* (which may also have A bulla "cocked"). The ventrolateral carina is composed of short small support mural struts and thin connecting columns or ridges fused against the main carapace wall. It is not generally fenestrate. For illustrations of appendages see Figure 27.

DIMENSIONS.—Length of hypotypes 1.39 mm and 1.42 mm; height 0.77 mm and 0.79 mm.

DISTRIBUTION.—Indian Ocean and Indonesia; Pliocene to Recent.

#### *Agrenocythere pliocenica* (Seguenza, 1880)

FIGURES 44–50; PLATE 3: FIGURES 3, 4; PLATE 5: FIGURES 3, 4

*Cythereis pliocenica* Seguenza, 1880:192.

*Cythereis dictyon pliocenica* Seguenza.—Ruggieri 1953:78, pl. 2: figs. 10–10d, 11.

*Bradleya dictyon pliocenica* (Seguenza).—Ruggieri 1959: 186; 1960: 4, pl. 1: fig. 5.

*Bradleya pliocenica* (Seguenza).—Ruggieri 1962:21, pl. 1: fig. 22.—Colalongo 1965:91, pl. 11: fig. 1.

AGE.—Pliocene to early Pleistocene; Italy.

DIAGNOSIS.—Distinguished from other species of *Agrenocythere*, new genus, by the absence of reticular spines, a broad blade-like ponticulate ventrolateral ridge, a tendency toward subdivision of the fossae in the anterior reticulum, simple yet conspicuous muri, a somewhat more elongate overall shape and a consequent enlargement of the fossae in the postmedial region. The arx of the castrum encompasses the fossae arcis yet remains discrete from the rampart, which is generally featureless except for a bold parapectus extending several ballial fossae from pore conulus Leo. The pervial fossa may be semi-enclosed. The second

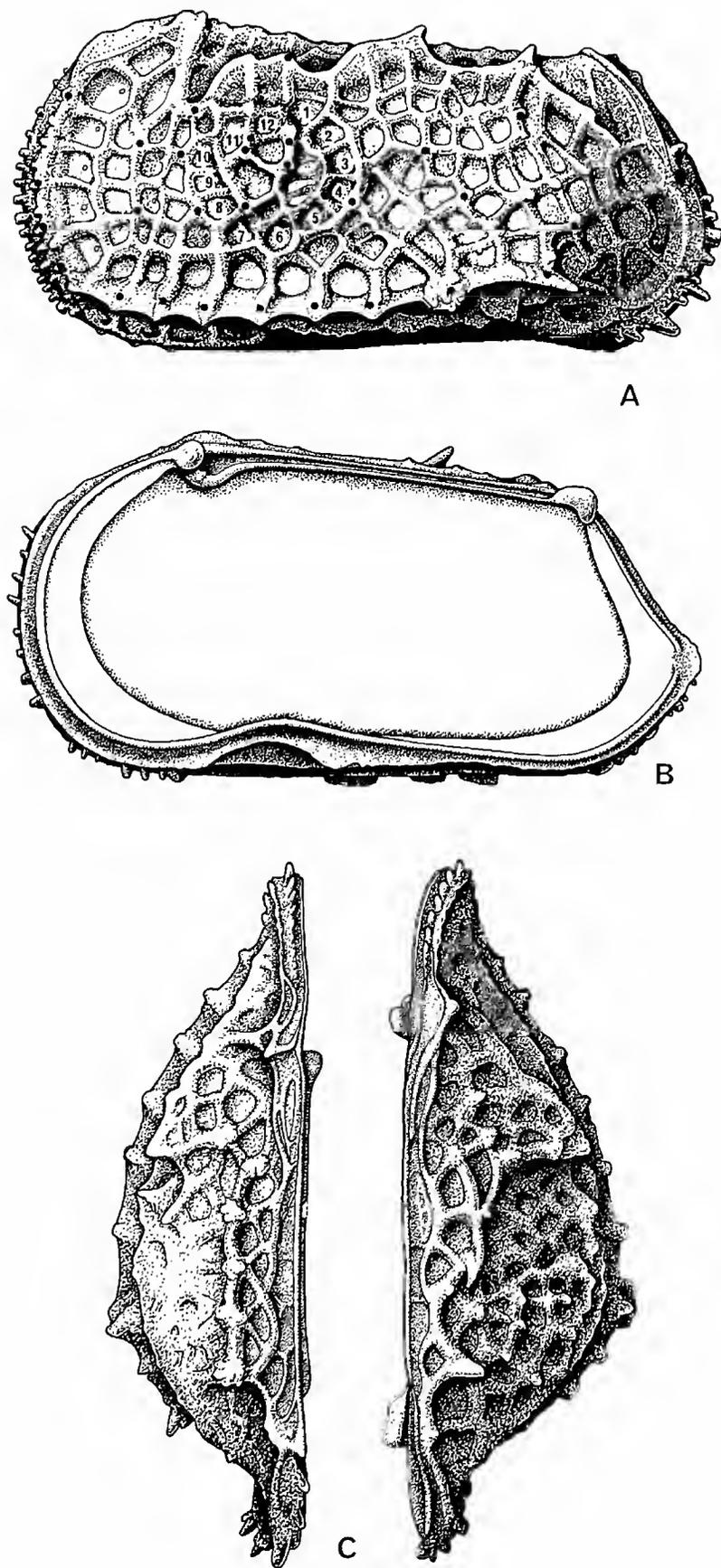


FIGURE 44.—*Agrenocythere pliocenica* (Seguenza, 1880); adult, male (USNM 174697): (A) exterior of left valve with the order of the fossae in the ballium and the locations of pore conuli indicated; (B) the interior of the right valve showing the narrow and delicate holamphidont hinge elements; (C) the right and left valves as seen in dorsal view. Specimen 1625 microns in length.

bullae (b) of the dorsal bullar series is often blade-like and prominent.

COMPARISONS.—The reticulum of *Agrenocythere pliocenica* is generally spineless (or very subdued spines) and without prominent pore conuli as in *A. spinosa*, new species, or many of the variants of *A. hazelae*. Dimorphism is very strong (Plate 3: figures 3, 4; Plate 5; figures 3, 4; Figures 44–50) due to the enlargement of the posteroventer in the male, a characteristic not unlike that in *Cletocythereis rastromarginata* (Brady). This feature was not noted to be as strong in other species of *Agrenocythere*, but dimorphism in these other species is quite apparent. The castral arx of *A. pliocenica* as described in the diagnosis is confined primarily to the central castrum. It is similar to the other H-like constructions of the more conservative forms of *A. hazelae* and *A. americana*, new species. Its similarity with these species strongly suggests phylogenetic ties with the stock of these forms rather than those of more radiate (*A. radula*) or promontory types (*A. antiquata*, new species). The ventrolateral carina is fused and blade-like with few fenestra noted (the muri may be strongly excavate, however). The dorsal bullar series are simple dorsal projections of the reticulum, less pronounced than *A. hazelae*; however, they may be attenuated into blade-like protuberances.

DIMENSIONS.—Length of hypotype male 1.49 mm, height 0.61 mm; length of hypotype female 1.40 mm, height 0.73 mm.

DISTRIBUTION.—Neogene (Pliocene and early Pleistocene) of Italy from near Bologna (San Ruffilo) in northern Italy to Sicily (Trubi formation) and Calabria (La Castella section, Pliocene and late Pleistocene); also in DSDP XIII 132 in the Tyrrhenian Sea floor.

#### *Agrenocythere gosnoldia*, new species

FIGURES 51–53

ETYMOLOGY.—Named for the R/V *Gosnold* of the Woods Hole Oceanographic Institute, which collected the material in which the specimen was found.

HOLOTYPE.—Left valve, adult male (?); Figures 52, 53; USNM 168375A; paratype USNM 174365B.

TYPE-LOCALITY.—Middle Eocene outcrop in Block Submarine Cayon at lat. 39°49'N and 71°12'W at a

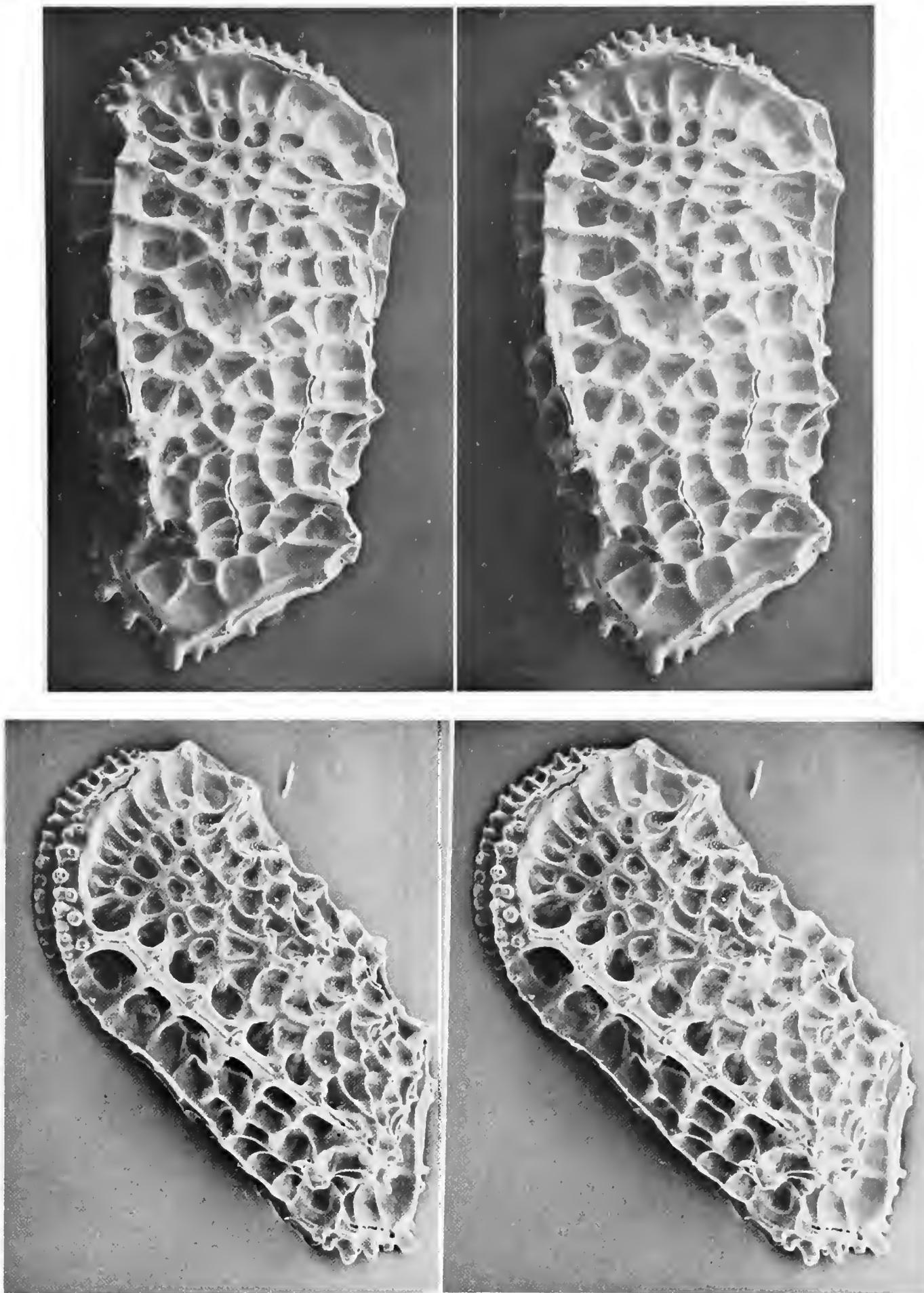


FIGURE 45.—Stereophotomicrographs of a hypotype (USNM 174350), an adult, female left valve of *Agrenocythere pliocenica* (Seguenza, 1880), from the Pliocene of San Ruffilo, Italy (ARL 4513) as seen from left lateral, and left anteroventral oblique views (x 55).

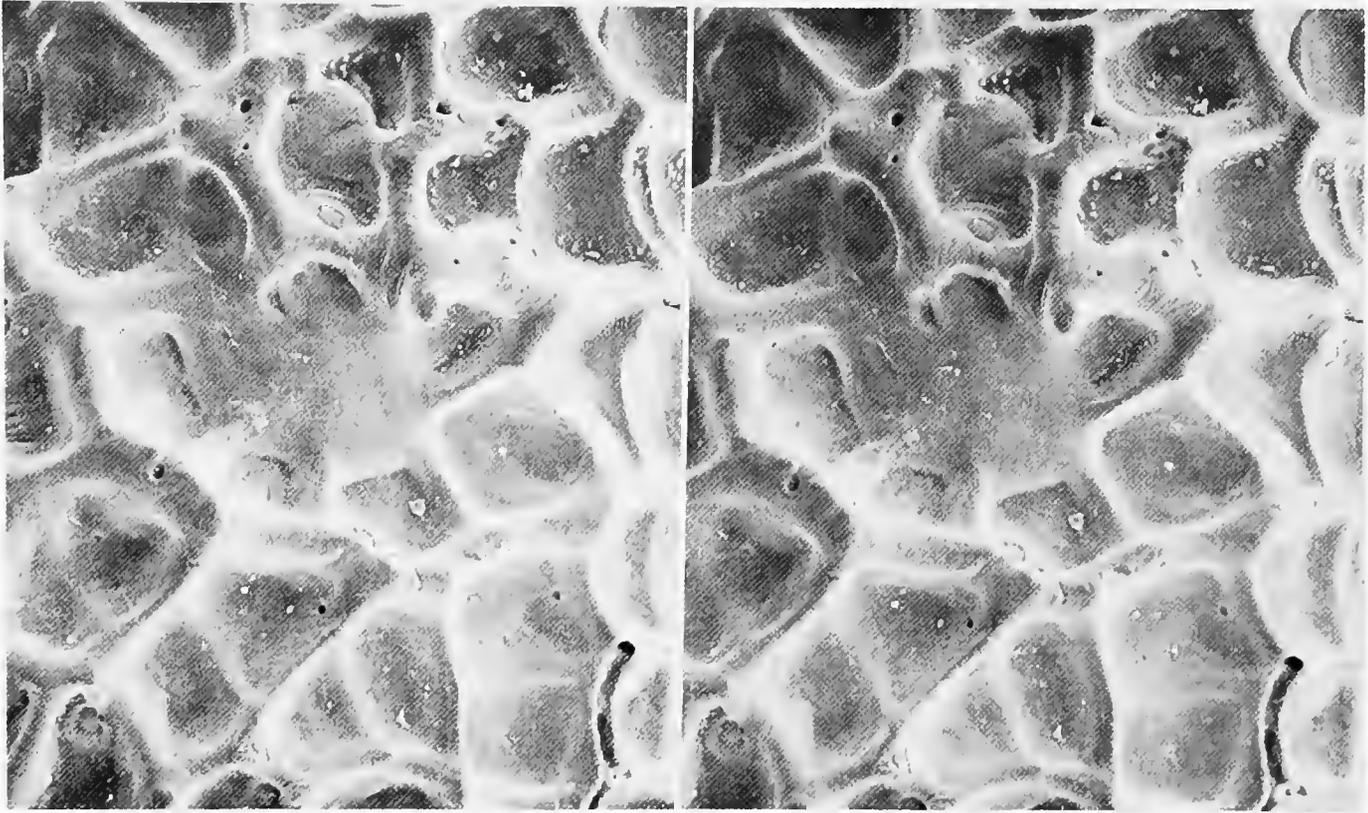


FIGURE 46.—Stereophotomicrographs of the castrum of a female hypotype (same specimen as Figure 45) of *Agrenocythere pliocenica* (Seguenza, 1880) (x160).

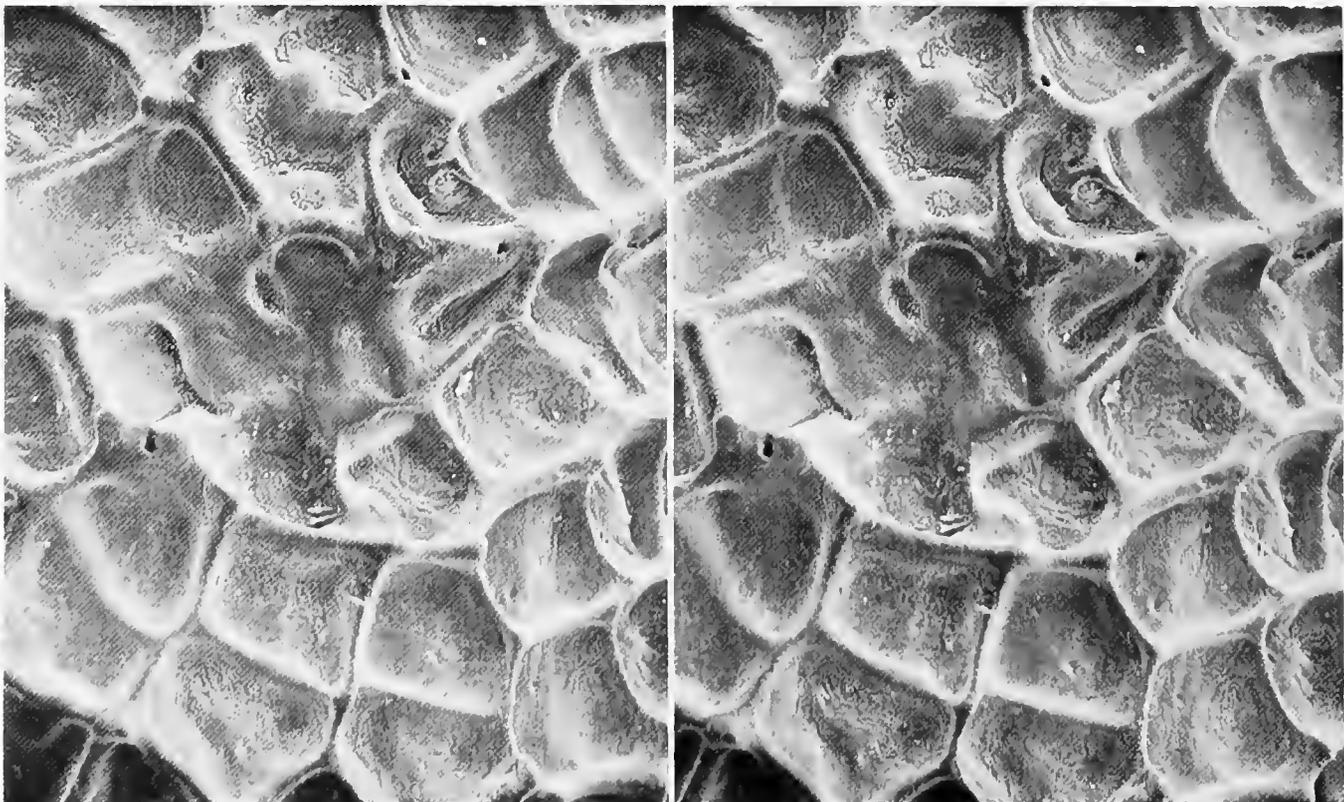


FIGURE 47.—Stereophotomicrographs of the castrum of a male hypotype (same specimen as Figure 48) of *Agrenocythere pliocenica* (Seguenza, 1880) (x160).

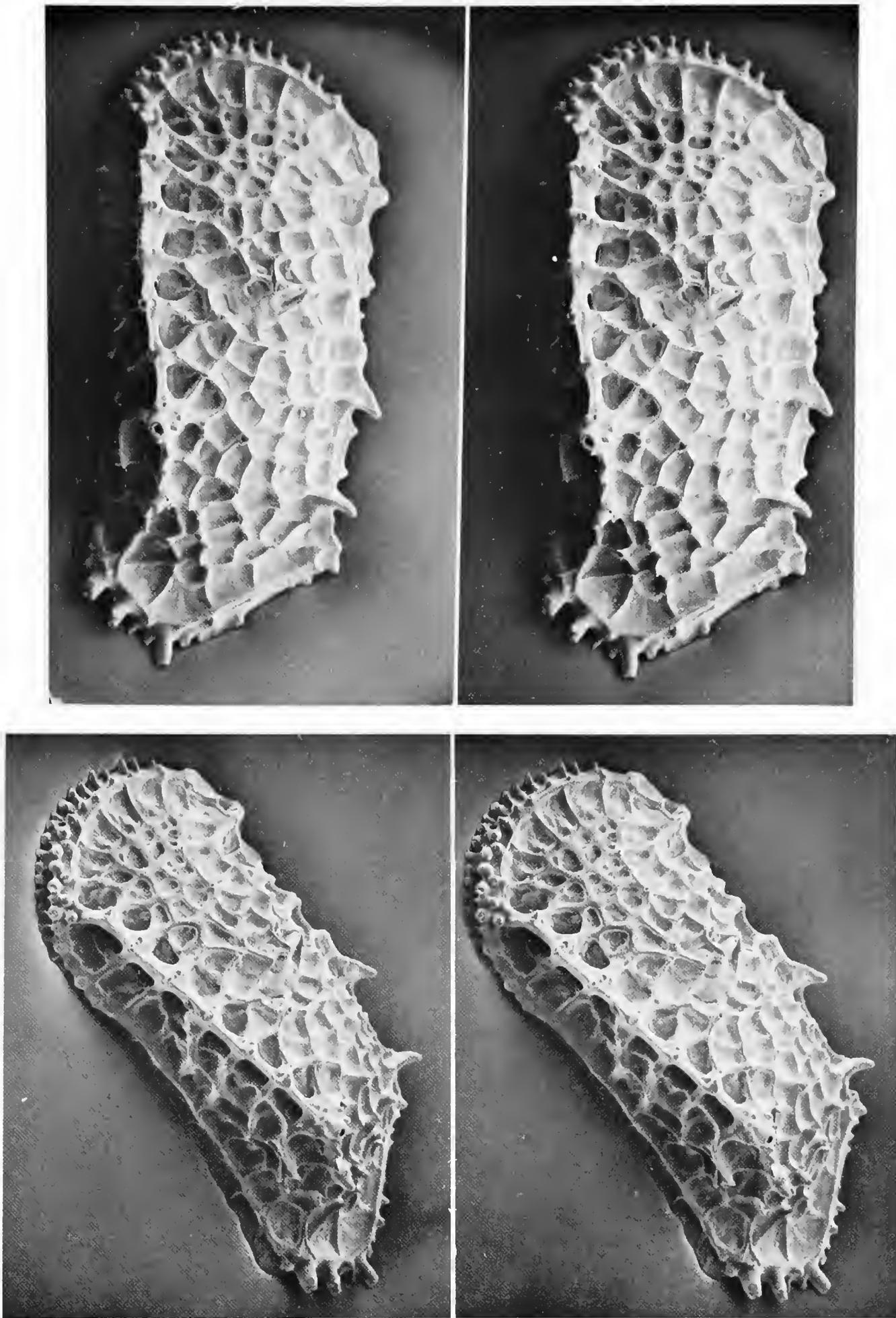


FIGURE 48.—Stereophotomicrographs of a hypotype (USNM 174349), an adult, male left valve of *Agrenocythere pliocenica* (Seguenza, 1880), from the Pliocene of San Ruffilo, Italy (ARL 4513) as seen from left lateral, and left anteroventral oblique views (x50).

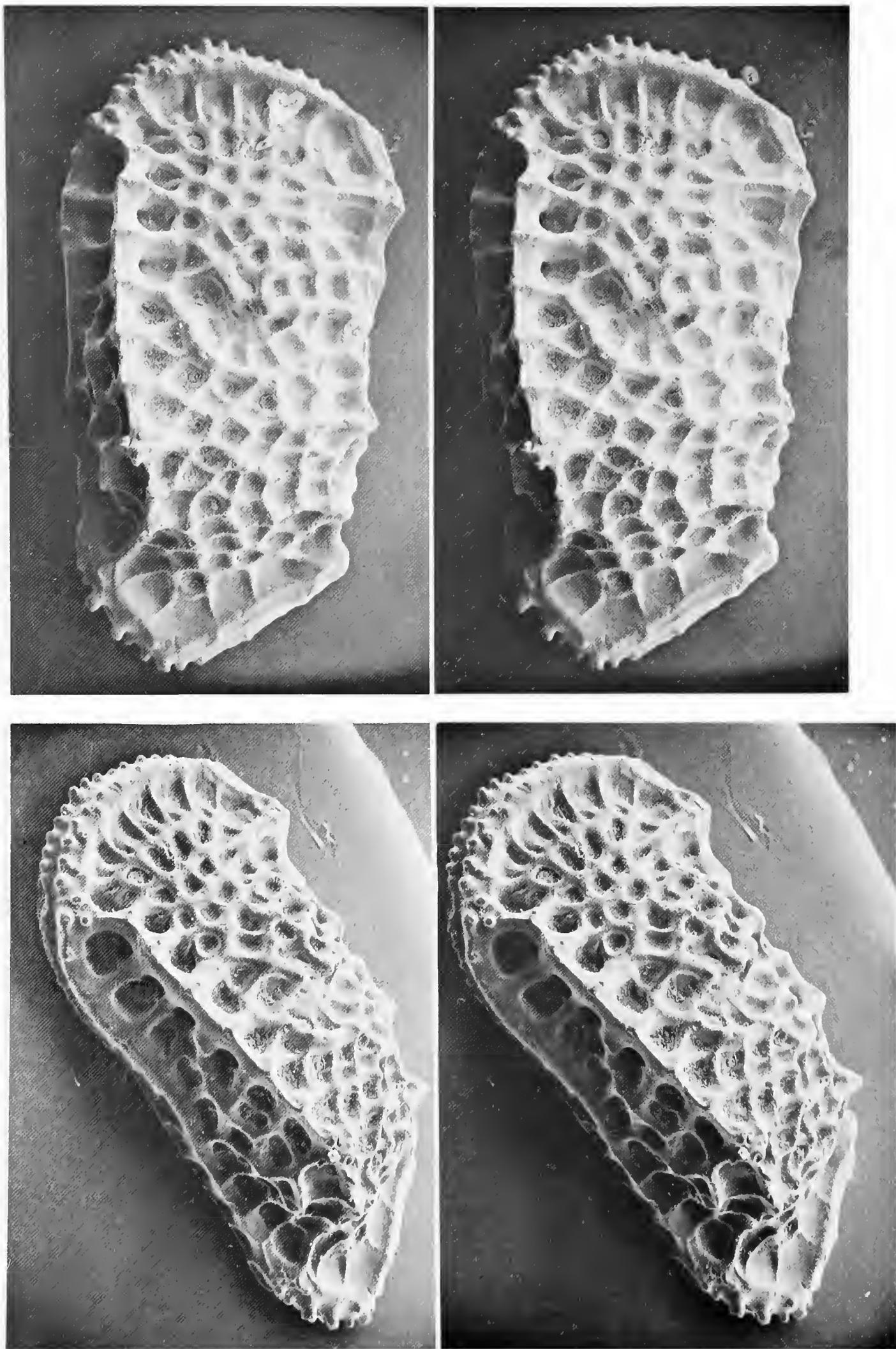


FIGURE 49.—Stereophotomicrographs of a hypotype (USNM 169376), an adult, female left valve of *Agrenocythere pliocenica* (Seguenza, 1880), from the Pliocene Trubi formation of Sicily near Licata (ARL 4468), seen from left lateral, and left antero-ventral oblique views (x60).



FIGURE 50.—Stereophotomicrographs of the castrum of a female hypotype (same specimen as in Figure 49) of *Agrenocythere pliocenica* (Seguenza, 1880). (x180)

depth of 1070 meters; yellow calcareous clay. Hazel sample 2621C (Gibson, Hazel, and Mellow 1968).

**DIAGNOSIS.**—This species can be distinguished from others of the genus by its high anterior, its massive muri, especially periferal to the margin as they form the blade-like bullar series, wide anterior and posterior marginal rims. Wide muri also join to support the ventrolateral ridge and arcis region. The castrum is massive yet simple with its many parts being subsumed under its generally bold architecture. Pore conulus Leo remains distinct as do many of the others, especially Charon. The ocular ridge is wide but not prominent as a tubercule.

**COMPARISONS.**—Although the basic patterns of the reticulum and the principal character complexes are those of *Agrenocythere*, new genus, the muri of the reticulum are exaggerated into wide blade-like or flange-like features in the castral region and especially around the periferal margins. Within the reticular fields the muri are not strongly excavate nor celate. There are many small conjunctive spines, in addition to the well-developed but short pore conuli. The posterior caudal extension is well formed and very trachyleberid. The ocular ridge is probably the widest of

the *Agrenocythere* species. The castral arx is similar both to *A. antiquata*, new species (which also has a specular promontory) and *A. hazelae* (whose arx extends over the ballial rampart in the anterodorsal sector) in that it is massive in relief (becoming highest between the specula and the anterodorsal ballial rampart) and tends to extend beyond the central castral region toward the posterodorsum. An inflation of the rampart near conulus Leo is also suggestive of the development of a local parapectus.

The ventrolateral carina is strongly excavate and flange-like. I have noted a large blunt perforate tubercule on the posteroventer between the terminal spine of the ventrolateral carina and the inner ventral margin. Such a large feature has also been noted in *Oertliella aculeata* and smaller homologous developments in other species as well. Its function is not guessed here, but its presence is conspicuous.

**DIMENSIONS.**—Length of holotype 1.14 mm; height 0.62 mm.

**DISTRIBUTION.**—One locality (Block Canyon) but many specimens from the middle Eocene of the canyons along the Atlantic shelf of North America.

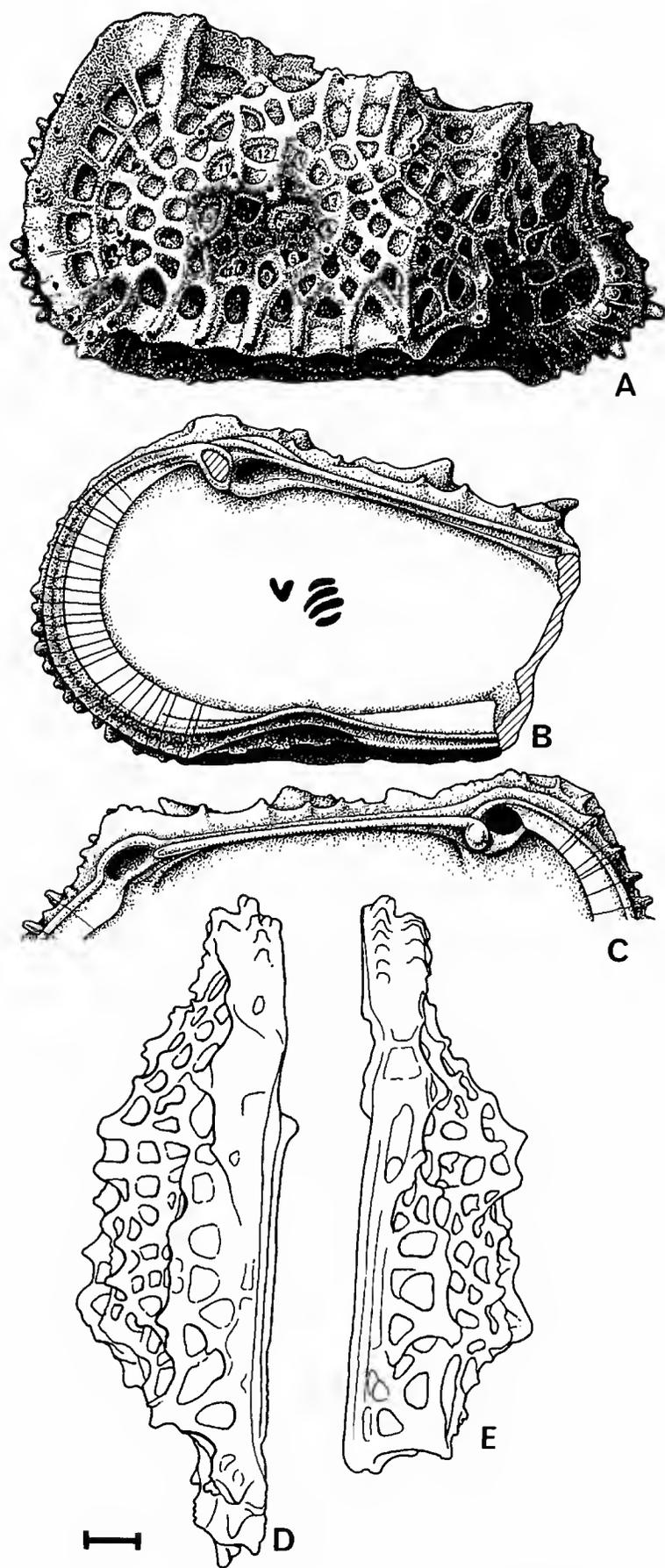


FIGURE 51.—*Agrenocythere gosnoldia*, new species, adult male (?): (A) exterior of the left valve (USNM 168375A) with the order of the fossae in the ballium and the locations of the pore conuli indicated; (B) the interior of a broken right valve (USNM 174365B) showing the muscle-scar pattern; (C) the hinge elements of the left valve; (D, E) the right and left valves as seen from dorsal views. Scale = 100 microns.

### *Agrenocythere antiquata*, new species

FIGURES 54–58; PLATE 4: FIGURES 5, 6; PLATE 6: FIGURES 5, 6

*Bradleya hazelae* (van den Bold).—Ascoli 1969:54.

*Trachyleberis? hazelae* (van den Bold).—van den Bold 1960: 165.

ETYMOLOGY.—*Antiquata*, Latin; the old one.

TYPE-SPECIMEN.—Holotype, whole adult specimen; Figure 55, USNM 174343.

TYPE-LOCALITY.—Trinidad; lower Eocene, Hospital Hill formation, van den Bold locality RHC 1054.

AGE.—Paleogene of Caribbean and Italy.

DIAGNOSIS.—Distinguished from other species of *Agrenocythere*, new genus, by its slightly smaller to moderate size (1.17 mm length), exaggerated and massive dorsal bullar series, central castrum, and prominent pore conuli Leo and Charon (which is developed into an elongate promontory). The anterior marginal rim is narrow; the posterior is caudate, flattened, and extended; the ventrolateral ridge is narrow and high. There are few spines and the muri are well formed but not prominent, often obscured by infilling of fine marly matrix. The specula is very prominent forming a Matterhorn-like projection with a long slope extending toward the murus between numbers nine and ten ballial fossae. The arx is best developed in the central region; however, in some middle to late Eocene specimens the arx may extend to the outer rampart in the anterodorsal sector. The rampart is poorly formed in the posterior sectors and there is no parapectus. The eye tubercle is poorly formed and the species is considered blind; however, there is a conspicuous short ocular ridge extending ventrally.

COMPARISONS.—This species is only slightly smaller among the Caribbean forms, but in Italy it is notably smaller than *Agrenocythere pliocenica*. Its castrum is most like that of the middle Eocene species *A. gosnoldia*, new species, but has its central part (including the specular region) much more accentuated and its arx sharper over the ballial region. The specimens are not usually well preserved. The arx is massive and the two muri that extend dorsally forming the H configuration, mentioned in other species descriptions around the fossa arcis and perval fossa, is poorly developed to well formed. The distal components of the H are usually subdued compared to the high ridge that is comparable to the cross-bar of the H. Examination of

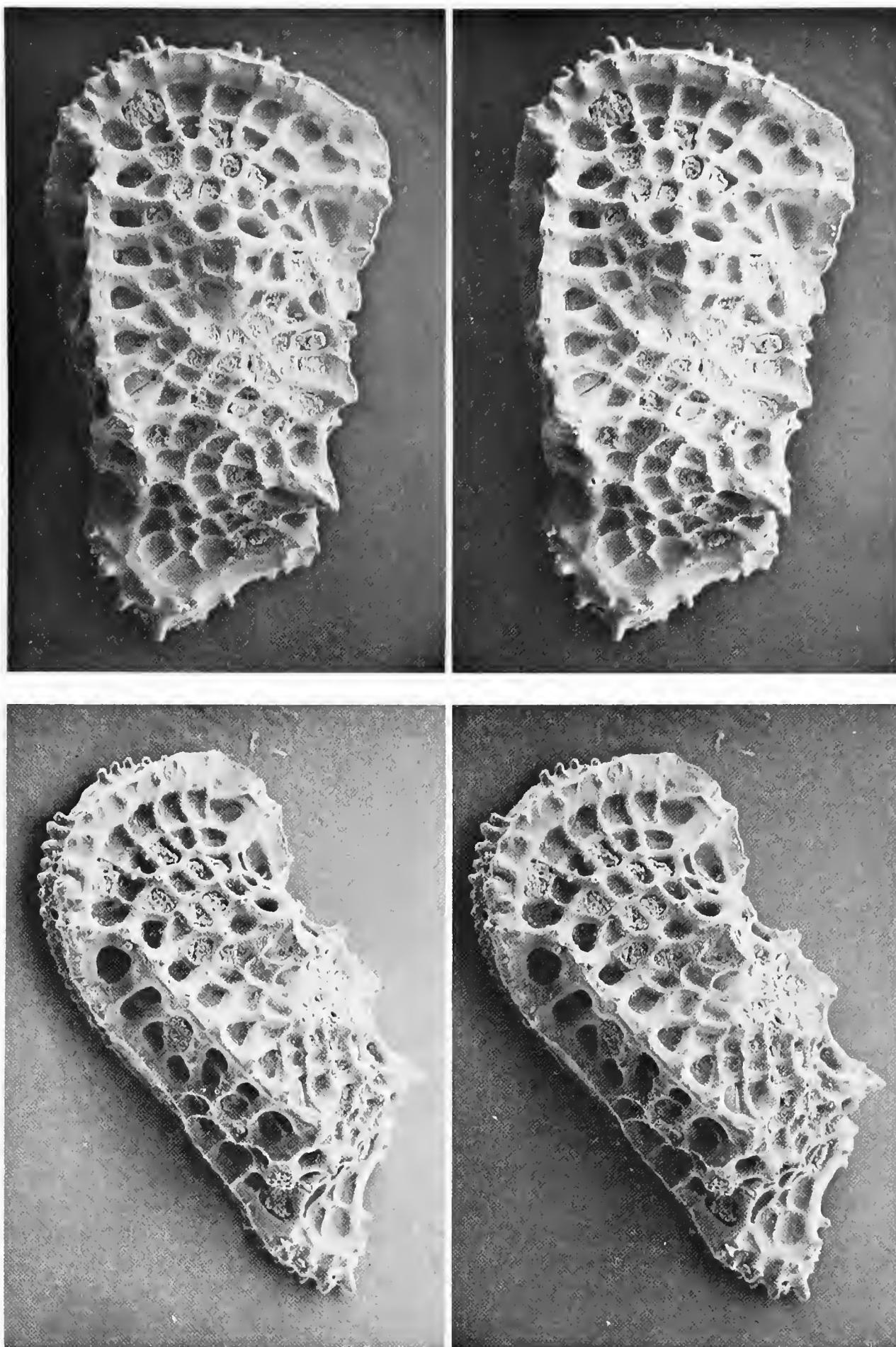


FIGURE 52.—Stereophotomicrographs of the holotype (USNM 168375) of an adult male (?), left valve of *Agrenocythere gosnoldia*, new species, from the middle Eocene of the continental slope of northeastern North America (H2621C), as seen from left lateral, and left anteroventral oblique views (x50).

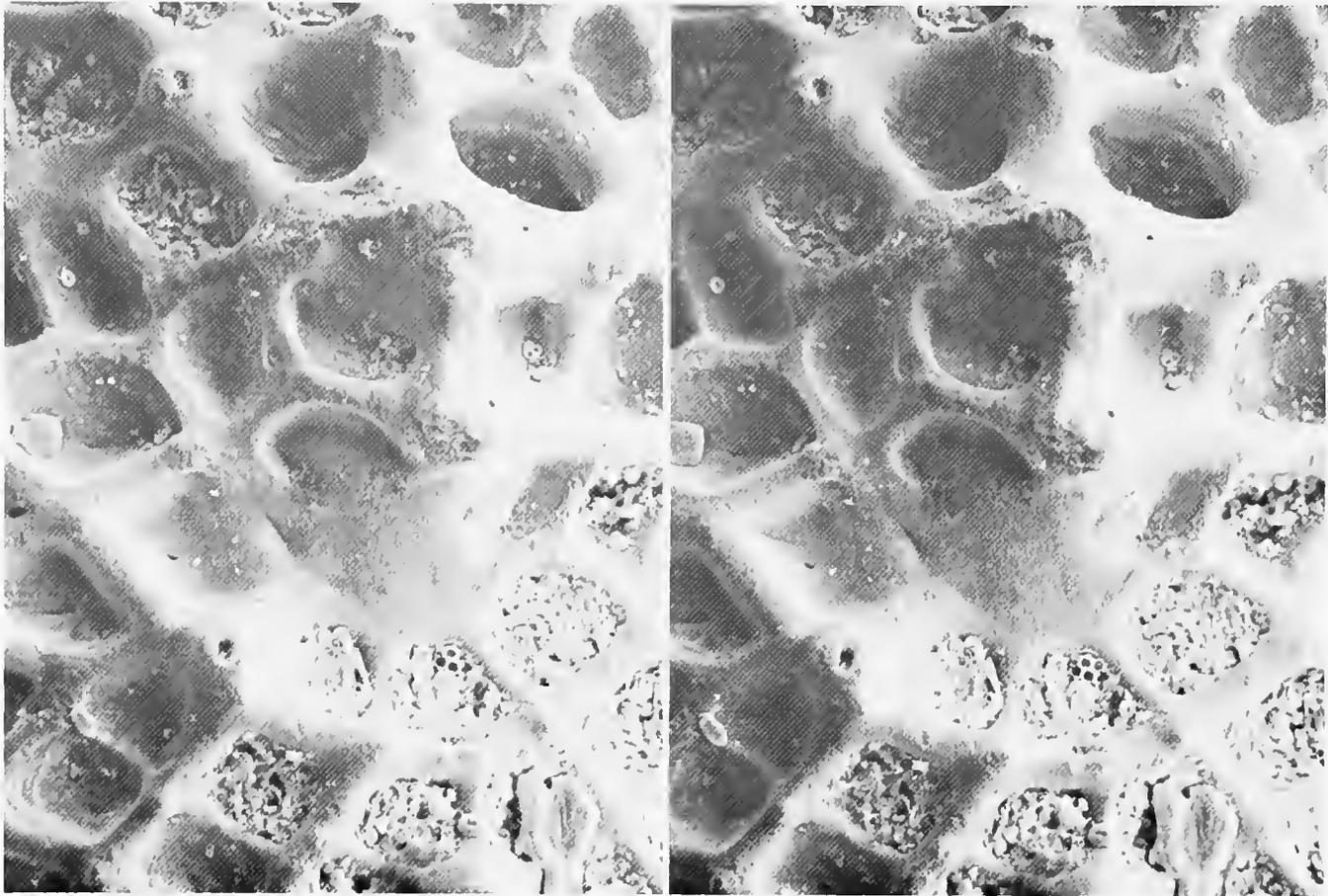


FIGURE 53.—Stereophotomicrographs of the castrum of the holotype of *Agrenocythere gosnoldia*, new species (x160).

van den Bold's Hospital Hill specimens (upper middle Eocene of Trinidad, RHC 1042 and Renz 75) shows an arx with the ballial segment well formed as in *A. hazelae*, yet smooth, narrow, and nonexcavate. The short ridge found in the posteromedian region (near pore conuli Charon) is prominent, unlike *A. hazelae*.

The dorsal bullar series is also pronounced. The similarity between the Italian specimens, first identified from the "scaglia rossa" of the Possagno section (lower Eocene; possibly upper Paleocene, Figure 54) by Ascoli (1969) is remarkable. From my examinations of the specimens of this region and those of Trinidad (Figure 56), I would agree with van den Bold (quoted in Ascoli's report) that they are the same form, but I would disagree that they are *A. hazelae* and I am making them a separate species. As discussed elsewhere, I believe that this species is obviously the best candidate for the ancestral form of *A. hazelae* and other Atlantic *Agrenocythere* species. I have included illustrations of an Eocene specimen from Cuba (Figure 55) and one from the Oligocene or Rockall Plateau in the northeastern Atlantic,

which seems transitional in form between *A. antiquata* and *A. hazelae*.

**DIMENSIONS.**—Length of holotype 1.17 mm; height 0.69 mm.

**DISTRIBUTION.**—Caribbean and Atlantic Paleogene (see Table 3) and Mediterranean lower Eocene.

#### *Agrenocythere? cadoti*, new species

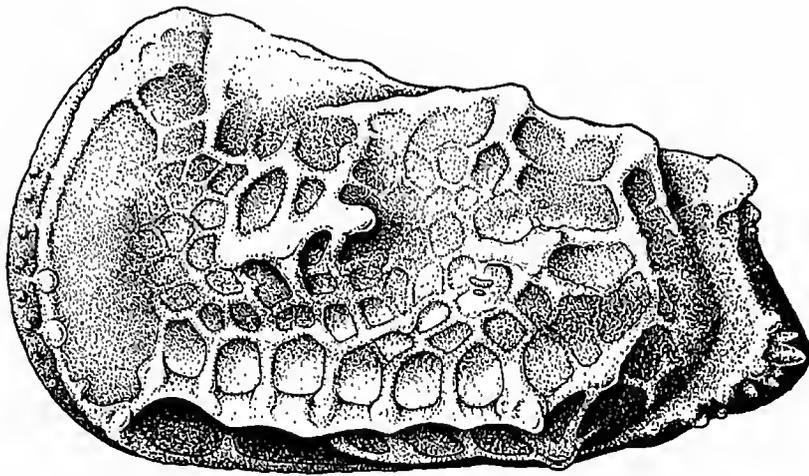
FIGURES 59, 60

**HOLOTYPE.**—Left valve, adult male; Figures 59, 60; University and Kansas collections, KU mip 1007900.

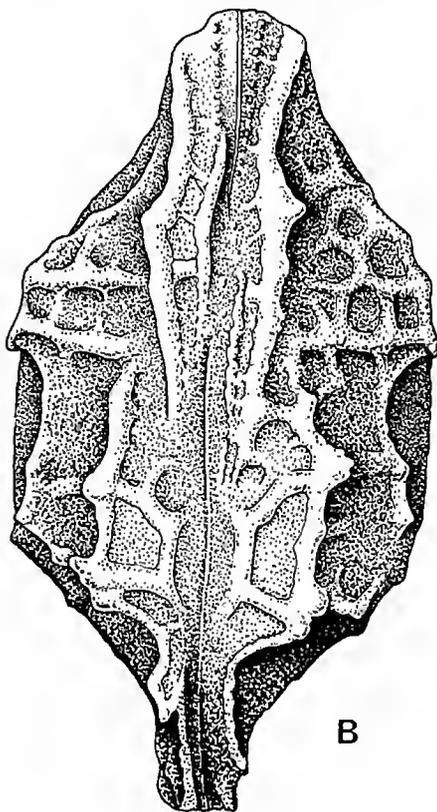
**TYPE-LOCALITY.**—Southern Ocean, south of Australia; Tasman Plateau vicinity of RV Eltanin station 32, Cruise 39, Grab 10; lat. 48°26.4'S and long. 148°17.2'E; 960 meters depth; bottom temperature unknown. Twenty specimens examined. Ten paratypes have been repositied in the University of Kansas collections.

**AGE.**—Recent; no living specimens found.

**DIAGNOSIS.**—Carapace elongate, rectangular with evenly rounded ends; reticulum with massive nodose muri; dorsal bullar series absent or very suppressed;



A



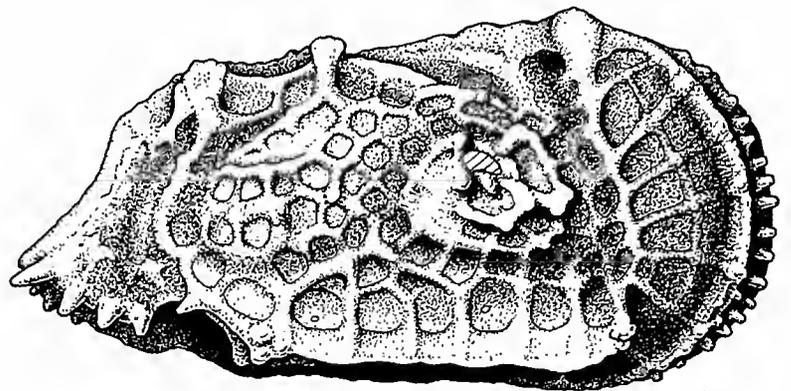
B

FIGURE 54.—*Agrenocythere antiquata*, new species, adult, female (?), from the Eocene of the Possagno section of northern Italy as seen from lateral (A) and dorsal (B) views (length of specimen 1100 microns, USNM 174685).

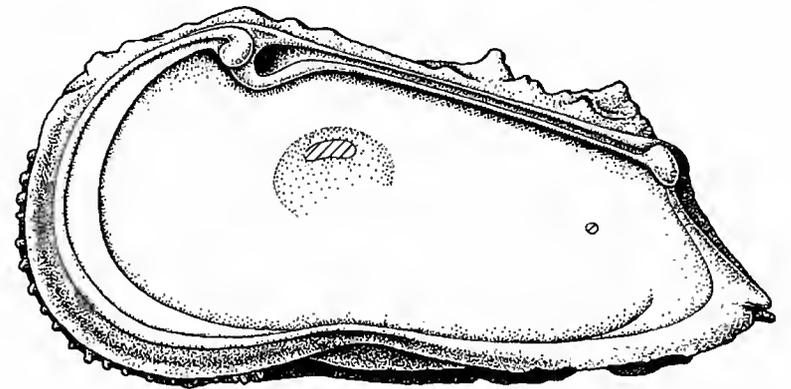
the castrum is evenly though irregularly muröse with indistinct subdivisions, no arx; no eye tubercule; the antennal muscle scar may be divided although the V-shape is at least residually present.

DISCUSSION.—This species, which is just now becoming known, may very well not belong to *Agrenocythere*, new genus. The similarity of the reticular pattern with species of *Agrenocythere* is striking, but as other genera also have this pattern this congruence may be misleading. The overall shape and even ex-

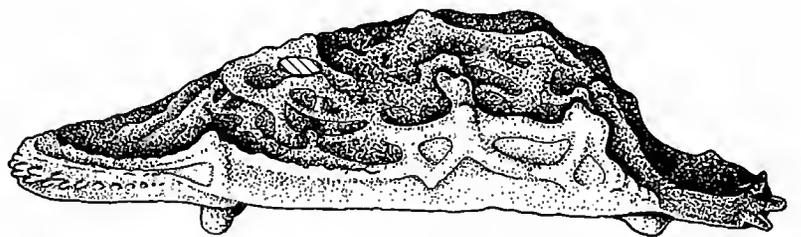
pression of feature complexes is not typical of *Agrenocythere*, yet it is not typical of related genera either. It is possible that this is an extreme derivative of *A. radula*, but this is conjecture. There are general similarities in the muscle-scar pattern with some species of *Cletocythereis* (broken V-shape). There are also similarities to specimens others have identified as *A. semivera* Hornibrook. Perhaps the publication of this species will bring these problems more to fore. It may be even more closely related to *A. semivera*. The specimens I have available of this species are not conclusive (their identity with the illustration of Hornibrook is in doubt).



A



B



C

FIGURE 55.—*Agrenocythere antiquata*, new species, adult male, right valve (USNM 174361), from the upper Eocene of Habana Province, Cuba (Cantera Kohly, Bosquet de Habana, Bank of Rio Almendares) as seen in (A) lateral, (B) interior, and (C) dorsal views (length of specimen 1230 microns).

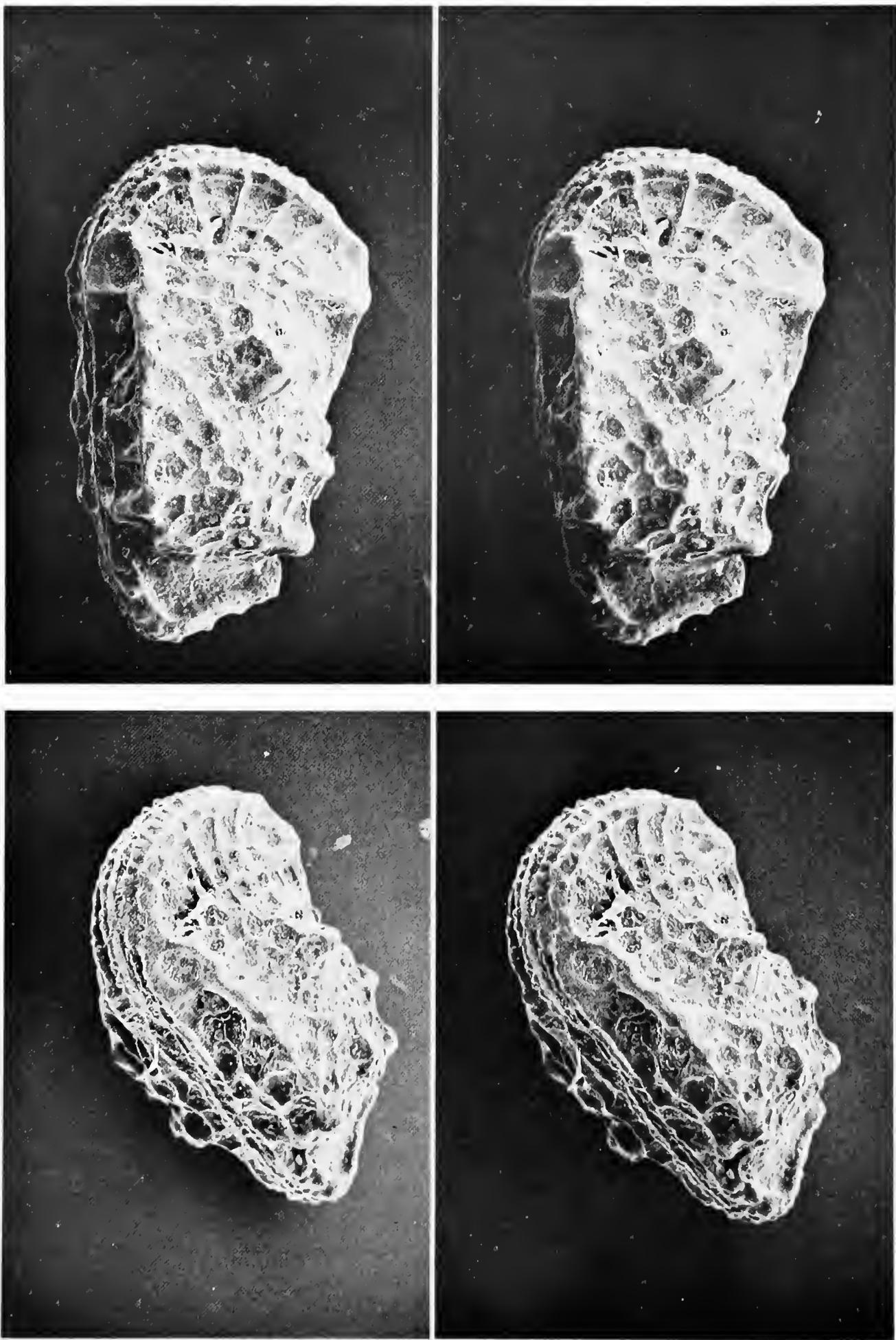


FIGURE 56.—Stereophotomicrographs of a holotype (USNM 174343) of an adult specimen of *Agrenocythere antiquata*, new species, from the Eocene of Trinidad (RHC 1054), as seen from the left lateral, and left anteroventral oblique views (x50).

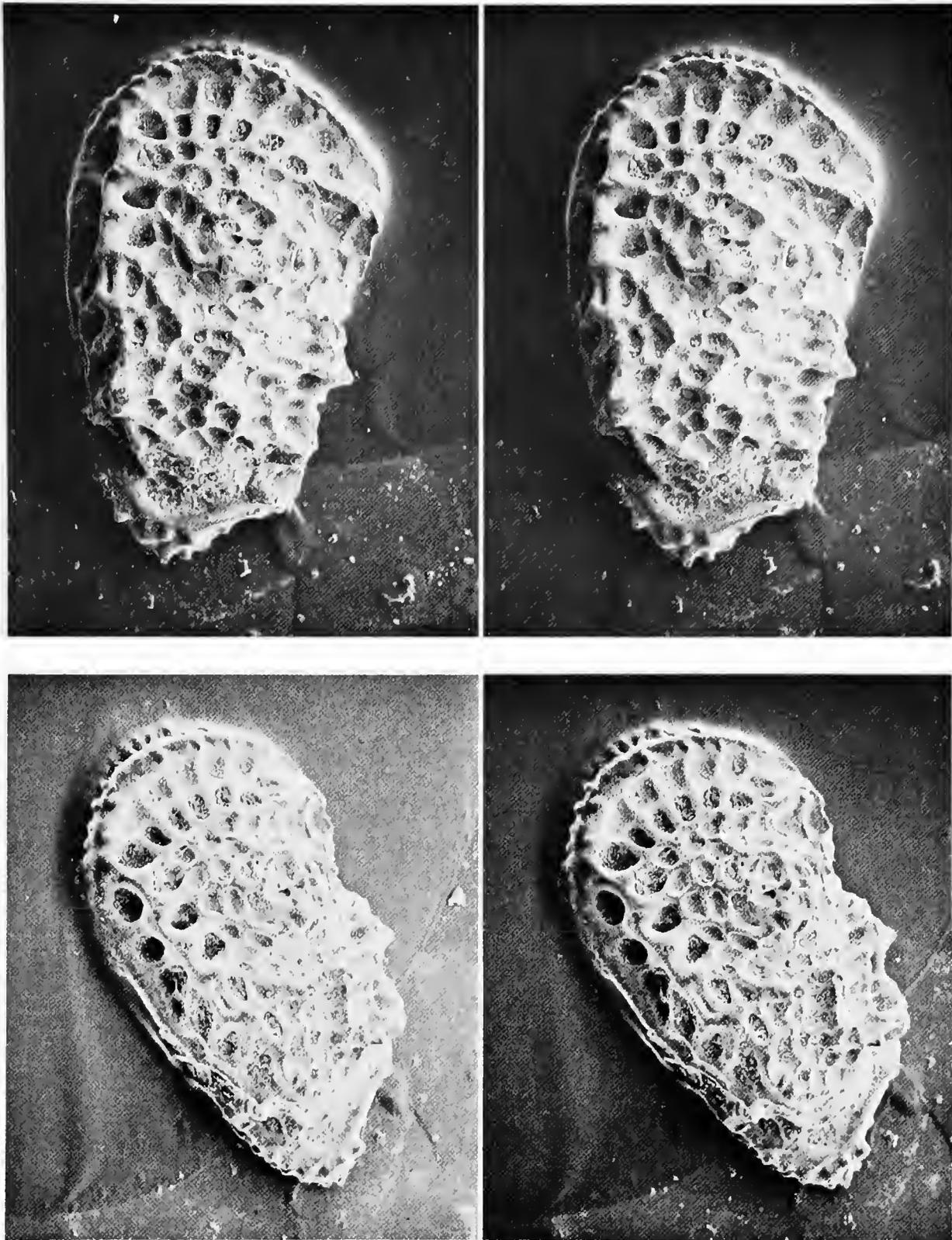


FIGURE 57.—Stereophotomicrographs of an adult, female left valve (USNM 174346) of *Agrenocythere* species from the Oligocene of the North Atlantic (Rockall Plateau, DSDP 117A, core 2, section 6) as seen from the left lateral, and left anteroventral oblique views (x50). This form appears to be transitional between *A. antiquata*, new species, and *A. hazelae*.

**DIMENSIONS.**—Length of holotype 0.99 mm, height 0.52 mm.

**DISTRIBUTION.**—Known only from one sample (the type-locality described above) south of Australia in 960 meters of water near the extreme southeastern limits of the known geographic range of *Agrenocythere*

(in conjunction with the possible member species *A. semivera* Hornibrook).

**Genus *Oertliella* Pokorný, 1964**

*Oertliella* Pokorný, 1964:283.

**TYPE-SPECIES.**—*Cythere reticulata* Kafka, 1886, from the Turonian of Bohemia, Czechoslovakia.



FIGURE 58.—Stereophotomicrographs of the castrum of an Oligocene specimen (same specimen as shown in Figure 57) of *Agrenocythere* species (x100).

**EMENDED DIAGNOSIS.**—Summarized and corrected from Pokorný (1964a). Carapace surface strongly reticulate with the reticulum bearing no castral structures (such as an arx or parapectus) except the pore conuli typical of the several related reticulate trachyleberid genera. Anterior marginal ridge narrow without ocular ridge. Dorsal ridge (carina) originating through the strengthening of several muri of the reticulum, low, reduced to spines (not protuberances such as a bullar series), or with an elongate crest formed by the fusion of the spines or extension of the carinae. Likewise the ventrolateral ridge (carina) may be weak or strong and it may be wide, and crest-like in certain species whose marginal carinae are well developed. Median ridge absent and the posterior reticular field is unadorned except with five or six pore conuli. The same is true of the anterior reticular field. With marginal rim around the ventral commissure. An eye tubercle is present.

Hinge hemi-holamphidont. Frontal muscle scar V-shaped, adductors undivided. Duplicature narrow to median in width. Radial pore canals numerous. Sexual dimorphism may be strong with the posteroventer of the male extended.

**AGE.**—Upper Cretaceous and Paleogene of Europe.

**REMARKS.**—Emended to include a greater range of species development than considered by Pokorný, and to be set in terms comparable to those used to describe *Agrenocythere*, new genus, and other related genera. The original description by Pokorný (1964) was very abbreviated. He credits Oertli (1963)—which statement I cannot find—with recognition of the independent status of the genus. Pokorný's paper included two illustrations of *O. reticulata* (Kafka) whose silhouettes are given in this report (Plate 3: figures 5, 6; Plate 5: figures 5, 6). It is noted that in the specimen considered the male (Pokorný 1964a, pl. 1: fig. 3) a long dorsal ridge is present (as compared to the supposedly more spinose female). More highly calcified species of this same generic form (especially those with celate muri) would not necessarily have such a sparse ornament as exhibited by *O. reticulata*. An example is the new species described here, *O. ducassae*, which is characterized by flange-like carinae, but in most other respects is like the type-species. Another extreme variation is *O. aculeata* (Bosquet) shown in Figures 61 and 62, which is very tuberculate due to enlargement of the pore conuli. *O. horridula* (Bosquet), the Maestrichtian predecessor of *O. aculeata* is similarly enlarged in this manner. Some latitude in the description of the genus must be allowed.

Another important addition to the diagnosis is the presence of eye tubercles. There is some room for doubt about the appropriateness of this character as being generically important, because any species could conceivably become blind as it invades deeper water. It also might become heavier and more massive as its species invade the surf zone. *Agrenocythere*, however, of which several species are described in the present report, is believed to have evolved from *Oertliella* or an *Oertliella*-like form. *Agrenocythere* is blind (assuming that it in turn evolved as a deep-sea genus) and began to develop several new characteristics (a castral complex, for example), as well as loss of the eye tubercle. Whereas some species of *Oertliella* may have become blind, it is not typical of this shallow marine genus.

Pokorný (1964a) made comparisons of *Oertliella* with *Hermanites* Puri, which has been a very confused genus. At that time the muscle scars of *Hermania reticulata* Puri, the type-species of *Hermanites*, were not known. The frontal scar is divided, with a U-shaped scar below and a single simple scar overly-

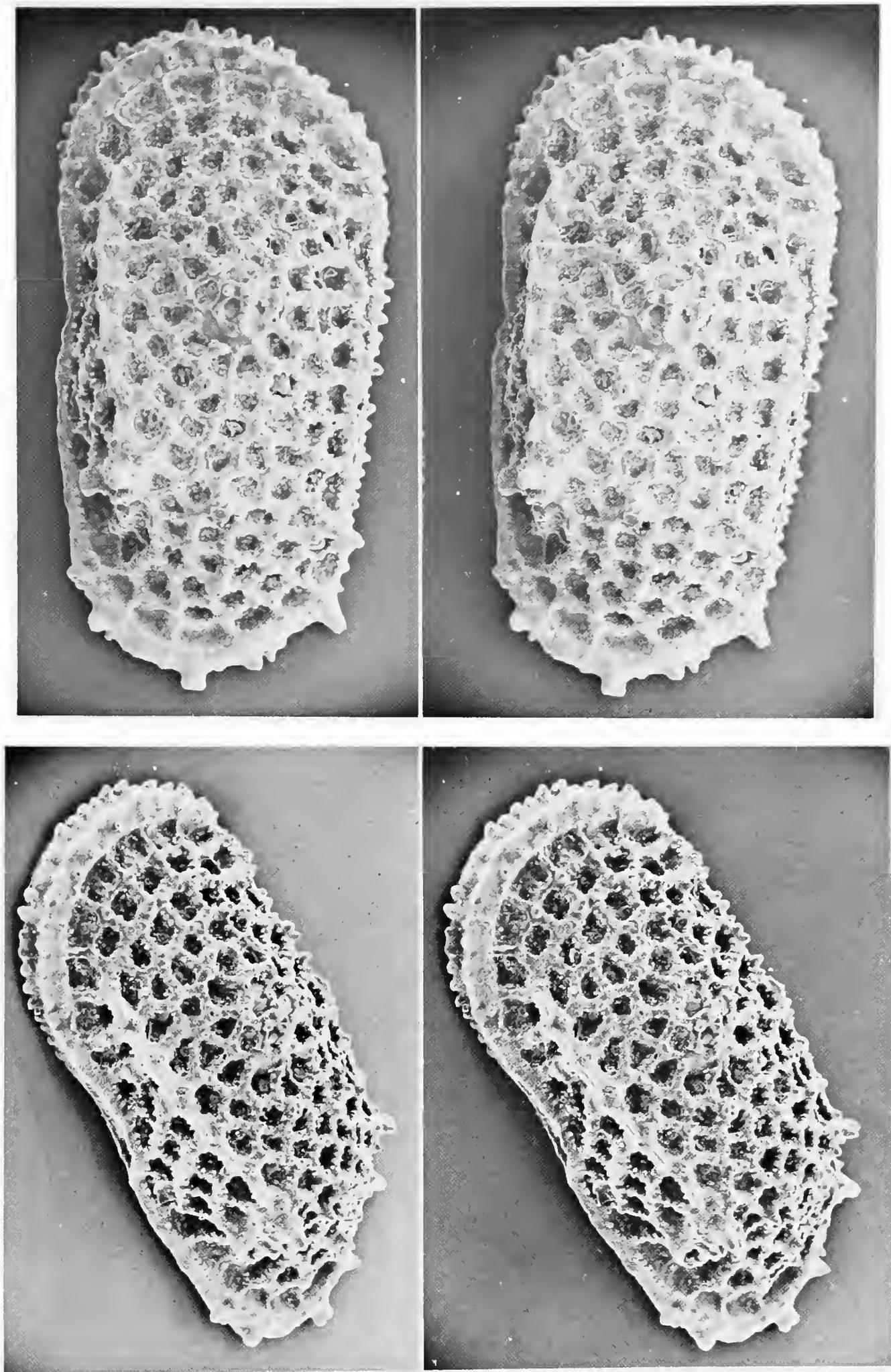


FIGURE 59.—Stereophotomicrographs of the holotype, a male (?) of *Agrenocythere? cadoti*, new species, from the Recent of the Tasman Plateau (ELT 39-32(10); lat. 48°26.4'S; long. 148°17.2'E; 960 meters; KUMP 1007900; x80), as seen from the left lateral and left anteroventral oblique views.

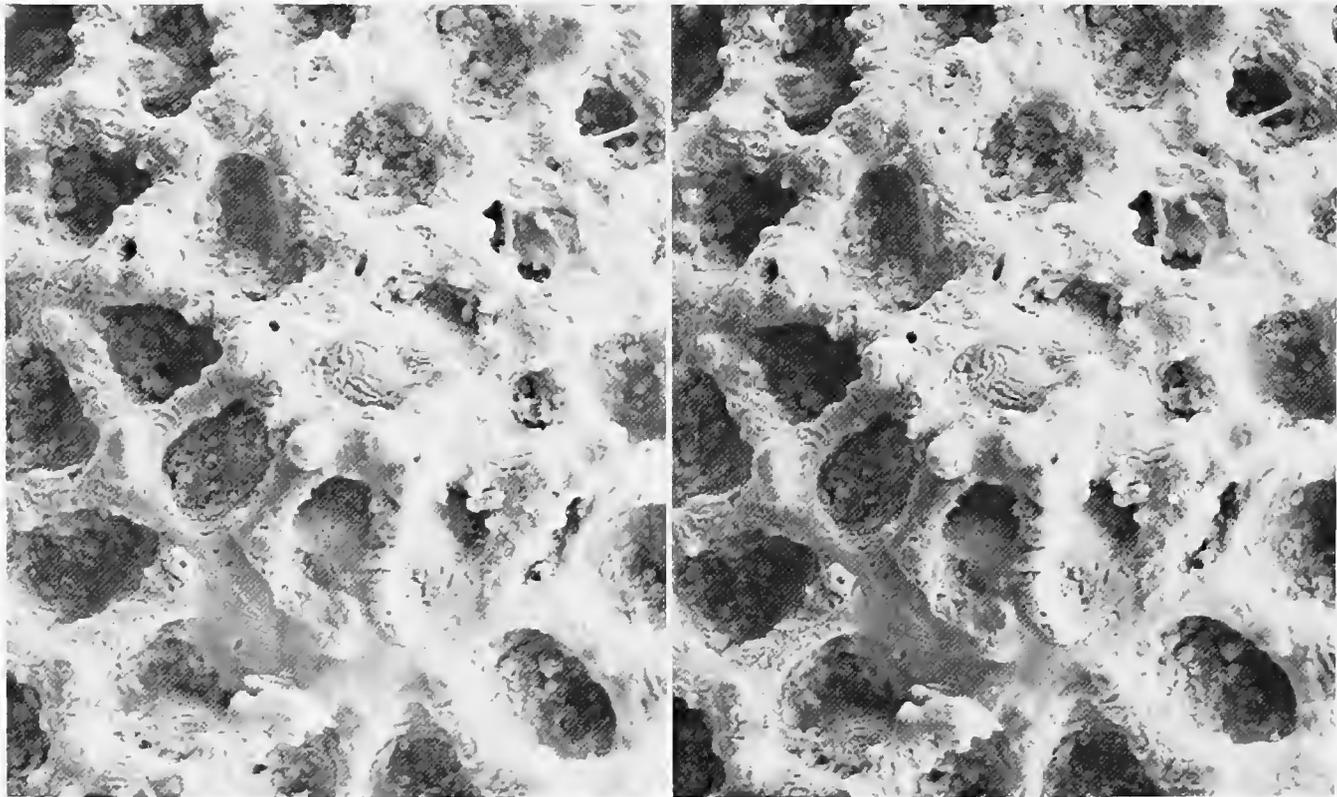


FIGURE 60.—Stereophotomicrographs of the central part of the castrum of the holotype (Figure 59) of *Agrenocythere? cadoti*, new species (x200).

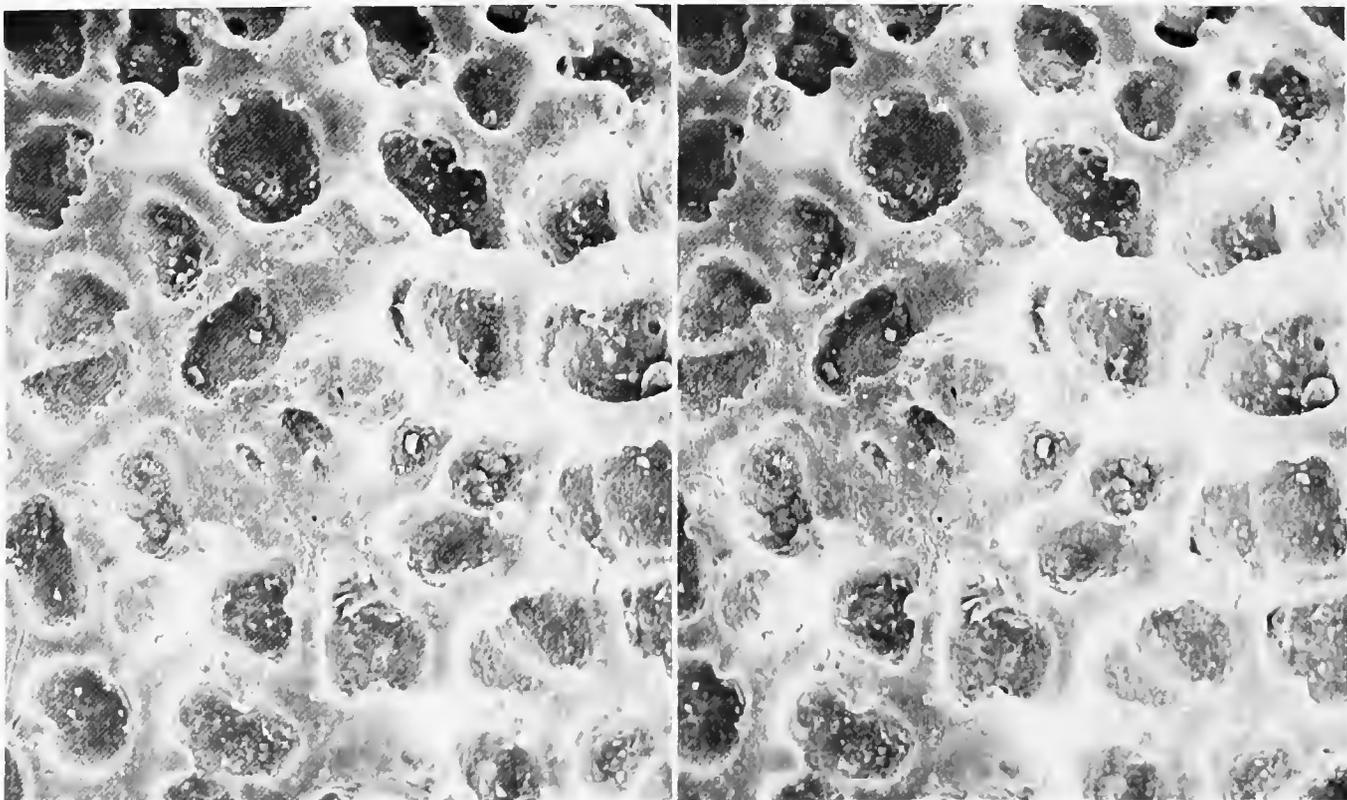


FIGURE 61.—Stereophotomicrographs of the castrum of the specimen in Figure 62, *Oerthiella aculeata* (Bosquet, 1852) (x180).

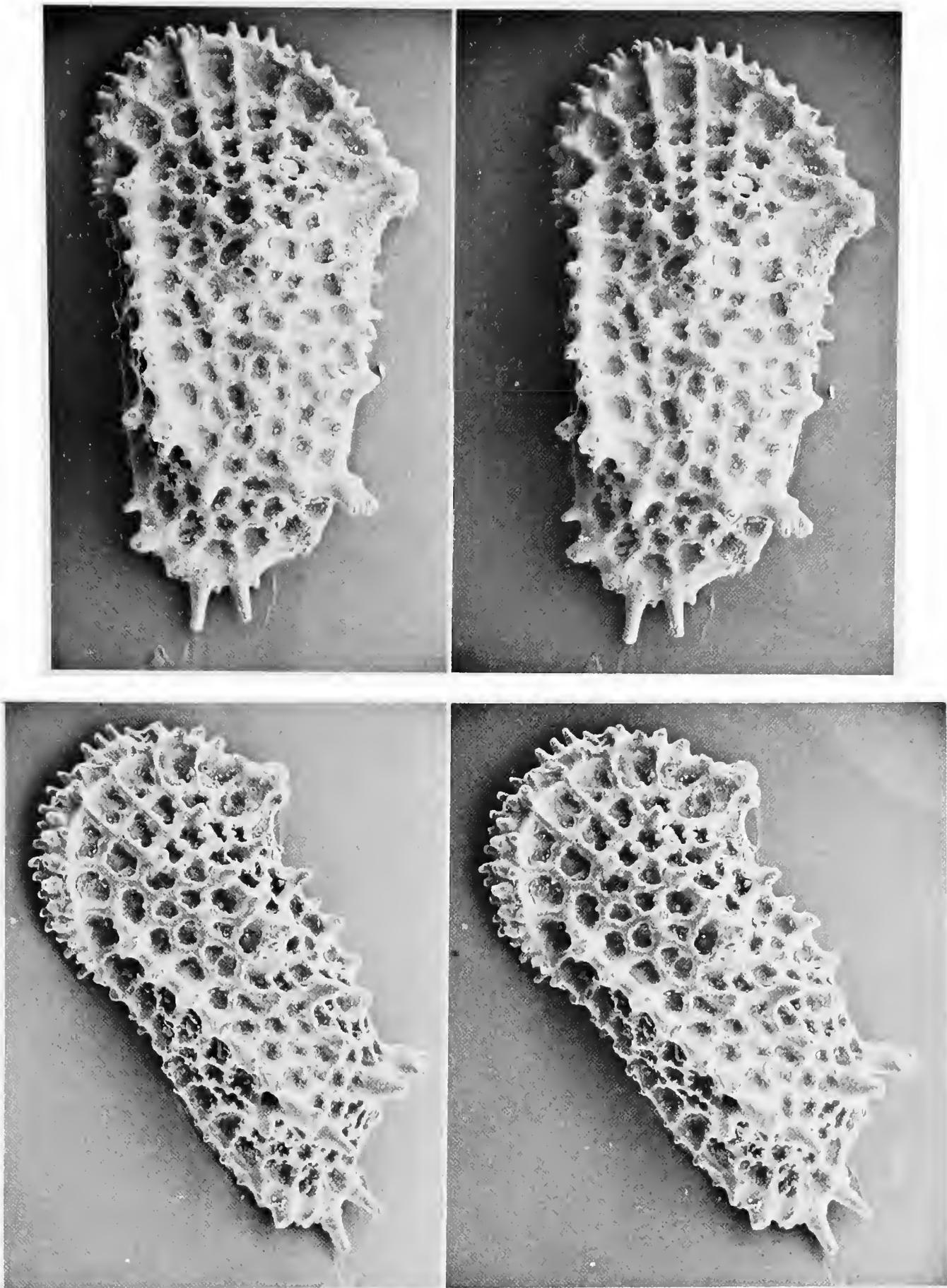


FIGURE 62.—Stereophotomicrographs of a hypotype (USNM 174340), an adult female (?) left valve, of *Oerthiella aculeata* (Bosquet, 1852), from the upper Eocene (Calcare de Blaye) of southwestern France (ASA, l'Octrol Commune, Blaye) as seen from the left lateral and left anteroventral views (x60).

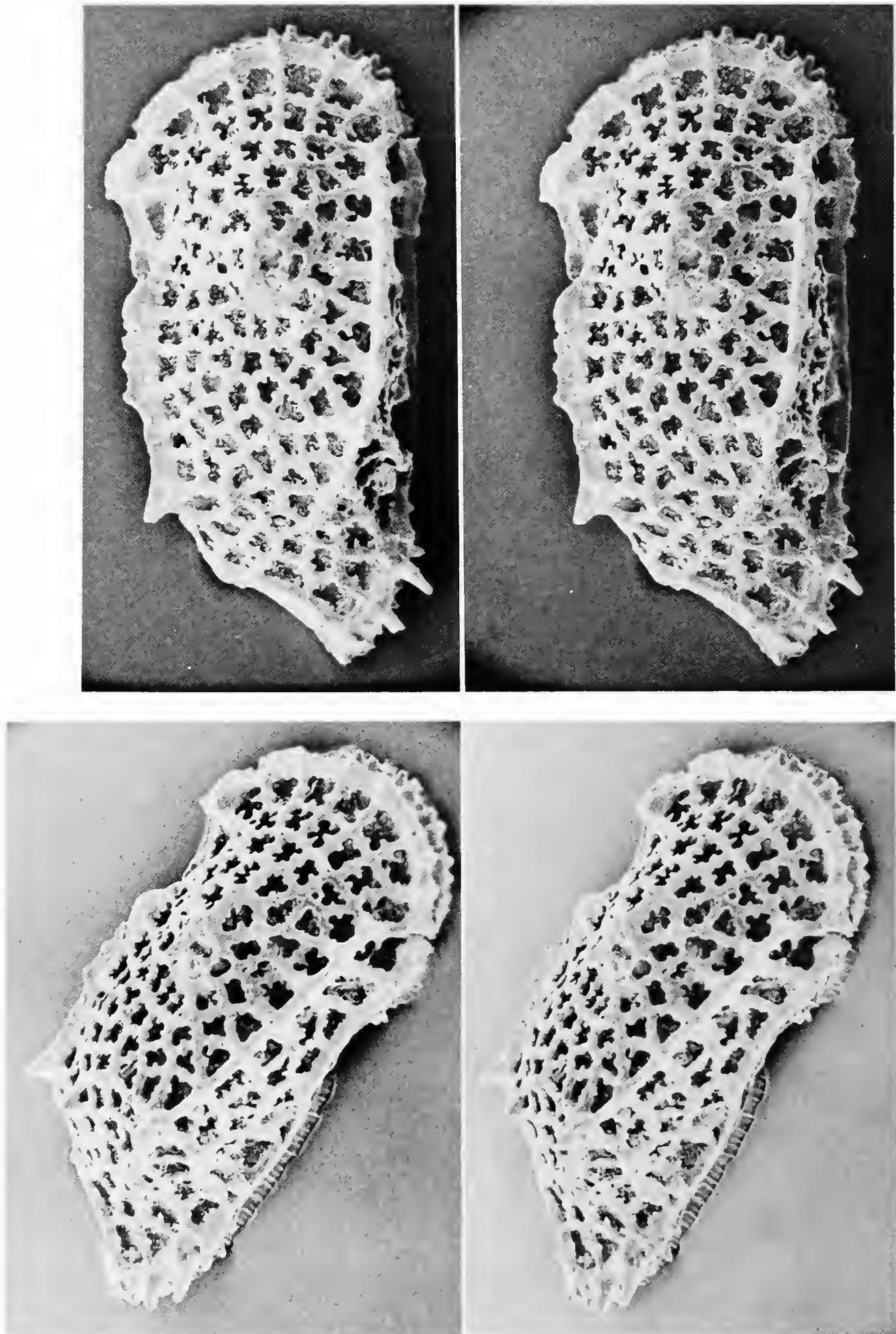


FIGURE 63.—Stereomicrographs of the holotype (USNM 174386) of a right valve of *Oerthiella ducassae*, new species, from the Eocene (Bartonian) of the Côte de Basque section, Biarritz, France (Cheetham 22 VIII 68, No. 7; x90).

ing one side of the U (similar to *Hornibrookella*). It is not a V-shaped scar typical of many trachyleberids or even as well developed as some divided V-shaped scars of *Cletocythereis* species. I do not consider it possible to establish a close comparison between *Oertliella* and *Hermanites*, sensu stricto, unless one allows for considerable adaptive change in both the reticulum and the frontal muscle-scar pattern. At present the consensus is that these two forms are of different genera and probably represent different families.

### *Oertliella ducassae*, new species

FIGURES 63-66

ETYMOLOGY.—Named in honor of Mlle. Odette Ducasse, whose ostracode work in southwestern France is becoming well known.

TYPE-SPECIMEN.—Holotype an adult right valve (USNM 174386) from the Eocene of southwestern France on the Côte de Basque (Figures 63, 64).

TYPE-LOCALITY.—Section on the Côte de Basque to the west of Biarritz, France, near the road and sea wall, Cheetham locality 22 VIII 68, No. 7.

AGE.—Bartonian, Eocene.

DIAGNOSIS.—A celate species of *Oertliella* with wide flared dorsal and ventrolateral carina (spines present but integrated into the carina) and fossae partly closed by spines directed inward from the outermost flanged portions of the muri (extensions of the tegmen). Pore conuli present but comparatively subdued.

COMPARISONS.—Celate muri and wide crest-like carina distinguish this species from either the type-species or *O. aculeata*, which is tuberculate (with extensions of the pore conuli) by comparison. A slight variation in form in this species is seen in specimens collected from the Paleocene of Rockall Plateau (DSDP XII 117A, Core 7, Section 1). This form abundantly in these samples (Figures 65, 66). The dorsal carina is not so crest-like, but the celation is present and the posterior is acuminate.

DIMENSIONS.—Length of holotype 1.0 mm, height 0.5 mm. Specimens from Rockall Plateau slightly larger (1.11 mm x 0.57 mm).

DISTRIBUTION.—Upper bathyal to outer shelf of western Europe and the northeastern Atlantic during the Paleogene.

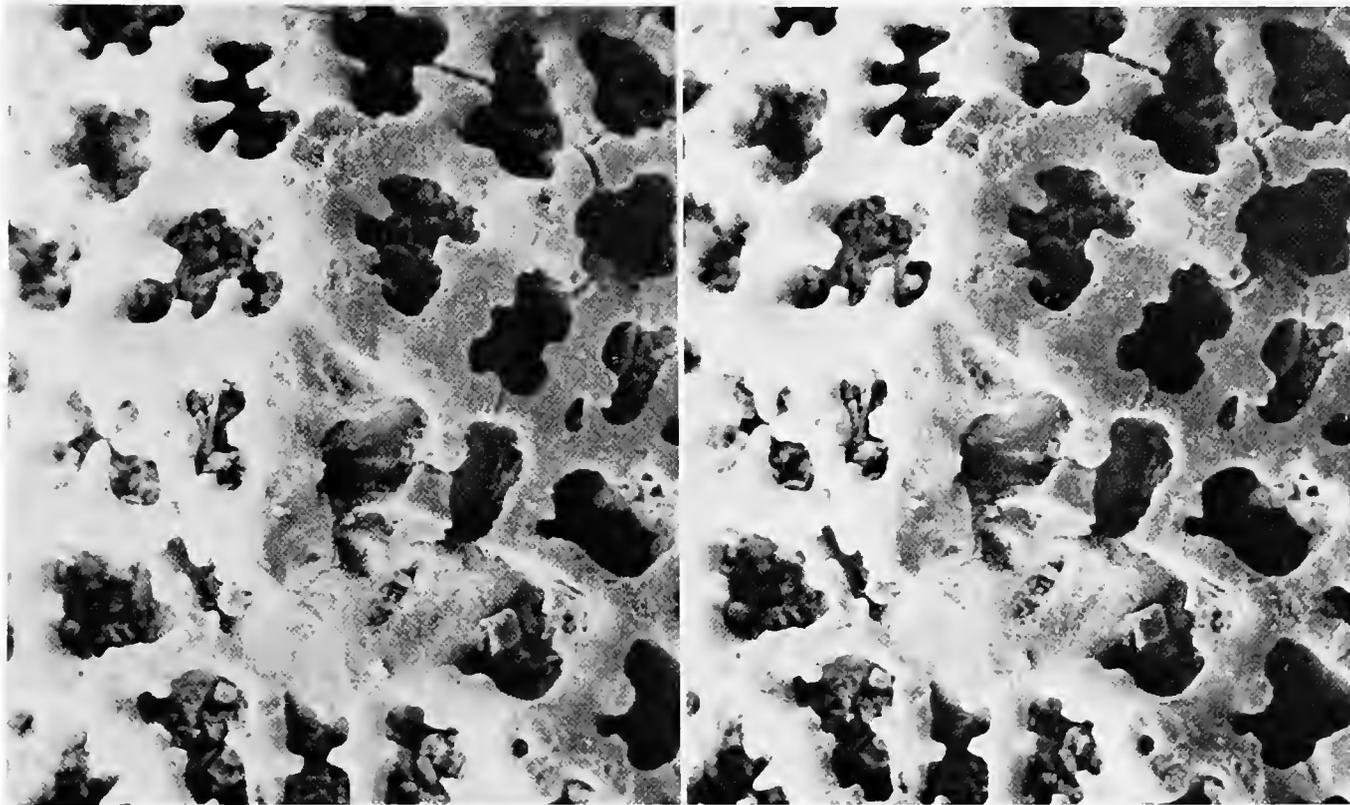


FIGURE 64.—The castral region of the holotype of *Oertliella ducassae*, new species (same specimen as in Figure 63; x200).

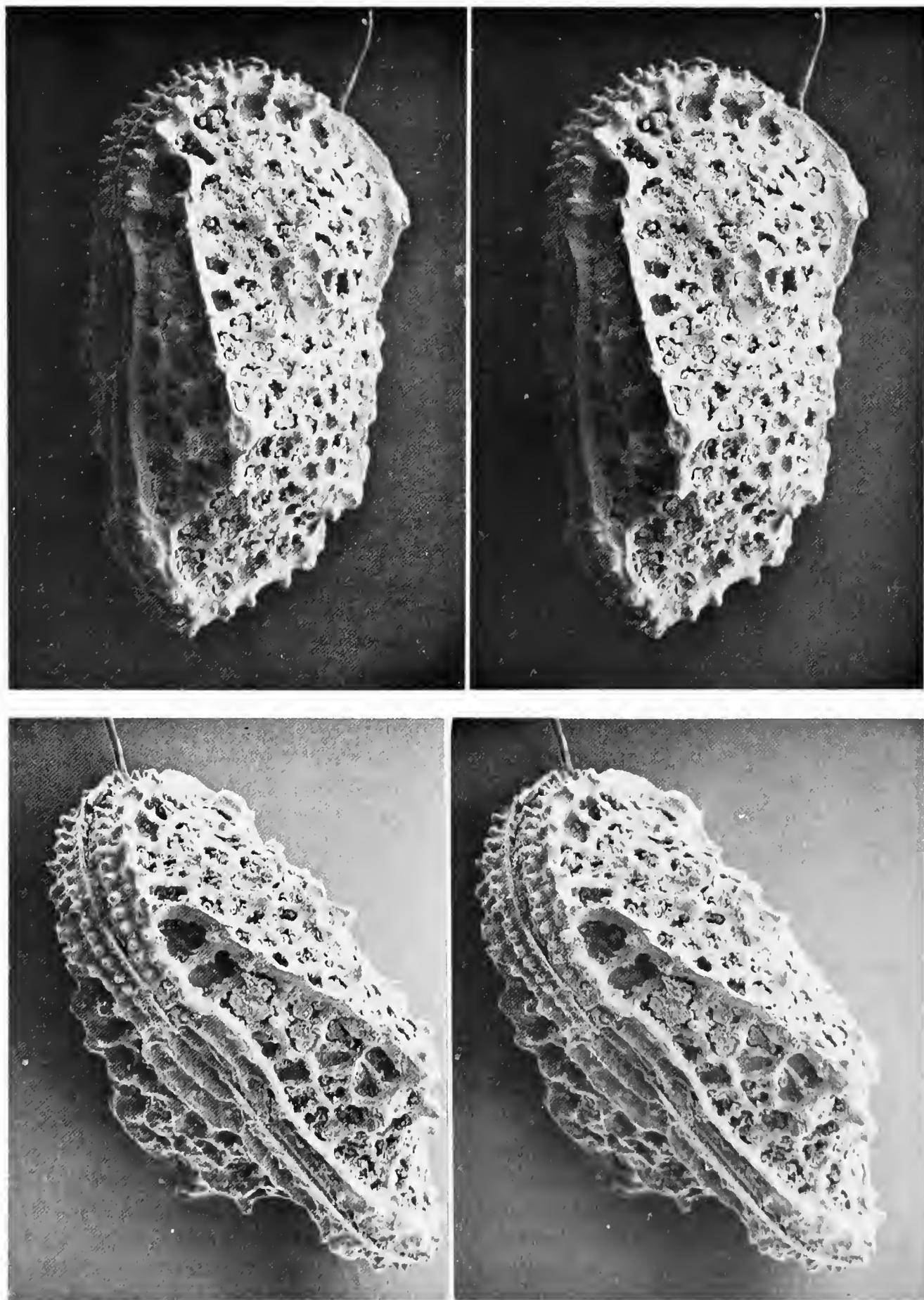


FIGURE 65.—Stereophotomicrographs of an adult female whole specimen (paratype, USNM 174338) of *Oertliella ducassae*, new species, showing eye tubercles and celate muri, from the Paleocene of Rockall Plateau (DSDP XII, Hole 117, core 8, section 1) as seen from lateral and anteroventral oblique views ( $\times 75$ ).



FIGURE 66.—Stereophotomicrographs of the castrum of a specimen (same as in Figure 65) of *Oertliella ducassae*, new species (x200).

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## Appendix: Distribution Data

Within the Appendix are included primary reference data regarding the distribution of the material studied for the description of the taxa in the text. Figure 67 is a bivariate plot of the length/height ratios of the *Agrenocythere* species showing the differences in size among the adult or late instars examined. This is followed by Tables 1-4 with locality information referred to previously in the text and maps (Figures 1, 2, 3, and 30) unless included in their captions.

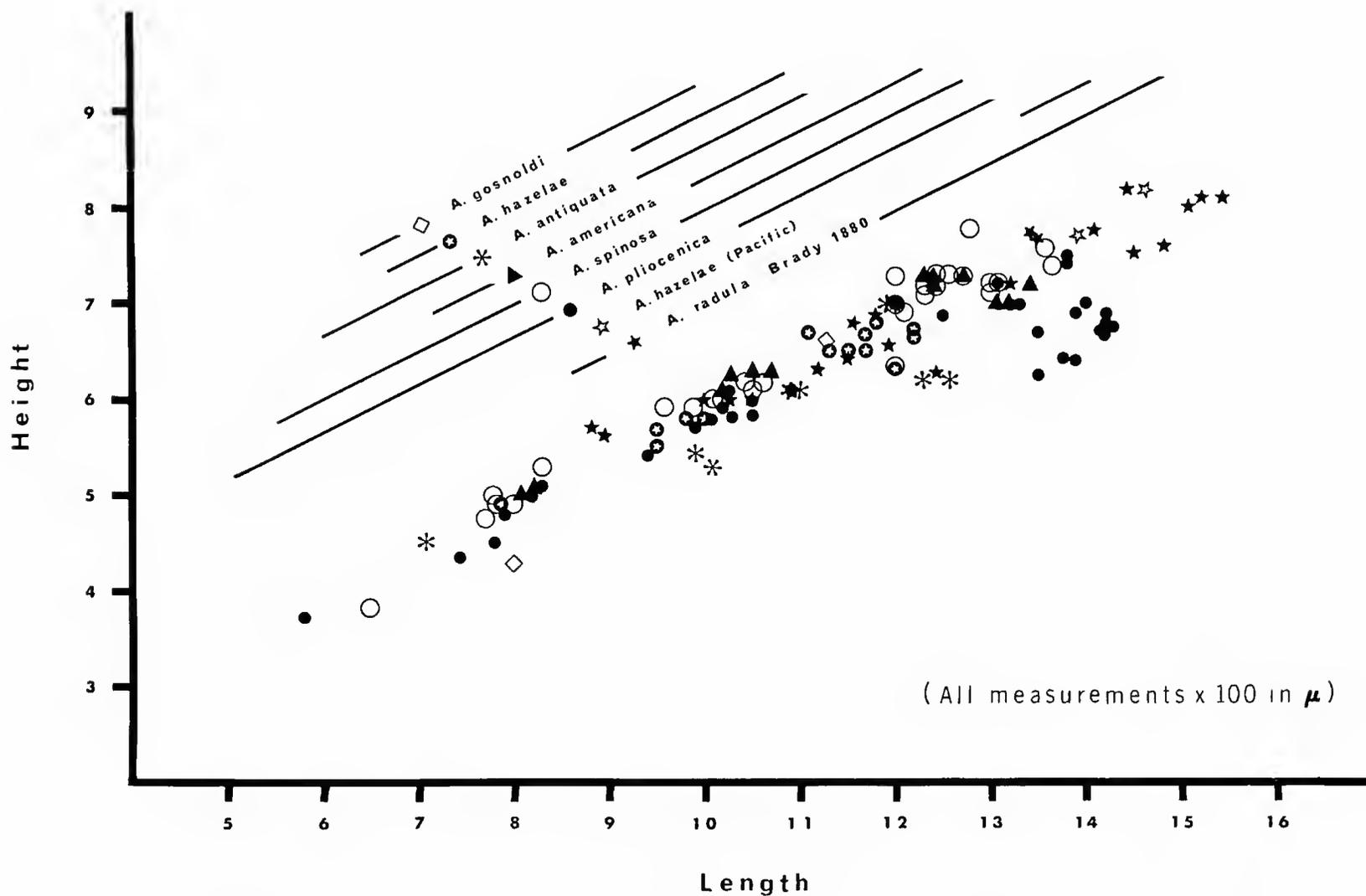


FIGURE 67.—Variation in maximum size among the different species of *Agrenocythere*, new genus. A bivariate plot of length-height ratios of eight species. The lower ends of the ranges (indicated by lines) are subject to considerable error for the respective instars, because of sample inadequacies; however, the upper ends of the observed ranges (the adult stages) are considered to be more faithful to the real size differences.

TABLE 1.—*Distribution of Bradleya species, new genus*

<i>Map Designation*</i>	<i>Station Number</i>	<i>Depth (meters)</i>	<i>Latitude</i>	<i>Location</i>	<i>Longitude</i>
1	ELT. 21-21		53°01'S		75°43'W
2	CHAL. 302	2610	42°43'S		82°11'W
3	ELT. 21-10	3137	36°41'S		93°37'W
4	CHAL. 300	2475	33°42'S		78°18'W
5	DWBG 99	3220	20°33'S		81°51'W
6	DWHG 74	3030	28°29'S		106°30'W
7	DWBG 121	3320	27°09'S		109°50'W
8	DWHG 79	3440	23°35.5'S		118°13.5'W
9	CHAL. 280	3492	18°40'S		149°52'W
10	ALB. 4723	3475	10°14'S		107°45'W
	ALB. 4728	1930	13°47.5'S		114°22'W
11	SWP 766C	1860	4°21'S		81°27.8'W
	SWP 770C	960	3°16'S		81°9.3'W
12	ALB. 2808	1144	0°36.5'S		89°19'W
	ALB. 2817	496	0°48'S		89°8.9'W
13	V20-27	4076	6°28'N		111°45'W
14	ALB. 3375	2197	2°34'N		82°29'W
	ALB. 3376	1132	3°9'N		82°8'W
15	ALB. 3363	1789	5°43'N		85°50'W
16	V19-19	3760	13°14'N		78°22'W
	V19-20	3539	12°31'N		78°18'W
	V19-21	3168	10°36'N		79°21'W
17	V12-122	2756	17°2'N		74°23.9'W
	A179-4	2965	16°36'N		74°48'W
18	ALB. 2751	1257	16°54'N		63°12'W
19	V3-72	3746	23°26.5'N		94°3.5'W
	V3-74	3733	22°49'N		92°21'W
20	ALB. 2379	2683	28°15'N		87°42'W
	ALB. 2381	2433	28°05'N		87°56'W
	ALB. 2382	2295	28°19'45"N		88°1.5'W
	ALB. 2383	2160	28°32'N		88°06'W
	ALB. 2385	1335	28°51'N		88°18'W
	ALB. 2392	1324	28°47.5'N		87°27'W
21	V3-41	832	29°12.5'N		87°02'W
22	ALB. 2659	931	28°32'N		78°42'W
23	ALB. 2679	1430	32°40'N		76°40.3'W
24	AII 118A	1135-1153	32°19'N		64°34'W
	AII 119	2095-2223	32°16'N		64°32'W
25	TR. 13	1955	49°38'N		13°28'W
26	CHAL. 78	1800	37°26'N		25°13'W
27	V9-29	4675	3°47.5'N		34°37'W
		Lower Miocene			
28	AII 156	3459	0°46'S		29°26'W
29	AII 159	834-939	7°58'S		34°22'W
	AII 169A	587	8°2'S		34°24'W
30	ALB. 2763	1227	24°17'S		42°48.5'W
31	RC8-91	2723	33°25'S		41°54'W
32	V12-54	4082	41°14.4'S		6°7'W
33	RC8-41	2897	43°38'S		51°16'E
34	V16-66	2995	42°39'S		45°40'E
35	V19-222	2005	33°22'S		34°24'E
		Cretaceous-Miocene			
36	IIOE 380A	935	32°58'S		43°37'E
	IIOE 380C	950	32°58'S		43°41'E

TABLE 1.—*Distribution of Bradleya species, new genus—Continued*

<i>Map Designation*</i>	<i>Station Number</i>	<i>Depth (meters)</i>	<i>Latitude</i>	<i>Location</i>	<i>Longitude</i>
37	IIOE 360B	1360	27°39'S		33°23'E
	IIOE 374C	1335	27°09'S		34°09'E
	IIOE 397D	665	26°14'S		34°04'E
38	IIOE 361G	2750	25°50'S		37°21'E
	IIOE 369D	1720	24°04'S		36°16'E
	IIOE 369G	1140	24°12'S		36°01'E
	IIOE 369J	910	24°25'S		35°47'E
	IIOE 370B	925	22°33'S		36°10'E
	IIOE 399	1530	21°12'S		36°24'E
	IIOE 400B	1530	21°12'S		36°24'E
39	IIOE 363B	2980	23°45'S		43°10'E
	IIOE 363G	1350	23°38'S		43°24'E
	IIOE 363J	1280	23°36'S		43°24'E
	IIOE 363K	1190	23°43'S		43°25'E
	IIOE 367C	3250	22°37'S		41°22'E
	IIOE 367G	3140	22°42'S		39°19'E
40	IIOE 407D	1360	17°32'S		43°05'E
	IIOE 409A	?	16°12'S		43°41'E
41	IIOE 413A	3530	12°32'S		45°50'E
42	IIOE 418B	3050	8°5'S		41°37'E
43	IIOE 418F	1550	4°14'S		40°59'E
44	MSN-20D	1390	9°23'S		109°16'E
45	RC9-148	2056	29°41.3'S		113°42.4'E
	RC9-150	2703	31°17'S		114°33.1'E
46	NZOI B303	2888	45°7.8'S		177°55'E
47	O-170L	2781	30°43.2'S		156°24.39'E
48	NZOI A293	2689	28°59.3'S		172°28'E
49	ALEX BANK 2	2560	11°5'S		175°10'E
50	CAP 6 HG	3363	4°15.5'S		171°55.5'E
51	RC11-158	3177	20°55'N		149°54.5'E
52	RC10-164	3766	31°43.5'N		157°30'E
	RC10-163	3550	32°43'N		157°30'E
53	ELT. 47-5056	613	50°13.67'S		74°36.27'E
54	ELT. 47-5057	613	49°43.53'S		71°02.16'E
55	ELT. 47-5064	1728	51°09.54'S		75°46.27'E
	ELT. 47-5061	1408	51°05.48'S		76°35.34'E
	ELT. 47-5068	2308	51°08.88'S		76°03.82'E
56	ELT. 47-5072	3584	51°33.40'S		78°56.19'E
57	DSDP II 11	3571	29°56.58'N		44°44.80'W
	(1, 4)			Plio-Pleistocene	
58	DSDP III 16	3527	30°20.15'S		15°42.79'W
	(2, 6)			U. Pliocene	
	DSDP III 15	3927	30°53.38'S		17°58.99'W
	(7, 3; 8, 3)			L. Miocene	
59	OZAWA F			Outcrop	Kaga Prov. Japan
	25510			U. Pliocene	
60	ALB. 3708	130		Off Ose Zaki, Honshu, Japan	
61	ALB. 5301	400	20°37'N		115°43'E
62	ALB. 5218	38	13°11'15"N		123°02'45"E
63	Briggs 1	75		Off N. Cape, N. Z.	
64	DSDP III 21	2102	28°35.10'N		30°35.85'W
	(4, 4)			U. Cretaceous	

\*See Figure 1.

TABLE 2.—*Distribution of Poseidonamicus species, new genus*

<i>Map Designation*</i>	<i>Station Number</i>	<i>Depth (meters)</i>	<i>Latitude</i>	<i>Location</i>	<i>Longitude</i>
1	DWBG 68	2820	48°27'S		114°18'W
	DWBG 70	2580	48°28'S		113°17'W
	DWBG 71	2790	46°35.5'S		113°34'W
2	DWHG 48	4240	42°00'S		102°00'W
	DWBG 77	3820	44°09'S		101°34.5'W
3	DWBG 76	3840	43°45'S		104°28'W
4	DWBG 73	3080	43°48'S		108°9'W
	DWBG 74	3220	43°43'S		107°36'W
	DWBG 75	3650	43°33'S		108°18'W
5	ELT. 21-10	3137	36°41'S		93°37'W
6	CHAL. 300	2475	33°42'S		78°18'W
7	DWBG 120	3060	27°56'S		106°55'W
	DWBG 121	3320	27°9'S		109°50'W
	DWHG 74	3030	28°29'S		106°30'W
8	ALB. 4693	2089	26°30'S		105°45'W
9	CAP 41 HG	3394	15°55.5'S		117°13.8'W
10	DWBG 137	2770	9°53'S		110°41'W
11	SDSE 58	4440	6°44'N		129°28'W
12	ALB. 4611	3292	10°32'N		88°25'W
13	V7-16	2635	25°20'N		77°36'W
	A167-43	2605	25°27'N		77°03'W
14	A156-1	1005	28°35.5'N		77°10'W
15	AII 120	5018-5023	34°42'N		66°34'W
16	A180-9	4060	39°37'N		45°57'W
17	A180-15	4610	39°16'N		36°42'W
18	R5-34	3750	42°23'N		21°58'W
19	KMI-36	4300	30°28'N		28°38'W
20	SP8-12	3252	32°37.4'N		36°46'W
21	V17-165	3924	32°45'N		41°54'W
22	V22-230	5048	32°39'N		52°11.8'W
23	V10-90	4030	23°02'N		47°03'W
24	V16-205	4045	15°24'N		43°24'W
25	V9-29	4675	3°47.5'N		34°37'W
		Lower Miocene			
26	V16-200	4095	1°58'N		37°04'W
27	ALB. 2763	1227	24°17'S		42°48.5'W
28	V9-11	4120	3°13.4'S		32°12.9'W
29	AII 155	3730-3783	0°3'S		27°48'W
	AII 156	3459	0°46'S		32°38.5'W
30	A180-76	3510	0°46'S		26°02'W
	A180-73	3750	0°10'N		23°00'W
31	V12-81	3671	0°18.6'N		18°25.8'W
32	V19-297	4120	2°37'N		12°00'W
33	V9-19	3730	11°23'S		14°15'W
34	V16-39	4510	24°43'S		4°45'W
35	RC8-91	2723	33°25'S		41°54'W
36	V12-53	3797	40°53.4'S		20°22.9'S
37	V12-60	3115	30°20.2'S		14°10.4'E
38	V12-54	4082	14°14.4'S		6°7'W
39	V16-66	2995	42°39'S		45°40'E
40	V19-222	2005	33°22'S		34°24'E
		Cretaceous-Miocene			

TABLE 2.—*Distribution of Poseidonamicus species, new genus—Continued*

<i>Map Designation*</i>	<i>Station Number</i>	<i>Depth (meters)</i>	<i>Latitude</i>	<i>Location</i>	<i>Longitude</i>
41	IIOE 360B	1360	27°39'S		33°23'E
	IIOE 361B	1829	26°34'S		35°59'E
	IIOE 361G	2750	25°50'S		37°21'E
	IIOE 369D	1720	24°04'S		36°16'E
	IIOE 369G	1205	24°12'S		36°02'E
	IIOE 374C	1335	27°9'S		34°9'E
42	IIOE 363B	2980	23°45'S		43°10'E
	IIOE 363E	1860	23°40'S		43°21'E
	IIOE 363K	1190	23°43'S		43°25'E
	IIOE 366A	2300	23°9'S		43°9'E
	IIOE 366C	2710	23°9'S		43°7'E
	43	IIOE 362D	3950	24°18'S	
IIOE 367C		3250	22°37'S		41°22'E
IIOE 367D		2200	22°15'S		40°21'E
IIOE 367G		3140	22°42'S		39°19'E
IIOE 368C		2995	23°0'S		38°31'E
IIOE 369A		2270	23°48'S		37°47'E
44	IIOE 409A	?	16°12'S		43°41'E
	IIOE 410A	3100	15°7'S		44°21'E
45	IIOE 416A	3850	8°45'S		43°39'E
46	DODO 117P	3398	18°21'S		62°4'E
47	O-121G	3994	5°39.1'N		82°13.4'E
48	RC9-147	2479	29°19.6'S		113°22.2'E
	RC9-148	2056	29°41.3'S		113°42.4'E
	RC9-150	2703	31°17'S		114°33.1'E
49	RC9-143	4396	41°21.8'S		114°08'E
50	V18-222	1904	38°9'S		140°37'E
51	O-170L	2781	30°43.2'S		156°24.39'E
52	NZOI D593	3020-3100	41°00'S		178°25'E
53	NZOI A293	2689	28°59.3'S		172°28'E
54	CAP 8 BG	2560	13°39'S		174°58'E
55	ALEX BANK 1	2560	11°5'S		175°10'E
56	RC10-161	3587	35°5'N		158°0'E
	RC10-163	3550	32°43'N		157°30'E
	RC10-164	3766	31°43.5'N		157°30'E
57	ELT 47-5062	1400	51°05.48'S		76°35.34'E
	ELT 47-5064	1728	51°09.54'S		75°46.27'E
	ELT 47-5068	2308	51°08.88'S		76°03.82'E
58	ELT 47-5072	3584	51°33.40'S		78°56.19'E
59	ELT 47-5110	2900	53°21.27'S		70°58.47'E
60	DSDP II 11	3571	29°56.58'N		44°44.80'W
	(1, 1)	Quaternary			
61	(1, 4)	Plio-Pleistocene			
	DSDP II 12c	4457	19°41.73'N		26°00.03'W
	(1, 3)	Quaternary			
62	(4, 2)	? Pliocene			
	DSDP III 14	4343	28°19.89'S		20°56.46'W
	(2, 3)	U. Oligocene			
	(8, 3)	L. Oligocene			
	DSDP III 15	3927	30°53.38'S		17°58.99'W
(1, 3)	Pleistocene				
(2, 1)	L. Pleistocene				
(2, 5)	U. Pliocene				
(3, 5)	L. Pliocene				
(7, 3; 8, 3)	L. Miocene				

TABLE 2.—*Distribution of Poseidonamicus species, new genus—Continued*

<i>Map Designation*</i>	<i>Station Number</i>	<i>Depth (meters)</i>	<i>Latitude</i>	<i>Location</i>	<i>Longitude</i>
	DSDP III 16	3527	30°20.15'S		15°42.79'W
	(1, 2)	Pleistocene			
	(2, 2)	L. Pleistocene			
	(2, 6; 3, 3)	U. Pliocene			
	(4, 3)	L. Pliocene			
	(5, 3; 7, 3; 10, 3; 11, 3)	U. Miocene			
63	DSDP III 17	4265	28°02.74'S		06°36.15'W
	(1, 2)	Pleistocene			
	(2, 3)	L. Pliocene			
	(3, 2)	L. Miocene			
64	DSDP III 21A	2113	28°35.10'S		30°35.85'W
	(1, 5)	L. Pliocene			
	?(3, 4)	U. Paleocene			

\*See Figure 2.

TABLE 3.—*Distribution of Agrenocythere species, new genus*

Map Designation*	Station Number	Location		Depth (meters)	Temp. (C°)	Core Level (cm)	Agrenocythere Species	Speci- mens	Age
		Latitude	Longitude						
1	ALB 3376	03°09'N	82°08'W	2080	2.6	Beam Trawl	<i>A. malpeloensis</i>	1	Recent
2	ALB 3375	02°34'N	82°29'W	2197	2.4	Beam Trawl	<i>A. malpeloensis</i>	3	Recent
3	ALB 2383	28°32'N	88°06'W	2160	4.3	Beam Trawl	<i>A. americana</i>	48	Recent
4	ALB 2352	22°35'N	84°23'W	833	7.2	Beam Trawl	<i>A. hazelae</i>	1	Recent
5	ALB 2140	17°36'N	76°46'W	1738	4.3	Beam Trawl	<i>A. hazelae</i>	11	Recent
6	ALB 2751	16°54'N	63°12'W	3250	—	Beam Trawl	<i>A. hazelae</i>	46	Recent
7	ALB 2754	11°40'N	58°33'W	1645	3.3	Beam Trawl	<i>A. hazelae</i>	2	Recent
8	GF 7871		Trinidad	outcrop	—	Lengua fm.	<i>A. hazelae</i>	1	L. Miocene
	KR 18192		Trinidad	outcrop	—	Lengua fm.	<i>A. hazelae</i>	1	L. Miocene
	DM 154		Trinidad	outcrop	—	Lengua fm.	<i>A. hazelae</i>	1	L. Miocene
	EL 1145b		Trinidad	outcrop	—	Cipero fm.	<i>A. hazelae</i>	1	M. Miocene
	RM 15715		Trinidad	outcrop	—	Cipero fm.	<i>A. hazelae</i>	1	M. Miocene
	Bo 202		Trinidad	outcrop	—	Cipero fm.	<i>A. hazelae</i>		Miocene
	Br 229		Trinidad	outcrop	—	Cipero fm.	<i>A. hazelae</i>		E. Miocene
	CH 4148		Trinidad	outcrop	—	Cipero fm.	<i>A. hazelae</i>		E. Miocene
	RHC 1042		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	RHC 1047		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	RHC 1049		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	RHC 1054		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	RHC 1065		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	Renz 75		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	1	L. Eocene
	Ky 7		Trinidad	outcrop	—	Hospital Hill	<i>A. antiquata</i>	3	L. Eocene
9	Rio Almendares		Cuba (Habana Prov.)	outcrop	—	van den Bold location	<i>A. antiquata</i>	1	L. Eocene
10	A 156-1	28°35.5'N	77°10'W	1005	—	200, 280	?	2	Pleistocene
11	H 2621C	39°49'N	71°21'W	1070	—	Barrel Dredge	<i>A. gosnoldi</i>	11	M. Eocene
12	Stet. 12-36	39°45'N	70°58'W	880	—	Core	<i>A. antiquata</i>	9	M. Eocene
13	DSDP III 19 (4; 6)	28°32'S	23°40.6'W	4677	—	Fram Ooze	<i>A. hazelae</i>	1	Rupelian
13a	DSDP III 22 (4; 4)	30°01'S	35°15'W	2134		<i>Globigerina ampliapertura zone</i>	<i>A. hazelae</i>	1	Chattian
14	DSDP III 14 (1a; 3)	28°20'S	20°57'W	4343	—	Endeavor Ooze	<i>A. hazelae</i>	2	Aquitanian
15	DSDP III 16 (6; 3)	30°53'S	17°59'W	3526	—	Blake Ooze	<i>A. hazelae</i>	1	Messinian
16	DSDP III 17a (1; 3)	28°03'S	06°36'W	4277	—	Albatross Ooze	<i>A. hazelae</i>	1	Pleistocene

TABLE 3.—*Distribution of Agrenocythere species, new genus—Continued*

Map Designation*	Station Number	Location		Depth (meters)	Temp. (C°)	Core Level (cm)	Agrenocythere Species	Speci- mens	Age
		Latitude	Longitude						
	DSDP III 17a (4; 3)	28°03'S	06°36'W	4277	—	Fram Ooze	<i>A. haxelae</i> (?)	1	Bormidian
17	DSDP XII 117 (6)	57°19.5'S	15°23'W	1048	—	—	<i>Oertliella atlantica</i>	18	Oligocene
	DSDP XII 117a (7; 8)	57°19.5'S	15°23'W	1048	—	—	<i>Oertliella atlantica</i> **	19	Paleocene
18	C22 VIII 68 (7)	Cote de Basque, Biarritz, France		outcrop	—	—	<i>Oertliella atlantica</i> **	5	Bartonian
19	Ascoli (1969) Ascoli (Ancona loc.)	Possagno section, Treviso Prov., Italy		outcrop	—	—	<i>A. antiquata</i>	5	E. Eocene
20	ARL 4513	Near Ancona Italy		outcrop	—	—	<i>A. antiquata</i> (?)	3	E. Miocene
		Near San Ruffilo, Bologna, Italy		outcrop	—	—	<i>A. pliocenica</i>	164	Pliocene
21	ARL 4468	North of Licata, Sicily		outcrop	—	Trubi fm.	<i>A. pliocenica</i>	65	Pliocene
	ARL 4473	Near Agrigento, Sicily; Greek Temple Loc.		outcrop	—	Trubi fm.	<i>Cythereis ornatissima</i>	84	Conacian
	Ascoli (3)	Crotona, Calabria Le Castella Section		outcrop	—	Trubi fm.	<i>A. pliocenica</i>	5	Late Pliocene
22	DSDP XIII 132 (11)	40°15.70'N	11°26.47'E	2813	—	Trubi fm.	<i>A. pliocenica</i>	4	Pliocene
	DSDP XIII 132 (18)	40°15.70'N	11°26.47'E	2813	—	Trubi fm.	<i>A. pliocenica</i>	2	Pliocene
23	Pokorny Kostice Loc.	Near Louny, Czechoslovakia		outcrop	—	—	<i>Oertliella reticulata</i>	—	Turonian
	Pokorny Kostice Loc.	Near Louny, Czechoslovakia		outcrop	—	—	<i>Cythereis kosticensis</i>	—	Turonian
24	Oertli Sample	Near Martiques (Bouches du Rhone), France		outcrop	—	Lima ovata zone	<i>Oertliella horridula</i>	—	Santonian
25	A2A l'Octroi	Commune Blaye, France		outcrop	—	Calcaire de Blaye	" <i>Oertliella</i> " <i>aculeata</i>	—	L. Eocene
26	DODO 117P	18°21'S	62°04'E	3398	—	108–110	<i>A. spinosa</i>	1	Recent
27	V19–222	33°22'S	34°24'E	—	—	505	<i>A. radula</i>	2	Pliocene
28	MSN 20D	09°23'S	109°16'E	1390	—	—	<i>A. radula</i>	1	Recent
29	Chal 191A	05°26'S	133°19'E	1061	4.9°C	Dredge	<i>A. radula</i>	1	Recent
30	Elt 39–10 (32)	48°26.4'S	148°17.2'E	960	—	Dredge	<i>A. cadoti</i>	22	Recent

\*See Figure 3.

\*\*Eye tubercules.

TABLE 4.—*Distribution of Agrenocythere species in Mozambique Channel*

Map Designa- tion*	Station Number	Location		Depth (meters)	Temp. (C°)	Core Level (cm)	Agrenocythere Species	Speci- mens	Age
		Latitude	Longitude						
1	IIOE 360B	27°39'S	33°23'E	1360	—	Grab	<i>A. spinosa</i>	11	Recent
2	IIOE 374D	27°09'S	34°09'E	1335	—	Grab	<i>A. spinosa</i>	28	Recent
3	IIOE 361B	26°34'S	35°59'E	1829	2.5	Grab	<i>A. radula</i>	2	Recent
4	IIOE 370B	24°25'S	35°47'E	910	5.6	Grab	<i>A. spinosa</i>	1	Recent
5	IIOE 368C	23°00'S	38°31'E	2995	1.6	Grab	<i>A. radula</i>	1	Recent
6	IIOE 367D	22°15'S	40°21'E	2200	2.5	Grab	<i>A. radula</i>	1	Recent
7	IIOE 363B	23°45'S	43°10'E	2980	2.1	Grab	<i>A. radula</i>	5	Recent
8	IIOE 363D	23°45'S	43°11'E	1605	3.8	Trawl	<i>A. radula</i>	24	Recent
	IIOE 363G	23°38'S	43°24'E	1350	4.2	Grab	<i>A. radula</i>	3	Recent
	IIOE 363G	23°38'S	43°24'E	1350	4.2	Grab	<i>A. spinosa</i>	10	Recent
	IIOE 363J	23°36'S	43°24'E	1280	4.7	Trawl	<i>A. spinosa</i>	16	Recent
	IIOE 363J	23°36'S	43°24'E	1280	4.7	Trawl	<i>A. radula</i>	1	Recent
	IIOE 363K	23°43'S	43°25'E	1190	4.9	Trawl	<i>A. radula</i>	1	Recent
	IIOE 363K	23°43'S	43°25'E	1190	4.9	Trawl	<i>A. spinosa</i>	9	Recent
9	IIOE 365B	23°19'S	43°33'E	420	12.0	Grab	<i>A. spinosa</i>	1	Recent
	IIOE 365D	23°20'S	43°32'E	475–695	—	Trawl	<i>A. spinosa</i>	18	Recent
10	IIOE 399A	22°33'S	36°10'E	925	5.5	Trawl	<i>A. spinosa</i>	4	Recent
11	IIOE 400A	21°12'S	36°24'E	1530	3.5	Trawl	<i>A. spinosa</i>	119	Recent
	IIOE 400A	21°12'S	36°24'E	1530	3.5	Trawl	<i>A. radula</i>	6	Recent
12	IIOE 407D	17°32'S	43°05'E	1360	4.5	Trawl	<i>A. spinosa</i>	142	Recent
13	IIOE 409A	16°12'S	43°41'E	400	—	Dredge	<i>A. radula</i>	37	Recent
14	IIOE 410A	15°07'S	44°21'E	3100	2.2	Trawl	<i>A. radula</i>	17	Recent
15	IIOE 413A	12°32'S	45°50'E	3530	1.5	Trawl	<i>A. spinosa</i>	5	Recent
16	IIOE 416A	08°45'S	43°39'E	3850	1.3	Trawl	<i>A. radula</i>	2	Recent
17	IIOE 418A	05°11'S	41°38'E	3050	—	Trawl	<i>A. radula</i>	4	Recent

\*See Figure 30.



## **PLATES**

## PLATE 1

1–4. *Cletocythereis rastromarginata* (Brady), the lectoholotype (designated herein, British Museum specimen BM 80.38.105). The left valve (of a whole specimen, separated for study) from Brady's *Challenger* locality "off reefs at Honolulu, 40 fathoms." Photographs (vegetable coloring stain) taken in incident and transmitted light showing (1) reticular pattern with castrum, (2) exterior morphology of the carapace, (3) holamphidont hinge, and (4) V-shaped frontal scar (with posterodorsal part slightly severed). Designated as the type-species of *Cletocythereis* by Swain in 1963 (approximately x80 and x225).

5. *Agrenocythere? semivera?* (Hornibrook, 1952), a left valve, female (USNM 174678) from the upper Eocene of South Island, New Zealand (Totara Limestone; locality of W. M. Briggs, Jr., SI-25, N.2. Sheet Fossil No. S136/f 1199). The identification of this specimen is not certain. Hornibrook's drawing (1952, pl. 8: fig. 103) is stylized (x55).

6. *Limburgina quadraxea* (Hornibrook, 1952), a left male valve (USNM 174679), from the upper Paleocene Tioriori Limestone (Mangaorapan), Chattam Islands, New Zealand (New Zealand Geol. Survey loc. F5080; Courtesy W. M. Briggs, Jr.). This species contains several of the characteristics common to the ancestral group of several of the genera discussed in the text (x70).

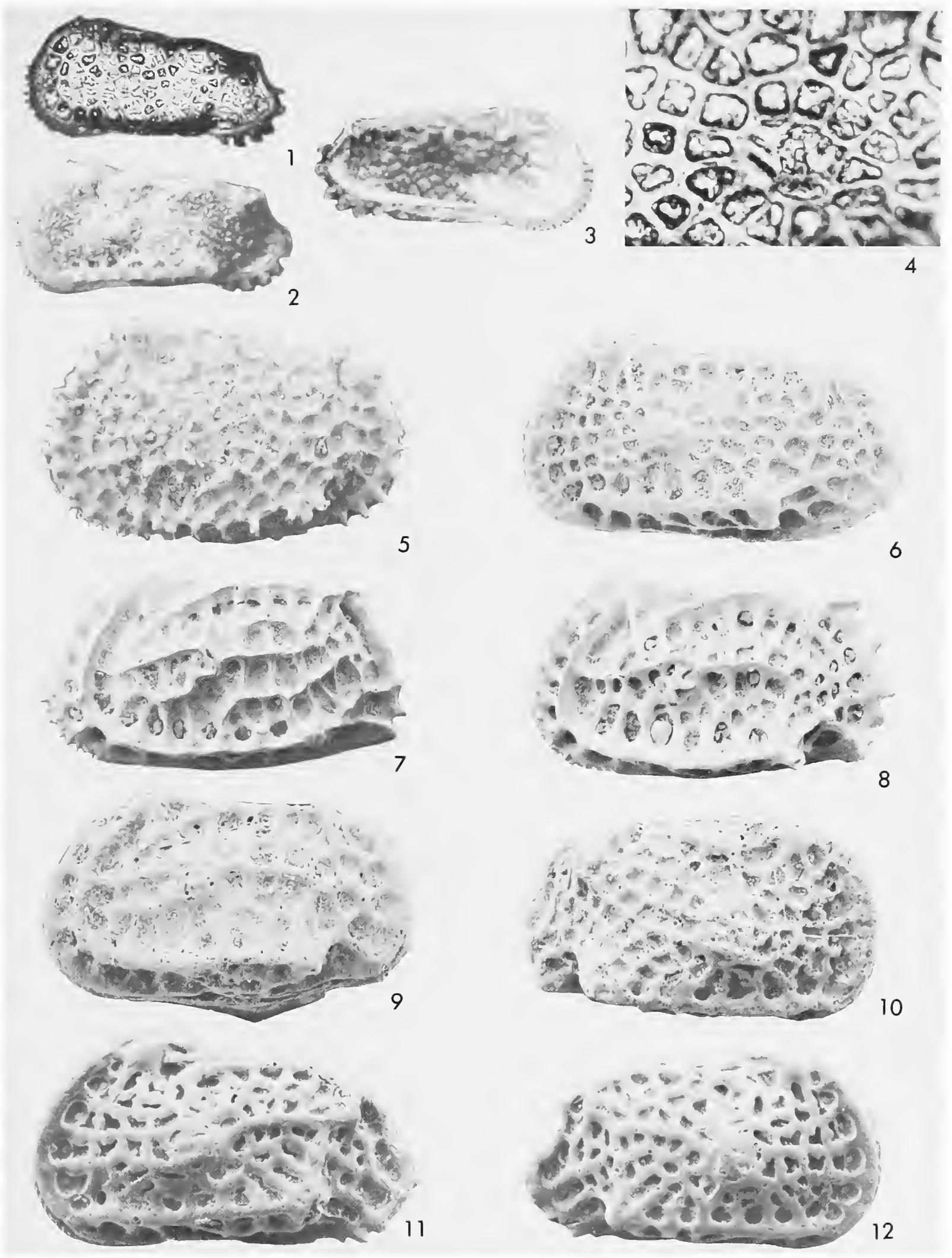
7. *Bradleya* species, left valve (USNM 174680) of a yet unnamed species of *Bradleya* from the Recent of New Zealand (NZOI E258, lat. 34°39'S; long. 172°10'E, 380 meters depth; courtesy W. M. Briggs, Jr.) showing strong box-work mural structure in the posterior, a diminished bridge (see p. 35) and the remainder of a median ridge (x50).

8. *Bradleya (Quasibradleya)* species, left valve (USNM 174681) of a yet unnamed species from the Recent of New Zealand (locality same as *Bradleya* species of Plate 1: figure 7). This Recent form is very similar to and descendant from *B. (Q.) dictyonites* of Oligocene age. They differ primarily in the reticular pattern of the posterior (x50).

9. *Bradleya* species, a whole female specimen (USNM 174682) from the upper Paleocene, Tioriori Limestone, from Chattam Islands, New Zealand (locality same as for specimen in Plate 1: figure 6) transitional in form between *Bradleya* and *Limburgina* (x70).

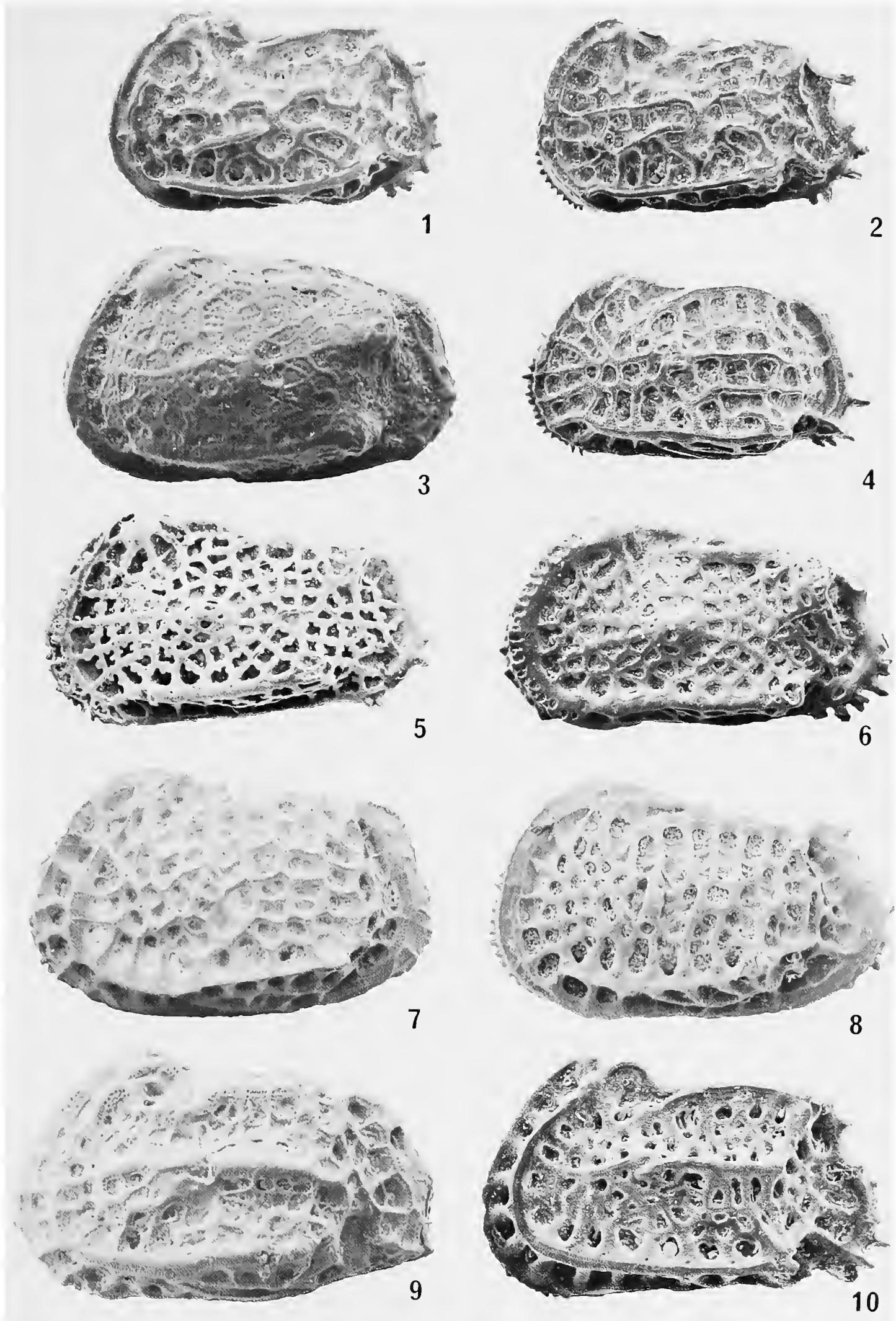
10. *Hermanites reticulata* (Puri, 1954); one of the two right valves repositied by Puri as paratypes (USNM P3286) of the type-species of *Hermanites*. From the Miocene, Alum Bluff stage, Chipola formation; Washington Co., Florida (x85).

11–12. *Hermanites* cf. *H. fungosa* Butler, 1963, (1) left and (2) right valves from the Oligocene (USNM 174683–4), Chickasawhcy formation, Taylor Mill Creek (Hazel locality), just below the *Chione* Limestone. This species is the closest, well-preserved specimen available to the type illustrated as Plate 1: figure 10 and is probably immediately antecedant (x85).



## PLATE 2

1. *Jugosocythereis pannosa* (Brady, 1869), left valve (USNM 174686) from the south shelf (Recent) of Puerto Rico (sample PA-2) (x75).
2. *Jugosocythereis vicksburgensis* (Howe and Law, 1936), left valve (USNM 174687) from the Byram Marl (Oligocene), a road cut east of Engineers Warf, Vicksburg, Mississippi (x70).
3. *Thaerocythere crenulata* (Sars, 1865), left valve (USNM 174688) from the Atlantic shelf (Recent) off of Maine, United States (Hazel, 1970, Sample 90, lat. 42°41'N and long. 67°22'W; 203 meters depth) (x80). The type-species of the type-genus.
4. *Bradleya* species, left valve (USNM 174689) of an undescribed species from about 800 meters off Brazil (ALB 2756; lat. 3°22'S and long. 37°49'W) (x70).
5. *Cletocythereis haidingerii* (Reuss, 1846), left valve (USNM 174690) from the "Amphistegina" Marl (Tortonian-Miocene) of Nussdorf in the Vienna Basin (Reuss, 1846, locality, sample courtesy of P. A. Sandberg) (x70).
6. *Cletocythereis* species, left valve (USNM 174693) from Wynyard Beach (Recent) of Northern Tasmania, more massive and shorter than the type-species (x85).
7. *Bradleya normani* (Brady, 1865), left valve (USNM 174694) from near Kerguelen Island (Recent; Eltanin station 47-5064, lat. 51°09.54'S and long. 75°46.54'E; depth 1728 meters), just north and west of the station (*Challenger* 150) from which Brady (1880) identified this species (x70).
8. *Poseidonamicus major?*, new species, left valve (USNM 174695) of a coarse variant of this species (possibly female) of Miocene age (Messinian) from the South Atlantic (DSDP III 16, core 8, section 3) (x65).
9. *Bradleya? telisaensis* (Le Roy, 1939), a paratype from the "Miocene" of Sumatra (Loc. HO-1512; Tapoeng Kiri area near Aliatan, Telisa; USNM 56147b) (x100).
10. *Bradleya (Quasibradleya)* species, a left valve (USNM 174696) from the Philippine Islands (Recent; ALB 5218, lat. 13°11'15"N and long. 123°02'45"E; depth 20 fathoms) (x70).



**PLATE 3**

(Page 118)

Reticular silhouettes of eight forms including *Agrenocythere*, new genus, and two other genera with positions of pore conuli (dots) indicated. [All illustrations reduced approximately to common size.] This series (and that of Plates 5 and 6) shows the degrees of similarity of major features among the forms listed below and basic changes in allometry.

1. *Argenocythere gosnoldia*, new species, middle Eocene of eastern North America.
2. *Cythereis ornatissima*, Reuss, 1846, Coniacian of Sicily.
- 3-4. *A. pliocenica* (Seguenza, 1880), (3) female and (4) male, San Raffilo, Italy, Pliocene.
- 5-6. *Oertliella reticulata* (Kafka, 1886), (5) female and (6) male, Turonian, Bohemian, Czechoslovakia.
7. *A. spinosa*, new species, Recent, Mozambique Channel.
8. *A. radula* (Brady, 1880), Recent, Mozambique Channel.

**PLATE 4**

(Page 119)

Reticular silhouettes of eight variations of *Agrenocythere*, new genus, with positions of pore conuli (dots) indicated. [All illustrations reduced approximately to common size.] This series (and that of Plates 3 and 4) shows the degrees of similarity of major features among the forms listed below and the basic changes in allometry. See page 4 for discussion of method.

- 1-4. *Agrenocythere hazelae* (van den Bold, 1946), (1) Recent of eastern Pacific (right valve, reversed), (2) Miocene of South Atlantic, (3) Miocene of Trinidad, and (4) Recent of Caribbean.
- 5-6. *Agrenocythere antiquata*, new species, Eocene; (5) Possagno, Italy (male); and (6) Eocene of Trinidad (female).
7. *Agrenocythere americana*, new species, Recent, Gulf of Mexico.
8. *Agrenocythere pliocenica* (Seguenza, 1880), Pliocene, Sicily.

**PLATE 5**

(Page 120)

Reticular silhouettes of eight forms of *Agrenocythere*, new genus, and two other genera with positions of pore conuli (dots; Plate 3), fossal pattern and constellar framework (Plate 5) indicated. [All illustrations reduced approximately to common size.] This series (and that of Plates 5 and 6) shows the degrees of similarity of major features among the forms listed below and basic changes in allometry.

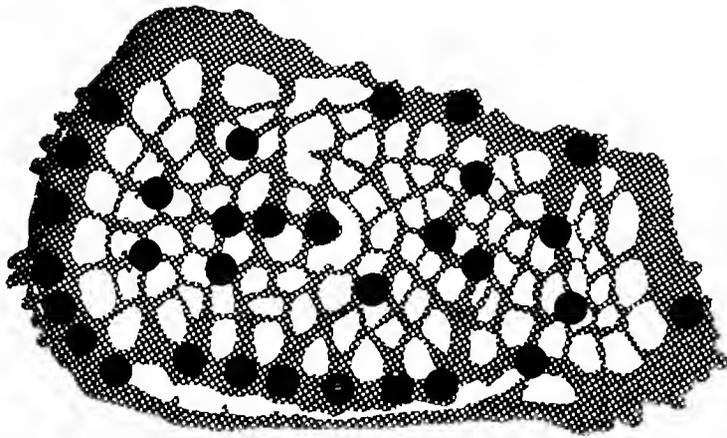
1. *Agrenocythere gosnoldia*, new species, middle Eocene of eastern North America.
2. *Cythereis ornatissima*, Reuss, 1846, Coniacian of Sicily.
- 3-4. *A. pliocenica* (Seguenza, 1880), (3) female and (4) male, San Raffilo, Italy, Pliocene.
- 5-6. *Oertliella reticulata* (Kafka, 1886), female and male, Turonian, Bohemian, Czechoslovakia.
7. *A. spinosa*, new species, Recent, Mozambique Channel.
8. *A. radula* (Brady, 1880), Recent, Mozambique Channel.

**PLATE 6**

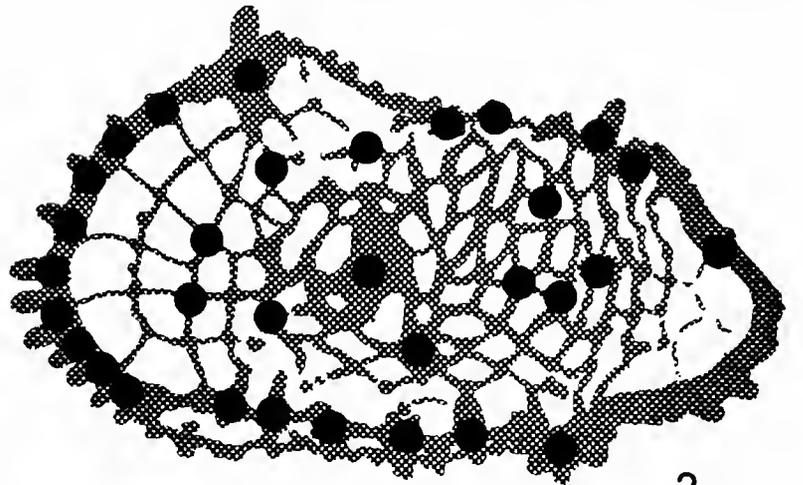
(Page 121)

Reticular silhouettes of eight variations of *Agrenocythere*, new genus, with positions of pore conuli (dots; Plate 4) fossal pattern and constellar framework (Plate 6) indicated. [All illustrations reduced approximately to common size.] This series (and that of Plates 3 and 4) shows the degrees of similarity of major features among the forms listed below and the basic changes in allometry. See page 4 for discussion of method.

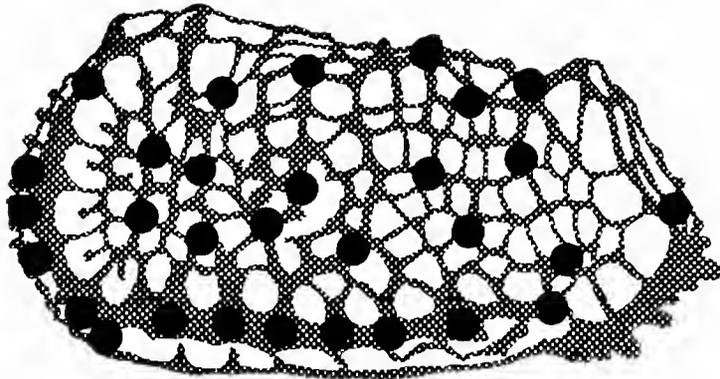
- 1-4. *Agrenocythere hazelae* (van den Bold, 1946), (1) Recent of eastern Pacific (right valve, reversed), (2) Miocene of South Atlantic, (3) Miocene of Trinidad, and (4) Recent of Caribbean.
- 5-6. *Agrenocythere antiquata*, new species, Eocene; Possagno, Italy (male); and Eocene of Trinidad (female).
7. *Agrenocythere americana*, new species, Recent, Gulf of Mexico.
8. *Agrenocythere pliocenica* (Seguenza, 1880), Pliocene, Sicily.



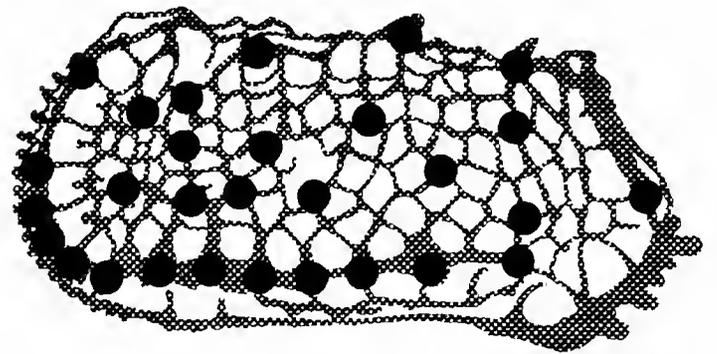
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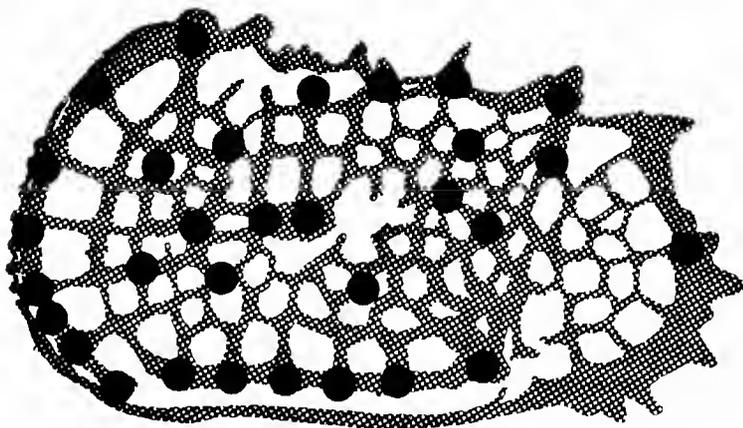
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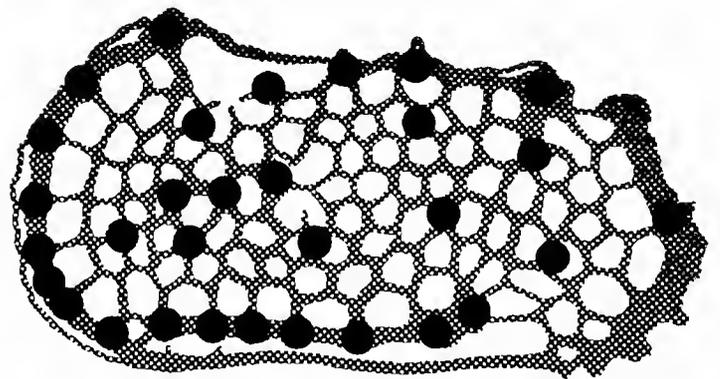
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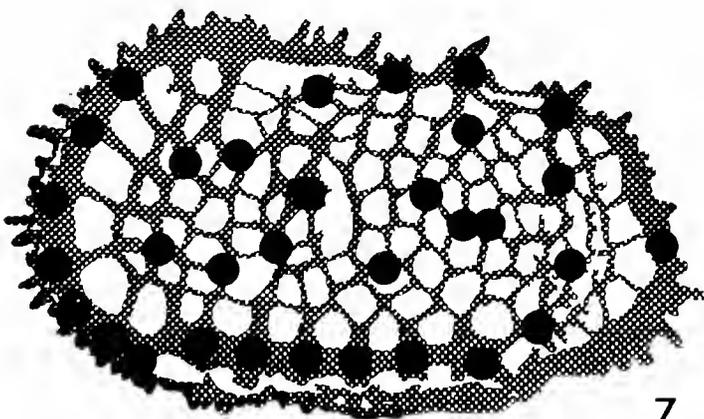
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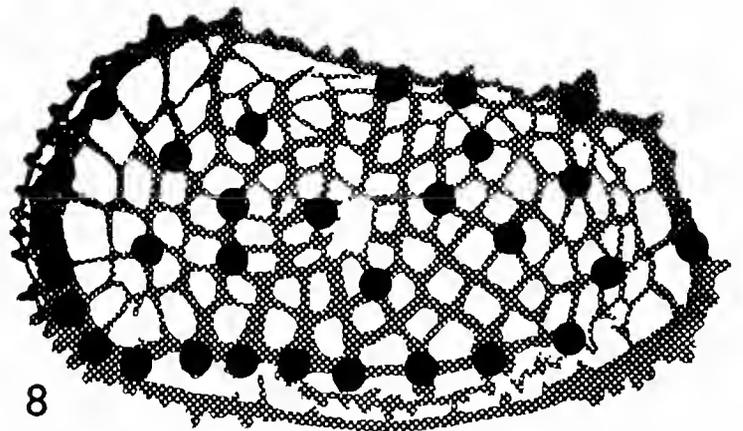
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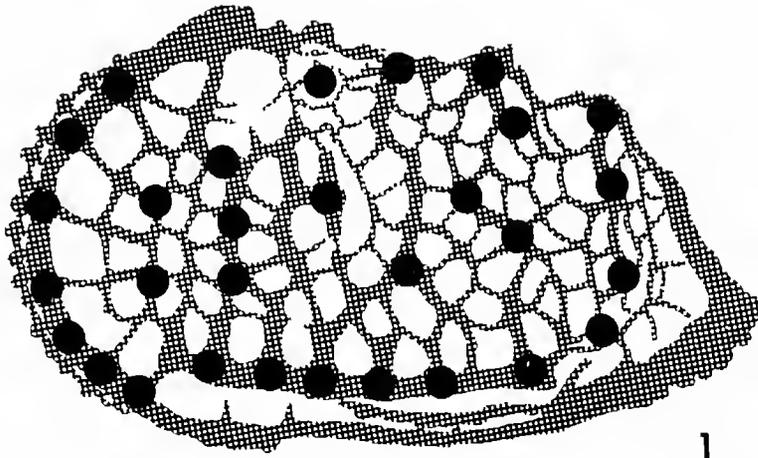
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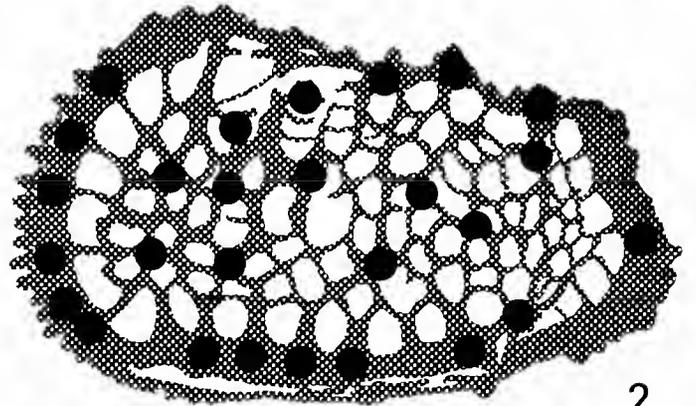
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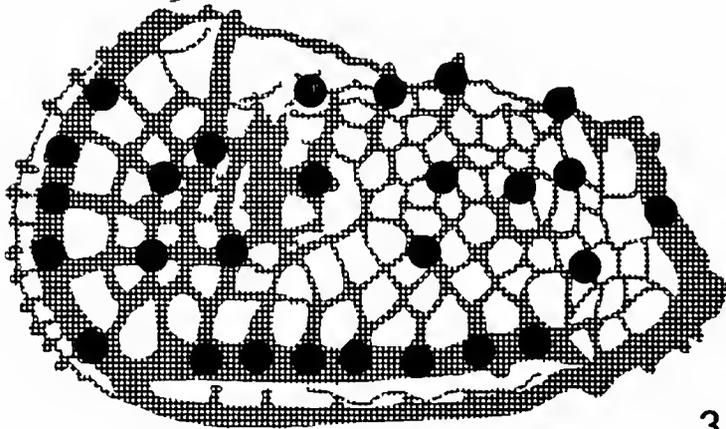
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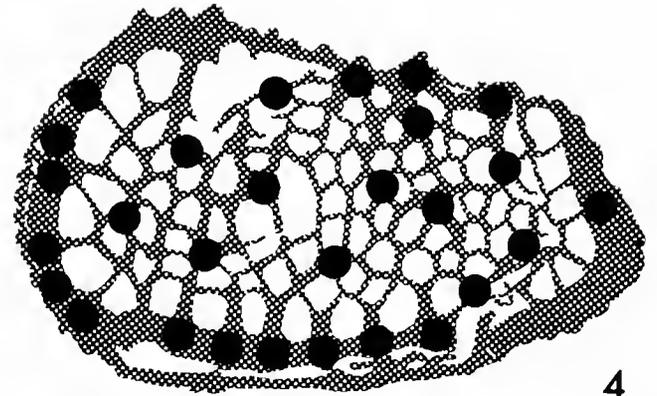
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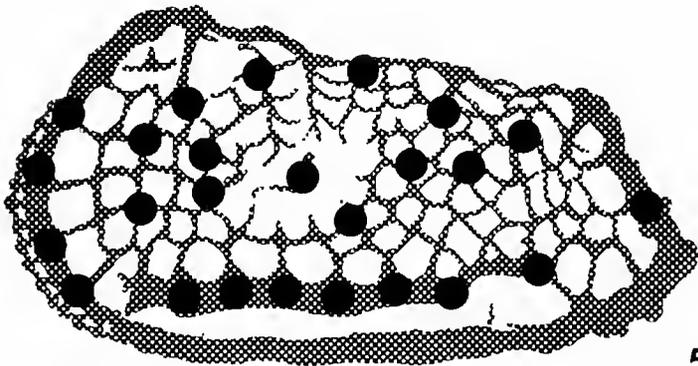
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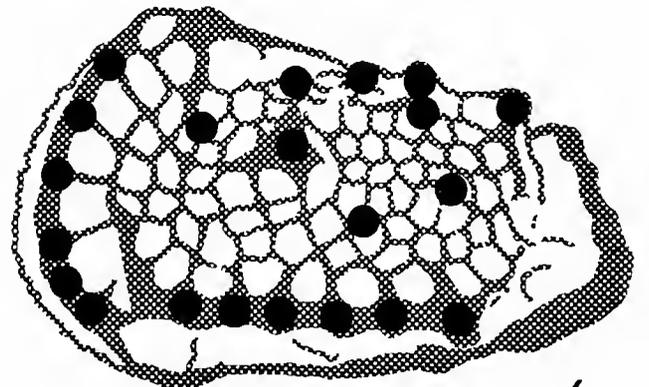
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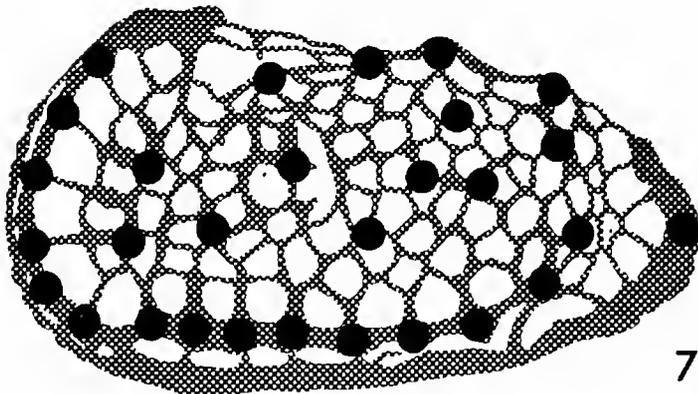
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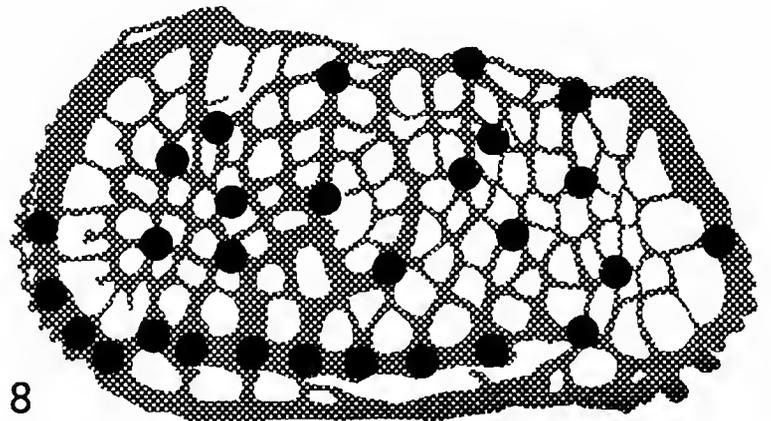
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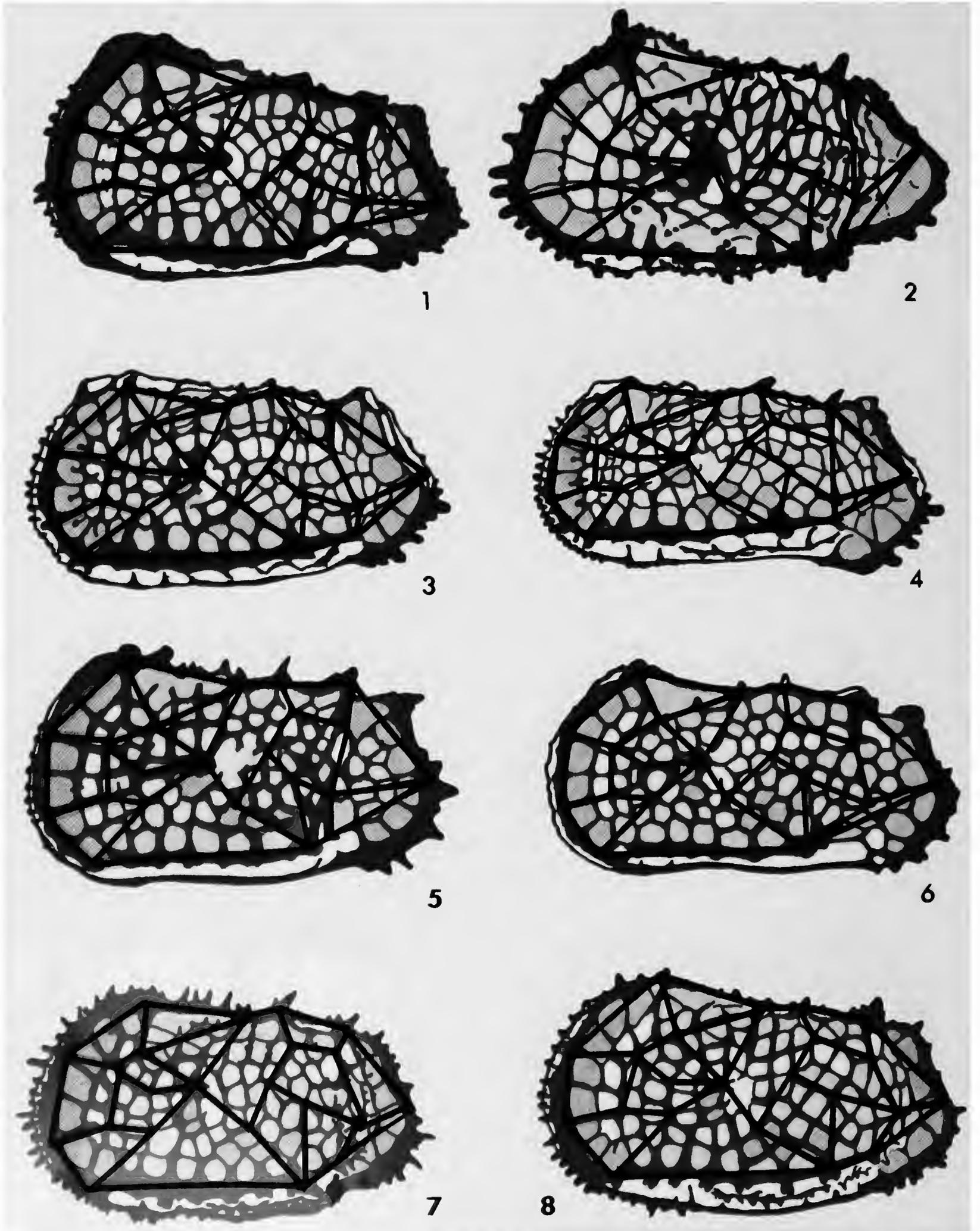
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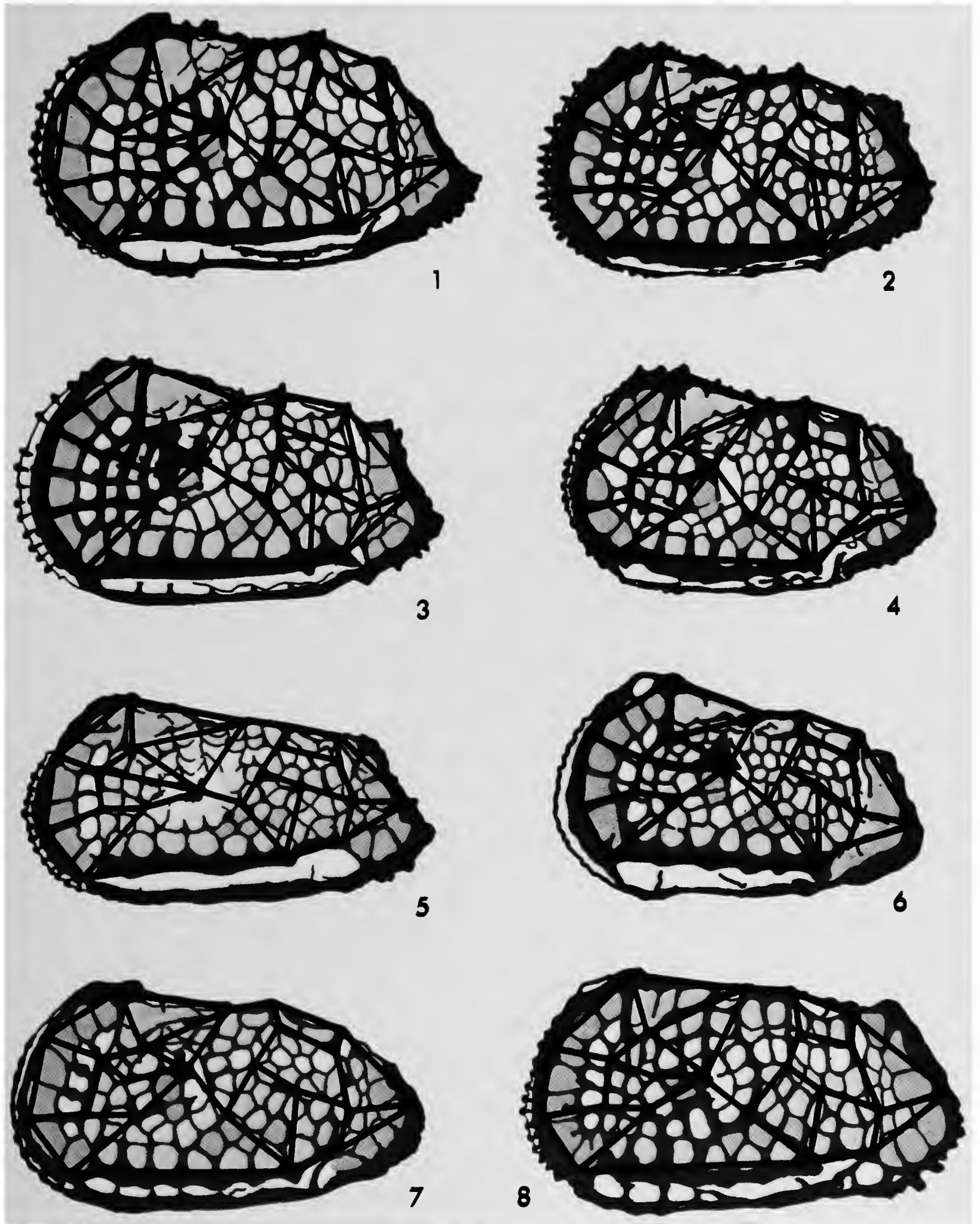


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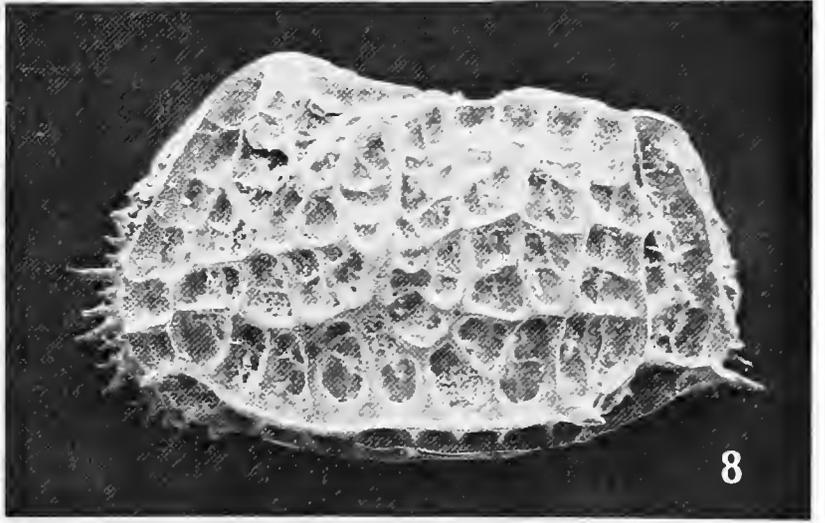
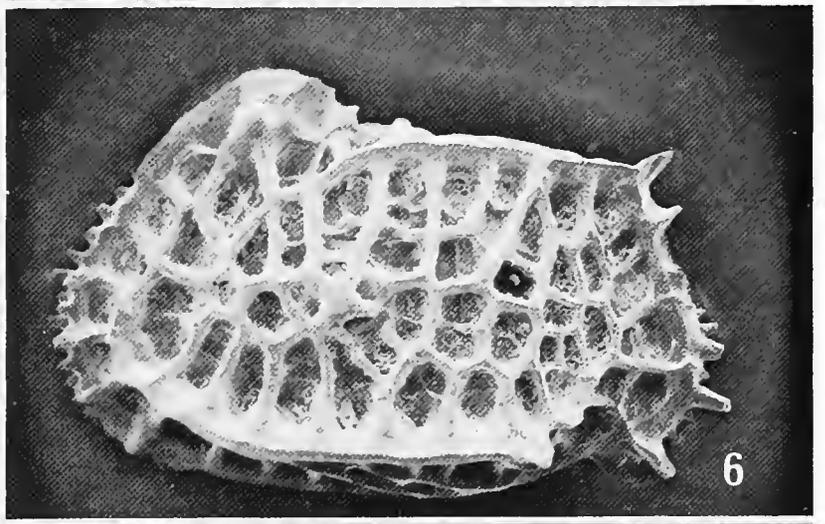
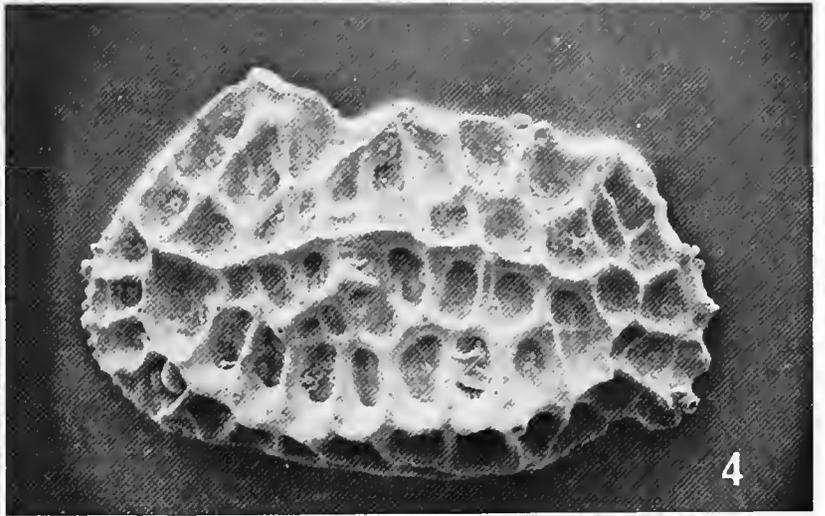
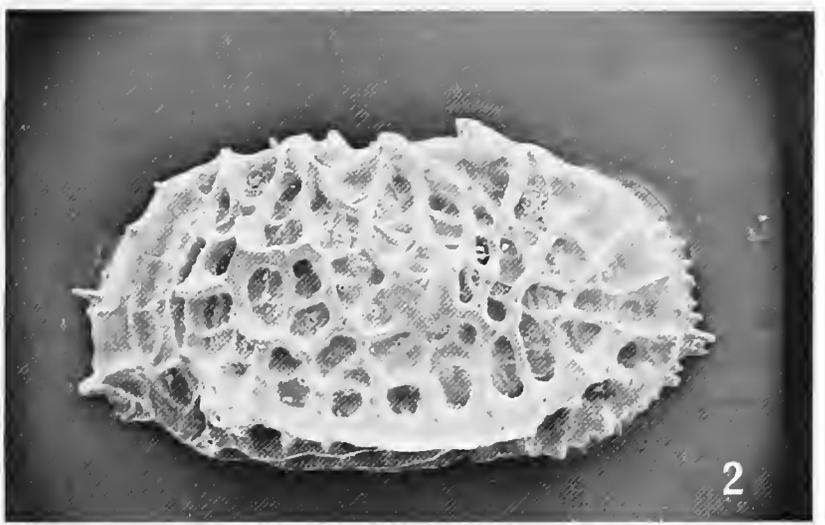
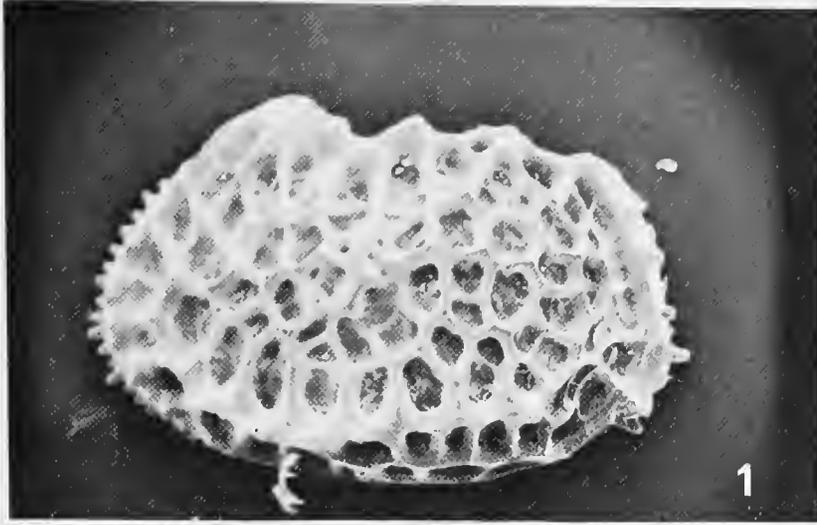
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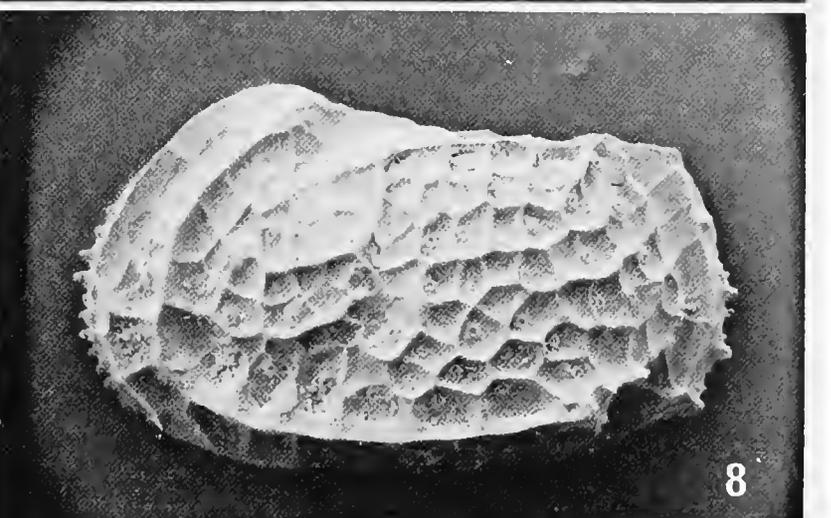
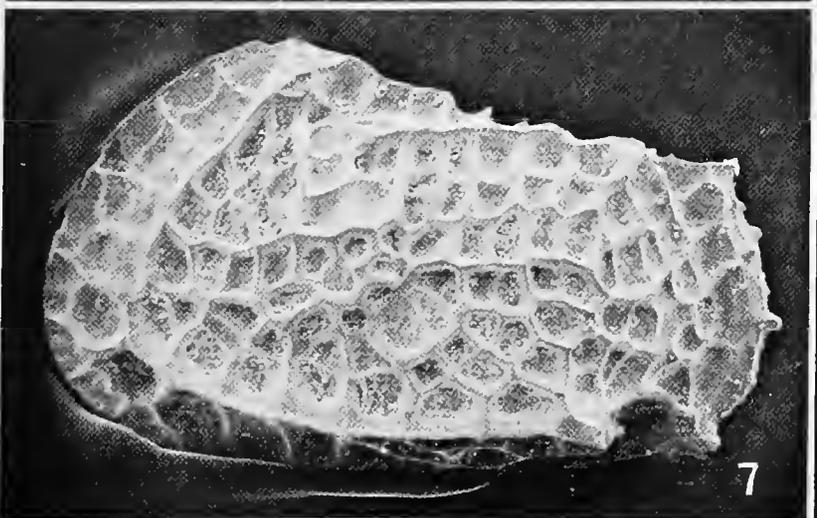
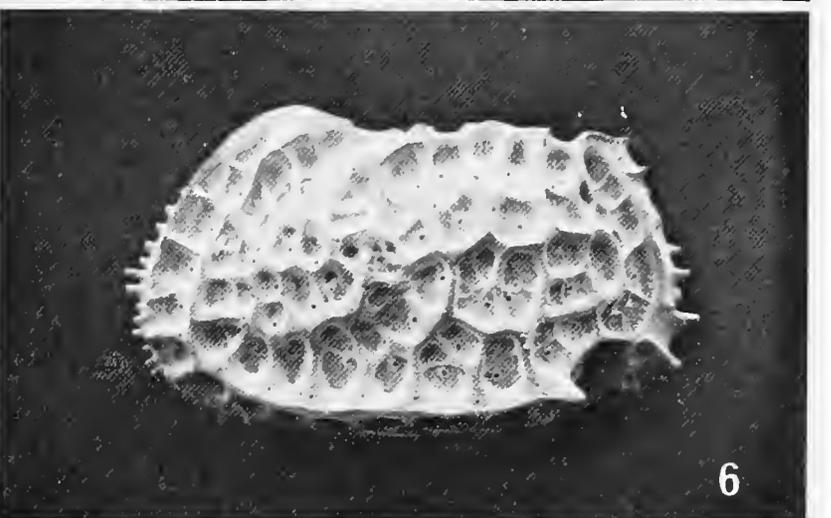
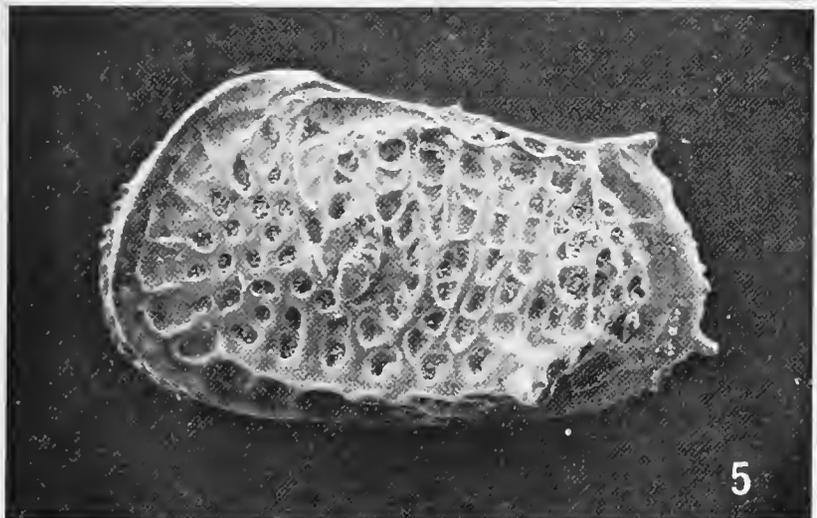
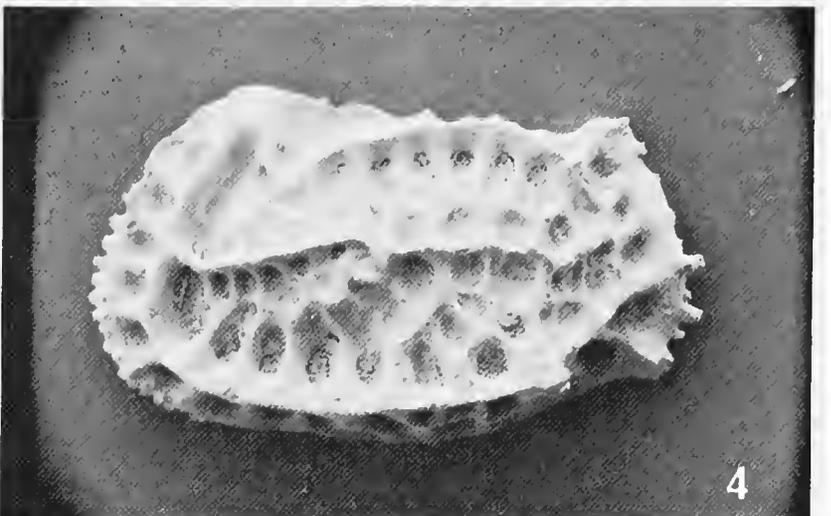
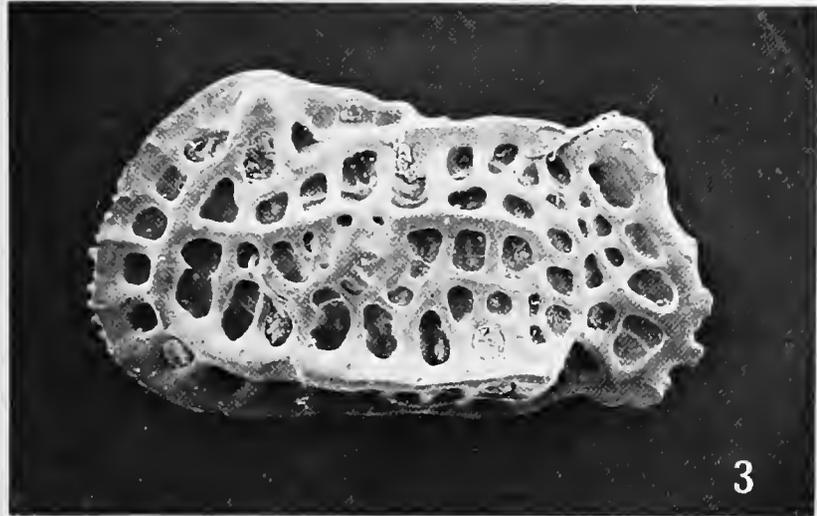
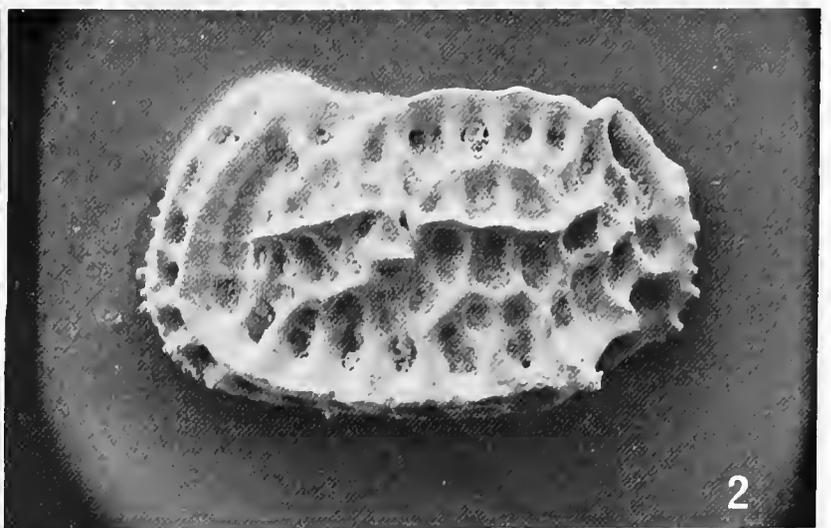
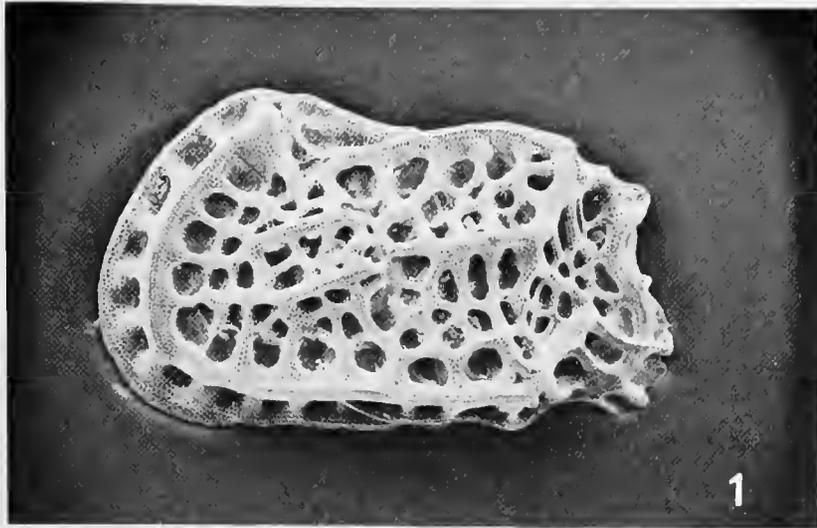
## PLATE 7

1. *Bradleya albatrossia*, new species; left valve adult; note boldness of muri, yet no median ridge or anterior bridge; Recent, China Sea off Hong Kong; *Albatross* station 5301, lat. 20°37'N, long. 115°43'E, 208 fathoms; holotype USNM 174318 (x70).
2. *Bradleya albatrossia*, new species; right valve of the same species as Plate 7: figure 1, but with slightly bolder muri and still no longitudinal ridges except for the ventrolateral carinae; Recent, Sample Alex No. 2, Alexa-Penguin Bank, lat. 11°5'S, long. 175°10'E, North Fiji Basin, 2560 meters; paratype USNM 174319 (x70).
3. *Bradleya japonica*, new species; left valve adult with nude anterior marginal region, broad ventrolateral carina, and irregular murate development; Recent, *Albatross* station 3708 off Honshu Island, Japan, 60–70 fathoms; holotype USNM 174320 (x50).
4. *Bradleya andamanae*, new species; left valve adult showing a very coarse reticulum forming a median ridge traversing the entire length of the side, a posterior ventral segment of the bridge, and an eye tubercle; Recent, *Oceanographer* station OSS-01, 260G in the Andaman Sea, lat. 06°39.4'N, long. 98°52.0'E, 78 meters; holotype USNM 174322 (x85).
5. *Bradleya nuda*, new species; left valve of adult showing absence of muri except for faint traces of parts of the reticular pattern similar to that of the specimen in Plate 7: figure 3; upper Pliocene, Okuwa, Kaga Province, Japan; Ozawa locality F25510; holotype USNM 174323 (x50).
6. *Bradleya mackenziei*, new species; left valve adult, a small form with prominent and sharp ocular, dorsal and ventrolateral carinae and remnants of the bridge, fossae quite angular to "ragged", eye tubercle; Recent from Australia, Bass Strait, McKenzie sample M290; holotype USNM 174324 (x65).
7. *Bradleya paranuda*, new species; left valve adult showing produced anterior, smooth surface except for the remaining traces of reticular pattern extending from the dorsal and ventral carinae and two near the posterior; Recent, *Albatross* station ALB 5250, Gulf of Davao, Philippine Islands, lat. 7°05'07"N, long. 125°39'45"E; 23 fathoms; holotype USN M174325 (x70).
8. *Bradleya normani* (Brady, 1865) left valve of adult showing a geographic variation of reticulum development (secondary reticulation) and with a slight indication of the bridge structure and a poorly developed ocular ridge; Recent, Straits of Magellan, R-V *Hero* station 57 (Cruise 69-5), 117 fathoms; USNM 174326 (x60).



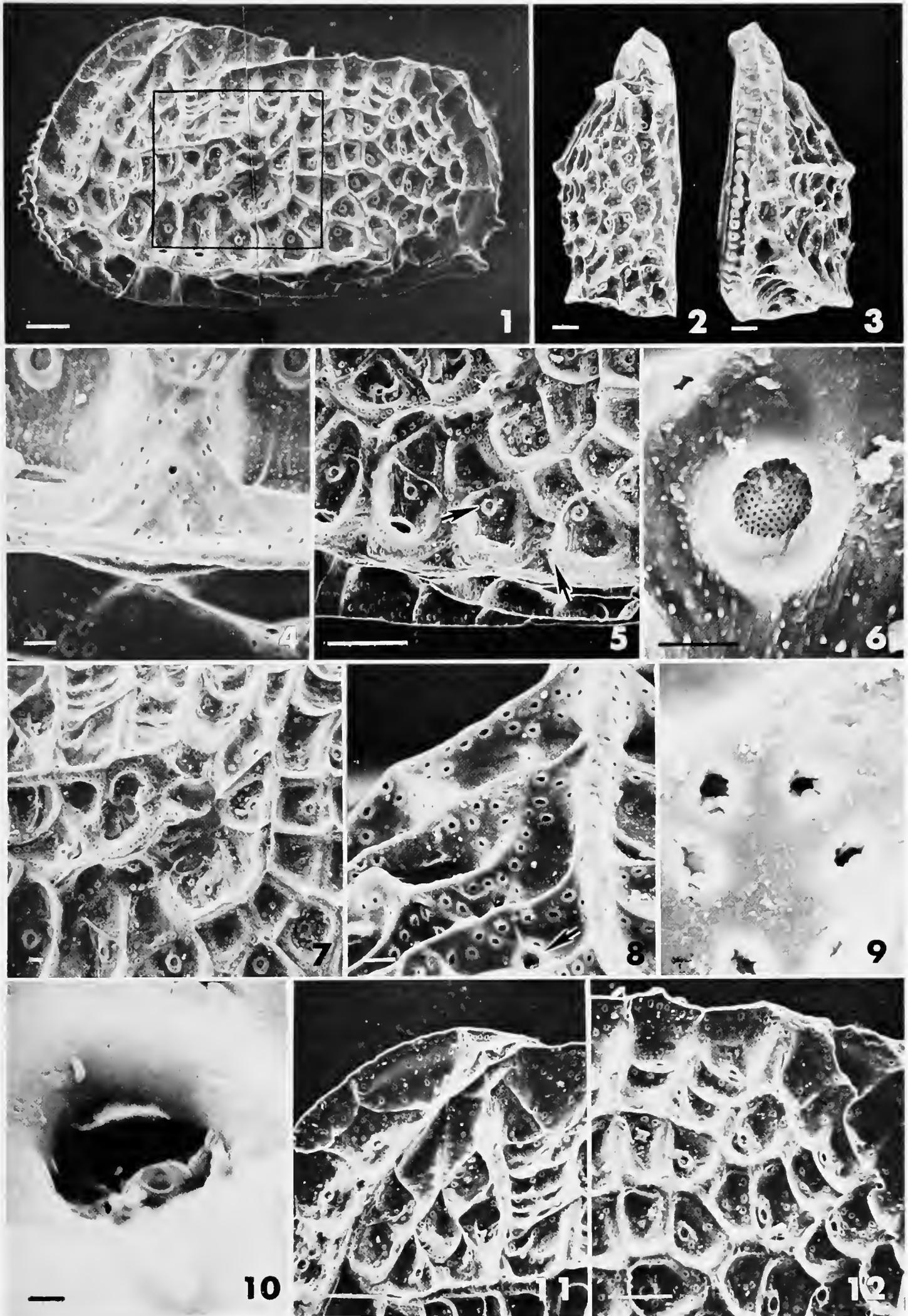
## PLATE 8

1. *Jugosocythereis* species; left valve of adult showing a well-developed bridge developed from the muscle-scar node region forward, the posterodorsal loop formed by dominant muri, and the similarity of the reticular pattern with those of *Bradleya*; Recent, Indian Ocean, Grand Comoro Island, 40 feet; USNM 174333 (x65).
2. *Bradleya* (*Quasibradleya*) *prodictyonites*, new species, left valve of adult showing variation in the strong ocular, dorsal and ventrolateral carinae, a disjunct bridge and median ridge continuing toward posterodorsum to form loop; lower Oligocene, New Zealand, Hornibrook sample F5052; holotype USNM 174327 (x55).
3. *Bradleya* (*Quasibradleya*) *paradictyonites*, new species; left valve adult showing massive muri, eye tubercle, "eared" posterodorsum and median ridge with diminished ventral portion of the bridge, Oligo-Miocene Fossil Bluff locality near Wynyard Beach, northern Tasmania; holotype USNM 174328 (x65).
4. *Bradleya* (*Quasibradleya*) *dictyonites*, new species (for *B. dictyon* of Hornibrook); left valve adult with strong ocular-ventrolateral and dorsal carinae, "eared" posterodorsum, eye tubercle, disjunct median ridge and remnants of lower portion of bridge; upper Oligocene (Awa-moah), New Zealand, Old Rifle Butts section, Hornibrook locality F6487; USNM 174328 (x55).
5. *Poseidonamicus major*, new species; an adult left valve with coarse vertical muri and enlarged bullate muscle-scar node; lower Miocene, South Atlantic, DSDP III, Hole 15, core 8, section 3 (see Table 2), holotype USNM 174329 (x65).
6. *Bradleya normani* (Brady, 1865); a small adult left valve showing increased mass in the muri and decreased secondary reticulation (see Figure 4 and Plate 7: figure 8); Recent, Galapagos Islands, *Albatross* station, ALB 2817, 271 fathoms; USNM 174330 (x40).
- 7-8. *Bradleya dictyon* (Brady, 1880); two variations in form of this cosmopolitan species (7) USNM 174331 (x65) from lower Miocene of the South Atlantic (DSDP III, Hole 15, core 8, section 3) showing traces of the median ridge and (8) USNM 174382 (x45) from the continental slope of northern Chile (ELT 63; lat. 25°44'S; long. 70°58'W; 1863 meters) showing a typical expression of the muri. This specimen is the one from which the soft parts were removed to be drawn for Figures 16 and 17.



## PLATE 9

1-12. *Bradleya dictyon* (Brady, 1880). Scanning Electron Micrographs of the left valve of a female specimen from Mozambique Channel (1) showing a full lateral view (box is view of Plate 9: figure 7); (2) posterior and (3) anterior views; (4) a conjunctive pore conulus (arrowed in Plate 9: figure 5) on a foveolate junction of the ventrolateral ridge and a supporting murus; (5) a ventromedian segment of the carapace; (6) a celate sieve pore (arrowed in Plate 9: figure 5) on a caperate solum; (7) the muscle-scar node region (boxed in Plate 9: figure 1) showing the thaerocytherid muscle-scar pattern, the local reticular pattern with three pore conuli mounted on the muri and the posterior section of the bridge structure; (8) an oblique view of the foveolate muri and (9) an enlargement of the foveolation and (10) a strongly celate pore (arrowed in Plate 9: figure 8); (11) the ocular region and (12) postero-dorsum. Scales = 1, 10, 100 microns.

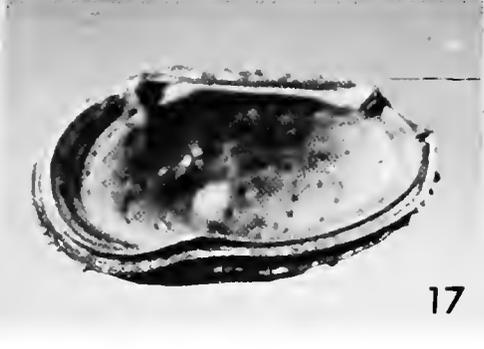
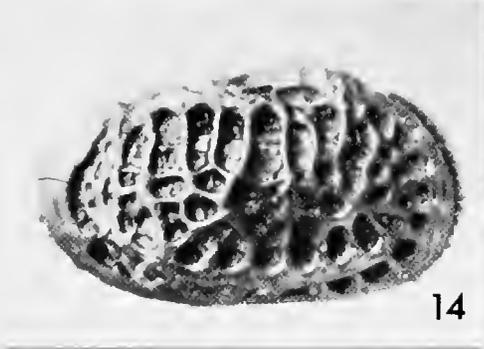
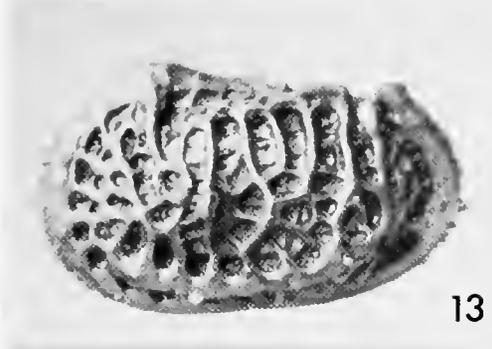
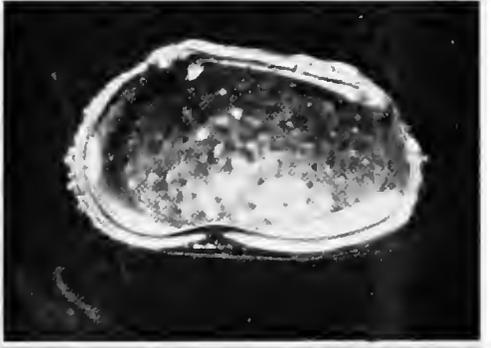
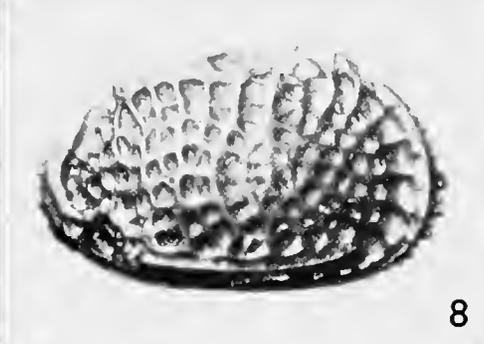
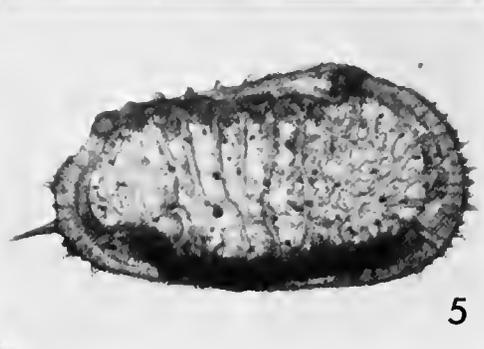
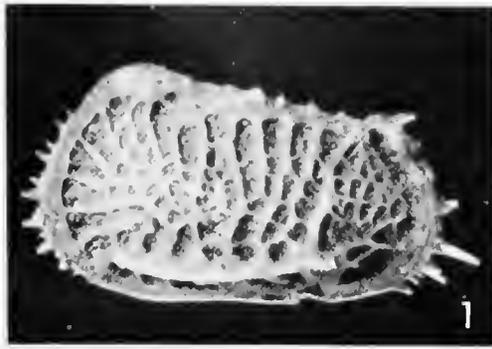


## PLATE 10

1–6. *Poseidonamicus major*, new species; paratypes (USNM 174354) as seen in reflected and transmitted light (1, 4) left valve, adult male; (2, 5) right valve, adult male; (3, 6) left valve, adult female. From Mozambique Channel, IIOE station 366A, lat. 23°9'S and long. 43°9'S and long, 43°9'E; 2300 meters; (x45).

7–12. *Poseidonamicus pintoii*, new species; separate valves of whole specimen as seen in (7) black light, (10) transmitted and (8, 9, 11, 12) reflected light; (7, 8, 10) right valve, female, paratype; (12) interior showing hinge, USNM 174356; (9) paratype left valve female (specimen lost); (11) holotype, left valve female, USNM 174355. From the continental shelf off Brazil; *Albatross* station 2763, lat. 24°17'S and long. 42°43'30'W; 671 fathoms; (x50).

13–18. *Poseidonamicus minor*, new species; two separate valves of the same specimen (13, 16) holotype, left valve, adult, USNM 174357; (14, 17) paratype, right valve, adult, USNM 174358, from the southeastern Pacific, Down Wind Expedition station DWBG 74, lat. 28°43'S and long, 107°36'W; 3220 m; and (15, 18 [dorsal view]), penultimate instar, right valve, paratype USNM 174359. From southeastern Pacific, *Eltanin* station 21–10, lat. 36°41'S and long, 93°37'W, 3137 meters; (x50).



## PLATE 11

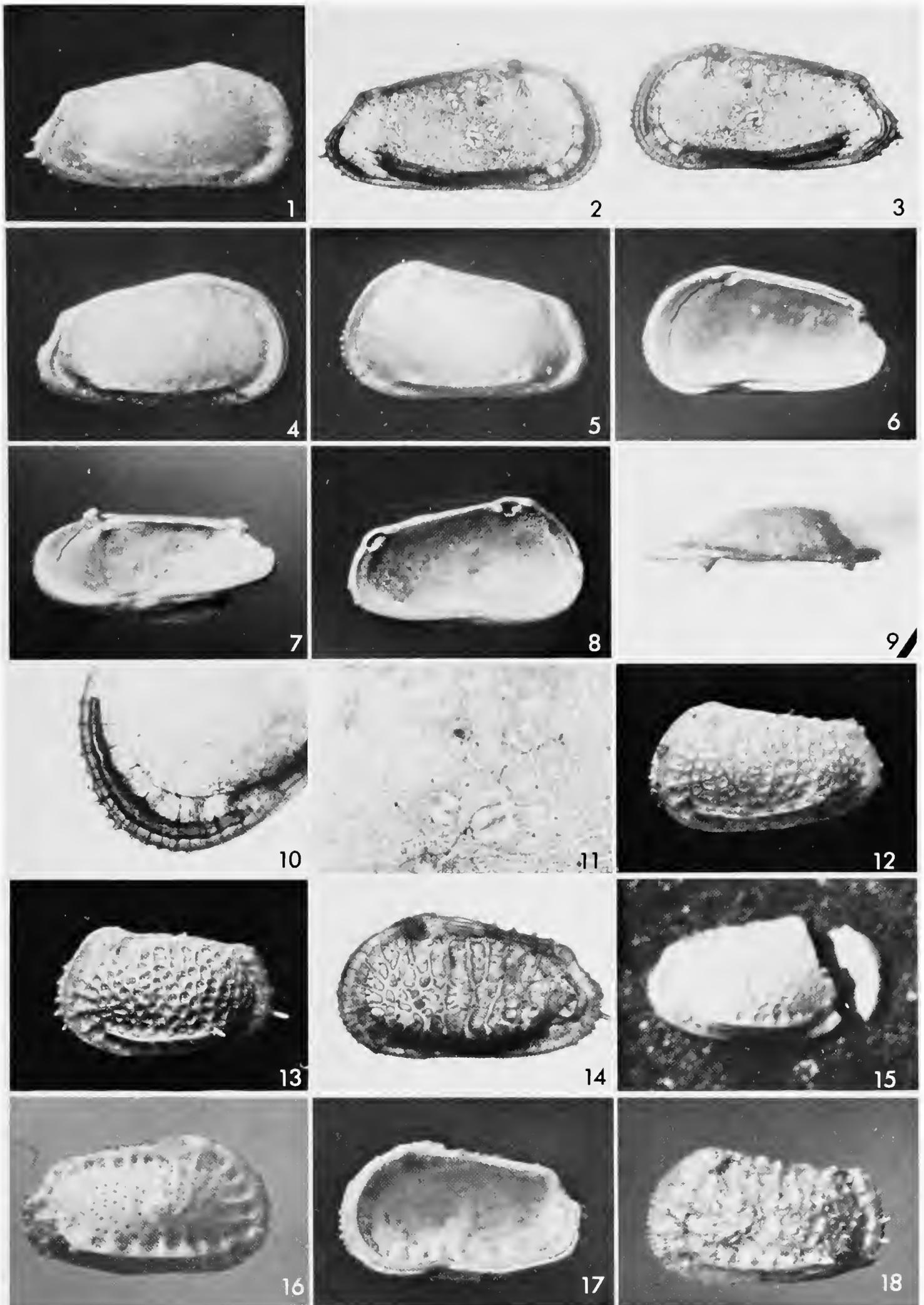
1–11. *Poseidonamicus nudus*, new species; as seen in (1) reflected and (2, 3) transmitted light; adult whole specimen (holotype USNM 174351) with valves divided; (1) right valve, (2) right and (3) left valves; (4–9) stained paratypes, right valve, adult, exterior view and showing several views of the hinge, USNM 174352; (10) anterior marginal area, (11) muscle-scar and reticular pattern of right and left valves. From the Mozambique Channel, IIOE station 367G, lat. 22°42'S and long. 40°21'E, 3140 meters (x40).

12–14. *Poseidonamicus major*, new species: (12) carapace of dissection 297, USNM 174353; *Eltanin* station 1248; (13) late instar from Mozambique Channel, IIOE 416A, USNM 174381; (14) left valve from above sample as seen in transmitted light for comparison of reticular pattern as seen in Plate 11: figure 11 (x45).

15. *Poseidonamicus viminea* (Brady, 1880), nomen dubium (see p. 50); holotype by monotypy, BM 80.5.33, from *Challenger* station 146 near Prince Edward Island (unstained, x55).

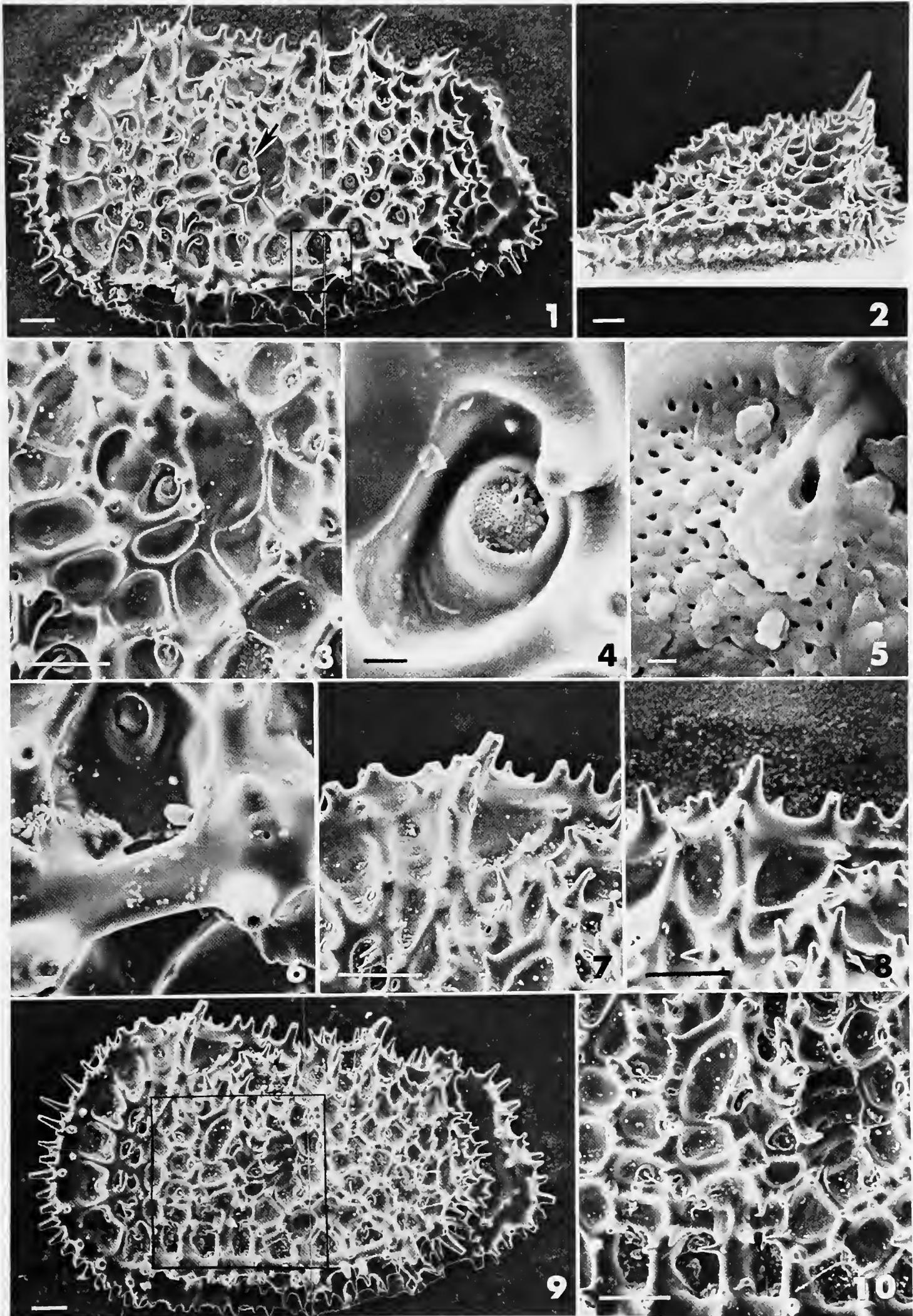
16–17. *Bradleya arata* (Brady, 1880), lectoparatype, a penultimate instar, BM 80.38.52, from *Challenger* station 167 in the Tasman Sea, as seen from (16) exterior and (17) interior views (unstained, x50).

18. *Bradleya dictyon* (Brady, 1880), the lectoholotype (designated herein), an adult left valve, BM 161.12.4.32, from *Challenger* station 78, North Atlantic, lat. 37°24'N and long. 25°13'W, 1000 fathoms (x40).



**PLATE 12**

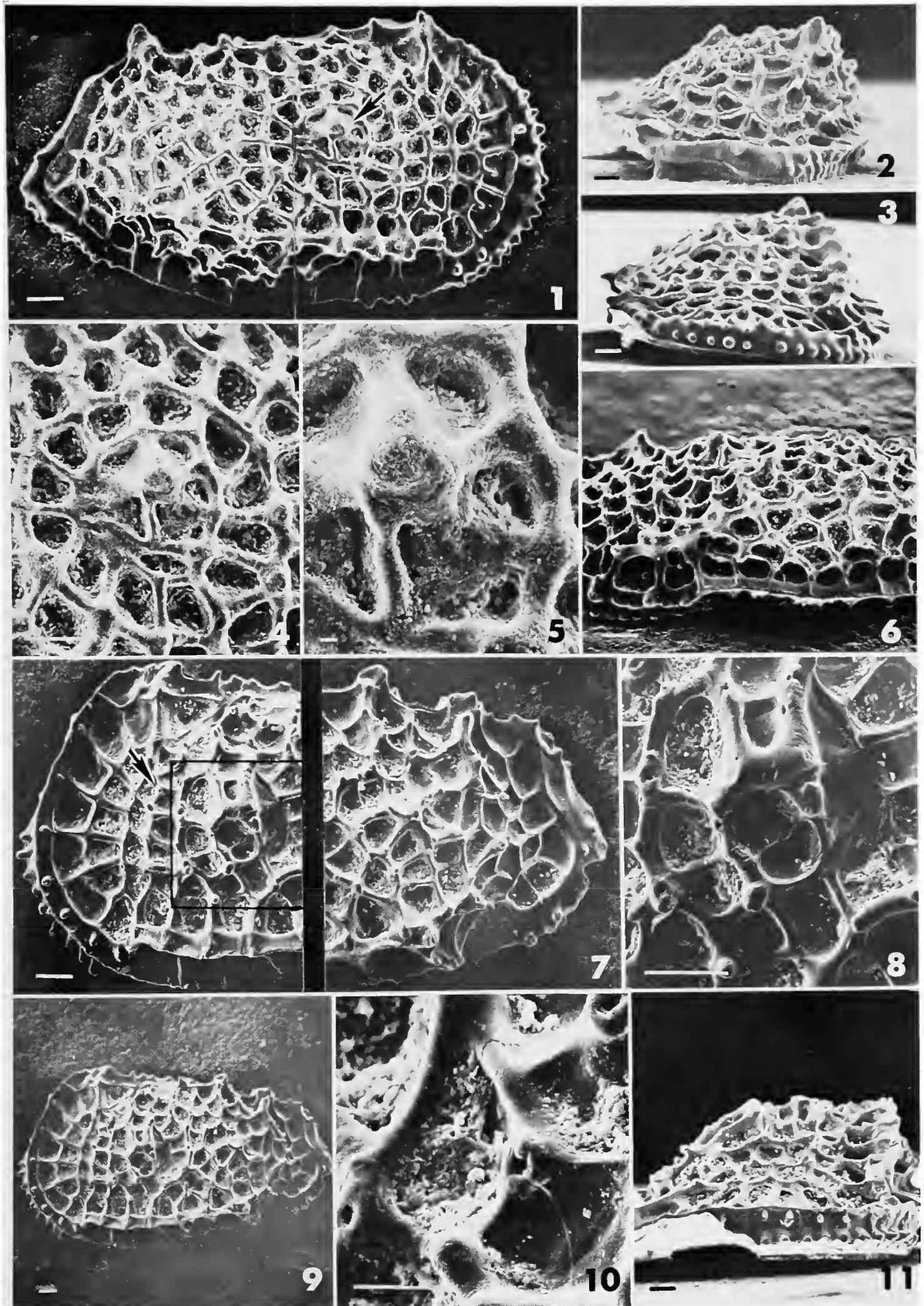
1-10. *Agrenocythere spinosa*, new species; (1) exterior lateral view and (2) anterior end view of left valve of paratype (USNM 174336, from IIOE 407, Recent), with (3) enlargements of the castrum, (4) the porus castri (arrowed in Plate 12: figure 1), (5) the sieve plate of the porus castri and setal mount, (6) a section (boxed in Plate 12: figure 1) of the ponticulum forming the ventrolateral ridge, and (8) the region of the ocular ridge. (9) Paratype, USNM 174365, from IIOE 365D, Recent, is shown in lateral view, with (7) enlargements of the ocular region showing the pore conulus Aquarius, and (10) the castral region (boxed section in Plate 12: figure 9). Scales = 10 and 100 microns.



**PLATE 13**

1-6. *Agrenocythere radula* (Brady, 1880), (1) lateral view, (2) posterior view, (3) anterior view, and (6) the ventral of right valve, with (4) enlargements of the castrum and (5) spicula (arrowed in Plate 13: figure 1). From the Recent of Mozambique Channel, IIOE 410A, hypotype USNM 174341.

7-11. *Agrenocythere hazelae* (van den Bold, 1946), from the eastern Pacific, ALB 3375, USNM 174342. (9) Lateral view, (7) enlarged and in (11) anterior view, with (8) enlargements of the castrum and (10) anterior pore conulus and intramural pore (arrowed in Plate 13: figure 7). Scales = 10 and 100 microns.



## PLATE 14

1–4. *Agrenocythere radula* (Brady, 1880); (1) exterior left valve of hypotype (USNM 168377, IIOE 363B); (2) exterior right valve of hypotype (IIOE 363B); (3) interior and (4) exterior of left valve of hypotype (USNM 174360, IIOE 363B; Mozambique Channel).

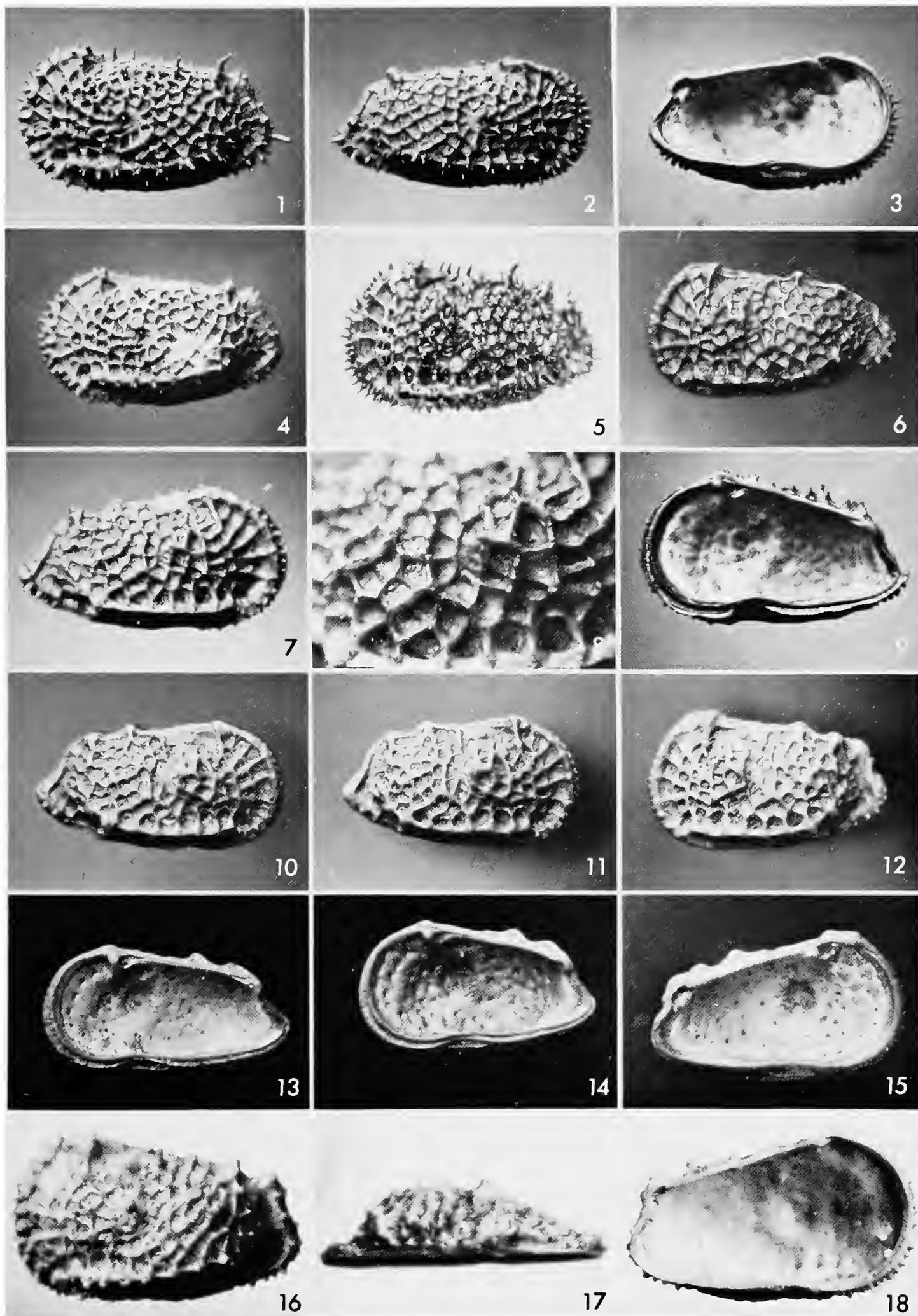
5. *Agrenocythere spinosa*, new species, left valve of paratype, USNM 174366, IIOE 407D; Mozambique Channel.

6, 10–15. *Agrenocythere americana*, new species, paratypes USNM 174363, from ALB 2383, Gulf of Mexico; (6) exterior view of left valve of male paratype; (10) exterior view and (13) interior view of right valve of male paratype; (11) exterior view and (14) interior view of right valve of female paratype; (12) exterior view and (15) interior view of left valve of female paratype.

7–9. *Agrenocythere hazelae* (van den Bold, 1946); (7) exterior view, (9) interior view and (8) enlargement of the central reticulum of a right valve of a male(?) paratype, USNM 174364; ALB 3375; eastern Pacific.

16–18. *Agrenocythere radula* (Brady, 1880), designated lectoholotype (left valve, penultimate instar) from the original Brady material of the *Challenger* Expedition (BM 81.5.28) collected from station 191A, Ki Islands, southern Indonesia at 580 fathoms depth, as seen in (16) exterior lateral, (17) exterior dorsal, and (18) interior views.

All illustrations on this plate were made by light photography and are approximately 35x magnifications except Figure 8, which is about 80x.



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