

Evolution of *Oblitacythereis*
from *Paleocosta*
(Ostracoda: Trachyleberididae)
during the Cenozoic in the
Mediterranean and Atlantic

RICHARD H. BENSON

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ABSTRACT

Benson, Richard H. Evolution of *Oblitacythereis* from *Paleocosta* (Ostracoda: Trachyleberididae) during the Cenozoic in the Mediterranean and Atlantic. *Smithsonian Contributions to Paleobiology*, number 33, 47 pages, 11 figures, 4 plates, 1977.—A new ostracode genus *Oblitacythereis* containing two new subgenera (the nominotypical form and the older *Paleoblitacythereis*) containing two new species (*O. (O.) mediterranea* and *O. (P.) luandaensis*) and one old species (new designation, *O. (P.) ruggierii* (Russo)) have been demonstrated to have descended from a common ancestral stock (new genus *Paleocosta*) of the genus *Costa*, the nominate form of the tribe Costini.

This genus contains heavily costate species whose history has been one of invasion of the greater depths of Tethys, which became thermospheric in the middle Miocene. Species of subgenus *Paleoblitacythereis* became adapted to upper slope and warm basinal habitats and underwent considerable modification of its carapace structure. When Tethys became extinct as a marine environment at the end of the Miocene, subgenus *Paleoblitacythereis* was eradicated in the Mediterranean region but survived in the Atlantic, where it lives today. Its descendant subgenus *Oblitacythereis* invaded the newly formed Mediterranean in the Early Pliocene, structurally modified to live in cooler water.

The history of *Oblitacythereis* was traceable because of a detailed analysis of structural and form homology, substantiated by quantitative Theta-Rho test.

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Evolution of *Oblitacysthereis* from *Paleocosta* (Ostracoda: Trachyleberididae) during the Cenozoic in the Mediterranean and Atlantic

Richard H. Benson

Introduction

The formerly great Tethys ocean-sea complex became progressively restricted during its final years of existence. Its deeper basins were progressively isolated from oceanic circulation leading to the eradication of the deeper bathyal and abyssal faunas. To occupy the warming and still habitable regions, many tolerant upper slope animals descended into the geologically active basins to evolve new, and modify old, structures forming new species and genera. One of these became the older of two ostracode subgenera of a new genus called "*Oblitacysthereis*." Subgenus *Paleoblitacysthereis* is a significant indicator of the history of the last moments of Tethys. At least one of its species escaped into the Atlantic, and when the Mediterranean formed after the Messinian salinity crisis, the species returned as a cooler water form, *Oblitacysthereis* (*Oblitacysthereis*) *mediterranea*, new species.

Among ostracodes in general, *Oblitacysthereis* (which includes the two subgenera *Oblitacysthereis* and *Paleoblitacysthereis*) belongs to that architectural group of heavily reticulate costine forms

whose principal ridges became enlarged to assume the load of stress distribution over the carapace formerly carried by more massive and uniformly distributed muri. The evolution of the genus *Oblitacysthereis* starts in the early Paleogene of Tethys, in an area now in the eastern Mediterranean, from an ancestor, now called *Paleocosta*, new genus, whose reticulum is just beginning to differentiate in several ways into secondary ridge systems. The evolution of *Oblitacysthereis* climaxes in the Late Tortonian development of an Atlantic invader, which became typical of the Mediterranean "Ocean" proper (the earliest stages of the "Sea" were in part psychrospheric) during the Pliocene. The ridges of the Pliocene *Oblitacysthereis* became ponticulate to extend a maximum distance outward, giving strength and lightness to the rest of the reticulum. The recognition of the tendency for organization of the secondary, structural system from an underlying coarser reticulum provides the foundation for the present analysis and classification of this complex group.

The trend of differentiation of the reticulum from many reticulate muri into a few prominent ridges is known in other groups of ostracodes besides *Oblitacysthereis*. It has been described for the Bradleyinae (Benson, 1972) and can be seen also in *Costa* (Benson, n.d.a.). In fact forms now distin-

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guished as *Oblitacysthereis* have been identified both as *Bradleya* and *Costa* in the past (Sissingh, 1971; Bassiouni, 1969; Russo, 1968). As will be demonstrated later, however, the same parts of the reticular pattern are not utilized by these different groups to achieve the same general and convergent architectural solution. *Costa* and *Oblitacysthereis* both arise from *Paleocosta* but in different manners. It has been one of the more interesting aspects of the present study to trace the differences on a similar underlying reticular and pore-conuli pattern.

The general purposes of the present work are (1) to describe the morphological and ecological changes that occur through time in this small but important ostracode group; and (2) to show how its structural modification reflects the final destruction of western Tethys and the beginning of the Mediterranean. I will conclude from this study that this ostracode evolves separately from other heavily reticulate forms; that its origins can be

traced into the Paleogene to converge with those of *Costa*; and that because of its eventual bathyal character, it is very useful in unraveling the water-mass changes that occurred in Tethys just before the Late Miocene "salinity crisis" and during the Pliocene invasion of cooler waters that formed the Mediterranean.

Also I would like to call attention to the method of analysis that I am using. It is my conviction that many evolutionary relationships in ostracodes are either overlooked or poorly explained because too much attention is paid to appearance rather than structure in their morphology. Questions of function must be addressed. Obviously we have much to learn about how the ostracode evolves and why its carapace changes through natural selection. I have sought to provide a theoretical beginning that may seem cumbersome in future years. Nonetheless, as Francis Bacon has said, "Truth emerges more readily from error than confusion" (in Kuhn, 1962).

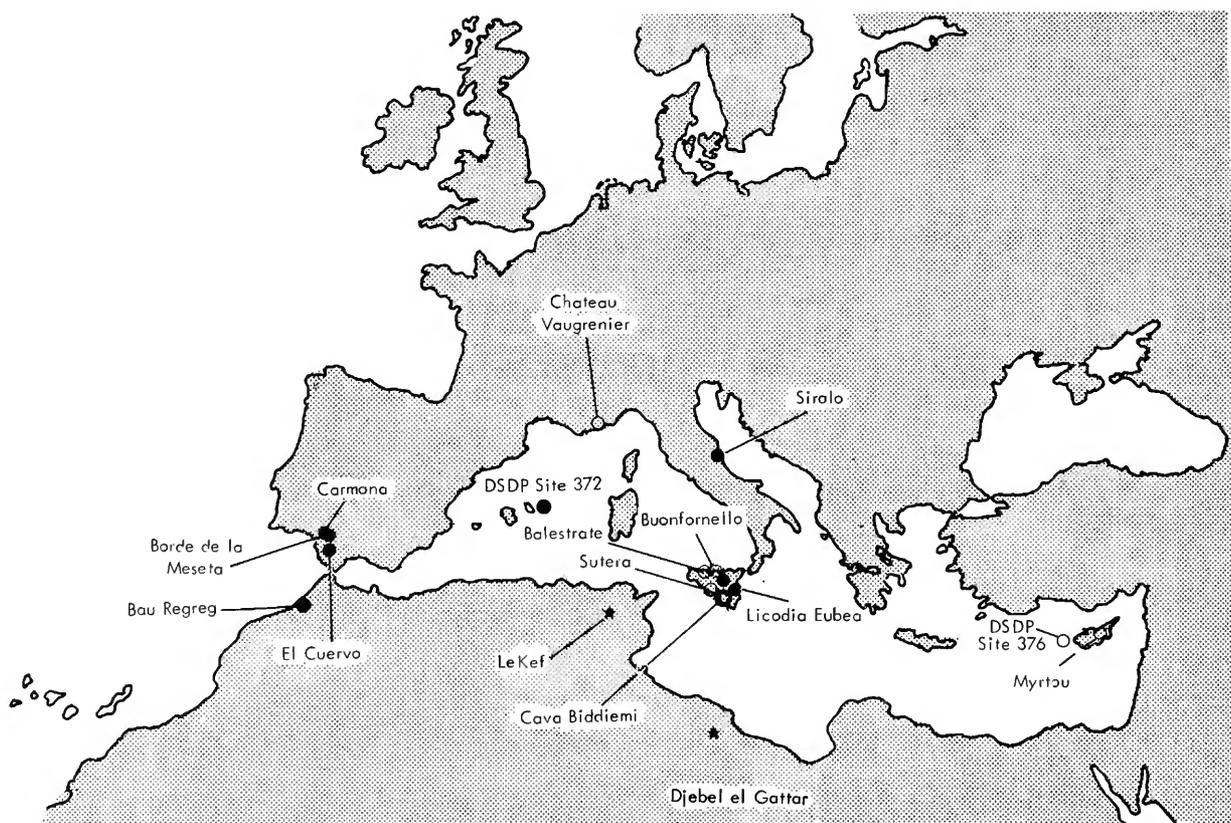


FIGURE 1.—Localities in the Mediterranean region where specimens (except the Recent species off Angola) were found.

○ subgenus *Oblitacysthereis* ● subgenus *Paleoblitacysthereis* ★ *Paleocosta*

ACKNOWLEDGMENTS

This work was begun with the mutual interest of myself and Professor Giuliano Ruggieri, who has advised and encouraged me to continue and complete it. In other works (Benson, 1973a, n.d.a., n.d.c.), I have mentioned the ostracode *Oblitacythereis*, and, in fact, credited Professor Ruggieri with its name. As we have worked on many problems together, I am honored that he would endow me with this trust and I hope that the results live up to his expectations.

I also would like to thank H. J. Oertli, J. E. Hazel, and G. Ruggieri for their reviews of the manuscript and helpful suggestions, and especially Mrs. Laurie Brennan who helped expedite the manuscript in its final stages while I was absent. Funding for this study came from the Smithsonian Research Foundation Grant SRF No. 450101.

COLLECTING LOCALITIES

The specimens used in this study were obtained

from 18 samples from 17 localities in the Mediterranean region (Figure 1) and the South Atlantic, ranging in geologic age from Paleocene to Recent with the greatest concentration in the Middle Miocene and Early Pliocene (Figure 2). The Middle Miocene is best represented in outcrops of *Oblitacythereis* from western Andalusia, which, although it faces the Atlantic, was probably contiguous with deeper basins of Tethys through the Iberian Portal and with Italy (especially Sicily), which may represent another threshold within Tethys. The Lower Pliocene collections of *Oblitacythereis* were obtained from outcrops in Sicily, France, and Cyprus. Cores from sites 372 and 376 of the Deep Sea Drilling Project Leg 42A yielded specimens of Lower Pliocene age from both the eastern and western Mediterranean; however, only the western Mediterranean yielded Middle Miocene specimens from the present deep basins. *Paleocosta* has been found only in North Africa in Tunisia and Libya. Two collections from Sicily were given to the author by Professor G. Ruggieri for which I am indebted.

SAMPLE NO.	LOCATION	AGE
<i>Oblitacythereis (Oblitacythereis) mediterranea</i> , new species		
RHB 730301	Buonfornello, Sicily, E of Palermo at Imera Museum	Trubi Fm. (Zanclian)
ARL 4458	Chateau Vaugrenier, N of Antibes, France, 43°24'N, 7°12'E	Lower Pliocene
Ruggieri Coll.	Balestrate (Palermo), Sicily, along the Forgitello River, 38°01'48"N, 13°00'36"E	Trubi Fm. (Zanclian)
S69 CYM3	Myrtou type-locality, Cyprus, 35°18'N, 33°06'E	Zanclian
DSDP	DSDP Site 376, Florence Rise, W of Cyprus, core 5, sec. 5, interval 70–80 cm, 34°52'19"N, 31°48'27"E, 2101 m depth	Zanclian- Piacenzian
DSDP	DSDP Site 372, Algero Provencal Basin, E of Balearic Is., core 3, sec. 3, interval 103–109 cm	Zanclian
<i>Oblitacythereis (Paleoblitacythereis) ruggierii</i> (Russo, 1964), new combination		
RHB 71809	Cava Biddiemi, at the bridge between Santa Croce Came- rina and Marina Ragusa in SE Sicily, 36°42'N, 14°48'E	Langhian
RHB 71827	S of Ancona, near Sirolo, 43°03'N, 13°03'36"E	Tortonian
Ruggieri Coll.	NW of Sutera, near Agrigento, Sicily, 37°15'N, 13°36'E	Langhian
Ruggieri Coll.	Licodia Eubea, E Sicily, 37°9'N, 14°39'E (GR 2539)	Tortonian
AG-2	Borde de la Meseta, Spain (Andalusia), NW of Carmona, 37°42'N, 5°18'W	Tortonian
C-12	Carmona (Andalusia) Spain, Andalusian Stratotype, 37°27'N, 5°39'W	Andalusian (allochthonous)
14	El Cuervo section, Andalusia, Spain, Madrid-Cadiz Road, km 607	Serravallian
DSDP	Site 372, Algero-Provencal Basin, core 33, sec. 3, interval 53–59 cm	Burdigalian (allochthonous?)

	<i>Oblitacythereis</i> (<i>Paleoblitacythereis</i>) <i>luandaensis</i> , new species	
AII42-203	Off Angola, 8°48'S, 12°52'E, 527-542 m depth	Recent
	<i>Paleocosta libyaensis</i> , new species	
2M-2/19	Djebel el Gattar, ESE of Tripoli, Libya, 31°30'N, 14°22'E	Eocene?
	<i>Paleocosta kefensis</i> , new species	
RHB 57	Le Kef, Tunisia	Middle Paleocene
	<i>Paleocosta?</i> sp.	
RHB 57	Le Kef, Tunisia	Middle Paleocene

THE *Oblitacythereis* PROBLEM

To give focus to the very great complex of ostracode development in the Neogene history of the Mediterranean region, it is helpful to concentrate on a few critical genera that would most likely leave a decipherable record of change and adaptation to the events that accompanied the onset and the aftermath of the Messinian salinity crisis. *Costa* is one of these, *Agrenocythere* another, and *Oblitacythereis* a third (Figure 3). *Oblitacythereis* lived near the ecologic and stratigraphic boundaries of greatest alteration during these critical times, and although it continued to survive in the warmer eastern Atlantic just outside of the Mediterranean "largo mare," it cannot be traced from the Miocene into the Pliocene within the Mediterranean region, nor has it yet been found living in that area today. Its fossil record is discontinuous at critical depths within the marine environment of Tethys and ceased as this environment deteriorated. It was then reinstated in the Mediterranean and then again apparently deteriorated.

To place so much emphasis on the importance of the history of one animal, it is necessary to formulate not only a historical model but also a logical analytical strategy so that adequate tests can still follow. In this way, it is hoped that the considerable historical conclusions can be subsequently and systematically modified as mistaken assumptions are identified, hopefully without having the whole structure of the model come tumbling down as a "house of cards."

The unique properties that one would look for in the testing of a historical progression within a

particular kind of ostracode could include (1) the availability of a sufficient number of adaptive characters, whose structural modification in a succession can be mapped; (2) an adequate structural theory that can explain and anticipate an adaptive development in any similar series of ostracode morphological changes; (3) the recognition of convergence in form in other still living ostracodes, so that analogous architectural solutions of extinct species can be compared from their Recent distribution; and (4) the faunal association of forms and taxa within assemblages whose modern distribution is known.

Therefore, with *Oblitacythereis* I have attempted to demonstrate (1) changes in the reticular pattern by reference to a basic plan followed by the mapping of these changes; (2) the rational progression of increased organization and simplification of the ridge system emerging from the reticulation; (3) an architectural explanation of these changes from one structural type to another as responses to different requirements of shell strength and differences in potential availability of shell material; (4) the significance of the present distribution of a living species and its soft-part morphology to others analogous in form; and lastly, (5) the likelihood of paleoenvironmental distribution by reference to the known ecological distribution of associated species, especially those from deep basin deposits. These properties are analytically separate, but obviously linked in the basic assumption that the general "ornamentation" of the ostracode carapace is adaptively responsive to significant historical changes. This latter point has become axiomatic among most ostracode students.

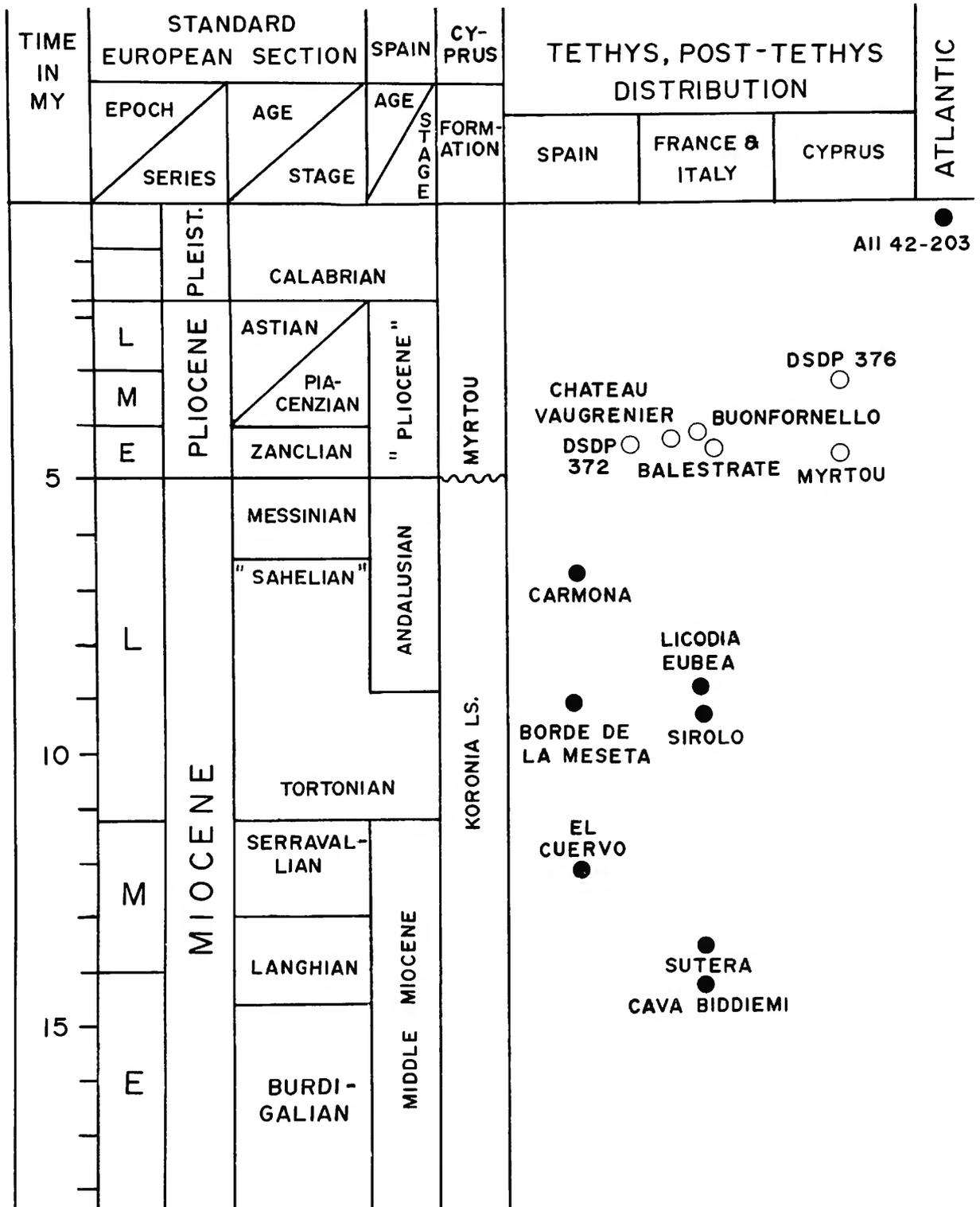
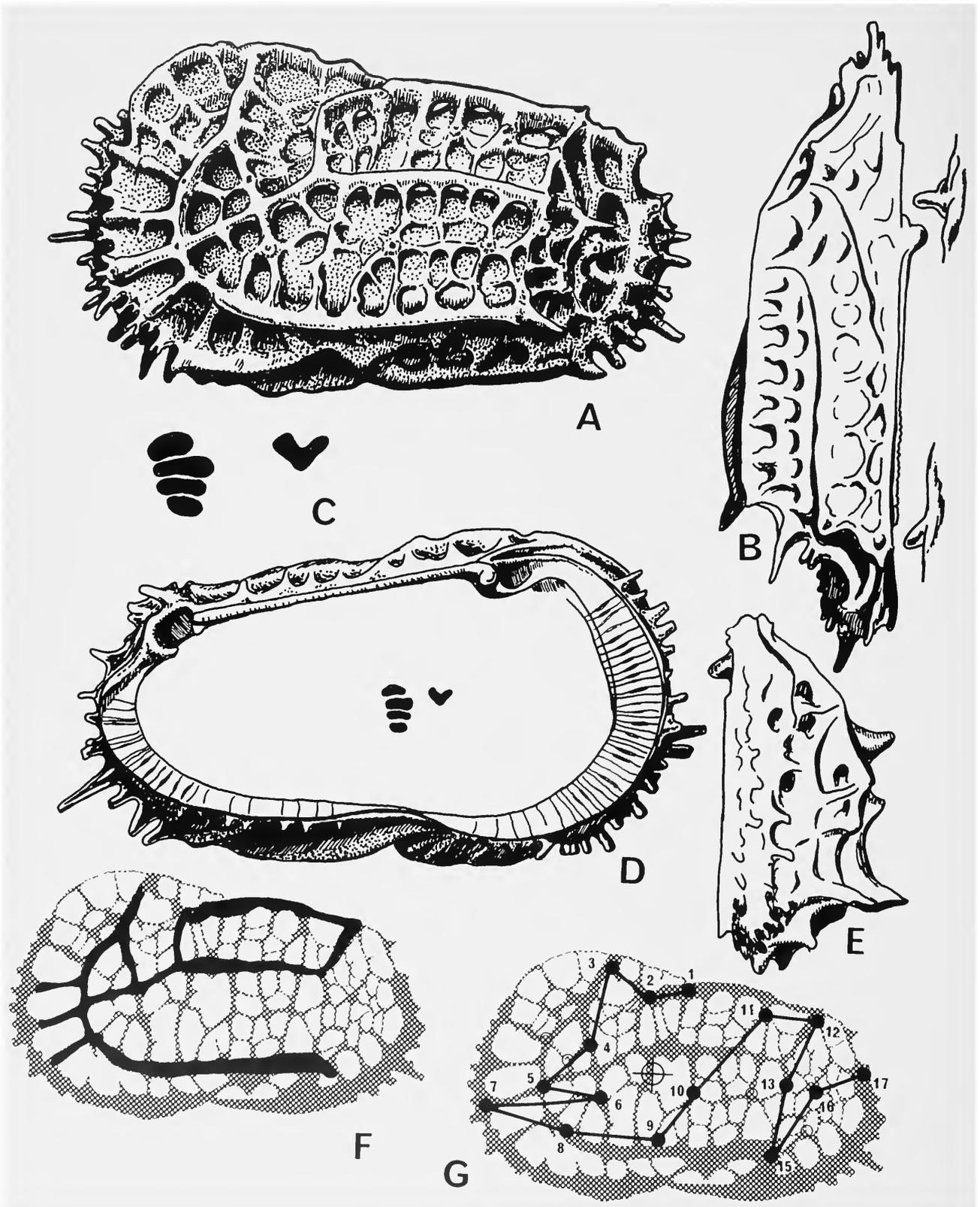


FIGURE 2.—Stratigraphic occurrence of the collecting localities of Miocene age and younger where *Oblitacythereis* was found.

○ subgenus *Oblitacythereis* ● subgenus *Paleoblitacythereis*



As an attempt to test relationships by an independent means, some selected representatives of *Oblitacythereis* from seven localities were compared morphometrically by Theta-Rho analysis. This method, which has been used and described elsewhere (Benson, n.d.a.), assumes that differences in phyletic allometry within the pattern of principal pore-conuli are least among most closely related forms. The results in general corroborate the other observations, but scarcity of well-preserved specimens of left valves of the same sex prohibit its universal usage. Also variability within better known species is still not sufficiently known to explain some of the results of testing a rare species.

In the classification of *Oblitacythereis*, I have found no difficulty in assigning it to the Tribe Costini of Hartmann and Puri (1974); however, I disagree with many of their assumptions on which this and other cytheraceans are classified. I have endeavored to explain why these disagreements exist.

ON CONSIDERING MORPHOLOGICAL COMPLEXITY

The "ornate" ostracodes often have very complicated carapaces that are highly sculptured with reticulation (the general structure is called the "reticulum"), pore distribution patterns, and superimposed, sometimes ponticulate ridge systems. Pokorny (1969a,b), Liebau (1969), and Benson (1972, 1974, 1975) have attempted to discover the intrinsic order within these reticular, pore-system, and structural ridge patterns and the relative amount of change that occurs among them. In this report, I have once again attempted to discover how these patterns change within the present group of costine ostracodes; but at the same time, I believe that something more has been learned about the study of patterns in general. A few remarks about this are

warranted in order to add to some of the ideas expressed earlier (Benson, 1972).

First, to re-emphasize a point made earlier, there is a difference in analytical procedure between the description of morphological consistency within a pattern and the explanation of the causes of this pattern. I have attempted to keep these pursuits separate, procedurally at least, so that the operation of the theory of cause might emerge from the observed changes within the patterns themselves. This may be philosophically naïve, however, as no simpler underlying pattern founded on the enumeration of parts has yet emerged without the aid of an a priori causal theory—in this case a strong architectural theory. The hope that some intrinsic, self-evident logical pattern would emerge from the coded reticular pattern, which was more attractive than ones previously offered (Benson, 1972), has not happened. No "golden mean" or some other such marginal permutation of numbered combinations of identified fossae has yet appeared, to me at least.

Somehow, the quest for an "essential geometry" in the numerical arrangements within the fossal distribution is attractive, if for no other reason than it would be satisfying to learn that an inherent natural system of form and one logically derived (by mathematical means) concurred. The discrepancies between the numbering systems that Liebau, Pokorny, and myself have tried to employ in mapping reticular networks simply confirm the fact that a single one is not immediately obvious. We are well aware that the appearance of the numbers and their impression of complexity can seem greater than that of the underlying pattern. I would hasten to add that we could have no confidence in the homologies within the patterns from specimen to specimen without having first labeled and then followed them individually. We must reduce the apparent complexity and identify homologies, but I am still unsure about the mathematical ordering of the fossae to fit some alphanumeric plot, although I have attempted another here.

In the pattern analysis I presented in 1972 for forms of *Agrenocythere*, I believe that homology was successfully demonstrated within the reticular pattern. The reticulum of ornate ostracodes is very conservative in its variability and remains relatively unchanged among closely related ostracodes. Homologies can be found consistently within the pore-

FIGURE 3.—Important morphological features of *Oblitacythereis* (*Oblitacythereis*) *mediterranea*, new species: A, exterior of a male left valve showing the mural and ridge systems; B, dorsal view of the left valve (and hinge elements of right valve), showing the outward extension of the ridges; C, the adductor and frontal muscle-scar pattern; D, valve interior showing the hinge, marginal area, and muscle scars; E, anterior view of left valve; F, major ridge pattern; G, positions of pore conuli used and path of Theta-Rho difference analysis.

conuli, which change their relative positions even more slowly (to represent a primary inertial system of reference; Benson, n.d.a.). Those changes that do occur in the reticular patterns are probably related to changes in depth distribution (Benson, 1975).

Regarding the cause of the reticular patterns, I am more convinced than ever that the basic underlying pattern is controlled by a genetically responsive histological pattern in the internal structure of the carapace. The muri are not simply for space accommodation among the fossae, analogous to the divisions between so many soap bubbles. The muri do in a sense "accommodate," but within restraints of overall pattern, and as strengthened members of the reticulum, not just as cellular separations. This conviction arises from the consistency of the pattern in many different ostracodes and mass exchanges between muri to form ridges, as will be again shown in the present work. One cannot help but notice that the muri or walls separating the individual cells or fossae of the reticular pattern come and go in a manner best explained by the local increase or relief of strength in the particular region of the carapace. In this localized sense structural accommodation and structural redundancy does occur over a period of adaptive change.

In short, the most successful approach to the explication of the morphological complexity of the ornate ostracode carapace has been to prove that the major ridges develop in structural response to changes in strength requirements or to changes in carapace construction capability, and that this takes place within the constraints of a more conservative, genetically controlled underlying pattern within the shell itself. The structural theories that I have proposed elsewhere (Benson, 1974, 1975) now seem to contain the simplifying mechanism of morphological explanation more than the analytical manipulation of number series from the coding of the reticular patterns.

I would add to this a comment, which may have already been obvious to others, that reduction of a pattern to a mathematical state (alphanumeric) does not automatically lead to an ordering of that pattern. Some might suggest that some sort of statistical regression technique might be applied to demonstrate consistency in linkage between reticular or fossal elements. I would argue, at this stage in our

knowledge, that this linkage is already obvious by inspection of the coded patterns, and this is not the problem. The problem is still that of elemental topology; that is, knowing what to measure. At this stage the numbers enumerate the fossae; they do not imply measurement. When we have arrived at an allometric progression in the changes in the fossal arrangement that coincides with a mathematical progression, then we will have used the enumeration to express a growth function or an evolution that is more than a mathematical accident. One can perhaps see more of this now, especially in the anterior of the reticulum, but as yet consistency in the coding system does not imply confidence in its meaning.

BASIC MORPHOLOGICAL PLANS

Very often evolution can be seen more easily in complex animals. The carapace "ornament" of *Oblitacynthereis* can be made to appear morphologically complex, as can easily be seen by reference to any one of the analytical diagrams (Figures 4-8). These have been prepared to represent all of the divisions of parts of the reticular patterns (ridges, fossae, etc.). One hopes that there is utility in this analytical increase in complexity, but it is soon obvious that it must be reduced to simpler states to understand it. In each case the silhouette of the reticulum is first derived from the lateral view of the carapace as shown in its entirety in the SEM photographs. To these background patterns have been added the pore-conuli and either the major ridges emerging from the underlying reticulum (Figure 4) or the identification of homologous fossae (Figures 5, 6, 7). These attempts at the initial reduction of morphological complexity make comparisons easier as long as the departures from a basic plan can be recognized. It is imperative that the logical connection of a derived abstraction be maintained.

The basic carapace ridge pattern of *Oblitacynthereis* is shown in Figure 3. It consists of three longitudinal ridges over the median and posterior regions similar to those of *Costa*, *Bradleya*, or *Chrysocythere* (Figure 8), frequently with a connection between the posterior ends of the median and dorsal ridges. In the anterior, however, there is a great difference between *Oblitacynthereis* and these other genera and within *Oblitacynthereis* itself. *Ob-*

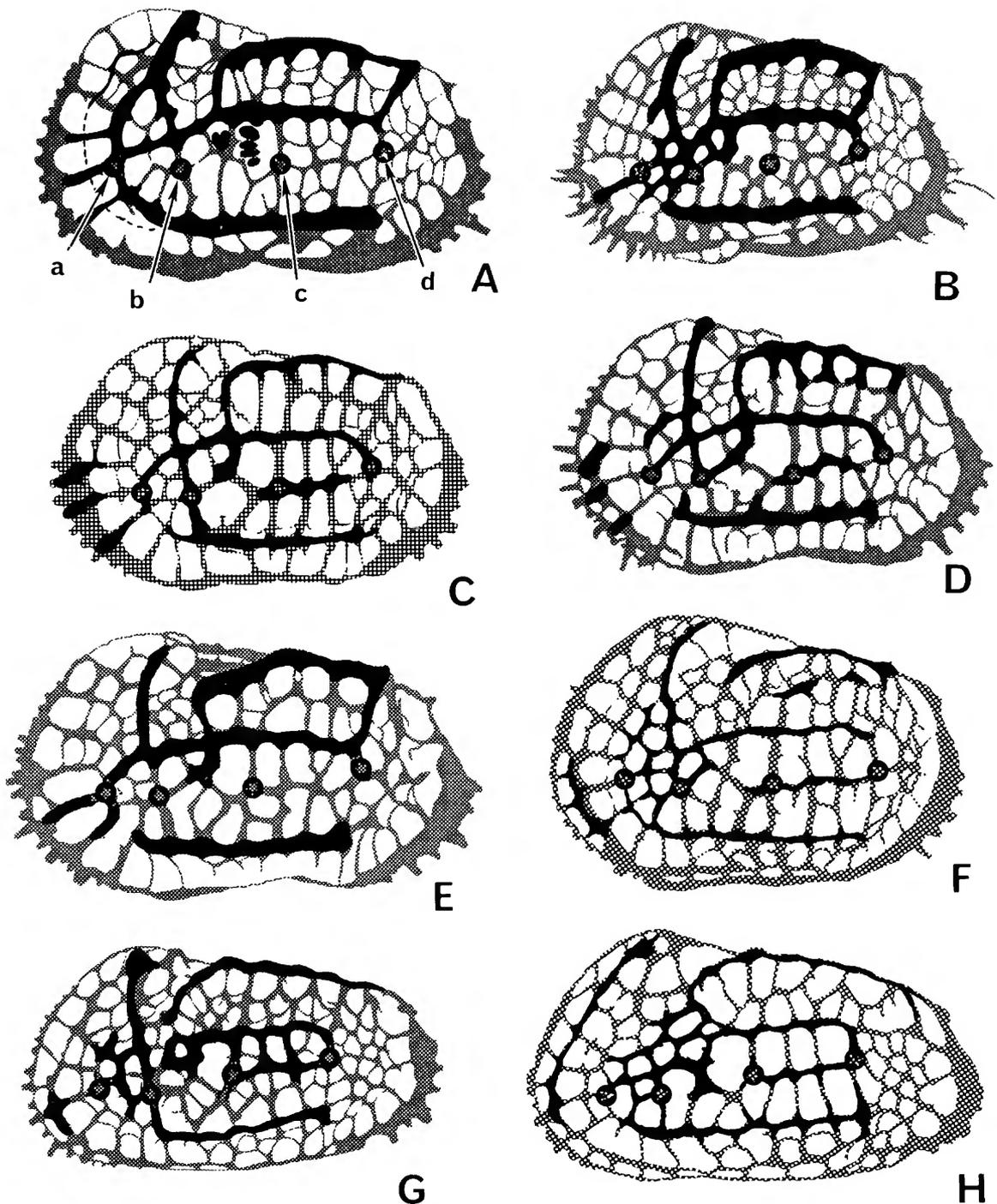
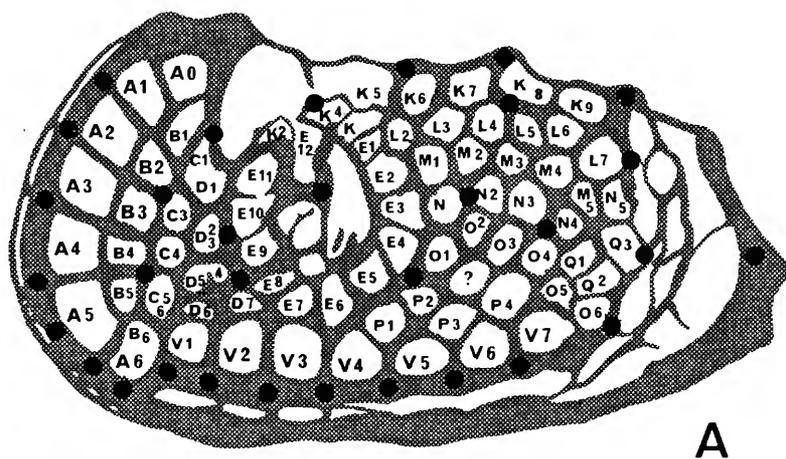
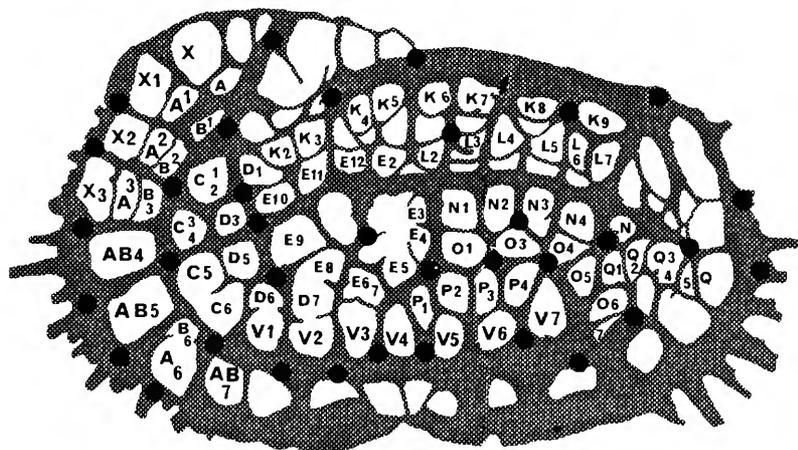


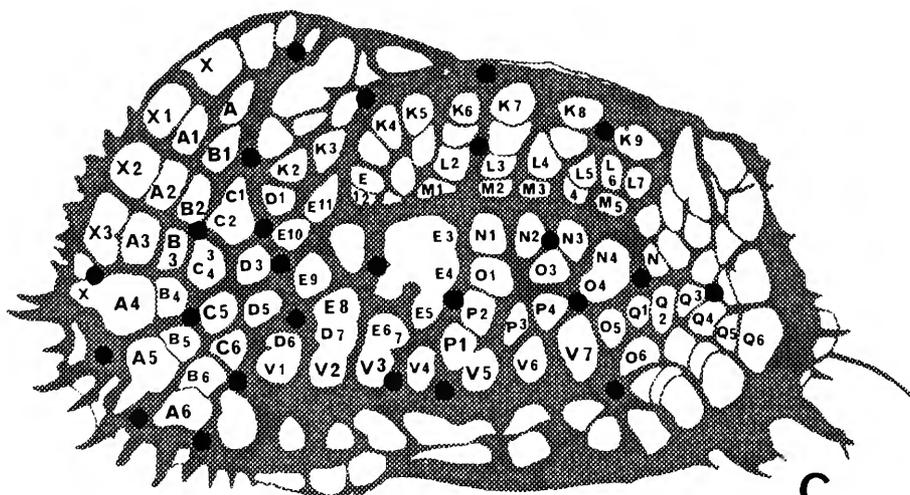
FIGURE 4.—Reticular silhouettes and ridge patterns: A, *Oblitacythereis* (*Oblitacythereis*) *mediterranea* from Myrtou, Cyprus (Zancian); B, *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis* off Angola (Recent); C, *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* from Licodia Eubea, Sicily (Tortonian); D, *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* from Borde de la Meseta (AG-2, Tortonian); E, *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* from Cava Biddiemi, Sicily (Langhian); F, *Oblitacythereis* (*Paleoblitacythereis*) sp. from El Cuervo, Spain (Middle Miocene); G, *Paleocosta kefensis* from Le Kef, Tunisia (Middle Paleocene); H, *Paleocosta libyaensis* from Djebel el Gattar, Libya (Eocene?).



A



B



C

litacythereis (*O.*) *mediterranea* has an anterior ridge extending parallel to the margin toward the ocular region of the ventral ridge. To form this ridge, it utilizes muri from more proximal portions of the reticulum than do the other genera just mentioned. This difference is very important as it represents architectural convergence or homeomorphy to strengthen the anterior, and yet the structure does not evolve from the same parts of the carapace. The structural difference causes a problem along the anterior margin in *Oblitacythereis mediterranea*. Because this ridge is so far removed from the margin, potential bending reactions are compensated by the three small ridges extending distally from the "marginal" ridge to the margin. Also a heavy connecting ridge extends downward from below the ocular region to join the median ridge anterior to the position of the frontal scar. Species of the subgenus *Paleoblitacythereis* do not have this ridge system completed. They use a redundant and irregular mural system to accomplish the same end but with more material. The history of this development will be discussed as will its taxonomic significance in later sections.

The basic plan or model of the distribution of fossae, which helps to compose or is the consequence of the reticular pattern and the pore-conuli, is shown in Figure 9. Everything but the basic order of the enumerative system of codification has been removed from the carapace morphology. Modifications in this plan as they occur in the animals themselves are shown in Figures 5, 6, and 7. These can be compared with *Agrenocythere americana*, which was one of the original group for which I attempted this kind of analysis in 1972. Some modifications in the *Agrenocythere* plan have been made as a result of the present study, wherein new homologies have been discovered that were previously obscured. This model is still considered a guide and possibly represents an improvement to that presented earlier for the pore-conuli alone (Benson, 1975, fig. 3).

At first it would seem that the fossae are simply the enlargements of pits and not the absence of

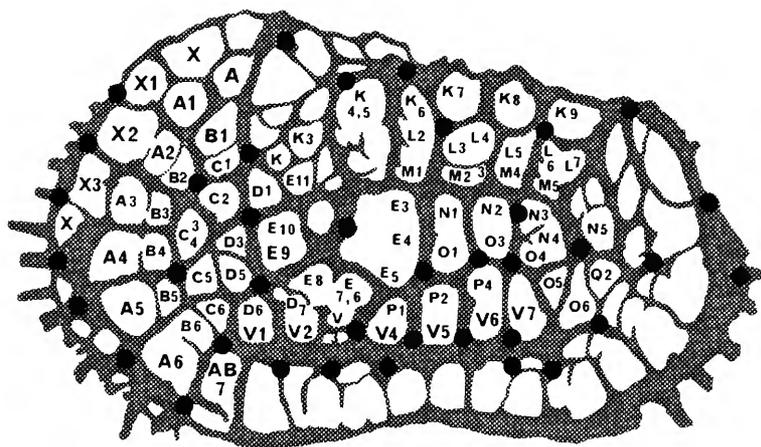
the muri that compose the reticulum. That this is not so can be demonstrated by tracing the disappearance of separating muri. The fossae are reflections of a system of cell division in the carapace. Inspection of the plan of fossae of a particular stage of reticular development in comparison with stages before and after may show where two or several fossae have joined. The muri do not occur at random, but they follow a predictable pattern. Without reference to the general plan of both fossae and pore-conuli, which is the consequence of examination of all of the developmental stages, such vestigial relationships and homologies of particular muri cannot be easily identified.

The fossal pattern, apart from the reticular pattern, can thereby be described as analogous to a matrix of alphabetic versus numerical factors approximately six deep and three sets of four or five wide. The reason for the discontinuity across the matrix is a result of trying to fit a rectilinear grid over the change in shape of the carapace from radial or semiconical in the anterior, to dorsal in the median region, to subrectangular in the posterior. It is obvious that the total system of codification is, at this stage in experimentation, at best incomplete and at worst a compromise; and yet, there is consistency within the sets that represents considerable improvement of the previous schemes.

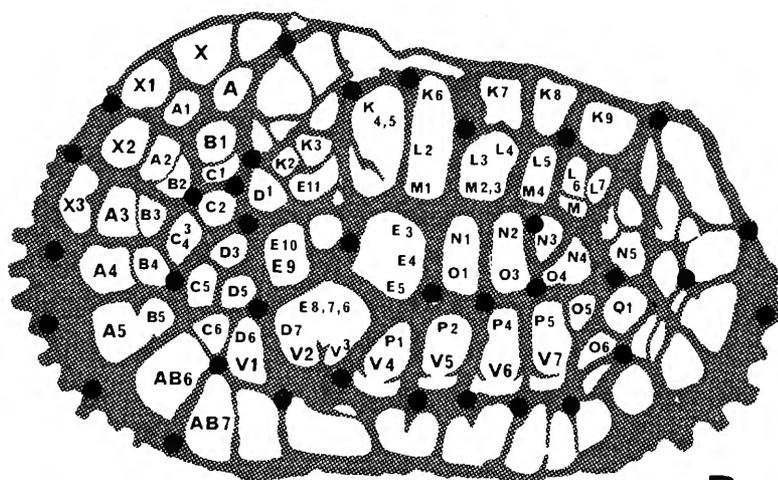
The anterior portion of the fossal matrix shows the greatest regularity numerically and in design. It will be used to show some of the most important changes that take place. In *Agrenocythere* this part of the matrix went from A to D. The anterior marginal rim of this ostracode obscured the distal-most row of fossae. This row is not covered in *Oblitacythereis* and is designated as X_{a-n} .

The median portion of the fossal matrix becomes confusing to analyze as it represents the transition around the muscle-scar node (hence its circular pattern). Of course the "scars," which are actually key-stone shaped crystals (anchors for the muscle tendrils), vary in arrangement and size. They are the source of stress within the carapace structure and slight changes in their arrangement are probably compensated for quickly in the muri around them. Also, it would seem that quite a few "adjustments" in the overall pattern take place above and below the muscle-scar node. This observation in itself may have important consequences in later comparisons of closely related species.

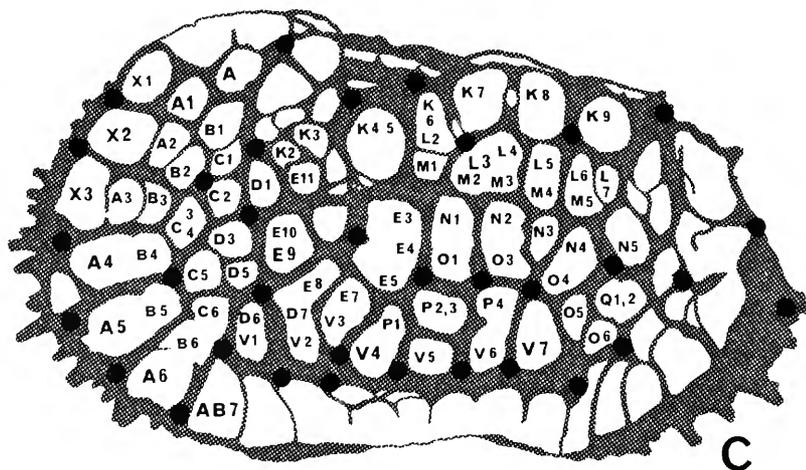
FIGURE 5.—Reticular silhouettes and fossal patterns: A, *Agrenocythere americana* from the Gulf of Mexico (ALB 2383, Recent); B, *Oblitacythereis* (*Oblitacythereis*) *mediterranea* from Balestrate, Sicily (Zanclian); C, *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis* off Angola (Recent).



A



B



C

The posterior portion of the fossal matrix tends to show regularity in a longitudinal manner. It may be shown that regularity in this region can be vertical as in *Poseidonamicus*, equispaced as in *Agrenocythere*, longitudinal as in the earliest stages of *Paleoblitacythereis* as it emerges from its ancestor *Paleocosta*, or irregular as it occurs between major, well-developed longitudinal ridges, such as occurs in *Costa sensu stricto* or *Bradleya*, and even *Oblitacythereis mediterranea*. This region was the most difficult to analyze in earlier studies, but it seems to be in the process of sorting itself out at this stage of investigation.

It is suggested that the reader take some time to examine for himself the patterns in Figures 5 through 7 to see how the homologies can be followed. Notice how the pore-conuli can be used as references. Unfortunately, not all of these pore-conuli could be seen in every specimen. Only those that could be seen are shown, so that their absence on a particular one of the diagram is not indicative of its absence in the species. It is believed that eventually all fossae can be homologized, but only those easier ones of the more central regions seen from lateral view have been so here. These amount to about 60 fossal references common to all specimens, which represent considerable control in tracing the development of any phyletic lineage.

In short, an alphanumeric plan is presented here as a guide to following the homologies in the fossal distributions among related ornate ostracodes. As I have said before, the plan is not yet stable and its elements may be changed when we find more complete animals. But it is useful here, because it brings an increased perspective of order to what has previously been confusing. I would hope that others are encouraged to attempt to test for further modifications.

MAPPING OF A MODIFIED SUCCESSION WITHIN THE RETICULAR PATTERN

Although not with this particular ostracode group, other workers (for example, Sissingh, 1971) have attempted to show how the major ridges of

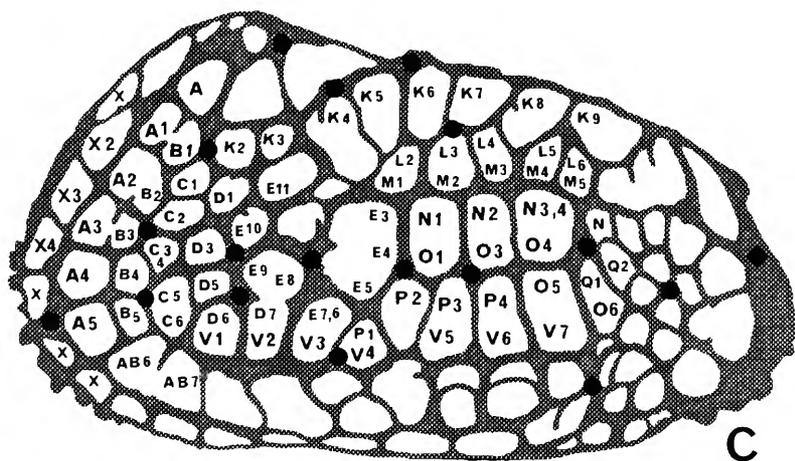
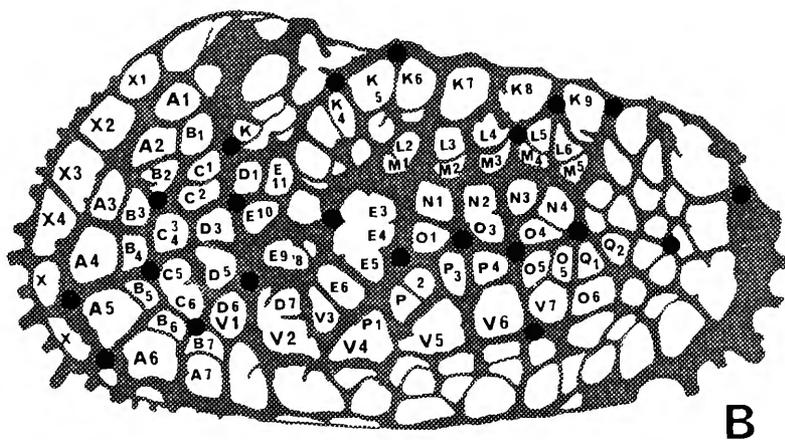
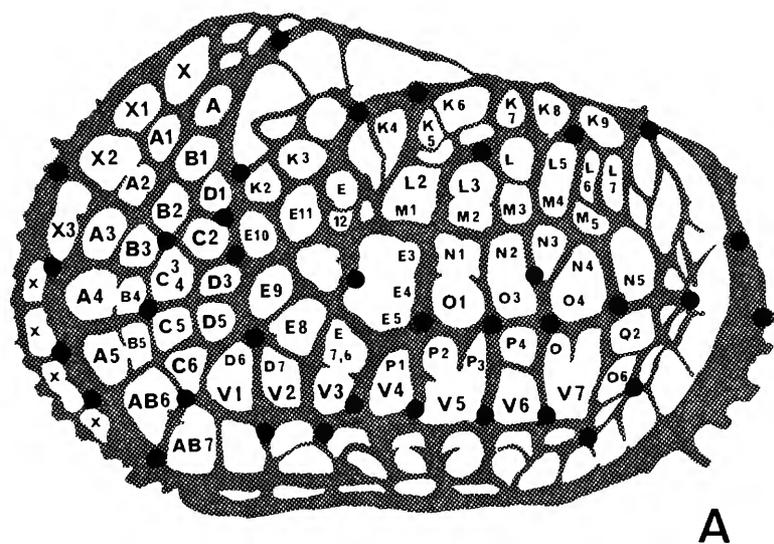
related ostracodes change through time. Until these changes are related to the reticular pattern, however, some serious errors can be made. The misidentification or failure to distinguish *Oblitacythereis* (the "forgotten" *cythereis*) from *Bradleya* demonstrates this point. The major changes of ornament are tied closely to the reticular pattern, and they can only be followed accurately relative to it. Therefore, the description of a possible evolution of *Oblitacythereis* from *Paleocosta* must begin with a description of the gradual changes in the reticular pattern and end with the description of the stabler phases of change or establishment of the principal ridges.

As one examines the stages of reticular development represented by the silhouettes on Figures 5 to 7, the major changes seem to be focused in (1) the anterior ventral region, (2) the region just antero-dorsal to the pore-conulus, which I have called "Capricornus" (adjoining D3 and E10; Benson, 1972, fig. 8), and (3) the area that will form the posterior median field between the median and ventral ridges (principally rows N, O, and P).

Without referring too strongly to the emergence of ridges that accompanies the separation of the reticulum (joining of adjacent fossae), it is noticeable that A4, A5, and A6 join to form AB4, AB5, and AB6 in these series, whereas A1-A3 and B1-B3 remain divided. Diminishment and the vestigial states of dividing ridges are plainly evident. Only when one examines first the disappearance of the anterior rim previously dividing rows X and A, and secondly sees this ridge replaced by a major ridge between rows B and C with ridges radiating distally between rows ABC5, ABC6, and ABC7, does the transformation through the intermediate stages begin to make sense. Whereas circumferential ridges near the margin have strengthened the frontal edge of the carapace, these have been replaced by radiating, finger-like meridional ridges. Between the end member stages in this succession a disordered series can be observed with many redundant structural parts.

In the case of the region near Capricornus, the pore-conulus anterior to the frontal scar (between D3 and E10), the fossa C1 is combined with fossa C2, and the B1-3 series is narrowed as the anterior ridge (between the B and C series) and the ridge connecting the ocular region, Capricornus, and the median ridge are formed. Through the mapping procedure and the discovery of the combination of

FIGURE 6.—Reticular silhouettes and fossal patterns of *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii*: A, from Borde de la Meseta (AG-2, Tortonian); B, from Licodia Eubea, Sicily (Tortonian); C, from Cava Biddiemi, Sicily (Langhian).



many fossae in this region as compared with the gain of prominence of fossae in row X, it would seem that allometric compensation is occurring with expansion near the margin and contraction inward.

In the earlier stages of individual development the reticular pattern of the lateral region posterior of the adductor scars and above the weak ventral lateral ridge consists of about eight fossae, which begin to differentiate as the median ridge becomes stronger with cooler water species. This differentiation may occur both in the Paleogene and the Pliocene. The evolution of this section is shown in Figure 4. The overall structural trend here is from fewer fossae and more connecting ridges (a box-frame design) to more fossae and fewer but better defined connecting ridges (an arch-beam design). The allometric changes as shown in the gain or loss of fossae, are not so much related to expansion or contraction of areas as to growth of the ridges.

Details of the separate stages of development will be given in the species descriptions, but the summary of overall changes given here hopefully will aid the reader in seeing the usefulness of mapping the fossae and their changes. For the most part the diagrams as maps speak more eloquently for themselves than a long written alphanumeric description.

CHANGES IN THE RIDGE SYSTEM

The system of major ridges that forms from enlargement and reorganization of the muri of the reticulum shows greater change than the reticular pattern, which in turn shows more change than the relative positions of the principal pore-conuli. Therefore, among the three systems of pore-conuli, the reticulum (by fossal mapping), and the major ridge system, the latter is most responsive to short-term environmental, adaptive change. The rearrangement is for a more efficient or different distribution of structural members of a frame to meet new strength requirements.

Comparison of Figures 5, 6, and 7 with Figure 4 shows how the ridges of one form have given way to the design of another. Even the vestigial remnants of the former are indicated as the second begins to form through a series of intermediates. The structural trend is not complicated, although the path to a new orderly arrangement may not seem very apparent at first. A Paleogene box-frame design of *Paleocosta* (few fossae and many interconnecting ridges of about equal weight and length) with a major ridge adjacent to the anterior margin is replaced by a more disordered form of a more massive quality. It is assumed that the irregularity of the muri in the anterior of subgenus *Paleoblitacythereis* distributes the stress through a field of which some members tend to be redundant.

The anterior rim of *Paleocosta* degenerates to just a remnant along the anterior venter, while the anterior region in general is crossed by an irregular network of ridges that seem to first strengthen one pathway and then another. In one instance (the Paleocene, Le Kef form; Figure 4c), a major ridge is formed extending from the ocular region ventrally, but this is later supplanted in part by parts of a "bridge" (crudely similar to that of *Bradleya*, Benson, 1972), which in turn is supplanted in the Miocene by the irregular pattern of subgenus *Paleoblitacythereis* that tends to enjoin with fingers reaching for the anteroventral margin. Order returns to the anterior design as the remnants of former marginal and longitudinal ridge elements disappear in subgenus *Oblitacythereis* during the Pliocene and a major ridge system is formed to join the middle with both the dorsum and the ventrolateral regions by way of major transverse ridges set well in from the margins. The marginal rim has been replaced or reinforced by a few strong outward-projecting struts. There is a considerable difference in height between the new ponticulate ridge system and the underlying mural network, which strengthens well-defined fields and reflects the intrinsic complexity of the basic reticular pattern.

As will be seen in the examination of the actual record of these evolutionary changes, the path was not necessarily a direct one, although the morphotypic trend was; neither was it necessary for the end result to exist or be predicted in any one of the intermediate stages. Obviously the hindsight presented here should not be confused with volition

FIGURE 7.—Reticular silhouettes and fossal patterns: A, *Oblitacythereis* (*Paleoblitacythereis*) sp. from El Cuervo, Spain (Middle Miocene); B, *Paleocosta kefensis* from Le Kef, Tunisia (Middle Paleocene); C, *Paleocosta libyaensis* from Djebel el Gattar, Libya (Eocene?).

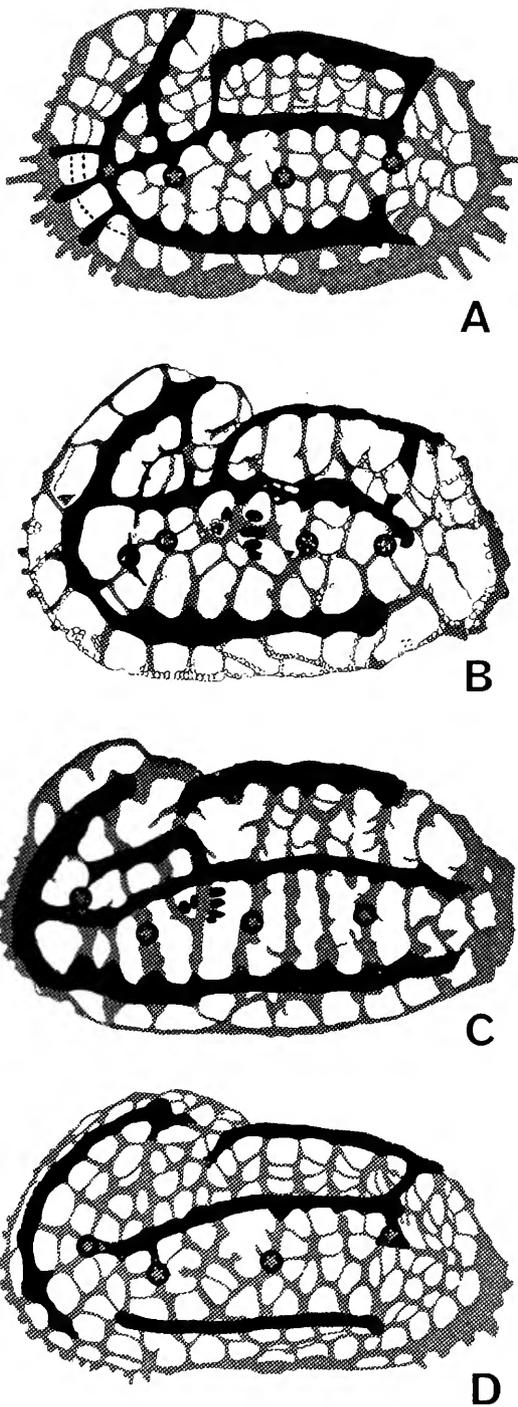


FIGURE 8.—Reticular silhouettes and ridge patterns of tricosine genera: A, *Oblitacythereis* (*Oblitacythereis*) *mediterranea* from Balestrate, Sicily (Zanclian); B, *Bradleya* (*Quasi-bradleya*) sp. from the Malacca Straits (Recent); C, *Chryso-cythere cataphracta* from Enna, Sicily (Tortonian); D, *Costa hermi?* from Korytnica, Poland (Tortonian).

on the animal's part or some kind of orthogenetic guidance. Structural redundancy and variation in design occurring in times of metabolic surpluses is all that is needed to explain how adaptation can be allowed to follow what is later interpreted as a successful structural trend.

STRUCTURAL EVOLUTION

Elsewhere (Benson, 1974, 1975), I have attempted to explain form in ostracode carapaces as structure responding or reacting to the transfer of compressive or tensile stress through its various parts. I have used this concept freely in the description and evolution of the ridge system in the foregoing sections of this report. I contend that there is considerable evidence to show that morphological changes in most ostracode carapaces can be explained by the replacement of one architectural solution with another as the overall shape or environmental demands of the animal are altered. Certainly the process of description of carapace evolution is made easier by the use of structural terms. I do not claim to know whether the dominant causes for the need of such structures, after calcification of the carapace is completed, are more on the outside of the animal or internal. I suspect that they are both.

Löffler (in Swain, 1975:46) has said that in his opinion the evolution of ostracode "structure" [sculpture?] does not require explanation in terms of mechanical principles. It is a fact that evolution among ostracodes has been described, or at least hypothesized, by increasing or decreasing complexity in the hinge or muscle-scar patterns. Little has been said, however, about adaptation of shell sculpture, especially at the species level. I contend that mechanical principles are active in most organic structures, whether we know them or not, especially in skeletal structure. Scale has little to do with the presence of mechanical reactions, only their proportions. *The argument that ostracodes are too small to have exoskeletons that behave in static equilibrium has no basis in any theory I know.* It is also a fact that the understanding of mechanical principles has provided satisfying explanations to morphological changes in ostracodes where none previously existed (especially the refutation of the concept of a bilamellar shell structure

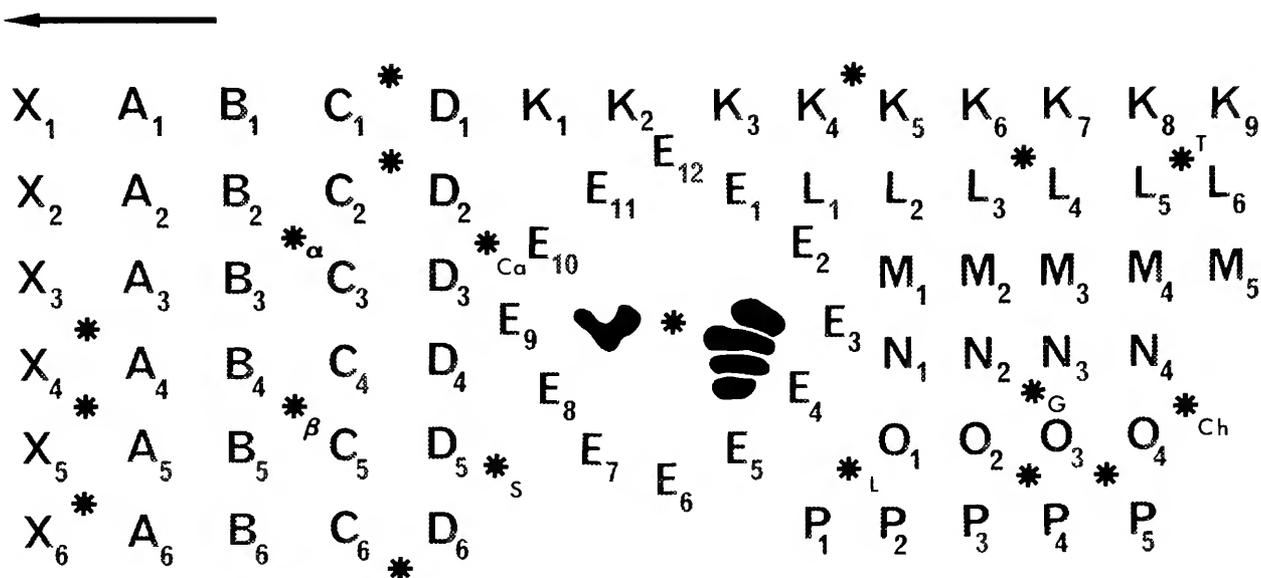


FIGURE 9.—Basic plan or model of the distribution of fossae of *Oblitacythereis* and similar genera with the anterodorsum indicated by the arrow. The rows are enumerated alpha-numerically from anterior to posterior with the sum of the pore-conuli positions (*) homologized with those of the genus *Agrenocythere* (Benson, 1972).

and its subsequent explanation; Benson, 1975). This does not mean, however, that all carapace features are automatically explained. I remind those who are skeptical of the use of such principles that the power of explanation does not lie solely in its completeness, but in its attractiveness to do at least some things well and hold promise for others.

This is probably not the place to enter into a polemic on the basic interaction of concepts of causation and "objective" description. Some at one extreme would argue that a description of a continual change is as close to causation as science can attempt to go. Others would counter that descriptive taxonomy cannot construct classifications without comparison of organs among different organisms. *I have chosen to consider the exoskeleton of the ostracode as an evolving organ, a functioning system undergoing changes in the balance of its parts.* I will let the descriptive positivists who consider their work done when they have enumerated correlation or coincidence among parts, whose names may have no purpose other than to identify these parts, to be limited by their own philosophy. I have used this methodology in the analysis of patterns among the fossae and thus far

have found it conceptually sterile, except as a part of a larger causal hypothesis.

The replacement of elements in the reticular pattern of *Oblitacythereis* to bring about a change in its appearance through time is a matter of observation. Descriptive evidence is presented here on at least three levels of morphologic complexity. One can argue whether the taxonomic divisions given here are appropriate. They represent three developmental stages in architectural change. Only further sampling will show how close this initial effort was to the one that will prove to be the most helpful.

From the structural view, the purpose of muri, and ridges that developed from muri, is to transfer the stress load formed by the inward pull of the adductor, or other muscles and load points, from the central part of the valve eventually to be resolved at the edges. The edges or commissure of the valves are reinforced to absorb the "thrust" and transform it laterally. At the same time the edges or margins of the valves may, as may the rest of the valve, form spinuous projections for defense. The muri may broaden and add to the mass of the valve to increase its weight ("sinking factor"), or they may become rough and clavate to act as an in-

creased irregular surface for the attachment of sediment, which also increases the weight, and possibly acts as camouflage. Whatever secondary benefits the mural, reticular, or ridge systems may have, their basic designs are determined by their ability to react as a static framework. The shell is mostly calcite, which is strong to resist compression but weak under tension.

The valve designs are selectively adapted for their greatest potential strength, depending upon the amount of calcite metabolically available, and this strength may be achieved by more than one structural pattern. It may not always be required during the existence of the species so that redundancy and freedom to carry unused structure in any given individual or population at a single moment in history allows the animal form to suddenly or gradually change in appearance.

The position of a particular ridge or reticular segment is a function of its role in a larger static system. The ridge or segment can be removed as other elements of this system assume their roles of load carrying. It can become stronger more economically by growing higher and thinner than it can by spreading out at a lower level, given the same mass. Muri in a reticulate pattern become discrete ridges because they translate load across a curved surface more effectively, not because of increased mass, but as a geometric product of the removal of mass away from the center of curvature. Because the direction of impact loads cannot be predicted in all environments, that is, ostracodes cannot know genetically if sediment particles will always strike the carapace at a consistent angle; the highly ridged (even ponticulate) ostracode, which is strong and efficient for internally induced stress, may be extremely vulnerable to external breakage in or on a mechanically active substrate. As the same species of reticulate ostracode, which is uniformly and massively reticulate in warm water, shallower than effective wave base, may be efficiently delicate with high ponticulate ridges in colder, deeper or more protected waters.

The evolution of *Oblitacysthereis* is a structural change from an evenly reticulate, medium sized, Paleogene forebearer (*Paleocosta*), with a marginal rim, living in warm shallow water to a tricostrate and marginally spinose, larger descendent living in deeper and ultimately colder water. Its morphologic history is primarily one of reorganization of its

skeletal frame to meet the stress requirements of a mechanically less arduous, but chemically more starved environment.

The most significant structural change takes place in the anterior of the carapace. As in many ostracodes the anterior margin along the commissure is broadly and evenly rounded with the reticular pattern tending to increase in number of fossae and the muri radiate toward the edge. In the early ancestral forms (*Paleocosta*) the margin is narrowly rounded. A marginal ridge is formed along the first mural row away from the edge. This ridge serves to strengthen the edge whose infold is welded to the inner side. The marginal spines are short. The marginal ridge is sufficiently massive so that muri parallel and adjacent to it on the next row inward diminish in size or are discontinuous. The more proximal muri are not so well organized. They begin to be more massive and raised as the region just in front of the muscle-scar node is approached. With a few exceptions the fossae are separate with intervening muri or partial muri, and they are about equal in size, although irregular in shape and organization.

This design is probably responsive to the rigorous habits of the shallow-water ostracode, whose anterior appendages are shorter, simpler and stronger than those of its deep-water relative. The focus of activity and need for valve-edge strength tends to be in the direction of the anteroventral margin. The curvature of this margin is prolonged. Also there is an emphasis in the marginal ridges (sometimes a rim or flange in other ostracodes) as they are directed or extend from the ocular regions toward the anteroventer of both valves to converge with the ventrolateral ridges. One can see many of the muri in other parts of the carapace align themselves toward this active and vulnerable region of the valve margins. This focus of strength by the convergence of major ridges in the anterior of the ostracode carapace never entirely disappears, even in the planktonic myodocopids, yet it diminishes significantly in depth zones of less mechanical agitation in the substrate, and the realignment of muri follows this change.

Therefore, were the ostracode to change its habitat from one where its activity was less focused in one direction, to where those bending moments near the anteroventral edge of the valves are potentially lessened, the stresses of the ridges and muri

of this region might become more uniformly distributed around the margin and a new arrangement would be selectively preferred.

In *Paleocosta* the eye tubercles are well developed suggesting that it lived in waters of less than a few hundred meters deep. The subgenus *Paleoblitacythereis* is blind. This morphologic change, and evidence of its faunal associations, indicates that the animal is moving into deeper water. However, there is strong indication to suggest that the relative amount of carbonate or mass in the shell is decreasing or that the water temperatures were appreciably lower. The anterior margin becomes more rounded, more spinose. The size of the carapace is not greatly changed (still around 900 microns).

The anterior marginal ridge of the subgenus *Paleoblitacythereis* disappears in the anterodorsal region. In the anteroventral region, the ridge either remains in part or forms into a flange or rim, spines form at the junction of the three muri that are normal to the edge, or the ridges in the critical anteroventral focal region form buttresses with the margin. The remainder of the carapace architecture is also being affected by the increased size of the longitudinal ridges, but it is in the anteroventral marginal area where the greatest change in the mechanical load can be observed. The marginal spines are becoming elongate and the largest ones are concentrated in the anteroventral sector of the margin. It is obvious that the strength requirements are being projected outward and not concentrated just along the edge of the shell. *Oblitacythereis*, in the last stages of its development has buttresses that support a heavily framed spinose margin and extend inward at right angles to the direction of the former marginal ridge. The anterior margin has become very broadly rounded and the distalmost row of fossae (X_{a-n}) are well developed and discrete. The anterior has expanded outward allometrically.

In other parts of the carapace, the shell design in *Paleocosta* is changing from a series of large equidimensional and normally opposed frame members, distributed over most of the lateral surface, to concentration of the stress loads into longitudinal series of some of these members of *Oblitacythereis*. Ridges arise from some muri, other muri diminish in size, some that have disappeared reappear. The reorganization can be followed in the diagram of Figures 5, 6, and 7. In general a few ridges with less

relative mass now do the mechanical work that was formerly done by a more massive frame. This is a common happening in ostracodes, and I have previously described it in *Bradleya* (Benson, 1972, 1975). It can be seen in many other ostracodes.

What is particularly interesting in the history of *Oblitacythereis* is how the structural support of an outwardly growing anterior margin is shifted inward, and the work of the marginal ridge is assumed by a ridge, two fossal rows inward toward the adductor region. Three longitudinal ridges arise in the lateral posterior, but we can see this happen in many ostracodes, as I have shown in Figure 8B-D with *Costa*, *Bradleya*, and *Chrysocthere*. The major difference here in the climax of *Oblitacythereis* development is in the use of a ridge that is formed from the ocular region extending downward to structurally tie the inner peripheral ridge to the median ridge. This provides a very strong inner structure comparable with the bridge of *Bradleya*, the castrum of *Agrenocythere*, or the dorsal muscle-scar node of many other ostracodes.

Lastly, the overall structural change in *Oblitacythereis* results in a general change in shape of the whole carapace from ellipsoid to rectangular. These terms are frequently used in older descriptions of carapace form. This rectangularity is often seen in ridged ostracodes, and sometimes heavy taxonomic emphasis is given to it. G. S. Brady was especially impressed with this difference in shape, and it is emphasized in many of his species descriptions. How important is this from a structural point of view?

The more rectangular and angular appearance of some "reticulate" cytherid ostracodes is a consequence, not of an increase in the amount of reticulation (that is, the number of mural elements), but in the increased height of a few number of elements into higher often reticulate ridges. The increase in height of the ridges is an attempt to gain leverage, inertial moment, mechanical advantage for the transformation of stress from the adductors and hinge to the margin with the least possible material. Therefore, a strongly costate ostracode has moved its strength outboard (away from the center of form) and this should reveal to us most clearly where most of the mechanical work is being done. We have seen a shift of work load in the anteroventral marginal region of *Oblitacythereis*. To some extent it can be seen in the overall change of design from box-frame of *Paleo-*

costa to arch-beam of the Pliocene *Oblitacythereis*. The primary difference shown in the structural development of *Oblitacythereis* is not simple in the general emphasis of an outboard truss system, but in the way it solves the problem of forming a bridge (in the general sense and not just like *Bradleya*) from the adductor region of the anterior margin.

STRATIGRAPHIC SIGNIFICANCE

It is often stated that the best biostratigraphic indicators are those fossil taxa that are abundant in the fossil record, have a broad geographic distribution, and yet have a restricted stratigraphic range. Also they should be undergoing gradual and identifiable modification in morphology commensurate with the passage of time. How does the *Oblitacythereis* lineage described here fit these requirements?

It would seem that ostracodes in highly diverse populations tend to have shorter ranges, stratigraphically and geographically, than do those in assemblages with few species. Faunas of the deep-sea, brackish, and fresh water habitats fall into this latter category. Therefore, it is not surprising to find *Oblitacythereis* over the whole of the Tethyan and Mediterranean regions and the eastern Atlantic near the influence of Tethys; however, it was unexpected to discover it living today in the South Atlantic. No doubt it will be found as fossils in bathyal sediments in many places along the eastern slopes of Africa. As Sanders (1968) has indicated, it is more difficult for a species to cross the psychrospheric-thermospheric barrier than to migrate laterally thousands of miles. It is in this area of transition between the ocean floor and shelves, i.e., the active and passive marginal areas, that are of prime interest to students of the history of oceans. Therefore, if animals are found at all in this zone, and if these remains are sufficiently complex and understood to record the gradual passage of time, it can be stratigraphically important.

Until the drilling of Site 372 in the Algero-Provencal Basin, the oldest specimens that are called *Oblitacythereis* (i.e., *O. (P.) ruggierii* (Russo)), were found in sediments identified as Langhian (about 14×10^6 BP, according to Berggren and Van Couvering, 1974) by Ruggieri (the *Praeorbulina* zone,

N-8, 9; pers. comm.) from the Cava Biddiemi locality (between Santa Croce Camerina and Marina Ragusa) in southeastern Sicily. Also the type of *O. (P.) ruggierii* is from the Langhian of Sutera in northern Italy (Russo, 1964) from the same Zone N-8 or 9. At Site 372 two specimens of *O. (P.) ruggierii* were found at a level (core 33, section 3) identified as Burdigalian. These were found with *Agrenocythere hazelae* and are thought possibly to be allochthonous, which would make them older. Since they were not complete specimens, their developmental stage could not be identified.

The youngest specimens from the Mediterranean region are from Zone N-19 or close to this near the base of the *Globorotalia margaritae* zone at Balestrate and Buonfornello in Sicily. Intermediate occurrences are indicated on Figure 2. Of special interest is the presence of *O. (P.) ruggierii* in the upper Tortonian blue marl (the marine phase) at Licodia Eubea in southern Sicily. The exact position of collection of the sample relative to the lower Messinian boundary is not known. In fact, that boundary is still in doubt even at Capodarso, the stratotype. I would state the age of the Licodia Eubea specimen as just slightly younger than the one from AG-2 of the Borde de la Meseta section (Upper Tortonian, Perconig and Granados, 1973) in Andalusia, Spain (north of Carmona) on the basis of a further stage of development of the anterior region. The ages are very close, but the former specimen seems to have fewer relic ridges around the lower part of the anterior end of the median ridges, and the anteroventral margin is forming the massive rim and normal ridge elements more typical of the last stages of *Oblitacythereis* development. Further collecting and definition of the boundary will serve to test this developmental hypothesis.

If in fact the evolution of the structure of *Oblitacythereis* is in a direct series, identification of these stages could help to modify age determinations that fall within the longer foraminiferal zone intervals such as N-16 and N-17 that cover a five million year period without a significant break. I want to call attention to this potential so that others may also add the data we have at present as these are not many.

The identification of Lower Pliocene age for the Myrtaou Formation in Cyprus now seems readily

apparent from the presence of *O. mediterranea* in the Zanclean of Sicily, in southern France (Chateau Vaugrenier, 2 km north of Antibes), and at DSDP Site 372 in the Algero-Provencal Basin (core 3, section 3, interval 103–109 cm). A few years ago, however, there were quite different views of the age of the Myrtou Formation, which was thought to be Messinian, with the evaporites below being among the oldest in the Miocene of the eastern Mediterranean. I was confused about this age in suggesting the possible continuity of *Oblitacythereis* through the salinity crisis (Benson, 1973a), which in retrospect seems to have developed from not enough confidence in the ostracodes and too much in the opinions of others on stratigraphy.

The discovery of *Oblitacythereis mediterranea* in section 5 of core 5 (interval 70–80 cm) of DSDP Site 376 in the floor of the Mediterranean just west of Cyprus represents the youngest occurrence known of this genus in this sea. It was found in a moderate brown marl in a condensed Pliocene section on the boundary between nannofossil zones NN-15 and NN-16 (Middle Pliocene). Ramil Wright of Florida State University (pers. comm.) found that the benthic Foraminifera of this core were middle bathyal in habit, which corresponds to the ostracode fauna.

Of special interest has been the recent discovery of an abundant *Oblitacythereis mediterranea* fauna in the lower part of the Bou Regreg section (of Messinian age) east of Rabat, by Alexandro Bossio of the University of Pisa (pers. comm.) and examination of this fauna by me at Pisa in September 1976. Dr. Bossio is presently in the process of describing this important ostracode fauna and it would be inappropriate for me to comment in detail on his discoveries. However, it would seem that he has found the ancestral fauna of that which invaded the Mediterranean during the Pliocene. The advanced nature of the architectural development of *Oblitacythereis* suggests the influence of coastal upwelling and also the fact that *O. mediterranea* had existed in the Atlantic sometime before it came into the Mediterranean during the Pliocene.

In their study of the ostracodes of the Maltese archipelago, Russo and Bossio (in prep.) kindly loaned me their manuscript and SEM photos to review. They have distinguished eight different faunal assemblages of upper bathyal (Aquitanian

to Lower Tortonian) and shelf types (Middle Tortonian-Messinian) that contain an impressive sequence of subgenus *Paleoblitacythereis* developmental stages. In large part their results concur with those given here, although I believe their stratigraphic control for the upper part of the Middle Miocene in the central Mediterranean is much better than mine.

Of particular interest is the discovery of a single broken left valve by Dr. Russo in the Burdigalian of Malta (Zone N-6; interval 3, sample MTA6-C716) exhibiting form and architectural properties of subgenus *Oblitacythereis*; that is, the presence of the interoconcentricum or what first appeared to be this critical structure. Another form from the Tortonian of Montegibbio superficially looked like subgenus *Oblitacythereis* through the binocular microscope, but it proved to be less similar under the SEM. There seems to be no question that some forms of *Oblitacythereis* exhibit an increased boldness of the ridges that ultimately become the interoconcentricum in the Messinian of Morocco and the Pliocene of many parts of the Mediterranean; however, none of these has this or other parts of the primary ridge structure elevated (punctulated) away from the rest of the reticulum. All retain the typical open fossae of subgenus *Paleoblitacythereis* without the differentiation of primary and secondary ridge systems as are so distinct in subgenus *Oblitacythereis* and necessarily part of its extreme architectural development. This confusion in recognition by Dr. Russo and myself emphasizes the need for clean specimens and SEM photos, at least at this early stage in our understanding of the development of *Oblitacythereis*. It is my conclusion that in spite of efforts, or the appearance of efforts, of organization of the reticulum of *Oblitacythereis* in the Middle Miocene, this is not successful and stable until the Late Miocene or Early Pliocene.

FAUNAL ASSOCIATIONS AND ENVIRONMENT

The other ostracodes most likely to be found associated with *Oblitacythereis* can only be estimated from one sample of a Recent assemblage and 14 samples of fossil assemblages of Neogene age. It was noted that *Oblitacythereis* is infrequently found associated with allochthonous valves of shal-

low species. However, as in the case of sample C-12 of the upper part of the lower marl of the Andalusian stratotype or in the Burdigalian sample of DSDP Site 372, it may itself occasionally be found as allochthonous, reworked specimens. Therefore, as this ostracode is an inhabitant of slopes that could be unstable, some care and notice of field conditions must be given for possible mixing.

In the fossil record *Oblitacothereis* is most frequently associated with the genera *Krithe*, *Cytherella*, and *Henryhowella*; less often with *Bairdia* and *Ruggieria*; and it has been found with the psychrospheric genera *Agrenocythere* and *Bythoceratina* (esp. group *scaberrima-vandenboldi*). It is seldom found abundantly in assemblages with more than eight other species. This low diversity, even with samples containing more than 100 specimens, suggests a deep assemblage.

In the sample of living ostracodes from off southwestern Africa (AII42-203) containing over 200 specimens, *Oblitacothereis luandaensis* comprises three-fourths of this number with only five other species present. The other genera present were *Bathocythere* (a post-Miocene genus also found in the Mediterranean), *Cytherella* (a smooth species), a variant of *Bosquetina*, and *Bythoceratina scaberrima* (found in the Pliocene "Trubi" of the Mediterranean and in the deep sea of many parts of the world).

In its deepest range, as exemplified by samples from the Lower Pliocene of Buonfornello and DSDP Site 372 in the Algero-Provencal Basin, or the Serravallian of Cava Biddiemi in Sicily, or in the "El Cuervo" section of southern Andalusia, *Oblitacothereis* is associated with upper psychrospheric ostracodes such as *Agrenocythere*, *Bythoceratina*, and even *Bradleya*. However, this deeper association is not common, and these samples may in fact represent near-threshold conditions (Benson, n.d.b.), where mixing of basin and oceanic water-masses and faunas occur.

At the shallower extreme of faunal association, such as might be represented in the Lower Pliocene Myrtou Formation at its stratotype locality in Cyprus or in the Pliocene section near Antibes in France, such shelf genera as *Costa*, *Buntonia*, *Pachycaudites*, and *Urocythereis* have been found with *Oblitacothereis*. These cases of mixing with shelf ostracode species are not thought to be common, however.

The size and architectural range of associated forms seems to be that expected of an ostracode of an intermediate depth and temperature range. Those of Miocene age seem more robust than those of Pliocene age, however. This reduction in calcification during the Pliocene is believed to be caused by lower temperatures when the psychrosphere was present. Such vertical mixing of cooler bottom waters with the warmer upper layers was probably diminished as the Mediterranean became a series of isolated basins during Late Pliocene when *Oblitacothereis* seems to disappear.

In summary, the faunal association of *Oblitacothereis* today and in the Neogene of the Mediterranean both before and after the "salinity crisis" is upper bathyal. Some of the ostracode genera associated with *Oblitacothereis* are known to extend down into the deeper areas of the psychrosphere. But *Oblitacothereis* is not commonly associated with typical psychrospheric ostracodes. Therefore, a temperature range equivalent to that now occurring in the world ocean on its eastern shelf boundaries where upwelling is known could be extrapolated into the Tethys-Mediterranean at somewhere near 12° to 14° C. This estimate needs much more study, but for the present represents that range above the psychrosphere (<10° C) and below that of a shelf of intermediate latitudes (16° to 20° C). Of course, the depth of this temperature range may vary considerably from that in a restricted basin satellite to that of the world ocean. *Oblitacothereis* would follow the emergence or submergence of such isotherms and be strongly affected by the control of thresholds on restricted basins. During the Middle Miocene, *Oblitacothereis* may well have lived in several thousand meters in a restricted thermospheric basin such as Tethys. This must have been the circumstances of the fauna just before the "salinity crisis." Today in open ocean, its depth range is far less because of the very rapid change to colder waters down slope.

EXTINCTION OF *Oblitacothereis* IN THE MEDITERRANEAN

Although *Oblitacothereis* has never been a common ostracode within the Tethys-Mediterranean, the failure to find any record of it younger than Pliocene begs the question of its extinction in this region. Among those ostracodes with which it is

most commonly associated, *Krithe*, *Bairdia* (*Neonesidea*?), *Cytherella*, and *Henryhowella*, all except *Oblitacysthereis* are found in abundance in the Pleistocene and the present deeper areas of the Mediterranean. Does this represent a failure to report *Oblitacysthereis*, or did it become extinct because of the re-occurrence of thermospheric conditions within the basins after the Pliocene?

TESTING THE MESSINIAN SALINITY CRISIS HYPOTHESIS

This historical question (Benson, 1973a) should be made as simple as possible: Is *Oblitacysthereis* morphologically and developmentally continuous in its record of morphological change from before the Messinian salinity crisis to afterward? Because all fossil records are inherently discontinuous, it must remain a matter of judgment as to whether a morphological series is necessarily an unbroken succession or not. The judgment of continuity rests on the *inability* to imagine or measure a significant intermediate step not already considered.

The argument that a significant evolutionary change, coincident with the Messinian salinity crisis, takes place in *Oblitacysthereis* is as follows:

1. Changes in the distribution of pattern of the pore system are measurably greater (by Theta-Rho analysis) between pre-Messinian Tethyan species (including the one living in the Atlantic today) and the Pliocene Mediterranean species than within these groups. This significant shift in shape allometry suggests there has been more environmental change inside than out of the Mediterranean region. Whether the Mediterranean species came in from the Atlantic cannot be resolved by the analytical method, only that it did not likely come directly from Tethys.

2. The multiplication of the number of muri that divide fossae occurred more quickly between the last known Miocene forms and the earliest Pliocene forms than at any time in the overall history of the group. This is a measurable property that is probably a secondary effect of a more important structural adaptive change. The same tendency is observed in Recent species of other genera ranging into deeper or colder waters (Benson, 1975). It may suggest simply that at the depths where *Oblitacysthereis* was found the Mediterranean was colder in the Pliocene than the Tethys was during earlier epochs.

3. The development of a coherent structural system among the major ridges is completed in the Mediterranean Pliocene. No transitional structural phases were found in the latter stages from subgenus *Paleoblitacysthereis* in the Miocene of Tethys to subgenus *Oblitacysthereis* in the Pliocene of the Mediterranean. The closest link yet known in this structural succession is from the Moroccan Upper Miocene of the Atlantic, and this morphology has yet to be studied in detail. A similar change was noted in *Agrenocythere*, a deeper psychrospheric ostracode (Benson, 1972:23).

What about a counter-argument that the changes in shape allometry, reticular pattern, and ridge structure could have just as easily taken place within a refugium in the Mediterranean region? This is to argue the likelihood of the existence of an unknown relic population within the Mediterranean as compared to accepting another just outside of the Iberian Portal. One actual sequence of recorded change in fossil evidence inside the Mediterranean will demolish much of the argument presented here, but so far it does not exist. This sequence, however, is only inferred outside of the Mediterranean. Moreover, *Oblitacysthereis mediterranea* of Messinian age in Morocco recently discovered by Bossio seems to have demonstrated the origin of the Pliocene fauna.

The above arguments are related to changes in measured properties of the carapace of *Oblitacysthereis*. One is change in proportion (allometry), another is change in number (divisions of fossae), a third is change in continuity (joining of muri to form ridges). The result is evidence of a discontinuity in form in development as seen in the Mediterranean region. The appearance of change, however, is not enough. It is equally important to show that these changes are coincident with structural adaptation that could have been caused by the conditions of a coming crisis and its aftermath. Otherwise, it is conceivable that proportions, numbers, and continuity in features can suddenly change and yet not represent anything more than a simple structural realignment of these parts.

The historical significance of the subgenus *Paleoblitacysthereis* is its architectural adaptation to *deep warm water* in the Miocene Tethys Sea. It contrasts in structural features with the subgenus *Oblitacysthereis* that was adapted to *not so deep cooler water* in the Pliocene Mediterranean. The

fact that these conditions are incompatible environmentally and coincide with other geological evidence of the salinity crisis is to me the most compelling argument for the extent of the crisis.

In a study based on visual morphological inspection of what were their considered diagnostic characters, I stated (Benson, 1973a) that "*Oblitacythereis*" (nomen nudum and including both subgenera) furnished evidence (Figures 5, 6) of the continuity of the marine environment at considerable depth in the Tethys-Mediterranean complex through the Messinian salinity crisis. Deep faunas with similar generic content appear just before and just after the crisis. This assertion was based on less than half of the samples now available and on comparison with the depth distribution of the presently extant species *O. (P.) luandaensis*. At the same time, the continuity of "*Oblitacythereis*" was compared to that of the genus *Costa* and the discontinuity of the psychrospheric genus *Agrenocythere*.

The morphologic continuity of "*Oblitacythereis*" at that time seemed self evident. The animal was thought to be unusual and rare, unknown outside of Tethys. The differences between the specimens of *Oblitacythereis* from the Miocene and Pliocene did not seem to be much greater than the range of form that might be expected in an ostracode of outer shelf or upper bathyal depths. Many ostracode workers had identified several of the same species of *Costa* from the Tortonian and the Pliocene in the central Mediterranean. In retrospect this was too much to assume. I now believe the conclusions were partly in error; that is, the depth to which continuity might be demonstrated was incorrect. The criteria for morphological continuity did not have sufficient resolution, and it now seems that *Oblitacythereis* did not cross the Mio-Pliocene boundary in the Mediterranean.

CLASSIFICATION OF *Oblitacythereis* AND ITS RELATIVES

Oblitacythereis, *Paleocosta*, and *Costa* should be assigned under the new Tribe Costini Hartmann and Puri, 1974, within the Trachyleberidinae Sylvester-Bradley. Hartmann and Puri (1974:38) diagnosed the Costini as follows:

Subrectangular, elongate carapaces with three to four elongate ridges with secondary ornamentation; of pits prominent anterior and posterior denticulations; both normal and

sieve type pores.

The following genera were included:

Costa Neviani, 1928 (= *Trachyleberidea* = *Spinicythereis*)
Carinocythereis Ruggieri, 1956
Cativella Coryell and Fields, 1937
 ?*Hazelina* Moos, 1966 (= *Curfsina* Deroo, 1966 = *Repandocosta* Hazel, 1967)
Protocosta Bertels, 1969
Paracosta Siddiqui, 1971
Chrysocythere Ruggieri, 1961
Moosella Hartmann, 1964
Ponticythereis McKenzie, 1967
Puriana Coryell and Fields, 1937
Robertsonites Swain, 1963

Nine other genera were considered by Hartmann and Puri (1974) with uncertainty to belong to the Costini. These included *Cistacythereis*, *Gyrocythere*, *Falunia*, *Kingmaina*, *Oertliella*, *Platycosta*, *Platycythereis*, *Quasihermanites*, and *Stigmatocythere*. Altogether 19 genera were included with 5 subgenera. This would make the Costini the largest tribe in the Family Trachyleberididae and possibly the largest tribe of ostracodes known or suggested.

What about the validity of this concept of the Tribe Costini? A few points should be brought out about this group, as much as can be learned about the underlying assumptions of our evaluation of characters of ornate ostracodes.

First, *Costa* in itself is a complex genus that consists of two large groups of forms with a definite divergence between the American group known especially from the Neogene of the Caribbean (van den Bold, 1970) leading to *Cativella* and those known from Europe (Benson, n.d.a.). These groups are quite likely to be separate valid genera. The Paleogene ancestors of the Tethyan *Costa* and *Oblitacythereis* are known in *Paleocosta*, possibly in *Paracosta*. The Paleogene ancestors of the American "*Costa*" may be known in *Protocosta* and *Platycosta*. The affinities of the Paleogene Tethyan and American groups are not known to me at present, but I suspect that they also include close relationships to *Trachyleberidea* and *Hazelina*.

I agree with the skepticism as expressed by Liebau (1975) of the Costini as the group described by Hartmann and Puri. I know the Cretaceous and Paleogene ostracodes less than he, but I agree that forms like *Oertliella*, *Curfsina*, *Spinicythereis*, *Platycythereis* are not closely related to *Costa*, and that *Puriana* and *Agrenocythere* are quite different ostracodes from *Costa*.

The important question is not, "How would Dr. Liebau and Dr. Hartmann arrange these groups such as the Costini?", but "Why would I, others, and they arrange them differently?"

Hartmann and Puri (1974:35, 41) have been critical of the "balance of systematical weight" of some of the ostracode families that Hazel (1967) and myself (1972), among others, have proposed for the more ornate ostracodes, especially those with important fossil records. It is obvious that from their overall viewpoint, these latter groups seem to contain considerably more systematic complexity derived from the study of the carapace than is reflected in the diversity of their "soft-part" anatomy. They are equally concerned about the escalation of the rank of these groups to higher taxonomic levels.

These are valid concerns, if not secondary in their importance to other pursuits of the study of ostracode morphological diversity. Classification is always an ephemeral pursuit and may depend heavily on one's sense of proportion, as well as on different opinions about the value of certain characters. I have written elsewhere (Benson, 1972, 1974, 1975), as in this report, that I believe our understanding of what constitutes the characters used for descriptive morphology in ostracodes is still incomplete. We continue to mistake form for structure. It will remain in a state of flux until a satisfactory developmental theory of morphological change is presented and used.

It is apparent that, so far as the ornate ostracodes are concerned, Hartmann and Puri attempt to classify ostracodes by (1) consideration primarily of the potential complexity of the antennae and the mandibles with their respiratory plates, (2) a sense of proportion of the number of taxa in each category, and (3) obviously the importance of prior classifications. Hartmann and Puri (1974:35) state very clearly that they "do not think it is possible even now, to trace the different evolutionary lines [of the Trachyleberididae, Hemicytheridae, Cytherettidae]." Since it is less easily done in other groups of ostracodes, we can conclude that Hartmann and Puri do not place much confidence in evolution at all as a basis of the classification of ostracodes. They present no developmental theory of soft-part evolution. They (1974:35) do state, however, that when "we regard the soft-part morphology (which includes characters more diverse than

the carapace alone) of other ostracodes and compare it with that of Hemicytheridae-Trachyleberididae, the closely related morphology of the latter is clearly visible." To them, diversity of form is of primary importance, but not of structure.

It is not my purpose to impugn the taxonomic judgment of Drs. Hartmann and Puri. It is too easy to simply disagree with their classification and present another scheme with different evidence. I would rather examine their assumptions and attempt to understand how they came to the conclusions they did so far as these affect the present problem of the Costini. I have heard them express all too often their a priori regard for the classificatory value of the soft parts and the handicap under which paleontologists must work with an insufficient fossil record. Is this an important issue? My experience tells me that it is not. However, perhaps they are correct; but if so, why?

The soft-part information at hand about *Costa* would come from Hartmann's drawings of *Costa variornata* (Hartmann, 1974, pl. 40). The fact is that, in spite of their remarks, three subfamilies and ten tribes of the Trachyleberidinae as diagnosed by Hartmann and Puri in their classification are based entirely on carapace characteristics. Nothing is said about soft-part characteristics for the Costini. To reach the Trachyleberididae in their key to the families, Hartmann and Puri (1974:22-24) require seven discriminatory steps. The first six consider soft parts and the last one is concerned with radial-pore canals (easily visible to transmitted light examination together with the soft parts). Of the soft parts used, the "Strahlen," referred by me and others (perhaps erroneously) as the mandibular epipodite, is noted as "equally constructed" or well developed (not reduced); the thoracic legs are symmetrical; the mandibular palp is not broad, has at least one terminal joint, and normal masticatory endites. In their diagnosis of the Trachyleberididae, however, they refer to a six-jointed "antennula" with the spinneret bristle reduced in the female and the absence of the knee apparatus. There are only two "Strahlen" (I count five) of the mandible.

In spite of their complaint of vagueness in some parts of the leg descriptions of the bradleyinae and trachyleberid soft-part morphology of my earlier study (Benson, 1972), I find no essential differences in my understanding of basic trachyleberid soft-part morphology than that of either Hartmann (espe-

cially his drawings of *Costa variornata*) or for that matter of Skogsberg (1928) of the drawings of Sars (1925). Hartmann and Puri state that the soft-part morphology of the type-species of the new [and old] subfamilies and tribes of the Trachyleberididae are not well enough known to use it for a further refinement of the classification. I challenge this to be factual. It is generally known that the appendage morphology just does not vary sufficiently to be of much value in discriminating among these forms. Skogsberg attempted to use the morphology of the hemipeni to discriminate among species. I suggest that those who would question this point to examine Skogsberg's (1928) attempts to discriminate among "*Cythereis*" forms from Tierra del Fuego in the context of modern genera or higher taxa.

Certainly one can discriminate between families with the hemicytherids on one end of the range of variation and the trachyleberids on the other. The thaerocytherids are transitional in appendage morphology between these two end points. Using Dr. Hartmann's (in Hartmann and Puri, 1974) criteria, where would you place *Procythereis torquata*? He has placed it in the Aurilini, but the knee apparatus he requires is absent (Benson, 1973b: 1:17:93-96). There are possibly three "Strahlen"; the carapace is thaerocytherid with two frontal scars. It is understandable why Dr. Hartmann places *Procythereis* in the Aurilini, because he has identified an obvious aurilid from South Africa as *Procythereis foveata* (Hartmann, 1974, pls. 58, 59). It is not *Procythereis*, as can be seen in the muscle scars, the carapace, and the appendages. It is easy to compare my studies with his own, but it is probable that so far as classification is considered, we both will be proven wrong. Some of these characters are polyphyletic.

The fact is that the soft parts do not consistently vary with one group of characters, such as the "Strahlen," or the knee apparatus, or the segmentation or fusion of the second antenna, so as to form even a single gap within all of the ornate ostracodes. It is very probable that reduction in number and fusion in these characters is polyphyletic or it is yet to be proven otherwise. The complex knee occurs in trachyleberids as well as hemicytherids; division of the muscle-scars occurs in several groups. There is a strong correlation between the length-thickness ratio of appendage segments, fusion, and

the shallowness of the water.

The value of carapace characters or the value of soft part characters is not predetermined as sacrosanct in the classification of ostracodes. It is only by attempting to group ostracode genera and species by their evolutionary history of phyletic proximity relative to their distribution can we approach a realistic ordering of diversity. I say "attempt," because no classification is more than a postulated relationship. The appendages of *Bairdia* (sensu lato) vary and the carapace is conservative. The appendage morphology is "useful" for classification (Maddocks, 1969), the carapace less so. In the Costini, the carapace varies systematically, and the soft parts do not, so far as I can tell at present. Both Hazel (1967) and I (1972) have emphasized the usage of the Thaerocytheridae as a transitional group of ornate ostracodes between the Trachyleberididae and the Hemicytheridae. It is admittedly a taxonomic convenience, but it is a useful one. It does contain many forms that have transitional carapace and appendage characteristics, including *Procythereis*.

Lastly, to address the adequacy of Hartmann and Puri's diagnosis of the Costini based on carapace characteristics, it would seem that by exclusion more than by study of this group, they have placed heavy emphasis on the presence of ridges. The reference to "secondary ornamentation" must mean the difference in prominence between the ridge system and the remainder of the reticulum. This is not diagnostic as it is found in almost every reticulate ostracode group as is the presence of sieve and normal pore canals and terminal marginal dentition of varying strengths. It should be clear also by the present study that ridges alone do not a costine make.

If I seem heavy in my criticism and if it has merit, it is because I wish to call attention to factual discrepancies in the results of classification based on inadequate morphological concepts. This is not the result of whether soft parts or hard parts have prime importance. I have shown that carapace morphology as practiced here is inadequate. Liebau (1975) has done the same only over a broader spectrum. The problem is not the lack of good faith or of effort by Drs. Hartmann and Puri, or even their concern for the presence of a comprehensive classification. It is first a lack of understanding of why ostracode morphology changes and second,

enough information of how it changes. The second depends on the first and is a task of many contributors. However, the first is one of conceiving an appropriate developmental theory and testing. It is hoped that this report contributes somewhat to this goal above all others.

THETA-RHO ANALYSIS

The principal results of the Theta-Rho analysis are shown in Figures 10 and 11. For details of this mathematical comparison of allometry the reader is referred to a similar and more comprehensive study by the author of the genus *Costa* (Benson, n.d.c.). The purpose of the analysis is to test for the retention of a genetically conservative pattern of pore distribution as an expression of possible closeness in hereditary or phylogenetic relationship. It is based on the supposition that this closeness, or least taxonomic distance, would tend to become obscured in morphologic features strongly affected by environmental differences, but be retained in an organ system protected by the more reactant systems. The pores are believed to represent the tactile ends of the nervous systems. Such systems are often conservative in invertebrates, and their network or pattern of distribution would tend to change less than some of the other patterns of homologous features that one might measure. They also have the advantage of being a series of points whose homologous positions can be accurately plotted. Lastly, there is the very great improbability that regardless of the biologic causes, no two animals would have an almost identical geometric pattern of any kind within a series of arbitrarily selected points unless there was some genetically controlled factors involved. The farther one gets away from this identity, the less valid this concept becomes. However, one can imagine many such arbitrary patterns to be expressions of homologous symmetry without being genetically significant on the level desired here. Therefore a cut-off point of values of 0.8 has been selected, above which the mathematical relationship rapidly becomes meaningless. This level is chosen in comparison with more conventional means of selecting species differences. A Theta-Rho value of less than 0.8 might indicate the same, closely related or sympatric species.

With this explanation and reference to Figures 10 and 11, it is obvious that the closest linkage

exists within species recognized on other morphologic grounds, and there is a gap between *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* and *O. (O.) mediterranea*. Also there is a close relationship between *O. (P.) ruggierii* and *O. (P.) luandaensis* in spite of differences in their age and geographic distance.

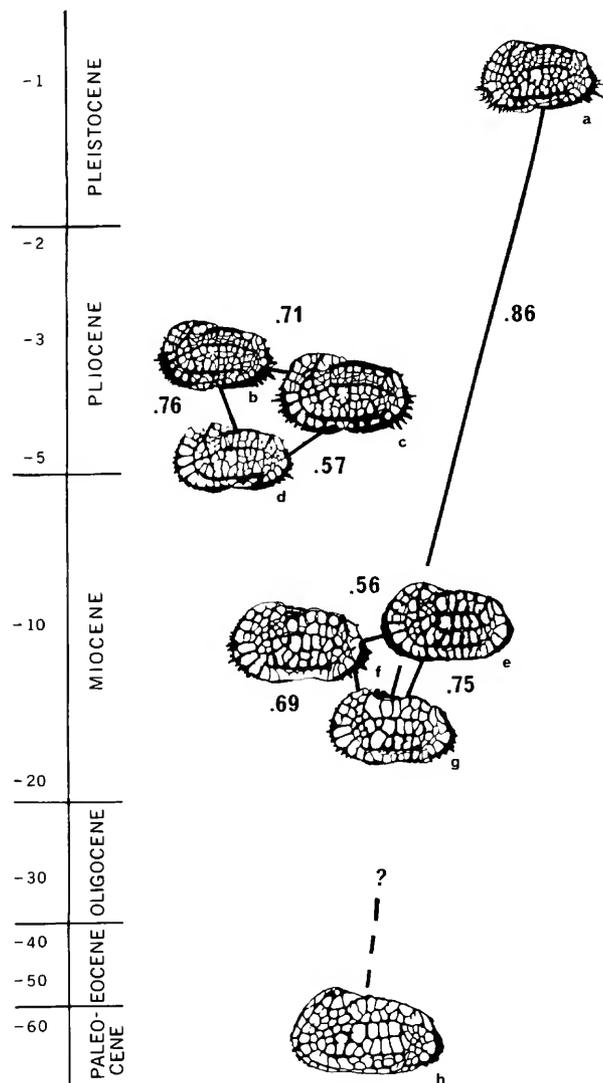


FIGURE 10.—Clustering of some *Oblitacythereis* specimens according to their age and smallest Theta-Rho values. The specimens are from the following localities: a, off Angola in the South Atlantic; b, Chateau Vaugrenier, France; c, Balestrate, Sicily; d, Myrtou, Cyprus; e, Carmona, Spain; f, g, interpopulation variation from Cava Biddiemi, Sicily; h, *Paleocosta libyaensis* from Djebel el Gattar, Libya (negative numbers represent millions of years B.P.).

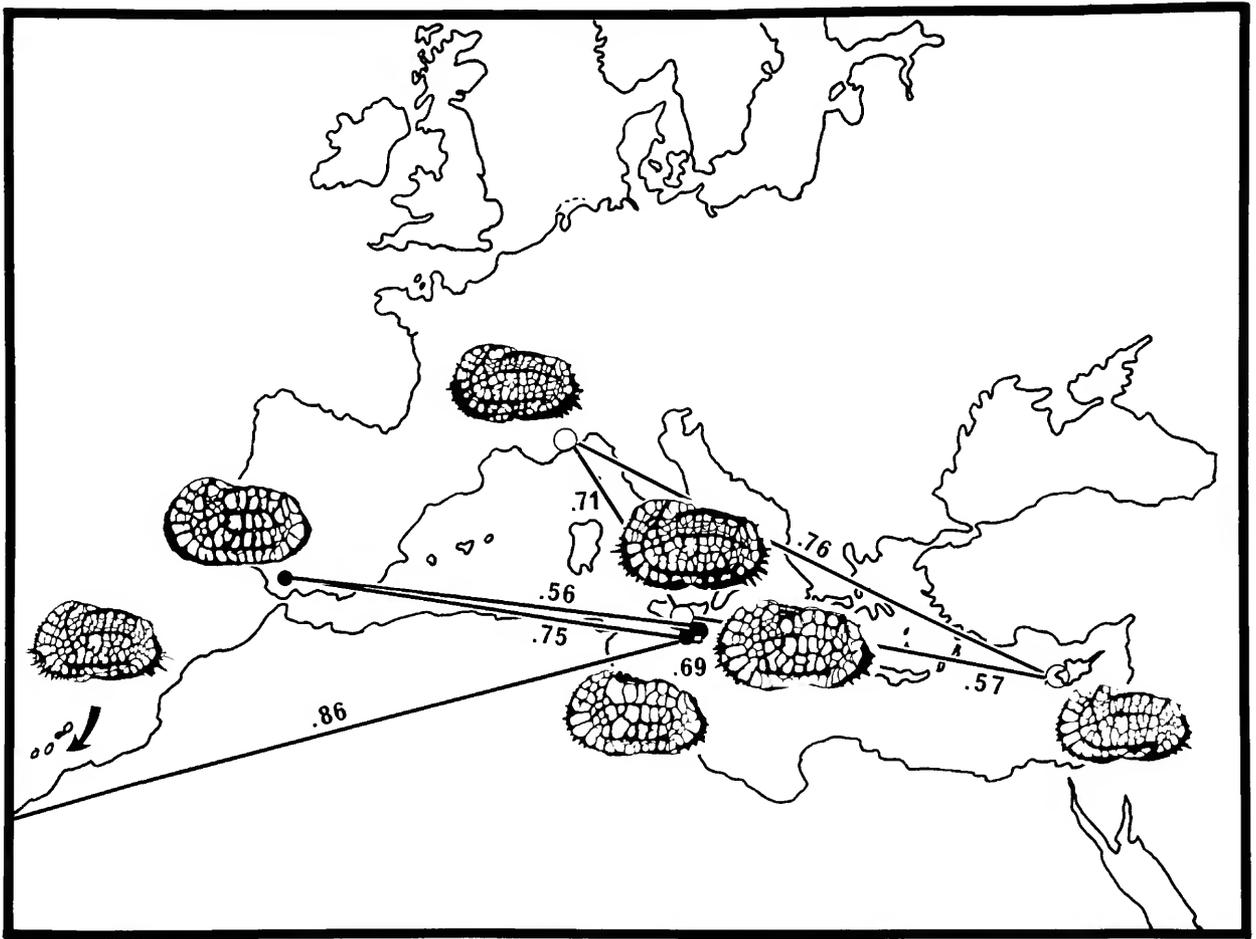


FIGURE 11.—Biogeographic linkage of six *Oblitacypthereis* specimens tested for Theta-Rho difference (average change in position of 17 homologous points). Open circle = subgenus *Oblitacypthereis* (Post-Messinian), closed circle = subgenus *Paleoblitacypthereis* (Pre-Messinian). Values indicating a greater difference than 1.0 have been omitted. Note lack of a significant tie between the subgenera across the Lower Pliocene boundary. The linkage to *O. (P.) luandaensis* (arrow) is suggested by the line with the value .86 running to the lower left.

This analysis shows nothing that cannot be seen in the other examinations of morphology given earlier in this report, but it does not reject any of them. This is perhaps its greatest use. Too little is known about the test or the variation within the genus to speculate further upon the significance of the variation within the values obtained.

Systematics

The following hierarchic classification is used in

this report:

- Subclass OSTRACODA Latrielle, 1806
- Order PODOCOPIDA Pokorny, 1953
- Superfamily CYTHERACEA Baird, 1850
- Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
- Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948
- Tribe COSTINI Hartmann and Puri, 1974

Family TRACHYLEBERIDIDAE
Sylvester-Bradley, 1948

In agreement with the sense of proportion suggested by Hartmann and Puri (1974), I would be willing to recognize the need to use the rank of tribe more than it has been in the past. Therefore, I believe that the costine ostracode can be suitably differentiated from other trachyleberids at that level. However, my own sense of proportion would not agree with that of Hartmann and Puri regarding the placement of the transitional group of ornate ostracodes that seems to transcend the morphology typical of trachyleberids to hemicytherids (Liebau, 1975). In my opinion the lowering of rank of the Thaerocytheridae to the rank of a tribe within the Hemicytheridae equivalent to that of the Aurilini or the Hemicytherini is unrealistic on the grounds of morphological difference and numbers of included taxa. I would prefer to retain Bradleyinae as a subfamily with the Thaerocytherinae in the Thaerocytheridae. Perhaps my experience with deep-water ostracodes and their evolution biases my own preference of their importance, but so be it. I view the prominence of such morphological factors as differences in overall shape, muscle-scar patterns, transition in numbers of "Strahlen" on the mandibular epipodite, the number of segments in the second antennae as important considerations; but it is the belief that most of the hemicytherids have developed separately from most of the thaerocytherids that is of prime importance.

An adequate diagnosis of the ornamentation of the Trachyleberididae has yet to be written, but as Liebau (1975) has suggested, it must include the conservative pattern of the reticulum (raised superficially or suppressed in the inner shell structure) and the distribution of pore-conuli. It is obvious that Liebau's diagnosis of *Cythereis* to include an anterior rib penetrated by special pores would not apply even in the *Costa-Oblitacythereis* phylogeny, because the anterior rib changes position. However, he is quite correct in that a basic ancestral plan of ridges seems to exist. The plan includes the anterior rib system as he describes it. Perhaps it is as well that a family diagnosis would include a statement that modifications of this initial plan is an important family characteristic. The muscle-scar pattern of a V-shaped frontal scar and four adductor

scars is diagnostic. There is no "fused zone" as Hartmann and Puri (1974:22) indicate; this old concept of a bilamellar wall structure is not valid (see "comments" after Bate and East, 1975). The infold in trachyleberids, however, is usually broad with numerous canals radiating through the zone of optical extinction where the shell crystals of calcite quickly change the orientation of their C-axes. The appendages are more segmented and contain more respiratory "Strahlen" than other closely related families, probably representing a more primitive or less specialized state of development.

Subfamily TRACHYLEBERIDINAE
Sylvester-Bradley, 1948

I have not considered the characteristics of this subdivision of the trachyleberids and refer the reader to the discussion of Liebau (1975), who has included some modifications of the array of tribes suggested by Hartmann and Puri (1974). It is my impression that it is a classificatory artifact resulting from the attempt to fill in all levels of rank to include the many tribes rather than having known natural properties. Further research may prove this view to be quite erroneous, however.

Tribe COSTINI Hartmann and Puri, 1974

ETYMOLOGY.—According to Article 29, *International Code of Zoological Nomenclature*, "a family-group name is formed by the addition, to the stem . . . of the name of the type-genus, of -IDAE in the case of a family . . . , of -INI, in the case of a tribe. (*Costa* = cost; used by Neviani, 1928 as one of a series of generic names of classical origin signifying obvious morphologic features; i.e., *Sacculus*, *Flexus*, *Costa*, *Fimbria*, as groups of "*Cythereis*" and not as a patronym.) Only when the name is not of classical origin can the first author arbitrarily determine the stem. Therefore, the tribe name should be "Costini," not "Costaini," as suggested by Hartmann and Puri (1974), and costine ostracodes are defined as those belonging to the Tribe Costini, as differentiated from costate ostracodes, which may belong to any taxon having this morphology.

CLASSIFICATION.—I have already discussed the views of Hartmann and Puri and my disagreement

with some of their judgments about the classification of the costine ostracodes, their characteristics, and included genera. It is a valid grouping of genera, however, and *Costa* is distinctive from most other ornate ostracodes. I would include all of those trachyleberids similar to *Costa*, many of which are ridged and reticulate or whose immediate ancestors were reticulate, with a pattern that tends to be divided longitudinally by a median ridge, unbridged (or whose immediate ancestors were unbridged) over the frontal scar, yet sometimes complex in the anterior. However, *Costa* does not have anterior or posterior "ears" on the dorsal margin as in the cytherettids. The animal can be blind or with eyes, with secondary reticulation (a well-developed reticulum under the ridges) or smooth.

Because of the tendency of some reticulate ostracodes to show phyletic convergence toward smoothness or massiveness (*Costa* to *Cativella*; *Costa batei*) on the shell surface, or for some bridged bradleyines (*Quasibradleya*) to lose one side of the bridge to appear like a costine, it is difficult to write a monothetic diagnosis of this tribe. Yet it does serve a useful purpose for placing *Costa*, *Oblitacypthereis*, *Paleocosta*, *Paracosta*, and *Protocosta* in a single group. All other genera are problematical as members at this time, as far as I can determine. I believe that an evolutionary case is necessary for inclusion of others at this time, and this is wanting.

Genus *Oblitacypthereis*, new genus

ETYMOLOGY.—From *oblitus* (Latin, past participle of *obliviscor*, to forget, because of this form having been overlooked).

TYPE-SPECIES.—*Oblitacypthereis mediterranea*, new species.

DIAGNOSIS.—Distinguished from other reticulate, ridged, and holamphidont costine ostracode genera by the movement of the anterior marginal ridge; superimposed on the reticulum, from close to the margin to several rows of fossae inward, and its marginal replacement by strengthening ridges in the anteroventral region aligned normal to the margin and reaching to or toward the newly forming displaced marginal ridge. In its earliest stages of development the ridge system shows vestigial

remnants of a marginal ridge next to the margin along the anteroventer with a disorganized system of ridges on the reticulum inward toward the frontal scar. In its latter stages of development, with which the type-species is associated, a complete ridge system is formed consisting of the new "marginal" ridge. This ridge is formed several rows of fossae inward but still parallel to the margin, continuing with the ventrolateral ridge to be joined with the median ridge that crosses it to form one of three ridges projecting from the "marginal" ridge to the margin. This new "marginal" ridge, better called the "interoconcentricum" as it is both interior and concentric to the old marginal ridge, is joined with the ocular ridge that is itself joined with the median ridge. There is no eye tubercle.

AGE.—Paleogene to Recent.

HABITAT.—Upper slope to outer shelf.

EXTERIOR CARAPACE MORPHOLOGY.—The shape of the reticulate carapace of *Oblitacypthereis* is dependent upon the robustness of the reticulum, the elevation of the major ridges, the broadening of the anterior margin and the attenuation or rounding of the posterior margin. The "ornamentation" is gross with large fossae or fossal fields due to their combination as individual meshes of the reticulum either as groups or their general suppression in importance relative to the enlargement of principal ridges. As seen from the side, most forms are subrectangular with broadly rounded anteriors. Some have their anteromargins focused in their narrowest curvature toward the anteroventer. The valves have abbreviated caudae, which can be attenuated in the left valves. From the dorsal view, the shape may be elliptical with prolonged and broadened terminal margins or subrectangular like some forms of *Costa* in the central portion.

The organization of the mural and fossal elements of the reticulum is consistent within the genus or changes gradually throughout its evolution. Certain parts of the mural pattern of the reticulum become enlarged to make principal ridges. There are three longitudinal ridges along the posterior two-thirds of the side of the carapace; one along the lateral venter, another extending through the region of the frontal scar along the median part of the valve almost to the posterior and a third along the dorsum from near the ocular region to the highest part of the posterior. A ridge

extends from the ocular region, that is devoid of an eye tubercle, to join the median ridge midway between the frontal scar and the pore-conuli known as "Beta" (Benson, 1972, fig. 8). In the most punctulate of the ridged species, another ridge may unite the ocular ridge, the median ridge, and the ventrolateral ridge along the muri between fossal rows B and C, parallel with the anterior margin. In less well-developed species the muri of the anterior region may tend to be equally enlarged so as to appear to be disorganized. Comparison of all of the stages of reticulum development shows this disorganized state to be a transition from an ancestral stage when a principal marginal ridge existed near the margin to the later stage wherein a parallel ridge, the "interoconcentricum," appears two rows of fossae inward. Near the anteroventral margin at least, three short perpendicular ridges may appear and join the inner ridge complex with the margin to strengthen an ever-widening and more rounded margin.

The individual fossae of *Oblitacothereis* may be homologized according to the plan shown in Figure 9, whose individual species expression is shown in Figures 5, 6, and 7. A key to following the homologies is the use of certain conjunctive pores, called "pore-conuli," whose development in other genera may take the form of spines or cones around the pores. These pores are extremely consistent in the relative positions of the carapace, even among different species.

The fossal pattern in the reticulum consists of a ring of 12 fossae (E) around the muscle-scar pattern, fine concentric rows of about six fossae each in the anterior, and about six longitudinal rows of four to eight fossae on the posterior. The E-ring of fossae is not clearly shown in *Oblitacothereis* as in *Agrenocythere* (Benson, 1972) with which it is homologized, but many of the elements can be seen. Of the three longitudinal ridges that lie above the V-row or below the K-row of fossae, the median ridge separates the M- and N-rows to run forward, bending downward toward pore-conulus Beta. The dorsal ridge bends around K4,5 to join the median ridge, and sometimes completes the circuit by extending from around K9 to near the posterior end of the median ridge. In the earlier forms of *Oblitacothereis* a ridge of intermediate importance may exist halfway between the median and ventrolateral ridges separating the O and P fossal rows and run-

ning through the pore-conuli Leo and Charon. These and the other anterior ridges can be seen in the diagrams of Figure 4, which are easier to follow than a written description. It should be noted, however, that as the vestigial parts of the anterior marginal ridge diminish or become re-oriented, the margin broadens and the X-row becomes better developed. This row is diminished or absent in ostracodes with strong marginal rims.

The venter of *Oblitacothereis* has not been studied herein in the manner of Liebau (1975). I have not observed any special advantage to compare these fossae, but perhaps further examination will prove otherwise.

INTERIOR CARAPACE MORPHOLOGY.—The interior exhibits a holamphidont hinge and a fused infold (marginal zone) of moderate width with many simple radial pore canals. The muscle-scar pattern consists of a vertical row of four adductors and a single V-shaped frontal scar (Figure 3; Plate 2, figures 3, 4, 6).

APPENDAGE ANATOMY.—The following description of soft-part morphology is based on the dissections of four specimens of *Oblitacothereis* (*P. luandaensis*, new species, two males (USNM 190014, 190067) and two females (USNM 190207, 190208; illustrated in Plate 4) from Atlantis II station 203 of cruise 42 off Angola in the South Atlantic.

The first antennae are divided into six segments with podomeres V and VI being unfused. The second antennae are relatively thin with either a very abbreviated epipodite or one entirely missing. There is no spinning bristle. The mandibular epipodite is probably "five-fingered" ("Strahlen"); however, it was damaged on all of the specimens examined and only three were actually observed. It is thought that the broken base of a fourth was seen, the fifth is inferred. One of the "Strahlen" is particularly long. The thorassic legs are long and slender, uniformly developed on both sides of the body and without a "knee apparatus," although there is a minor stiffening at the knee joint where two setae were also observed. The male copulatory organ is not in good preservation as the specimens had been dried before rewetting and dissection; however, it seemed smaller than was expected for an animal of this size.

The appendages of *Oblitacothereis* are typically trachyleberid with no special attributes, so far as I can determine. Photographs were taken, rather than

making drawings, so that some of the features I could have overlooked can still be observed. With the exception of the missing "knee apparatus" the soft-part anatomy of this form is very similar to that of *Agrenocythere radula* Benson.

COMPARISONS WITH OTHER GENERA.—*Oblitacythereis* has the grossly reticulate appearance of some shallow bradleyid species, *Chrysoythere* and *Costa*. The major difference is in the movement of the marginal ridge from near the front edge inward several rows of fossae or its interim removal. This distinction has been discussed at length in an earlier discussion in this report. Their genus arises from the same stock as *Costa* through *Paleocosta* and the subgenus *Paleoblitacythereis*. Its general architectural form is convergent with other ponticulate genera. At this point *Oblitacythereis* appears to have changed with the formation of the Mediterranean, but it has remained in its Miocene state of reticular development, living until the present on the slopes of the eastern Atlantic.

INCLUDED SUBGENERA AND SPECIES.—*Oblitacythereis* (*Oblitacythereis*) *mediterranea*, new species, Mediterranean, Lower Pliocene, designate type-species. *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis*, new species, Recent, slope of southwestern Africa. *Oblitacythereis* (*Paleoblitacythereis*) *ruggerii* (Russo, 1964), southern European Tethys, Middle and lowermost Upper Miocene.

The formation of two subgenera containing three species is more than just the judgment of the similarity between two being greater than those and the third. It is the conviction that the series is broken substantially in one major area, while continued outside of this area and changed dramatically on reentry. If this history of succession is proven wrong then the names can be elevated to emphasize this difference.

VARIATION WITHIN SAMPLES.—On examination of about 35 adult left valves of *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis* from the Recent off Angola, it was noted that some specimens were very spinose, that is, had very long spines around the terminal margins and at the posterior end of the ventrolateral ridge, whereas other specimens were almost devoid of spines. It was wondered if there was a corresponding difference in the development of ridges from the mural network that would exceed that considered significant to define a species

or, in particular, if there was an indication of transition from *Paleoblitacythereis* to *Oblitacythereis*. The observations are as follows:

1. Most very spinose specimens were also the most murate showing "secondary reticulation" with a vitreous surface. Conversely, many nonspinose forms showed a reduction in the number of secondary murae and they almost always showed either an etched surface or actual solution of murae. Therefore, difference in preservation makes a difference in the degree of reticulation in general. If this were the only criteria, mistakes in identification or designation of species or separation of fossae could occur.

2. As *Paleoblitacythereis* is characterized by the joining of fossae, especially in the posterior median area, is it possible that definition of this taxon is an artifact of preservation? On observation of the most poorly preserved forms, that is, those with solution and loss of spines, it was noted that the joining or clustering of fossae was seldom uniform over any area; and furthermore the major ridges, those that show changes between species were as likely to be broken or eroded as were the secondary muri. It is not thought likely that one would mistake this corrosion for morphologic difference.

3. Lastly, all specimens did not show the same degree of uniformity of emphasis in the muri of the anterior in that region where the interconcentricum would form. In a few specimens this ridge did appear to form at the expense of neighboring muri; however, a measurement of this change would be very difficult and probably overlooked completely were not its presence known elsewhere. The fact remains that the variation or emphasis in parts of the ridge pattern is very slight, and there is a far greater difference in preservation than in natural morphological variation.

In contrast to the examination of a Recent population, six adult left valve and four right valve specimens of *O. (O.) mediterranea* were examined from the Lower Pliocene Myrtou fauna of Cyprus. There were only 25 total specimens of all stages and sexes. Preservation was moderately good, but most of the spines were missing. The very fine marl, which was difficult to remove, emphasized the major ridges while concealing the rest of the reticulum. Except where it was broken the interconcentricum was always present in its entirety.

GEOLOGIC RANGE.—Known range Middle Miocene to Recent with the youngest form known in the Mediterranean from the Middle Pliocene. Projected range expected to be Oligocene to Recent.

GEOGRAPHIC DISTRIBUTION.—Eastern and western Mediterranean and the South Atlantic.

Subgenus *Oblitacythereis*, new subgenus

TYPE DESIGNATION.—Nominate subgenus with the type-species *Oblitacythereis mediterranea*, new species.

DIAGNOSIS.—Distinguished from the other subgenus *Paleoblitacythereis* by ponticulate ridge system, which forms a more separate structure from the rest of the reticular muri. The fossae of the midregion posterior of the muscle scars are more separated by muri (L through P series). The interoconcentricum is well developed.

AGE AND DISTRIBUTION.—Known from the Messinian of Morocco and the Pliocene of the Mediterranean.

Oblitacythereis (Oblitacythereis) mediterranea, new species

FIGURES 3, 4A, 5B; PLATE 1: FIGURES 1-4; PLATE 3: FIGURE 1
Bradleya? sp.—Sissingh, 1972:122, pl. 9: fig. 13 [Pliocene of Crete].

HOLOTYPE.—Right valve, male (Plate 1: figure 4), USNM 191301; unfigured paratype suite USNM 190592.

TYPE-LOCALITY.—Buonfornello, Sicily; east of Palermo at excavation of Imera Museum, Trubi Formation (Zanclian); RHB 730301.

AGE.—Pliocene of the Mediterranean.

DIAGNOSIS.—Distinguished from other species of *Oblitacythereis* by the complete development of the interoconcentricum, an increased ponticulate ridge structure, and the more discrete definition of the fossae in the posteromedian region of the reticulum.

COMPARISONS.—This species and its subgeneric separation from other species of *Oblitacythereis* has been discussed at length in previous sections. Its principal relationship with the other species is its end position in the morphologic series. Previous forms have shown incomplete stages in the organization of the muri to form continuous ridges par-

ticularly in the anterior region.

The monotypic nature of this subgenus is defensible on the basis of the extent of the morphological difference *Oblitacythereis mediterranea* has from the other species and also its separation stratigraphically and geographically.

DIMENSIONS.—Length of the holotype 1.02 mm; height 0.50 mm.

DISTRIBUTION.—Mediterranean region, from the Atlantic coast of Morocco to Cyprus. Found in cores from the eastern Mediterranean (DSDP Site 376) as well as in outcrop, especially in northern Sicily.

Subgenus *Paleoblitacythereis*, new subgenus

TYPE-SPECIES.—*Carinocythereis ruggierii* Russo (1964:242, pl. 44: fig. 4; pl. 45: fig. 1-2a,b), Languian of Pescale, northern Apennines.

DIAGNOSIS.—Distinguished from subgenus *Oblitacythereis* by the lack of an interoconcentricum in the anterior, the less elevated three longitudinal major ridges, the boldness of the other parts of the reticulum, and the vertical merging of many fossae in the posteromedian region.

REMARKS.—The limits of this subgenus and its merger with *Paleocosta* and subgenus *Oblitacythereis* are defined as that intermediate development of the reticulum between the disappearance of those *Costa*-like elements of its shape and ridge formation (especially its marginal ridge) and the acquisition of well-developed and joined ponticulate ridges with elements extending toward the anterior margin. The upper limit was made sharp by the crisis event. The lower boundary is another problem, however, which is made vague by the sparseness of samples and the gradual change that takes place in that structural area. Except for the placing of a generic name this is not a very important problem. The disappearance of eye tubercles from the preceding stages (*Paleocosta kefensis*) is thought to be an important indication of the adaptation to deeper water and is considered here as an important distinction or indication of change between *Oblitacythereis* and its ancestors.

AGE AND DISTRIBUTION.—Miocene through Recent. Found in Tethys before the Messinian and found living in the southeastern Atlantic at present.

Oblitacythereis (Paleoblitacythereis) ruggierii
(Russo, 1964), new combination

FIGURES 4C-E, 6A-C; PLATE 1: FIGURES 5, 6, 8;
PLATE 2: FIGURES 5-7; PLATE 3: FIGURES 2, 3, 8

Carinocythereis ruggierii Russo, 1964:242, pl. 44: fig. 4, pl. 45: figs. 1-2a,b.

Bradleya? sp.—Russo, 1968:23, pl. 2: fig. 7a [Tortonian of Montebaran zone].

TYPE SPECIMENS.—Described originally by Russo (1964:242) from the Langhian of Pescale (Modenese) in the northern Apennines of Italy ("F. 86, Tav. II, No. P13 a circa 170 m") near the confluence of Rivera della Costa and the R. Pescarola not far from (1½ km) and to the southeast of Pigneto in the "Strati del Pescale" in a well-stratified whitish, calcareous clay. The collection is in the Istituto di Paleontologia dell'Università di Modena (Cat. No. 1608). I have seen only the photographs for verification of this species, but I have Professor Ruggieri's opinion also that this species and those given here, at least positively the ones from the Langhian of Sicily, are the same.

AGE.—Positively Langhian to Tortonian, using these cenozoone concepts. Estimated age *Praeorbulina* Zone (N8, N9) to Messinian.

DIAGNOSIS.—The original description of the ornamentation considers the three longitudinal ridges and how they join each other, especially the dorsal ridge with the median. Mention is made of the subdivision of the median ridge to radiate anteriorly. Other properties are rather generalized and would not now differentiate among species of *Oblitacythereis*.

An emended diagnosis would include the following: Distinguished from other species of *Oblitacythereis* by its irregularly formed anterior ridge system with a ridge joining the position of the blind eye tubercle and vestigial parts of the anterior marginal ridge forming nodes or partial ridges. The three major longitudinal ridges of the posterolateral region and a fourth more subdued ridge between the median and ventrolateral ridges rise above the surrounding reticulum consisting of muri joining many vertical pairs of fossae of the L-M, N-O, and P-V series. The interoconcentricum is absent; however, there is a ridge extending anteriorly down from the median ridge just behind the frontal muscle-scar position. The median ridge tends to reach anteriorly to the Beta pore conulus

and terminate posteriorly at pore conulus *Charon*.

The infold seems unusually broad in some specimens.

COMPARISONS.—This species exhibits a development or variation (Figure 4C-F) in the ridge system from rather subdued and vestigial as left over from the ancestral form *Paleocosta* to strong and tending to be organized as in its descendant subgenus *Oblitacythereis*. This species, which is Miocene in age, is differentiated from the Recent species *O. (P.) luandaensis* by the more obvious fusion of the fossae in the posteromedian region and generally a more massive appearance.

It is different from its ancestor *Paleocosta kefenensis* in that it is blind, less elongate and *Costa*-like in shape and the ridge between the median and ventrolateral ridge is less pronounced. In common they have the strong ocular ridge extending downward from the eye tubercle area, but in *O. (P.) ruggierii* this ridge is not quite so strong at its lower end.

DIMENSIONS.—Adults generally are about 0.90 mm long, to about 1.20 mm in the longest as recorded by Russo (1964:242). The holotype appears to be unusually large. The younger adult specimens all tend to be about 0.90 mm long with the males being somewhat less high.

Oblitacythereis (Paleoblitacythereis) luandaensis,
new species

FIGURES 4B, 5C; PLATE 2: FIGURES 1-4; PLATE 3:
FIGURE 6; PLATE 4

TYPE SPECIMEN.—The holotype (USNM 190392) is an adult whole carapace, female (Plate 2: figure 1), from the South Atlantic (Atlantis II, cruise 42, station 203; lat. 8°48'S, long. 12°52'E, 527-542 m depth).

DIAGNOSIS.—Distinguished as a separate species of the subgenus *Paleoblitacythereis* by the less massive appearance of the carapace and its more spinose margin. The reticular pattern shows more muri separating the anterior rows and the posteromedian rows of fossae (A and B series separate, L and M series, N and O series, and P and V series mostly separate), lessening of the robustness of the anterior extension of the median ridge, dorsal ridge distinct as opposed to blade-like.

In interior view, the carapace is quite trachy-

leberid in shape with well-formed holamphidont hinge and V-shaped frontal scar. The infold is wide.

The appendages have been illustrated on Plate 4 and have been discussed earlier under the general question of classification. In my opinion they are not of value to differentiate this species or the genus from many other trachyleberids. The diagnostic characteristics are in the carapace.

COMPARISONS.—This species represents an end point in evaluation as it is the only surviving member of the genus yet known; yet it is intermediate in character between the oldest members of subgenus *Paleoblitacythereis* and *Oblitacythereis*. It is assumed that some day the link between *O. (P.) luandaensis* and the Pliocene Mediterranean form will be found, but this is conjecture. The longitudinal ridges of the posteromedian region are well formed and yet the anterior region is obviously retarded in its development.

DISTRIBUTION.—Found only at one locality in the South Atlantic on the upper slope (527–542 m), it is well separated from its Miocene forebearers. Many other Miocene elements of the Tethyan deeper fauna, however, are found living on the slope off or near equatorial Africa. *Carinocythereis* and *Buntonia* are two such ostracodes. The species occurrence in this region is the chief control on the comparative distribution of *Oblitacythereis* in the Tethyan Miocene and the Mediterranean Pliocene, yet the associated faunas are similar also.

DIMENSIONS.—Adults generally about 1.10 mm long and from 0.55 mm (male) to 0.60 mm (female) high. Males slightly more elongate, but no longer than females.

Genus *Paleocosta*, new genus

ETYMOLOGY.—From *palaios* (Greek, = ancient, referring to the ancestry of *Costa*).

TYPE-SPECIES.—*Paleocosta crassireticulata* (Bassiouni), 1969:403, pl. 28: fig. 4a–c (holotype), from Middle Eocene of Egypt (Mokattam Formation) and Jordan.

DIAGNOSIS.—Distinguished from other genera of the Tribe Costini by its coarse carapace reticulum to one smoothed between the major ridges with the three usual longitudinal ridges supplemented by a tendency to form a fourth (or relics) with cross muri between the median and ventrolateral ridges, plus a well-defined ridge running close to the ante-

rior margin. The reticulation over the muscle-scar area and in the anterior is gross and not well organized but with a tendency to form a ridge running through Beta pore conulus to the anteroventral margin. An eye tubercle is present; marginal spines are small and poorly developed. The hinge is holamphidont; the muscle-scars include four adductors and a V-shaped frontal scar.

INCLUDED SPECIES.—

Costa crassireticulata Bassiouni, 1969 (type-species)
Costa sp., in Bassiouni, 1969, Middle Eocene, Jordan

Costa mokattamensis Bassiouni, 1969

Costa humboldti Bassiouni, 1969

Paleocosta libyaensis, new species

Paleocosta kefensis, new species

Paleocosta? sp. (described herein)

REMARKS.—The variation in emphasis in this group of ostracode species from coarsely reticulate to almost smooth is very much like that of *Costa* into which it later evolves. *Costa* is a quite variable group of species of younger age, in which the three major ridges become well defined. Only the shorter anterior median ridge and the pore conulus (Leo) remain of the longer posteroventromedian ridge, which is more conspicuous in *Paleocosta*. There are, of course, many elements in common as one develops into the other. There is also a subtle difference in shape that is hard to define, perhaps most acute in the upward tilt of the posterior of *Paleocosta*.

Paleocosta shows development into *Oblitacythereis*, especially in the change of the anteromarginal ridge, the emphasis of an ocular ridge that begins to form toward the venter. *Paleocosta* has eye tubercles, like *Costa*; *Oblitacythereis* is blind, obviously a deeper dwelling animal. *Paleocosta* shows gradation in carapace architecture from very shallow waters (*P. mokattamensis*), similar to *Costa batei*, a massive variant (*Paleocosta* species, Plate 3: figure 5), to a coarse offshore form (such as, *P. libyaensis*) to where it becomes deep, more delicate, and begins to develop into *Paleoblitacythereis*.

Several Paleogene genera have been likened to *Costa*, at least in name and ostensibly in relationship, but they are probably only distantly related. These include *Protocosta* Bertels described from the Paleogene of Argentina. *Trachyleberidea* and *Hazelina*, often foveolate forms, both are parallel in ridge ornamentations to *Costa* only in superficial

ways, and they are not at all close to *Paleocosta*. How it is related in the larger sense, I do not know.

The subgenus *Paracosta* Siddiqui was proposed as a division of *Costa* to include three species from the Upper Eocene of West Pakistan. This taxon is described as a "*Costa* with a fourth ventral ridge intercalated between the third ridge and the ventral margin" (Siddiqui, 1971:29). From his subsequent species descriptions and the photographs of the three species (Siddiqui, 1971, pl. 14: figs. 1-11), it is not clear where this fourth ridge is found except as an alignment of muri near the ventral margin. The specimens are quite evenly reticulate and *Costa*-like (similar to *Costa runcinata*); however, they do not have the fourth short longitudinal ridge of *Paleocosta* between the median and ventrolateral ridge. I was concerned at first that the subgenus *Paleocosta* and *Paracosta* might be variations of the same thing. It is still possible that they are very closely related, but I am not able to demonstrate how this is beyond the inference of a close relationship. The structural connection between these two groups is not obvious to me now, but I have studied few specimens at this level.

AGE AND GEOGRAPHIC DISTRIBUTION.—KNOWN from the Paleogene of the Mediterranean region.

Paleocosta libyaensis, new species

FIGURES 4H, 7C; PLATE 3: FIGURE 4

Costa sp.—Bassiouni, 1969:405, pl. 28a-c.

TYPE SPECIMEN.—The holotype is a left valve (USNM 191544), one of a few specimens given to me by Janina Szczechura from sample 2M-2/19, Djebel el Gattar, ESE of Tripoli, Libya, lat. 31°30'N and long. 14°22'E. Szczechura says the specimen is lower Tertiary, but in my view it is probably Eocene.

DIAGNOSIS.—Distinguished by its coarse reticulation forming a box-work structure in the posteroventral region similar to subgenus *Paleoblitythereis* (Series L-M, N-O, P-V), yet with a well-developed marginal ridge (separating rows X and A). The fossae are large with high muri near and anterior to the frontal scar region. The median ridge runs from the anterior margin around both sides. Margin is poorly spinose, and there is an eye tubercle.

COMPARISONS.—This species is most similar to the form left unnamed (*Costa* sp.) by Bassiouni (1969) from the Middle Eocene of Jordan and in fact is probably conspecific with it. Notable is the common envelopment of the frontal scar by the median ridge. This species differs from the type-species *P. crassireticulata*, which is more rectangular in outline and whose principal ridges are more pronounced.

DIMENSIONS.—Length of illustrated Libyan holotype (female), 0.69 mm height, 0.39 mm.

DISTRIBUTION.—Eocene of southern shelf of Tethys.

Paleocosta kefensis, new species

FIGURES 4G, 7B; PLATE 1: FIGURE 7

TYPE SPECIMEN.—Adult left valve, male (USNM 191208), from the *Globorotalia angulata* Zone of the Middle Paleocene of the Le Kef section in Tunisia (RHB 57).

AGE.—Paleocene.

DIAGNOSIS.—Distinguished from other strongly reticulate *Paleocosta* species by its large carapace and by the boldness of a ridge (i.e., "ocular ridge") extending from the well-developed eye tubercle to the anterior end of the ventrolateral ridge.

COMPARISONS.—This species differs from the Eocene species *P. libyaensis* by the more obvious alignment of muri forming the "ocular ridge," but as shown in Figure 7B,C, there are more noticeable muri of secondary importance separating some of the fossae in the posterior. Otherwise the two species are simply variations of emphasis of muri forming ridges in the anteromedian region of the reticulum. The anterior marginal ridge of *P. kefensis* is somewhat more subdued in its central part. *Paleocosta kefensis* has many more muri separating the fossae than does *P. crassireticulata*, but the overall emphasis of primary muri is very similar, with the exception of the ocular ridge. This species is much larger in size as well.

REMARKS.—The similar development of the ocular ridge in this species of *Paleocosta* and in part in *Oblitythereis* (cf. Plate 1: figures 7 and 8) suggests a direct line development. If *Oblitythereis* did indeed evolve from *Paleocosta*, this would indicate that it did so in the Paleocene. *Paleocosta libyaensis* is part of the *Costa* phylogenetic line,

which joins the *P. kefensis*-*Oblitacythereis* line somewhere in the Middle or Lower Paleocene or southern Tethys.

DIMENSIONS.—Adults very large, 1.59 mm long and 0.63 mm high.

Paleocosta? sp.

PLATE 3: FIGURE 5

REMARKS.—This ostracode, which has not been identified beyond its possible generic affinities, has been included here to show its reticular pattern, which is very similar to the other two species just described. It is much smaller (0.80 mm long; 0.43 mm high) and more massive than *P. kefensis* with

which it occurs in the same sample of Middle Paleocene age from the Le Kef section. Its shape is *Veenia*-like and shows the likelihood of phyletic divergence of several groups including *Costa* and *Oblitacythereis* from this older form or one closely related to it.

I have not mapped homologies in the reticulum, but from inspection one can see that the basic pattern described for *Oblitacythereis* and *Paleocosta* is also present here. The pore conuli are also in the same positions. There are suggestions of four longitudinal ridges, a sloping anterior portion of the median ridge and a faint ocular ridge. This species has a well-developed holamphidont hinge and a wide inner marginal area.

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PLATE 1

1. *Oblitacypthereis* (*Oblitacypthereis*) *mediterranea*, new species, left valve (USNM 190134) of Pliocene age from Chateau Vaugrenier, north of Antibes, France (ARL 4458), \times 95.
2. *Oblitacypthereis* (*Oblitacypthereis*) *mediterranea*, new species, left valve (USNM 190872) from the Lower Pliocene of the Trubi Formation, along the Fongritello River, Balestrate, Sicily. \times 100.
3. *Oblitacypthereis* (*Oblitacypthereis*) *mediterranea*, new species, left valve (USNM 190835) from the Zancian of the Myrtou Formation of Cyprus (S69 CYM3), \times 100.
4. *Oblitacypthereis* (*Oblitacypthereis*) *mediterranea*, new species, holotype, right valve, male (USNM 191301) of Zancian age from the Trubi Formation of Buonfornello, Sicily (RHB 730301—excavation for foundation of Imera Museum), \times 100.
5. *Oblitacypthereis* (*Paleoblitacypthereis*) *ruggierii* (Russo, 1964), left valve (USNM 190861) of Langhian age from Cava Biddiemi, Sicily (RHB 71809), \times 110.
6. *Oblitacypthereis* (*Paleoblitacypthereis*) *ruggierii* (Russo, 1964), right valve (USNM 190878) of Langhian age (*Praeorbulina* cenozoone) from northwest of Sutera, near Agrigento, Sicily, \times 120.
7. *Paleocosta kefensis*, new species, a left male valve (USNM 191208) from the Middle Paleocene of Le Kef, Tunisia (RHB 57), \times 90.
8. *Oblitacypthereis* (*Paleoblitacypthereis*) *ruggierii* (Russo, 1964), a left female valve (specimen belonging to G. Ruggieri) from the Tortonian of Licodia Eubea, Sicily, \times 105.

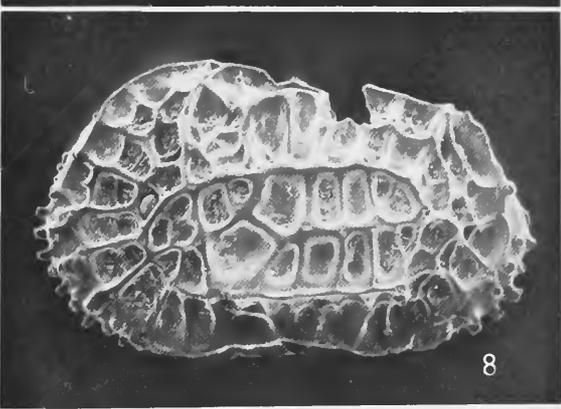
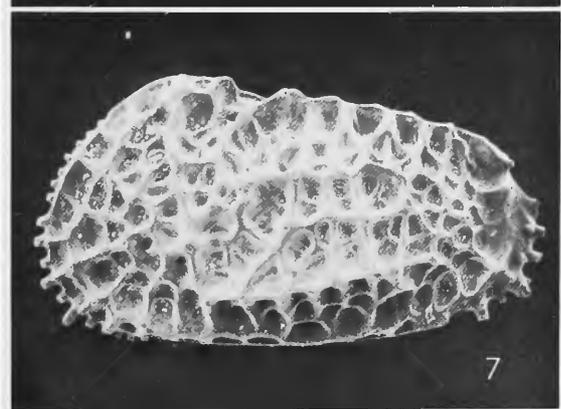
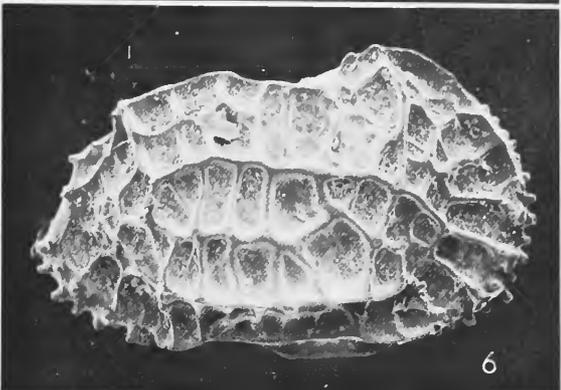
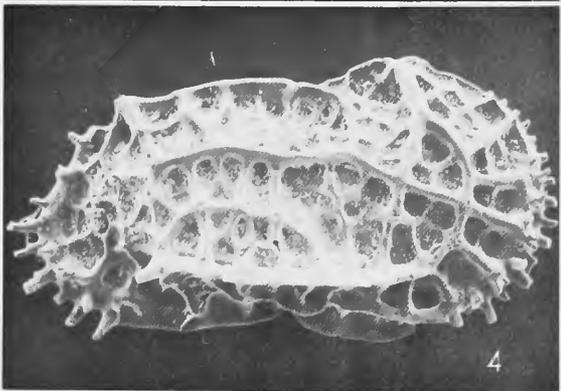
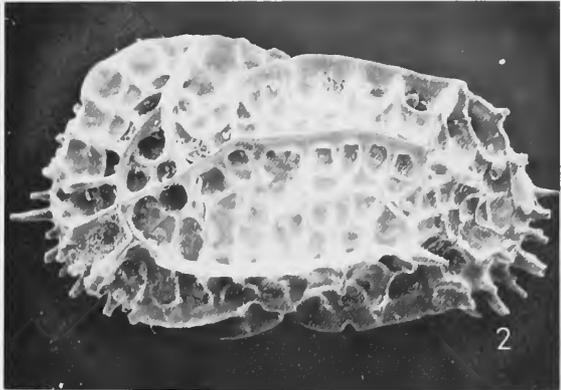
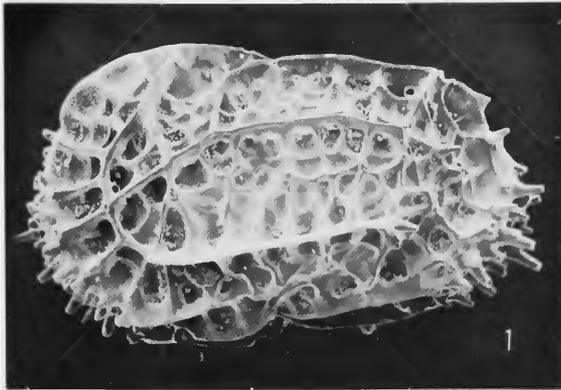


PLATE 2

1-4. *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis*, new species, all Recent from the South Atlantic (Atlantis II, cruise 42, station 203: lat. 8°48'S and long. 12°52'E; 527-542 m depth): (1) holotype, female, USNM 190392, whole carapace, × 70; (2) paratype, USNM 191303, whole carapace, × 95; (3) paratype, USNM 191358, left valve, × 90; and (4) paratype, USNM 191359, right valve, × 85.

5,6. *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* (Russo, 1964), both from the Tortonian of Borde de la Meseta, Spain (AG-2): (5) a left male valve, USNM 191142, × 115; (6) a left valve, USNM 191302, × 115.

7. *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* (Russo, 1964), left valve (USNM 191094) from the Andalusian of Carmona, Spain (C-12), × 115.

8. *Oblitacythereis* (*Paleoblitacythereis*) species?, left valve (USNM 191139) from the Middle Miocene of El Cuervo, Spain (#14), × 115.

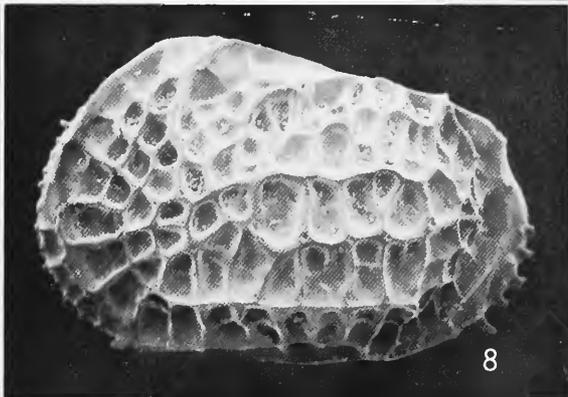
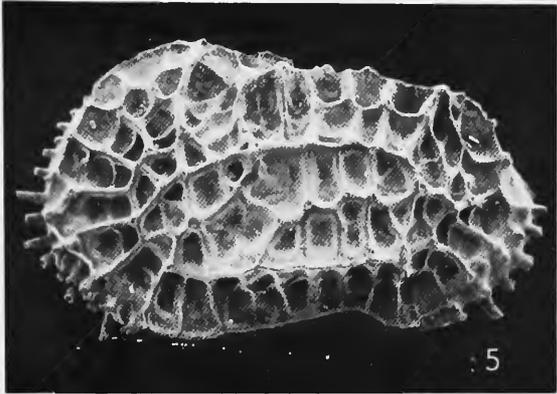
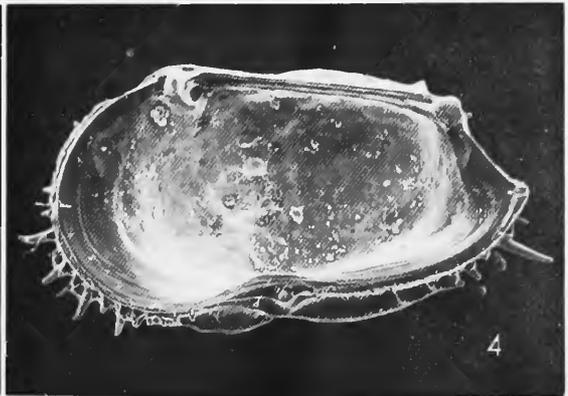
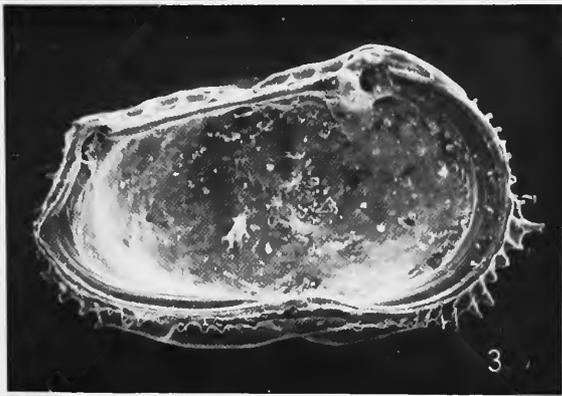
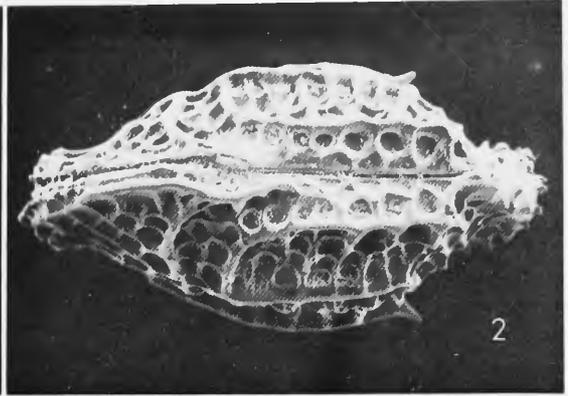
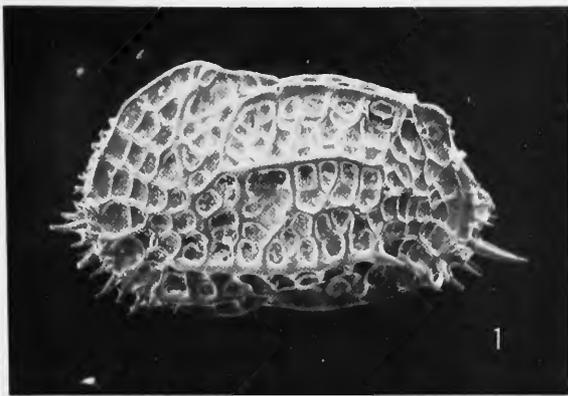


PLATE 3

1. *Oblitacythereis* (*Oblitacythereis*) *mediterranea*, new species, left valve (USNM 191520) of Zanclean-Piacenzian age from a core taken at DSDP Site 376, leg 42A, core 5, section 5, 70–80 cm (lat. 34°52.32'N, long. 31°48.45'E; 2101 m depth), × 110.
2. *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* (Russo, 1964), left valve (USNM 190420) from the Langhian, Cava Biddiemi, near the bridge between Santa Croce and Marina Ragusa, Sicily, × 100.
3. *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* (Russo, 1964), left valve (USNM 191615) of Tortonian age from Borde de la Meseta, Spain (AG-2), × 115.
4. *Paleocosta libyaensis*, new species, holotype, left valve (USNM 191544) of probable Middle Eocene age from Djebel el Gattar, ESE of Tripoli, Libya (2M-2/19), × 150.
5. ?*Paleocosta* sp., left valve (USNM 191205), from the Middle Paleocene of Le Kef, Tunisia (RHB 57), × 120.
6. *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis*, new species, paratype, whole carapace (USNM 190336), Recent from the South Atlantic (Atlantis II, cruise 42, station 203: lat. 8°48'S, long. 12°52'E; 527–542 m depth), × 175.
7. *Oblitacythereis* (*Paleoblitacythereis*) species?, left valve (USNM 191139), from the Serravallian of El Cuervo, Spain (14), × 200.
8. *Oblitacythereis* (*Paleoblitacythereis*) *ruggierii* (Russo, 1964), a left female valve (specimen belonging to G. Ruggieri) of Tortonian age from Licodia Eubea, Sicily, × 200.

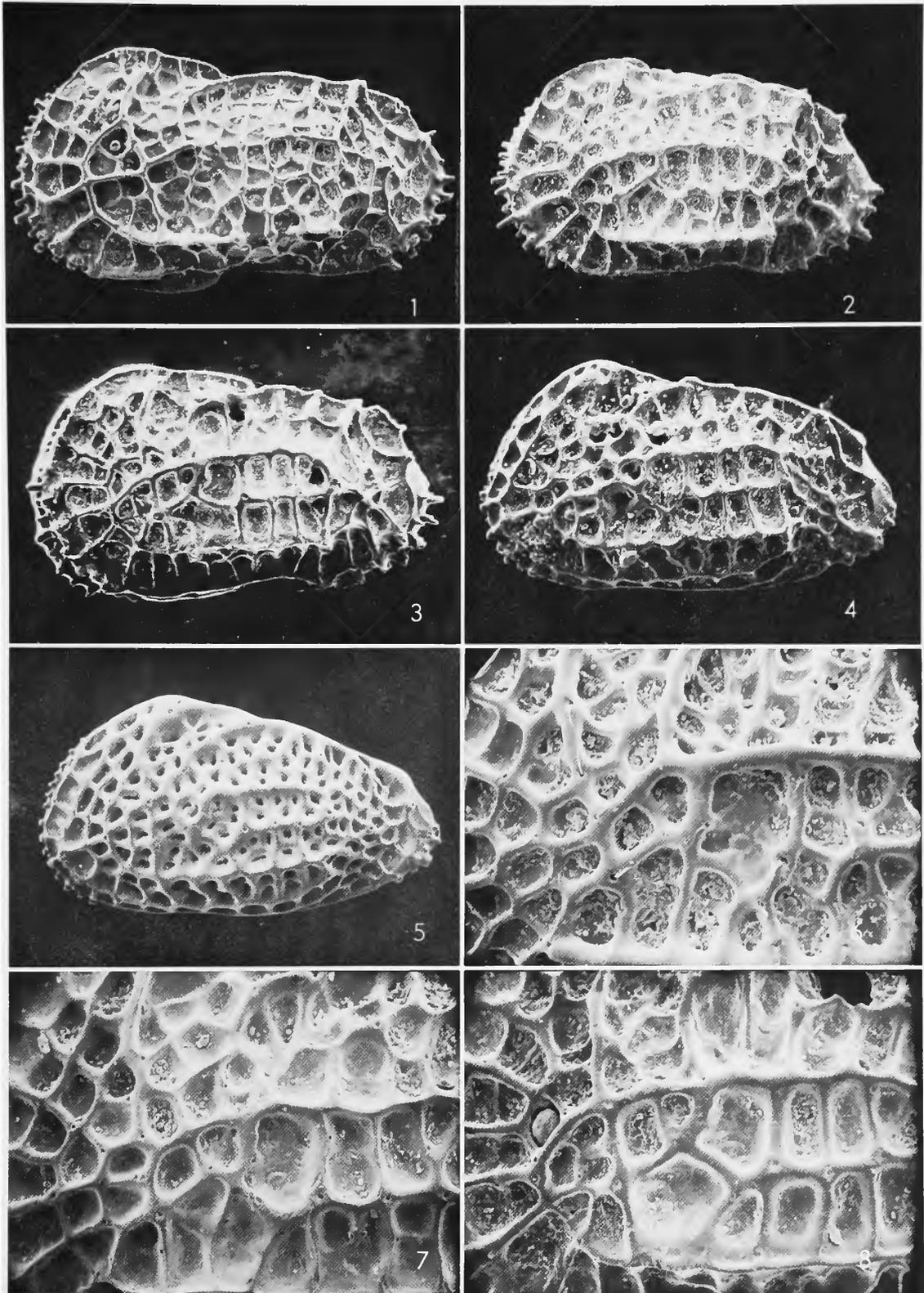
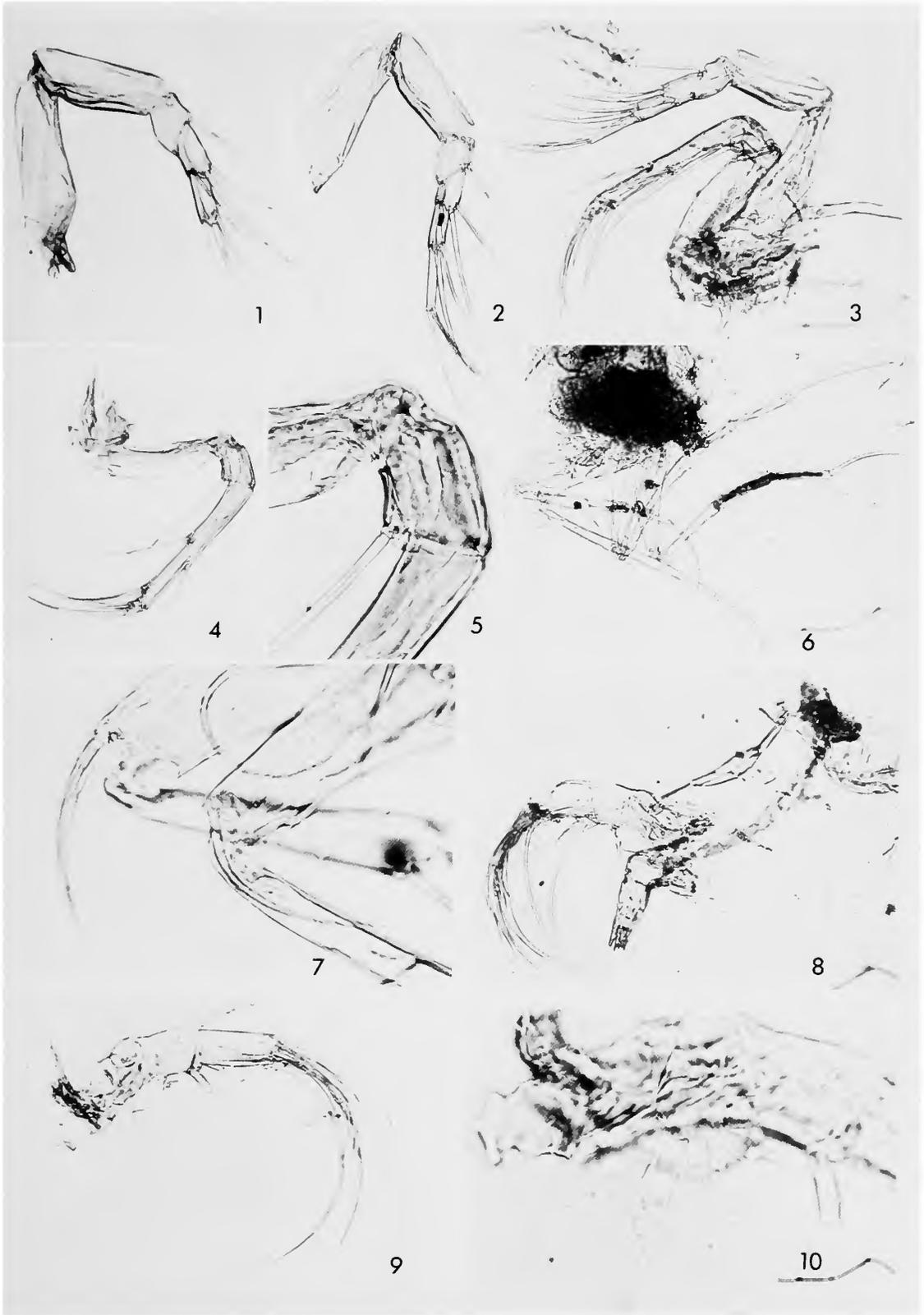


PLATE 4

1-10. *Oblitacythereis* (*Paleoblitacythereis*) *luandaensis*, new species, females from Atlantis II, cruise 42, sta. 203 off Angola, 8°48'S, 12°52'E, 527-542 m depth: (1,2) first antennae (USNM 190208), × 180; (3) first and second antennae (USNM 190207), × 180; (4,5) second antenna (USNM 190208), × 160 and × 480; (6,7) thoracic legs (USNM 190207), × 125 and × 625; (8) mandible (USNM 190207), × 220; (9,10) partial mandible showing the epipodite enlarged (USNM 190208), × 240 and × 270.



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