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Ontogeny, phylogeny, and systematics of recent species of the superfamily Soritoidea Ehrenberg, 1839

Gudmundsson, Gudmundur, Ph.D.

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U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

ONTOGENY, PHYLOGENY, AND SYSTEMATICS OF RECENT SPECIES OF THE SUPERFAMILY SORITOIDEA EHRENBERG, 1839.

by

GUDMUNDUR GUDMUNDSSON

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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Chairman of Examining Committee

3 NOV 1989
date

Executive Officer

Neil Landman

John Tietjen

John Van Couvering

Norman Platnick

Gareth Nelson

Supervisory Committee

The City University of New York

Abstract

ONTOGENY, PHYLOGENY AND SYSTEMATICS OF RECENT SPECIES OF THE SUPERFAMILY SORITOIDEA EHRENBERG, 1839

by

Gudmundur Gudmundsson

Adviser: Professor John J. Lee.

A classification and phylogenetic relationship of 18 species of the superfamily Soritoidea (Foraminifera) was established and one new species erected, *Marginopora kudakajimensis*. Thirty homologies were recognized which defined 16 groups as monophyletic, where 15 of these 16 groups could all be represented as branching points in a single diagram. The significance of this congruent data set is that it is consistent with the assumption that these homologous features originated in a common ancestor and were inherited in all of its descendant species. It was estimated that the probability of obtaining such results by chance alone was $(14/304745)^{27}$, practically a zero probability. Chance was defined in this context to signify the combined outcome of three different processes: 1) unique origin and inheritance of the homologues, 2) elimination or loss, and 3) convergence.

The ontogenetic change of all the homologies was documented. Twenty eight homologies were found to form a part of 6 different ontogenetic sequences. These sequences behave according to 3 general modes: transformation, divergence, and the combination of several unrelated ontogenies. Information on the ontogenetic succession of forms, was used to predict a definite sequence of fossils which is expected to exist in the sediments. This prediction was based on a reformulation of the famous thesis of parallelism or the biogenetic law.

The thesis was tested, that the morphological evolution of the soritids was driven by symbiotic relationships. The distribution of different types of symbionts is confined to the same species groups as are defined by a few homologies, which is consistent with the symbiosis thesis.

Acknowledgement

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INTRODUCTION

The Soritoidea include some of the largest animals of the Foraminifera, some exceeding 1 inch in diameter. They inhabit the shallow tropical seas of the world and captured the interests of many early naturalists because of their large size, complexity, and because they husband symbiotic algae. But why would anyone devote extensive labor and time to describe in such minute and prolix details the structure of organisms apparently so mean and insignificant as the Soritoidea? Carpenter (1856), in his monograph on this group, concluded, after considering this question, that it is desirable to elucidate the structure of any living form, to obtain a complete knowledge of the structural diversity of the whole biological world, and to relate one tribe of animals to another. It is also true that from such studies certain general principles can evolve, perhaps applicable to all groups of organisms. Such an acquaintance would benefit every department of the biological sciences. Even though many of Carpenter's general principles and taxonomic conclusions are rejected today, his rationale for practising systematics remains sound.

It is of interest to review briefly the history of ideas and principles that have in the past influenced the classification of the Soritoidea, in order to identify some of the problems that continuously have complicated the systematics of this group, and to evaluate possible solutions. The following historical survey is limited to the few selected authors who have presented original anatomical analyses of the Soritoidea.

The Soritoidea were first recognized as a natural group by Carpenter (1856). Carpenter was influenced by the doctrine that organisms were created according to a settled and comprehensive plan (or types). He believed it was his task as a systematist to discover both the number, and the essential characters of these original or primary types, the only basis of a true natural classification. The types were supposed to have proliferated into a vast multitude of diversified

forms, by the ordinary course of "descent with modification" in the long succession of geological ages. Within each primary type, Carpenter recognized an immense character variability, which he elucidated by observing a large variety of osculant or intermediate forms. Ontogeny was assumed to exemplify how a single organism changed within the type, from one plan of organization to another, further demonstrating the immense morphological plasticity within each type, all in response to fluctuating environmental conditions. Therefore, all attempts to discover defining characters for taxa, especially within the types, are futile since all characters are in principle intimately connected by gradational links. Recognition of subgroups within the original types was only to be adopted for the convenience of description and nomenclature, and therefore essentially an artificial task (Carpenter 1861, pp.569-586, Janal 1987). This type concept, then widely endorsed by the scientific community, had its origin in 18th century biology, especially in the works of Buffon and Linnæus (Zirkle 1959).

Carpenter suggested in a diagram (diagr.1), how the Soritoidea (= Orbiculine type) might have originated.

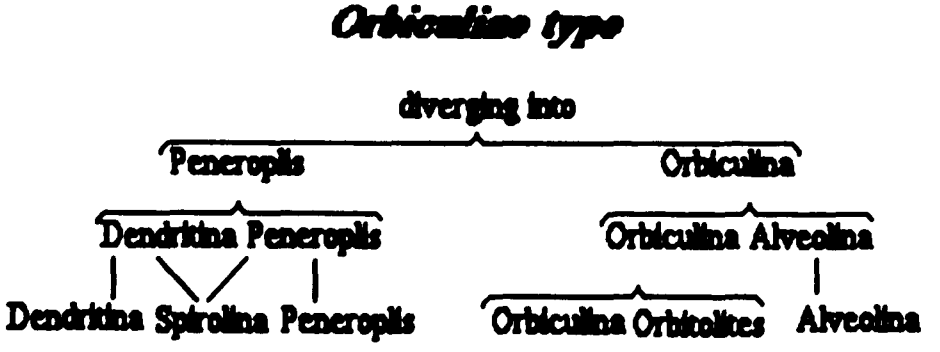


Diagram 1. "The following may be suggested as the mode in which the existing forms might thus have diverged from each other and their primary type" (Carpenter 1861, p. 575).

For the sake of clarity Carpenter's diagram is rearranged in diagram 2, such that it resembles the current cladistic fashion of drawing such diagrams.

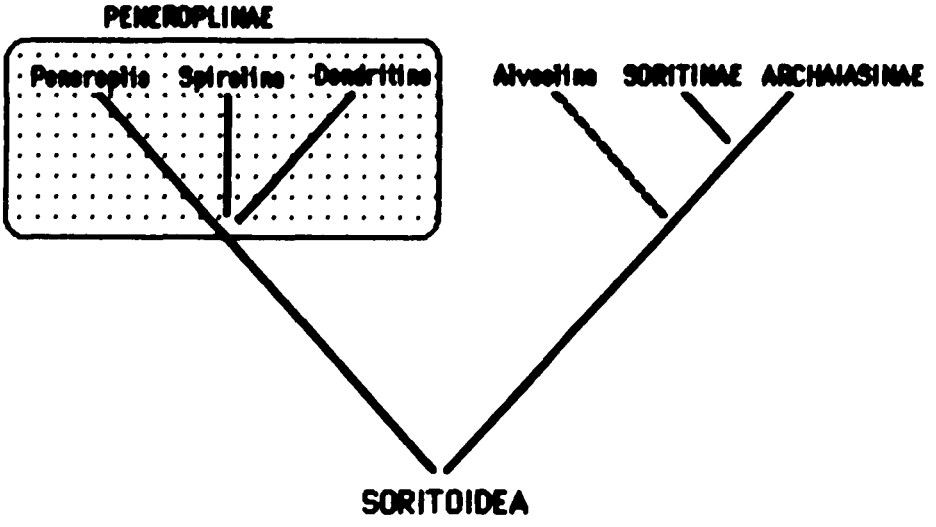


Diagram 2. A modified version of diagram 1. Each line corresponds to Carpenter's "diverging types". All names spelled in full in capital letters are adjusted to the usage adopted in this dissertation. *Alveolina* is not a member of the Soritoidea and this is noted with a dotted line (see page 44).

It is possible that Carpenter understood the "Orbiculine type" (Soritoidea) as a single species, and his diagram therefore would represent a hypothesis on how a complex morphology evolved within a single species. Carpenter was not explicit on this point, possibly because species appeared to him as uninteresting ephemeral phenomena, merely representing man's ignorance of the morphological gradation of living forms, through space and the eons of time. Further appraisal of organic variability led Carpenter et. al. (1862) to abandon the Soritoidea as a natural group, and its members were dispersed

among all the other porcellaneous forms within the larger type, Miliolida.

The taxonomic conclusion implied in diagrams 1 and 2 is that the Soritoidea are to be divided into three subgroups: the Archaiasinae (= *Orbiculina*), the Soritinae (= *Orbitolites*), and the Peneroplinae (= *Peneroplis*), and that the Archaiasinae and Soritinae are more closely related in comparison to the Peneroplinae.

Brady (1884) followed the conceptual tradition of Carpenter, but reinterpreted Carpenter's type concept to serve only as a basis of nomenclature. Brady correctly excluded *Alveolina* from the Soritoidea (= Peneroplidinæ), but erroneously included the genus *Cornuspira* within the Soritoidea. This was a consequence of another mistake, which was to include the species *Discospirina tenuissima* (a member of Opthalmidiaceae (Haynes 1981)) within the Soritoidea (see page 44-45).

D. tenuissima displays early in ontogeny a planspiral tubular growth stage, which Brady thought to be homologous with that of the genus *Cornuspira*. Brady's classification of the Soritoidea is summarized below.

Subfamily Peneroplidinæ

genus	*Cornuspira*
genus	*Peneroplis* (= Peneroplinae)
genus	*Orbiculina* (= Archaiasinae)
genus	*Orbitolites* (= Soritinae)

For comparison the above classification is represented in diagram 3.

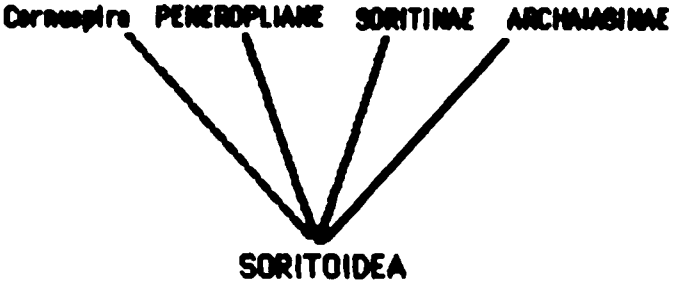


Diagram 3. A graphic summary of Brady's (1884) classification. All names spelled in full in capital letters are adjusted to the usage in this dissertation. *Cornuspira* is represented with a dotted line, because it does not belong to the Soritoidea.

The only taxonomic conclusion to be drawn from diagram 3 is that the three subfamilies Archaiasinae, Soritinae, and the Peneroplinae are somehow related, a less detailed conclusion that expressed by Carpenter (diagr. 2).

After 1927 Cushman recognized the Soritoidea (=Peneroplidae) as a natural group throughout his long career. Cushman based his classification on information derived from ontogeny, and the geological age of each group. Ontogeny was accepted as a general principle to infer phylogeny; to differentiate between homology and analogy. As a general example of Cushmans method consider species A and B both possessing a structure Z, similar in every anatomical detail, and therefore an apparent homology. If it is observed that structure Z develops from structure X in species A, but from a different structure Y in species B, then structure Z in species A and B is taken to be an analogy, developed (or by inference, evolved) from two different structures (or ancestors). Cushman never formally stated the usage of ontogeny in this manner, but there are enough examples of his usage to make this inference. Cushman's (1948) classification of the Soritoidea is summarized below.

Family Peneroplidae

Subfamily Spirolininae
Genus *Peneroplis*
Genus *Dendritina*
Genus *Spirolina*
Genus *Monalysidium*
Subfamily Archaiasinae
Genus *Archaias*
Subfamily Orbitolitinae
Genus *Sorites*
Genus *Amphisorus*
Genus *Marginopora*

To facilitate comparison the above classification is represented in a standardized format in diagram 4. The taxonomic conclusion implied in diagram 4 is identical to that reached by Brady (1884) (diagr. 3).

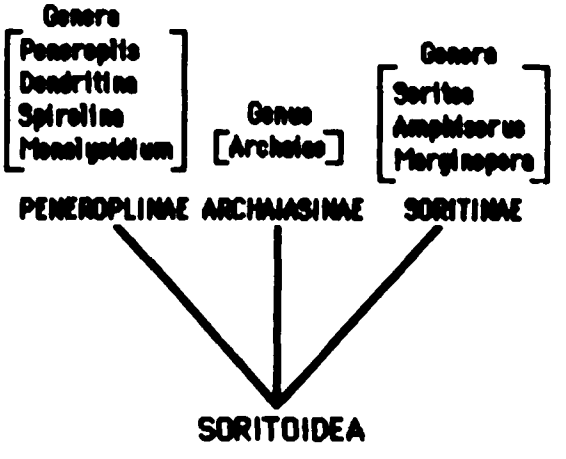


Diagram 4. A summary of Cushman's (1948) classification. All names spelled in full in capital letters are adjusted to the usage in this dissertation.

Hofker (1930) also recognized the Soritoidea (=Peneroplidæ) as a natural group. Later, in a slightly revised classification, Hofker (1953) presented a diagram which was supposed to summarize detailed evolutionary relationships among the Soritoidea. Hofker (1971) again presented a revised classification of the Soritoidea, almost unchanged from 1953, except that now both *Haueriina* and Alveolinidæ are properly excluded from the Soritoidea, but without any discussion. Hofker's (1953) phylogenetic scheme is reproduced in diagram 5.

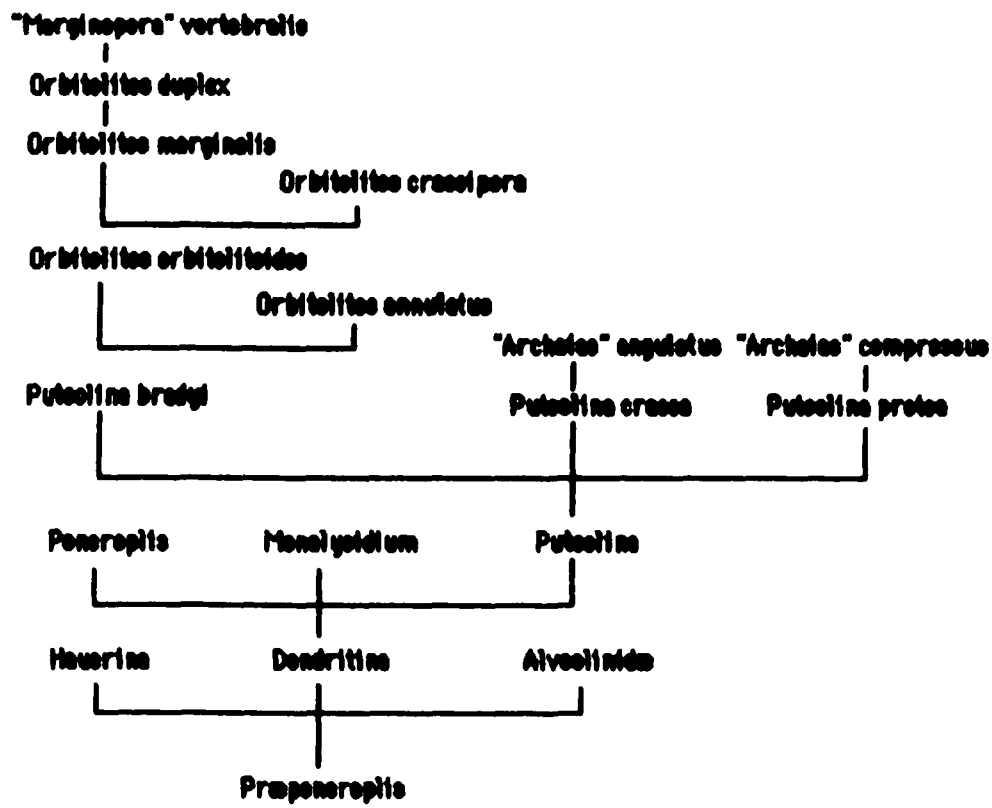


Diagram 5. Hofker's phylogram of the Soritoidea species and genera. (Modified from Hofker, 1953, p. 45.)

The relationship of the soritid species as Hofker probably understood it is presented in diagram 6 in a standardized format. In diagram 6 the Peneroplinae are represented as a group sharing a close relationship, which is not indicated in diagram 5. It was explicitly stated by Hofker (1953 p. 42) that from *Praepeneroplis* the dendritine forms developed and that from the dendritines the peneropline forms developed. This relationship was evidenced by the presence of striations on the exterior of these animals. From *Praepeneroplis* another group developed, including both the Archaiasinae and the Soritinae.

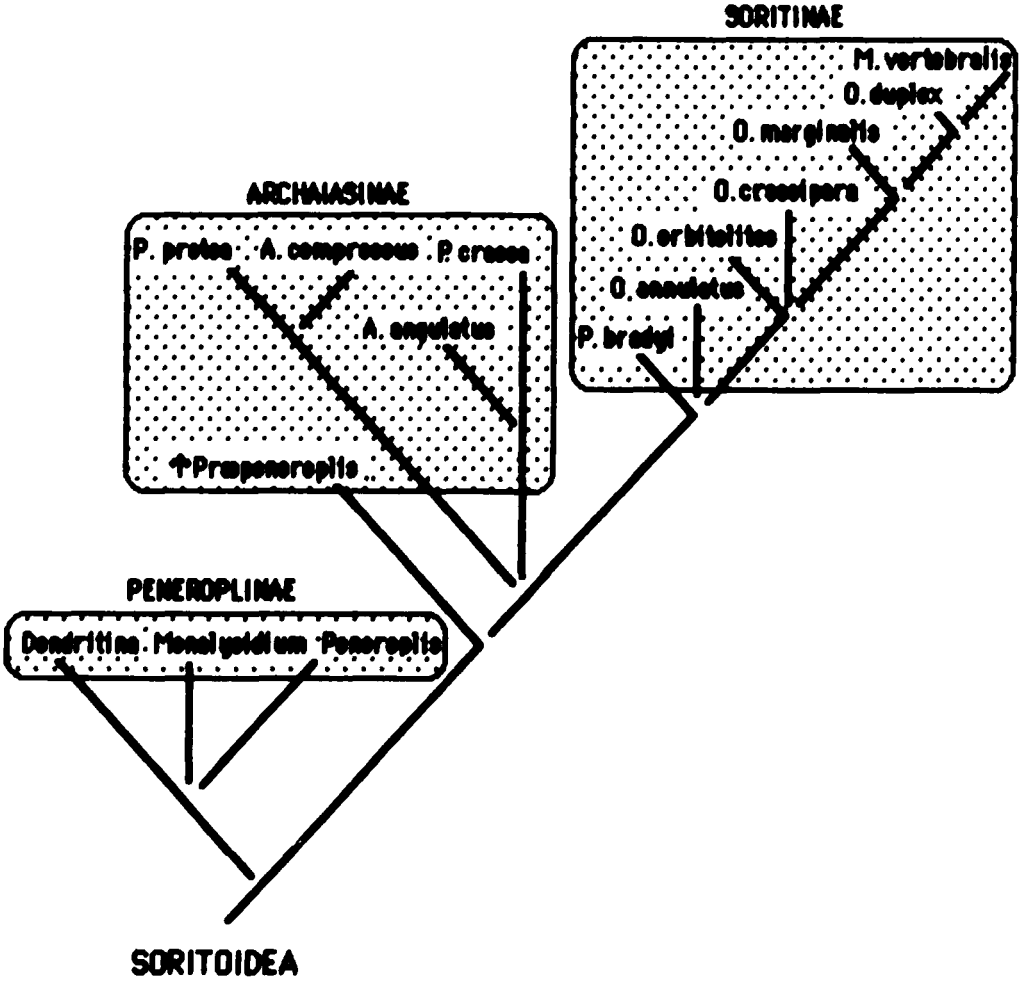


Diagram 6. A modified version of diagram 5. Each unbroken line denotes an evolutionary linage and the proximity of lines indicates an ancestor descendant relationship. The stippled boxes with names spelled in full in capital letters, refer to the subfamilies adopted in this dissertation.

The scheme presented in diagram 6, is a representation of Hofker's best judgement on how evolution occurred within the Soritoidea. Ancestor descendant relationship are derived from theories of homology and ontogeny, coupled with information on the age of taxa as derived from the fossil record. Structures were frequently assumed to be primitive if they appeared early in ontogeny and evolved if appearing only in adult stages. To ease comparison with previous diagrams, diagram 6 is simplified by reducing species linages to generic linages. The result is presented in diagram 7.

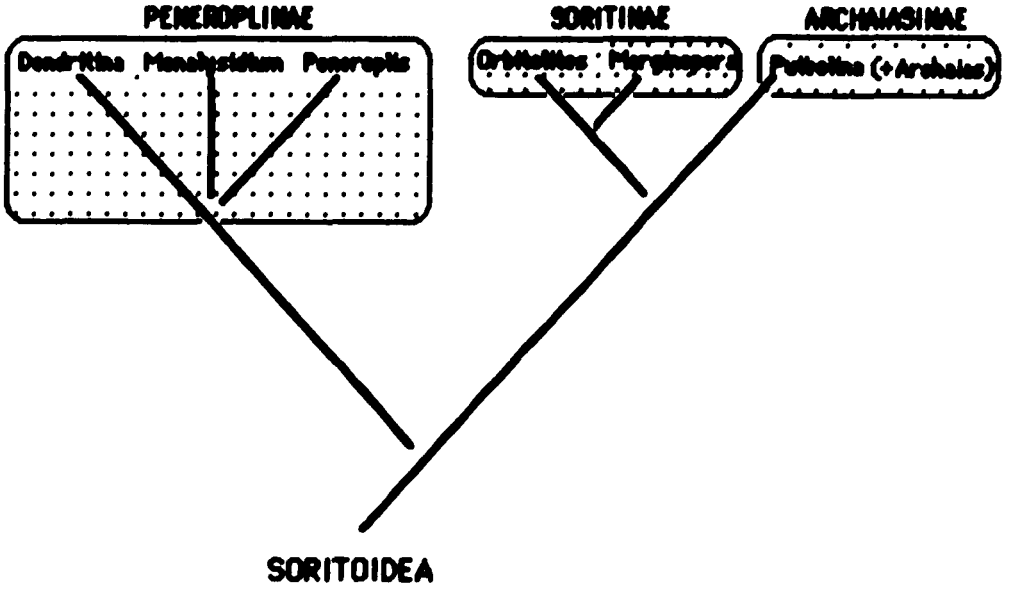


Diagram 7. A simplified version of diagram 6, representing evolutionary linages reduced to a generic level. The dotted

boxes labeled with names spelled in full in capital letters, refer to subfamilies adopted in this dissertation.

The branching pattern that emerges from diagram 7 is almost identical to Carpenter's diagram 2, except that diagram 7 is a little more detailed. As before the taxonomic conclusion is that the Archaiasinae and the Soritinae are more closely related in comparison to the Peneroplinae.

Ersu (1983, 1985), classified the Soritoidea into 4 subfamilies, Peneroplinae, Archaiasinae, Soritinae and Meandropsininae, and expressed taxonomic conclusions which at the subfamily level are identical to Hofker's (diagr.7), with the assumption that *Broeckina* the only recent Meandropsininae was to be lumped with the Soritinae.

Henson (1950) presented a classification on the Soritoidea (=Peneroplidae), treating both fossil and recent forms. A natural classification, as understood by Henson, should be based on the knowledge of a phylogenetic affinity. Henson noted that the morphology of the Soritoidea is an extreme case of variable series of integrated forms. Further, Henson asserted that similar forms have evolved repeatedly, in the same or different lineages, or in the same or different localities. Finally, different features occur in almost any combination in the same individual organism, subject to mechanical and functional compatibility. Henson echoed almost unchanged the ideas held over a century earlier by Carpenter, except that Carpenter's type concept had long become obsolete. In contrast to Carpenter, Henson called his classification artificial, an extremely simplified scheme, recognizing only two subdivisions of the Soritoidea. Henson's classification of recent Soritoidea is summarized in diagram 8.

Henson abolished the Archaiasinae and included its members within the Peneroplinae, but the Soritinae are retained as the second division of the Soritoidea. Henson's taxonomic conclusion is the least detailed of all the authors discussed, but understandable considering his

assumption that recognition of homologies is an almost impossible task.

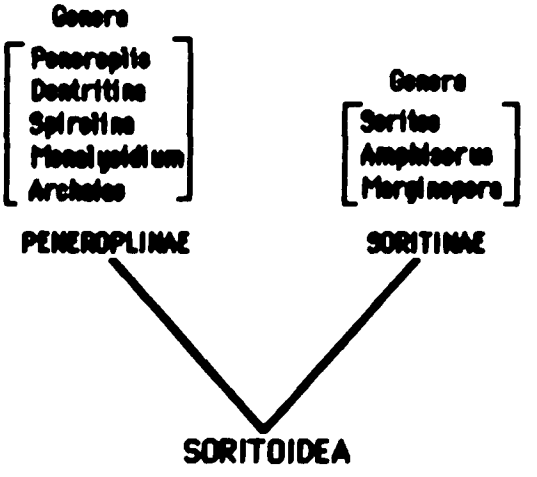


Diagram 8. A graphic summary of Henson's (1950) classification. All names spelled in full in capital letters are adjusted to the usage in this dissertation.

All the hitherto discussed authors based their studies on comparative anatomy and fossils. A slightly different contribution to the soritid systematics has been supplied by workers focusing on a symbiotic relationship present within this group. The Soritoidea are known to be hosts of a variety of photosynthesizing symbionts. This symbiotic relationship is postulated to be the driving force in the evolution of the Soritoidea, based on functional studies of the adaptive value of the symbiotic relationship (Lee and Hallock 1987). Interestingly, the three soritid subfamilies each harbor different types of symbionts. The Archaiasinae host several Chlorophycea, the Soritinae different Dinophycea, and the Peneroplinae host a Rhodophycea (Lee and Lawrance 1989, Leutenegger 1984).

Turning back to the opinion of Carpenter, one can ask in retrospect if there are any generalizations to be drawn from these foregoing studies. These can either be in the form of general principles, or conclusions in particular concerning the relatedness of the various soritid tribes.

As a summary of the above historical survey, it can be stated in particular as a taxonomic conclusion that the 3 subfamilies, Archaiasinae, Peneroplinae, and Soritinae, have consistently been identified by all the authors discussed above except Henson (1950). This threefold division is further evidenced by the presence of unique types of symbionts in each subfamily. Consistently the Archaiasinae and the Soritinae have been considered as more closely related, in comparison to the Peneroplinae (diagr. 2 and 7).

Concerning general principles, it is evident that all the above authors regarded the reconstruction of phylogeny as the grand incentive of their systematic research, where such knowledge was an end in itself. The justification for phylogenetic reconstruction rests on the assumption that evolution is orderly, producing anatomical structures recognizable as homologies and interpretable as indicators of past evolution. The anatomical features of ancestral species are assumed to be inherited in a modified form in all of its descendant species. Convergences and parallelisms can be detected by careful anatomical scrutiny, and an evolutionary loss of features does not occur. As a corollary it follows, that ontogeny is apt to exhibit a congruent orderliness among different species, where one structure develops or transforms into another, and further that ontogeny recapitulates phylogeny. Elements of self-skepticism have confounded all the above authors to a varying degree. Perhaps all homology theories are artifacts of human perception; a disorderly reflection of convergences, parallelisms, and lost features, as Henson lucidly advocated. As corollary, ontogeny would be apt to be conceived as disorderly, as a sequence of anatomical structures incongruent among different species. The discussion seems to be

stalled, and it would be superfluous here to express my opinion for or against either view without any new arguments.

Rather than assuming beforehand that the process of phylogeny is either orderly or disorderly order in itself will be identified as a problem that can be investigated independently. The objective of this study is to identify homologies on the basis of similarity of anatomical parts, among 18 extant species of the Soritoidea. The homologies in turn are utilized to divide the Soritoidea into subtaxa. If all the homologies identified form an inter-nested set of subtaxa, combinable in a single diagram, then the homologies as such form a pattern that is ordered and hierarchical. If in contrast, homologies do define sub-taxa not combinable in the same diagram, then the homologies form a disorderly pattern. Scrutinizing order from disorder in this sense is a prerequisite for any persuasive argument for or against the orderliness of phylogeny, the process that produced the pattern specified in the diagram. These matters, concerning homologies, analysis of order (congruence analysis), and species are further discussed in the analytical part that follows.

ANALYTICAL PART

HOMOLOGY AND CONGRUENCE ANALYSIS

The assertion that certain structures in different species are identical despite some minor differences, is traditionally known as a homology statement. Homology is the relation which defines a group of species as monophyletic, as the descendants from a common ancestor (Patterson 1982). There are three types of errors possible when homology hypotheses are erected.

1) Similar, but non-identical (analogous) structures are hypothesized to be comparable and homologous.

2) Comparable structures are hypothesized to be different when these in fact are identical and homologous.

3) Homologous structures are only observed in some but not in all of the taxa truly possessing the homology. The distribution or the generality of the homology is underestimated (Hennig 1964).

Patterson (1982) distinguishes three different tests of homologies. These are the tests of conjunction, similarity, and congruence. The test of similarity is based on the assumption that the homology of structures can in principle be recognized, investigated, and understood by everyone. The verisimilitude of a homology statement is accepted or rejected on its own merits, as an accurate description of homologous similarity. Convergent or analogous similarity should be possible to discriminate from homologous similarity by careful anatomical scrutiny. The conjunction test refutes a homology if the

supposed homologues occur together in the same organism. The conjunction test can be regarded as a special case of the similarity test. Patterson's (1982) formulation of the congruence test is an attempt to evaluate the probability that the same group of species is defined by two or more homologies, by chance alone. A similar test was devised by Wilson (1965) to estimate the probability of observing by chance alone, homologies which define an inclusive set of inter-nested groups. The procedures of both Patterson and Wilson can be interpreted as an evaluation of the premises that, 1) homologies are never lost in any descendants, and 2) convergent or parallel features are always discerned by careful anatomical scrutiny. If these premises are accepted then all observed homologies should define a completely congruent set of groups forming an inter-nested set of groups within subgroups. What follows is an attempt to combine the reasonings of Wilson and Patterson in order calculate the probability of observing a given number of particular homologies defining a congruent set of groups, by chance alone.

It is of general interest to realize that subdivisions of any N number of species into subgroups is limited to a finite number of possibilities. To be more exact, given any N number of species, in how many ways is it possible to group together these N species by forming groups of 2 species, of 3 species, 4 species, etc. up to a group containing all the N species. The solution is given by formula 1, where G is the total number of possible species groupings, N is the total number of species under investigation, and r is the number of species included in a group. The lowest possible number for r = 2, if it is to define a branching point in a diagram. I do not know if formula 1 has been noted before in this context.

$$G = \sum_{r=2}^{N} \frac{N!}{r!(N-r)!} \qquad \text{Formula 1}$$

Thus, if N = 2 species there is only 1 group possible, if N = 3 species there are in total 4 groups possible, if N = 4 species there are in total 11 groups possible, etc. However, only a limited number of the total number of possible groups G, can be combined in a single diagram, ranging from 1 up N-1 groups. The maximum, N-1 is a constant regardless of the topological structure of the cladogram (Roberts 1984). To conclude, given any N number of species there are at most N-1 congruent groups which can be combined in a single cladogram as branching points.

Diagrams containing N-1 groups are characterized by only bifurcating branching points. Given a G number of groups there is a finite number of bifurcating diagrams possible. It has been shown (Cavalli-Sforza and Edwards 1966) that the number of bifurcating diagrams (containing N-1 branching points) is enumerated by formula 2, where N is the number of species and D is the total number of bifurcating diagrams.

$$D = \frac{(2N-3)!}{2^{N-2}(N-2)!} \qquad \text{Formula 2.}$$

If it is assumed that ancestral features are never lost in any descendants and convergent features are always detected, then only a set of congruent group definitions is consistent with these premises. Congruent groups are used here in the sense that these groups can be represented in a single diagram as branching points (Nelson and Platnick, 1981). However consistency or congruence are not definitive proofs and even if character loss and parallelism are accepted as a factual reality, it is possible that these unrelated or random processes could produce a set of completely internested groups. Randomness is defined in this context to signify the combined outcome of three unrelated processes, 1) ancestral origin and inheritance of anatomical features in all descendants, 2) reversal or elimination of ancestral characters in some or all descendants, 3)

independent origin of the "same" structures in different species. Assuming this notion of randomness it seems clear that any of the G number of groups enumerated in formula 1 has some possibility of being defined by a homology hypotheses. In the absence of any evidence of the absolute rate of origin, convergence, and elimination of features, it is further assumed that all the G number of possible groupings have an equal chance of being observed by some homology. To give an analogy, suppose that there exists an unbiased dice with a G number of sides. Each throw of this multifaced dice can result in any of the G number of possibilities. The frequency of each group definitions would approach 1/G as the number of homology hypotheses increases.

Under these random circumstances one can ask, given any number of congruent groups what is the probability that the next defined group will be congruent with the already defined groups? Consider diagram 9, for 9 species as an example.

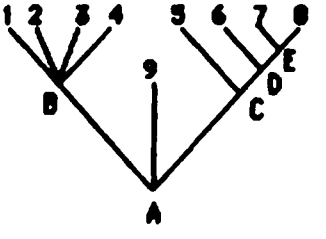


Diagram 9.

Given diagram 9, one can ask, what is the probability that the next observed homology defines a group by chance alone, that is congruent with species groups A, B, C, D and E? Given formula 1, it is possible to compute the total number of groups, that could be combined to diagram 9. In this case there are three computational steps involved 1) Number of groups possibly combinable with group B at a lower level of generality, or including less than 4 species (tips). Then in formula 1 N = 4 and r=2 and 3, and therefore G = 10.

2) Groups possibly combinable to groups B and C at a higher level of generality, or species groups including 5 or more tips. Groups B and C must be treated as individual tips (taxa) to calculate the possibilities. Then in formula 1 N =3 and r = 2 and therefore G = 3.
3) Replicates of the 5 existing groups, A, B, C, D and E are combinable with the cladogram.

To sum, there are only 18 species groups combinable to diagram 9 out of 502 possible groupings for 9 species. The probability that the next observed homology defines a group, combinable to diagram 9 by chance alone, is therefore 18/502 = 0.035, a low probability. For a 9 tip diagram as above, there are at most 8 groups combinable in single cladogram, and only replicates of exactly these same groups are combinable to it. Any such set of combinable or congruent set of groups could have been defined by chance alone, but the chances are 8/502 = 0.016, an improbable event.
A different question can be asked. Given any any x number of homologies, larger than N-1, the probability that these x homologies all define groups combinable in the same diagram by chance alone is simply $(N-1 / G)^X$.

Given certain number of congruent group definitions, it seems that the most likely or the simplest hypothesis is that the homologies originated in some common ancestor and were inherited in all of its descendants. It is of course possible that such a pattern of congruent groups could have originated randomly, but such a possibility can be judged not to be convincing given some specified level of significance as chosen by the investigator.

SPECIES

The Foraminifera even though diverse in form fall into more or less well defined "kinds" that have been hypothesized by systematists to be species. Species are here understood as lifecycles of self-

perpetuating populations of the same morphological structure. The assertion that different forms of organisms are parts of the same lifecycle has to be established by direct observation, where one life form develops or gives rise to another life form. An example of a study that utilizes this species concept is that of Medioli et. al. 1987. Cultures of clones of the arcellan species *Difflugia tricuspis* were kept in the laboratory and the morphological variability within successive clones was documented. When additional clones ceased to add new information, it was taken as an indication that the morphological variability of the species had been documented. The conclusion that emerged from this study was that 98 form groups, previously described as species, subspecies, varieties, and formae, were in fact parts of the lifecycle of *Difflugia tricuspis*. There remained, though, a large diversity of described arcellacean form groups that remained to be tested in the same exhausting way.

Two corollaries followed from this;

1) All morphotypes falling inside a given segment of morphological variability objectively belong to that particular species, and

2) all morphotypes falling outside a given segment of morphological variability objectively belong to another species, or were not observed during the experiment.

A morphotype is understood in this context to be a theory that describes a part of the lifecycle of a given species. Considering the whole lifecycle, any given species possesses certain defining structures that are qualitatively different from all other species, an assertion that can always be tested by life history studies.

In taxonomic studies that concern many species, lifecycle experiments are in practice either technically impossible or too laborious, so it is necessary to use substitute methods to infer the morphological life history of the species. There are two types of errors that can be made by inferring lifecycles only on the basis of preserved specimens. First, two or more different species can be mistakenly lumped together if the morphology is so similar that no significant structural difference is detected. Secondly, different

forms that appear to belong to two different groups can mistakenly be hypothesized to be different species when in fact these morphotypes are parts of the same lifecycle. The validity of all such hypotheses that are erected on the basis of conformity to some morphological structure can subsequently be confirmed (or falsified), by life history studies. The reality of species is in essence an empirical problem that can only be tested with lifehistory experiments.

Documenting the diversity of morphotypes encountered in nature, both within and among species, forms a basis for, or at least contributes to, all subsequent life history studies. If it can be shown by an experiment that form A can reproduce (sexually or asexually) with, or develop into, form B then the form groups A and B have to be considered as the same species, as different stages of the same life cycle. The significance of such experiments is however not crucial for systematics, although information on species groups can readily be incorporated into systematic diagrams. Assume for instance, that Carpenter was correct in that the whole family Soritoidea is nothing but a single but complex species. As Carpenter realized over 100 years ago this does not obviate the significance of the existence of distinct infraspecific morphotypes, each displaying an orderly ontogeny, and relationship, representable in a single branching diagram. All this still calls for an analysis to elucidate the natural factors that brought about such a marvel of a single, but regular and diverse species.

Organisms that belong to the same species (or morphotype) are never exactly alike due to both internal and external factors that determine morphology. Undoubtedly different anatomical parts display under different environmental conditions a varying amount of stability. Any descriptive theory of the anatomical structure of a species has to account for small or large amounts of morphological variability, both due to ontogeny and variability among individual organisms at the same ontogenetic stage. The anatomy of species is described as composed of variable structural units arranged and interconnected in a hypothetical system which is supposed to reflect a natural organic

design. Such structural systems are not only a matter of personal preference from an infinity of other possible descriptive schemes, but are subject to an objective evaluation. In an objective model each structural unit has to be defined with reference to an observation. Any description can either be proper or improper and the only way to evaluate a given description is to compare it with the described object and judge if it accurately reflects some natural reality. Objectivity is thus partly achieved by standardizing the observations with reference to some designated type specimens that are the actual standard of reference. A given descriptive theory of a species can be tested, if the described structures can in principle be recognized, observed, and justified by everyone (Blow 1979)

The objective and qualitative approach to systematics that has been argued for above, has in the past been criticized by some authors. Scott (1974) took a rather strong point when he stated, that population variability is the important taxonomic unit and the approach should be statistical and multivariate and that subjective assessment of variability is inadequate, in principle and in practice. The argument rests on the assumption that numerical measurements are objective in contrast to verbal descriptions and image-related presentations of species morphology which are subjective. Objectivity and subjectivity are used as opposite terms. Objectivity is supposed to be desired but subjectivity is undesired. Related to these are the terms quantitative and qualitative. Quantitative aspects of systematics are supposed to be desired but qualitative elements are undesired. Systematics should accordingly be objective and quantitative, and subjectivity and qualitativity should be excluded as much as possible (Burma 1948).

However, all quantitative measurements are only one type of observation and are not objective just because they are presented in the form of numerical measurements. Observations, including quantitative measurements, are always made in the light of some particular theory. All observations are dependent on and derived from a theory on what it is important to measure, and what the particular

significance of it is. If it is decided to quantify certain specified attributes of organisms, some measurements are selected as the most appropriate from an infinite number of possible sets of measurements. The preferred theory qualifies the quantity that is to be measured as an appropriate reflection of some natural reality. The preferred theory dictates which aspects of the organisms are to be recorded and analyzed; the rest are judged to be insignificant for the analysis. There is no a priori guarantee that quantitative measurements are always objective, for these could just as well reflect some arbitrary convenience imposed by the investigator. Measurements can at most supplement a theory, qualifying certain quantities as significant, but they can never supplant theories.

Popper (1959) defined objective and subjective knowledge according to Kant. Scientific knowledge and theories should be justifiable, independent of any personal speculation. Justification is <u>objective</u> if it in principle can be <u>tested</u> and understood by everyone.

> "Kant was perhaps the first to realize that the objectivity of scientific statements is closely connected with the construction of theories - with the use of hypotheses and the use of universal statements. Only when certain events occur in accordance with rules and regularities, as is the case with repeatable experiments can our observations be tested, -in principle - by everyone. We do not even take our own observations quite seriously, or accept them as scientific observations until we have repeated and tested them. Only by such repetitions can we convince ourselves that we are not dealing with a mere isolated 'coincidence', but with events which on account of their regularity and reproducibility, are in principle inter-subjectively testable" (Popper 1959, p. 45).

If objectivity is achieved through testability, what constitutes then a valid test? Theories are always tested with reference to some sort of observations which are always fallible. Theories cannot be conclusively falsified or verified, because any observation statement that forms the basis of a test may prove to be erroneous in the light of later developments. This is a curious situation where the argument for or against any scientific theory is based on fallible

observations. Nevertheless science as a research programme searches for objective knowledge, but there is no established formula or dictum to decide which observations are objective or subjective, true or false (Lakatos 1978).

To conclude, there are four main objectives of this study:

1) To demarcate groups of specimens as species, on the basis of anatomical features that are qualitatively different.

2) To establish relationship of species groups, based on homologies, interpreted as a shared and derived similarity due to common ancestry. Any such set of homologies will be analyzed with reference to congruence or non-congruence.

3) To evaluate the symbiosis thesis of soritid evolution with reference to homologies.

4) To document ontogenetic change of anatomical features at all developmental stages and to evaluate the significance of ontogeny for the study of fossils

TECHNICAL PART

One primary objective of this study was to document the ontogeny of the Soritoidea test. In order to achieve this it was necessary to dissect the test. Two methods were used, dissection with needles and by making thin sections. Dissection of the tests with needles was done by cementing the specimens to a frosted glass slide cut to 1 x 1 cm. Individual chambers were then peeled apart under a microscope, with steel needles, such as beading needles no. 15, insect pins no. 4, or fine glass needles (Troelsen 1954, Ponder 1972). The drawings were made with the aid of camera lucida and measurements were obtained with a micrometer. For the binocular microscope various stains were used to increase contrasts such as alizarin red, congo red, methylene blue and rose bengal (Henbest 1931).

Epoxy resin was used, following standard procedures, in order to make internal casts of the hollow compartments of the test (Hottinger 1979). The epoxy embedded specimens were ground down to the desired position, then the calcareous test was slowly dissolved by placing the epoxy block in 1N HCl solution for about 48 hours. This resulted in a relief epoxy copy of the hollow compartments of the test. Thin sectioning of the specimens followed the procedures in Finger and Armstrong (1984) with a few modifications. Sometimes, the preferred embedding medium over epoxy resin was Permount histological mounting medium because it is simple and quick in use, is easily cleaned from the specimens and generally gives good results. The specimens were cemented to a frosted glass slide in the desired orientation, and then submerged in the embedding medium. The hardening of the medium, free of air bubbles, was done by placing the preparates on a hot plate provided with a thermostat and

thermometer, and the temperature was gradually increased up to 95^{0}C for 3 hours. The specimens were then ground on a wet silicon carbide sandpaper, 200 grit, just enough to expose the interior. Then the specimens were reembedded, to fill the interior parts, and then the medium was hardened again. Afterwards the specimens were grounded to the desired plane and finally polished with a frosted glass slide. The embedding medium was cleaned off the specimens before examination, in serial solutions of touluene.

Preparation of specimens for the SEM involved cleaning the specimens for 3 hours in 5% hypochlorite solution at 90 ^{0}C., followed by washing in 5 steps in distilled water for 15 min. each. The specimens were lastly sputter-coated with gold or platinum.

The specimens for this study were picked from dried samples with a wet red sable brush no. 000, applying a standard 6 x 10 cm. extraction tray. The samples were supplied from the Department of Invertebrates of AMNH, by Dr. J. J. Lee and W. Faber. The following is a list of the 34 sample locations.

1) Sample no. VHS178(170) AMNH. Recent, Hawaii Island, Oahu, reef off Waikiki. Depositor, Henry Dodge, 6/15/49

2) Sample no. VWS190(170) AMNH. Recent, Midway. Depositor, Henry Dodge, 6/15/49.

3) Sample no. VHS191-II(170) AMNH. Recent, Alsaega, Manua Samoa. Depositor, Henry Dodge, 6/15/49

4) Sample no. VHS 177(170) AMNH. Recent, Hawaii Island, Oahu, reef off Waikiki. Depositor, Henry Dodge, 6/15/49

5) Sample no. 809 AMNH. Recent, Tunisia, Gabés. Collector, Robert King, Oct. 1. 1952

6) Sample no. 1529 AMNH. Recent, Pacific, Marshall Islands, from a lagoon at Eniwetok atoll. Collector, H. Hirschfield, 3/58.

7) Sample no. 1532 AMNH. Recent, Pacific, Marshall Islands, from a lagoon at Eniwetok atoll. Collector, H. Hirschfield, 3/58.

8) Sample no. 1538 AMNH. Recent, Pacific, Marshall Islands, from a lagoon at Eniwetok atoll. Collector, H. Hirschfield, 3/58.

9) Sample no. 1472 AMNH. Recent, Pacific, Marshall Islands, from a lagoon at Eniwetok atoll. Collector, H. Hirschfield, 3/58.

10) Sample from J.J. Lee, The Great Barrier Reef, off Heron Island.

11) Sample no. 2125 AMNH. Recent, Caribbean Sea, New Providencia Isl., British West Indies (Nassau), Lightbourne's Creek, 500' east of ocean, at 3' below low tide. Collector, H. Cousminer, 2/60.

12) Sample no. 2313 AMNH. Recent, Saudi Arabia, Ras Tanura, Tahrut Bay. Collector, B. F. Ellis, 2/60

13) Sample no. 2298 AMNH. Recent, Saudi Arabia, Ras Tanura, Tahrut Bay. Collector, B. F. Ellis, 2/60

14) Sample no. 1057 AMNH. Recent, The Bahamas, Bimini. Collector, A. R. Messina, Jan. 22. 1949.

15) Sample no. AMNH unknown, Ohunua, Eua, Tonga. Beach, 5' above high tide.

16) Sample no. 2071 AMNH. Recent, Egypt, Suez Canal, Just off False Ras Gharib, at anchor in 5 fms. of water. Collector, J. Dorreen, 12/3/41.

17) Sample no. 758 AMNH. Recent, Red Sea, station 20j, Mabaheth expedition, Lat.N. 27^0 21' 51", Long. E. 33^0 46' 30", depth 17-21 m.

18) Sample no. 1092 AMNH. Recent, Pacific, Kanton Island. Collector, I. M. Van der Vlerk, 9/10/54.

19) Sample no. 3416. Recent, Caribbean Sea, Providencia Isl. (Colombia), Brothers Cay, dredged sand. Collector, Sid Anderson, Jan.- March 1966. Deposited, 7/67

20) Sample no. 2744 AMNH. Recent, Australia, Great Barrier Reef, Heron Island, a beach sand. Collector, A. Messina, 7/66.

21) Sample no. 1295 AMNH. Recent, British Solomon Island, Faisi, Shortland I. D., South Seas. In coral sand beach drift. Depositor, AMNH Fish department, 6/56.

22) Sample no. 3176 AMNH. Recent, Hawaii Isl., Lat.N. 21^0 16' 58", Long. W. 157^0 53' 15", depth 320 ft. Deposited, 5/67.

23) Sample no. 1441 AMNH. Recent, Tunisia, Gabbés, beach sand. Depositor, Ben Uhl, 10/58.

24) Sample no. 1438 (and 1439) AMNH. Recent, Libya, $7\frac{1}{2}$ km. W. off Tunis road, strand line. Depositor, D. Hughes 6/57.

25) Sample no. 2477 AMNH. Recent, NW-part of New Caledonia, SE-side of bay Tuohfo(?), depth 4-7 ft. Deposited, 1/61.

26) Sample no. 2475 AMNH. Recent, U. S. Samoa, Fagasa bay. Depositor, Bill Christian, 1/23/64.

27) Sample no. 2479 AMNH. Recent, New Britain, Robaul. Deposited, 3/69.

28) Sample from J. J. Lee. Recent, Japan, Kudaka-jima, from a lagoon environment, 2 m. below low tide. July 1988.

29) Sample from W. Faber, Recent, Red Sea, Gulf of Aqaba, Taba, off the Steinitz Marine Biological Laboratory, depth 15 m.. January 1988.

30) Sample from W. Faber, Recent, Red Sea, Gulf of Aqaba, Taba, off the Steinitz Marine Biological Laboratory, coral reserve, depth 20 m.. March 14. 1988.

31) Sample from W. Faber, Recent, Red Sea, Gulf of Aqaba, Taba, off the Steinitz Marine Biological Laboratory, coral reserve, depth 30 m.. Collector Walter Faber, March 14. 1988.

32) Sample no. 2339 AMNH. Recent, Solomon Islands, Kieta, Bougainville, mixed with small shells from high tide line. Collector, W. J. Eyerdam, 8/25/29, depositor, W. K. Emerson.

33) Sample no. 1211(7-9-1) AMNH. French Oceanica, Tuamotu Archipelago, Raroia. Sand from small beach between seward reef flat and beach rock at traverse north of Garumaoa village. Collector, Sperrazza, 6/11/56.

34) Sample no. AMNH 3606, The Torres Strait.

SYSTEMATIC PART

DEFINITION OF TERMS

In the Soritoidea, as in most Foraminifera, the test is divided into chambers. When the animal grows each chamber is added to the test in successive steps, thus recording in the test the ontogenetic history of each individual. The morphological observations in this study are based on 6 anatomical aspects of the test, and the ontogeny of these. These are, the growth form, the ornamentation on the exterior wall, the internal skeleton, the sutures, the aperture, and to some extent the crystal structure of the wall. I recognize 4 different types of growth forms within the Soritoidea. Growth form refers to the shape of the chambers and the mode of how each chamber is added to the test. These are defined as following:

1) Planspiral, lenticulate growth. In planspiral growth the chambers are added to the test in a single plane. The plane of growth is determined by drawing an imaginary line through the center of all apertural faces in a single test. Each chamber is attached to one or more chamber in the previous whorl and covers the apertural face of the immediately preceding chamber. The lateral side of the chamber forms one continuous U-shaped wall. The distance between two subsequent apertural faces in the same test is defined as the length of a chamber. The distance between the lateral sides of a chamber is the width, and the height of the chamber is the distance between the keel and the base of the chamber. A chamber is defined here as lenticulate if the greatest dimension is the height of the chamber (fig. 1 a). (A chamber is fusiform when the greatest dimension is the width, and chambers are tubular when the greatest chamber dimension is the length).

Planspiral lenticulate growth in the Soritoidea can either be involutive or evolutive. An evolutive growth is when the lumen of the chamber is confined towards the keel of the test, such that all the chambers in the test can be viewed from the outside (fig. 1 a and 36). In some species (for example *Amphisorus hemprichii* and *Peneroplis acicularis*), the chambers in each whorl extend membranous layers of calcareous material towards the umbilici (center) of the test. This phenomena is not understood here to constitute an involutive growth. An involutive growth occurs only when the chamber lumen is extended towards the umbilical part of the test, such that only the chambers in the last volition can be viewed from the exterior. There are two types of involutive growth modes, the arciform and the planate-form. A planate-form of involutive growth occurs when the chamber lumen extends towards the umbilical part of the test, but the chamber is only slightly curved, extending in almost a single plane towards the umbilicus (fig. 1 b and 53 a and b). An arciform involutive growth is when the chamber lumen extends towards the umbilicus of the test in a curved plane (fig. 60 a and b). This type of growth has also been referred to as a vorticiform growth (Smout and Eames, 1958)

2) In a flabelliform growth mode the apertural face is connected at two sites to the previous chamber(s) of the test. The apertural face divides the lateral sides of the chambers into two discontinuous lateral walls (fig. 2).

3) In a rectilinear growth mode, each chamber is attached to the apertural face of only the immediately preceding chamber (fig. 2). The chambers in a rectilinear growth form only possess one cylindrical lateral side.

4) In annular or circular series, the chambers are only connected to the apertural face of the previous chamber, and form continuous rings around the test (fig. 2). The apertural face divides the lateral walls of each chamber into two discontinuous annular sides.

Certain members of the Soritoidea possess an internal skeleton. There are three basic types of internal skeletons recognized, pillars, buttresses and septula (singular, septulum) (Henson 1950, Hamaoi and

Brun 1974). Pillars are cylindrical structures that form a connection between the apertural faces of two succeeding chambers. Pillars never form a connection to the lateral sides of the chamber wall (fig. 3). Buttresses are thickenings of the lateral walls, forming a wall-like structure, extending toward, but never into, the center of the chamber (fig. 3). Septula are platelike partitions, dividing the chambers into distinct chamberlets. The septula form a continuous wall between the apertural faces of two succeeding chambers and also extend between opposite lateral walls in each chamber. The septula possess openings (stolons), located directly below the apertures. The stolons form a passage between the chamberlets in the same chamber. Thus, the septula, the stolons, and the apertures form a single structural complex (fig. 4).

Since the late eighteenth century it has been noted that there exists a dimorphism among Foraminifera. There are two categories of dimorphism that have been in usage, a size dimorphism and a structural (anatomical) dimorphism. It was probably first noted by Harpe (1879) that specimens identical in morphology are usually distributed in pairs differing only in size. The size dimorphism is characterized by two phenomena. First, the size of the whole test seems to fall into two distinct size ranges, at least in some species. Secondly, the embryo or the first chamber of the test (proloculus), also falls into two distinct size groups. The larger tests, usually contain the smaller prolocull, and are accordingly called microspheric (or the B form). The smaller tests, usually contain the larger prolocull, are called megalospheric (or the A form), terms first created by Munier-Chalmas and Schlumberger (1883).

The significance of the size dimorphism in the proloculus and the test was first elucidated independently by Lister and Schaudinn in 1895, who observed the life history of *Elphidium crispum*. In general two methods of reproduction occur, sexual and asexual, which alternate in occurrence (Lister, 1903). Asexual reproduction consists of a simple multiple fission (schizogony), in tests with a smaller proloculus (microspheric tests, also called the B form).

Asexually formed embryos have larger proloculus (megalospheric tests, or the A form). The animal with the megalospheric test, in turn, reproduces sexually (either uniparentally or biparentally) by forming gametes which fuse to form embryos which develop into individuals with microspheric test. Subsequently, it became customary in the Foraminiferal literature to assume that tests with a microspheric proloculus represent asexually reproducing organisms (agamonts). Thus, the terms agamont and the microspheric generation (B-form) became synonymous. Similarly the megalospheric generation (A-form) was assumed to represent sexually reproducing organisms (gamonts). Thus, the terms megalospheric generation (A-form) and the gamont became synonymous. Later studies undermined the postulate, that the size of the proloculus somehow manifested the mode of reproduction.

Arnold (1964) summarized the lifecycle studies of 9 species that had been studied since 1894. For 3 species the size of the proloculus was the same for both the sexual and the asexual generation. For 2 species the proloculus of the megalospheric test belonged to the asexual generation, which is opposite to the "classical" species *Elphidium crispum*. For 2 species there was a considerable overlap in the prolocular size range of the sexual and the asexual generation. For two species the prolocular size conformed to the "classical" life cycle. Originally Schaudinn 1895 had noted that there was an overlap in the prolocular size between the sexual and the asexual generation in *E. crispum*. Similar anomalies were discussed by Arnold (1964) concerning the size dimorphism in the adult test size. To conclude from the above, it seems that size difference information on prolocular size has a limited value as a general indicator of the mode of reproduction. It has been suggested that the terms megalospheric and microspheric generations should not be used at all because of these ambiguities, and also because apparently factors other than the mode of reproduction affect the size of the proloculus and the whole test (Boltovsky and Wright 1976).

The second category of dimorphism refers to anatomy, and was perhaps first used by d'Orbigny (1846) to indicate two modes of growth within an individual test. This concept of dimorphism refers to morphological differences in the test structure among or within specimens, without any reference to the relative size of the structures. In addition to the size dimorphism among specimens of the same species, Munier Chalmas and Schlumberger (1883) also noted two distinct types of growth forms, among these two generations. This original notion of dimorphism referred to a structural or anatomical dimorphism, sometimes correlated with size difference in the proloculus and the whole test. To give an example of anatomical dimorphism within the Soritoidea, it suffices to refer to the species *Marginopora vertebralis*. The embryonic apparatus in the A-form of *M vertebralis* is made of a proloculus, flexostyle and a vorhof, and the growth form is exclusively annular series in the post embryonic chambers (fig.13 b and c). In the B-form however, the embryonic apparatus consists of a single chamber, the proloculus. The growth form following the proloculus in the next 5-9 chambers is planspiral lenticulate, and then a flabelliform growth (fig. 13 a). The remaining chambers form annular series identical to the A-form. The criteria to detect a dimorphism is then primarily based on structural difference in the embryonic apparatus, rather than on a mere difference in point of size, which however usually correlates with structural differences. I use the term dimorphism in the original sense of Munier Chalmas and Schlumberger, to indicate an embryonic structural difference among generations of the same species.

THE SYSTEMATIC POSITION OF THE SORITOIDEA

The classification adopted herein and tabulated below, is based on the morphological relationship of the soritid species as is presented in diagram 10. This subdivision conforms to the division as presented in Loeblich and Tappan (1984).

Suborder Miliolina Delage and Herouard, 1896
superfamily Soritoidea Ehrenberg, 1839
family Soritidae Ehrenberg, 1839
subfamily Soritinae Ehrenberg, 1839
subfamily Archaiasinae Cushman, 1927
family Peneroplidae Schultze, 1854
subfamily Peneroplinae Schultze, 1854

The following is a list of the defining and diagnostig features of the soritids.

1) The Soritoidea are defined by a planspiral, lenticulate and evolutive growth in first juvenile chambers. The second characteristic is a special kind of ornamemtation on the apertural face, consisting of elongated pits, slightly fusing, forming a spongy texture.

2) The Soritidae are defined by multiple apertures, where each individual aperture ranges in shape from a circular to elongate to crescentic form.

3) The Soritinae are defined by possessing an internal skeleton, consisting of simple transverse wall partitions or septula. The septula are transformed into a more complex skeleton in *Amphisorus*

and *Marginopora*, but the septula is distinctly present in the juvenile chambers in these genera. The apertural characteristics in all the Soritinae form a single row of apertures, transforming later into a double row of apertures. The single and double apertural rows are only present in the juveinile stages in *Marginopora*.
4) The Archaiasinae are defined by the presence of an involutive, arciform growth mode, at some stage of development. The apertures always form a single row of apertures on the involutive part of the chamber (fig. 60 a). A double apertural row is present on the evolutive part.of the chamber, which sometimes extends onto the involutive part. The double apertural row is develops in adult specimens into a broad segment of anomalously disposed apertures in the *Archaias*, *Androsina* and in the large specimens of *C. compressa*
5) The Peneroplinae are defined by the presence of pits arranged into rows. The apertural characteristics form dendritic apertures, beginning in the juvenile as a simple X of Y shaped form, later transforming into a single (or multiple) irregularily dendrtic structure.

The Soritoidae belong to the Suborder Miliolina Delage and Herouard, 1896. All members of the Miliolina possess a porcellaneous test, constructed of three layers of calcite crystals. The external and the internal surface of the test are covered with thin inner and outer veneers of regular rhombohedric crystals. The central layer consists of a threadlike crystals arranged in a random array (Lynts and Pfister 1967, Haake 1971, Cherif and Flick 1974). The formation of calcite crystals in the species *Spiroloculina hyalina* takes place within a 6µm thick organic matrix. In each new chamber the crystals build up into scattered hummocks in the central area on the interior of an organic matrix. The hummocks gradually coalesce and spread, reaching the aboral and oral areas. There may be several waves of crystallization before the organic matrix is completely calcified (Arnold 1964). This type of calcification has been observed only within the Miliolina (Towe and Cifelli 1967).

Le Calvez (1938) described biflagellated gametes with axostyles for some miliolline species. However this was based on only 3 species and I know of no subsequent study concerning the anatomy of gametes in the miliolines.

It is well established that a bilocular embryo is present in all members of the Miliolina, at least in the A-form. The embryo consists of an ovate proloculus, followed by a tubular flexostyle (deuteroconch), which whirls around the proloculus (e.g. Haynes 1981).

The homology hypotheses that define the Miliolina as a monophyletic group are here summarized

1) Porcellaneous wall structure
2) Embryo constructed of a proloculus and a flexostyle, in the A-form.
3) Gametes with an axostyle.

Varying schemes of classifications have been presented for the Miliolina subtaxa but it is beyond the scope of this text to discuss the merits of these schemes. There are however at least 5 larger groups that I can recognize. First to mention are two groups apparently closely related, the Fischerinian and the Opthalmidean type, characterized by a planspiral tubular and later irregular growth. Second are the related groups of the Miliolinean and the Alveolinean type, with tubular chambers winding in various planes at least in the embryo. Last are the Soritoidea which apparently display a closer affinity to the group containing both the Miliolina and the Alveolinean types.

Superfamily Soritoidea Ehrenberg, 1839

In the course of this study I have recognized 18 species as properly belonging to this group, made among these 30 comparisons as homology statements, and among those identified 6 ontogenetic transformations. Each of these homologies are given equal weight in defining subgroups within the Soritoidea. The distribution among of

the homologues among the 18 species is summarized in table 1. In diagram 10 the distribution of the homologies (numbers 1 - 30), are represented as branching points (letters A - P), each defining one of the 16 species groups. A short description of each homology is listed below.

1. Evolutive, lenticulate, planspiral growth following the embryo in the B-form.
2. Flabelliform growth stage.
3. Chambers arranged in annular series.
4. Internal skeleton consists of septula.
5. Median skeleton present.
6. Apertures form a single row.
7. Apertures form double marginal rows.
8. Median apertures present between the marginal apertural rows in homology 7.
9. Ornamentation on lateral chamber surface consists of evenly dispersed pits, and sometimes partially fused pits, forming irregular depressions.
10. Internal skeleton forms the duplex plan.
11. Sutures wave-formed.
12. Apertures multiple, of a circular, elongate, to crescentic form.
13. Ornamentation on the apertural face consists of pits, elongated, slightly fusing of a spongy appearance.
14. The A-form embryo possesses a vorhof.
15. Pits arranged in a single row.
16. Pits arranged in double and triple rows
17. Pits irregularly disposed within multiple rows of pits.
18. An aperture of an X or Y-type.
19. An irregularly dendritic aperture.
20. Multiple apertures partly made of irregularly dendritic apertures.
21. Planate-form of an involutive growth.
22. Chambers flaring, evolutive, and compressed.

23. Involutive, lenticulate, and planspiral growth of the arciform type.
24. Internal skeleton elements consist of buttresses.
25 Internal skeleton elements consist of pillars.
26. Growth form consists of circular chambers.
27. Apertures form a single row of apertures.on the involutive part of the arciformed chamber.
28. Apertures form a double row of apertures, on the evolutive part of the chamber sometimes extending onto the involutive part of the chamber.
29 Cylindrical to flaring chambers, forming a rectilinear growth.
30 Apertures forming a multiple row of a circular, crescentic to elongate apertures, disposed anomalously over the apertural face.

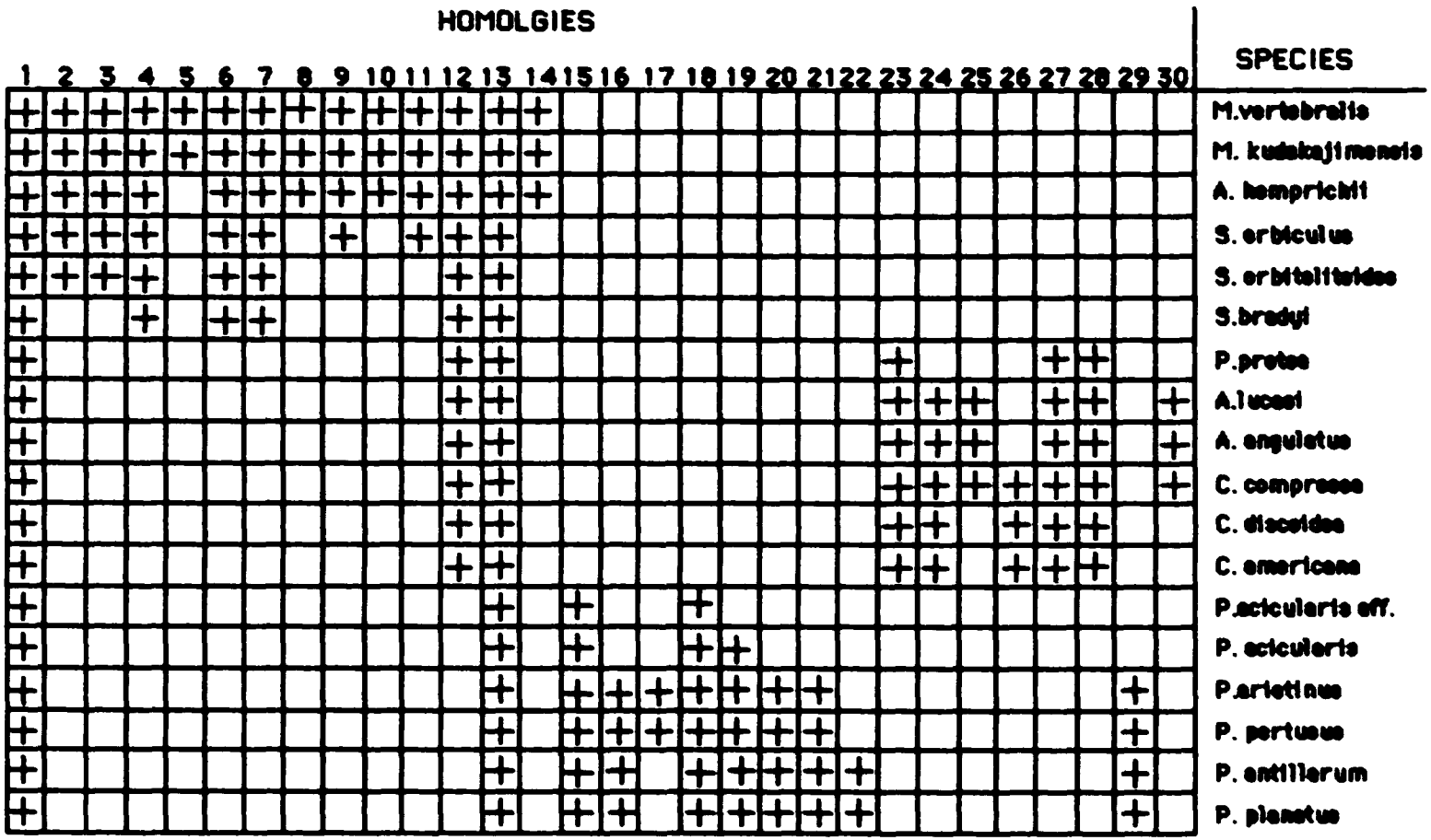


Table 1. A data-matrix showing the presence (+) of each of the 30 homolgies among 18 soritid species.

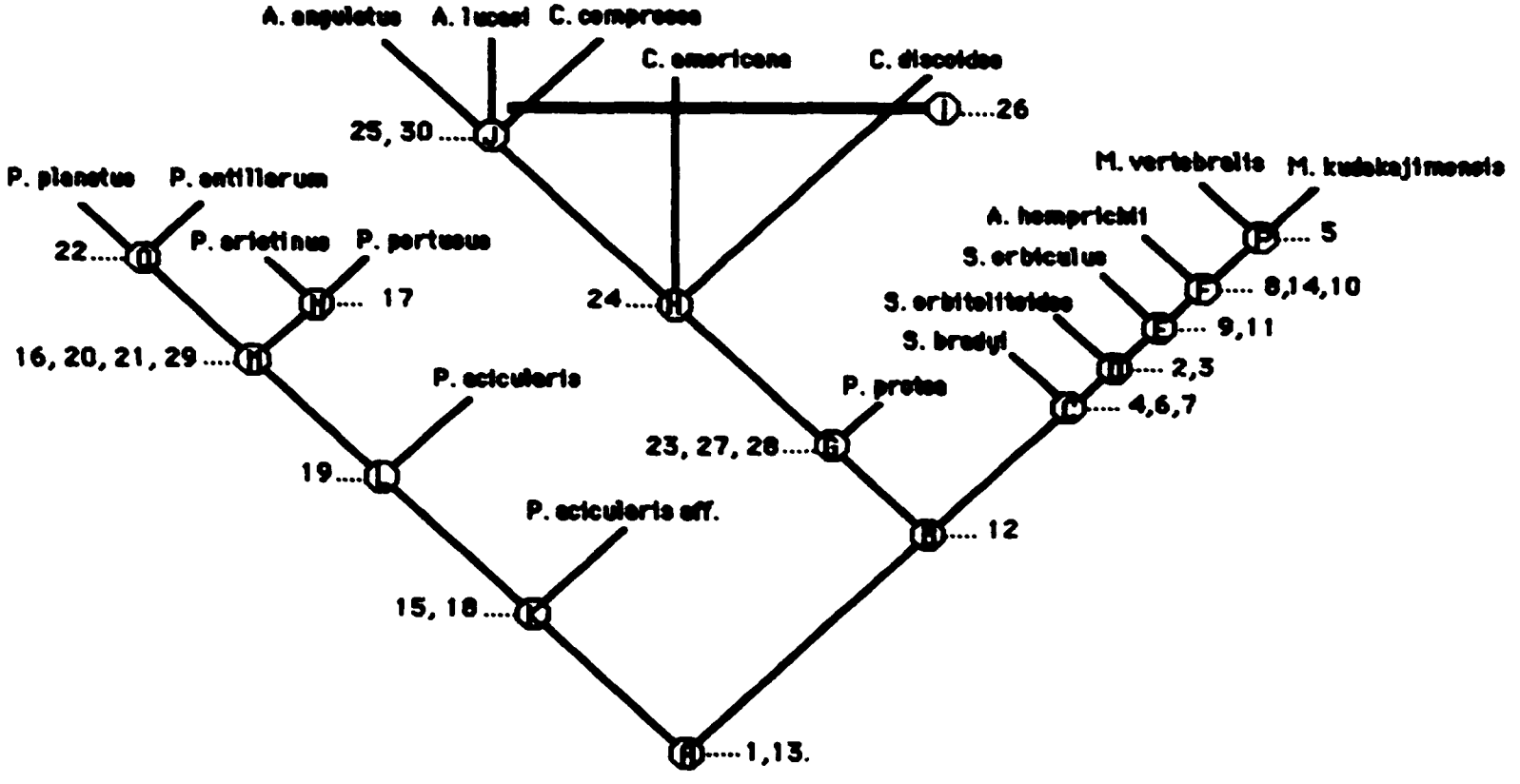


Diagram 10. A summary of the systematic relationship of the Soritoidea. The groups are indicated with the letters A-P, defined by homologies 1-30.

The presence of rectilinear growth, following the planspiral, lenticulate, and evolutive growth, is excluded as one possible homology on the basis of insufficient information. A number of juvenile specimens, (about 3-10 chambered) were encountered in most samples. It is impossible to identify these juvenile specimens, since the specific features develop only in the adult chambers. The samples from the Caribbean region revealed a number of juvenile specimens which are only possible to diagnose as belonging to some of the species included in group H (the Archaiasinae), based on homology 12 and poorly developed homology 23. A few of these specimens show a tendency to develop a rectilinear growth mode following homology 1. Several juvenile tests from Japan and the Red Sea were found showing 1 or 2 chambers growing in a rectilinear mode. As before the specific identity of these juvenile specimens is impossible to determine, but they do possess multiple rows of pits (homology 16) and multiple dendritic apertures (homology 19 and 20), and could belong to any species included in group M, although they lack a well developed homology 21. This suggests that a proportion of the population in some or all the species included in groups H and M, do possess a rectilinear growth at this growth stage. However in those few adult specimens, I have attempted to dissect, I have been unable to detect any signs of rectilinear growth following the planspiral growth.

The species *M. vertebralis* and *A. hemprichii* express homology 1 only in the B-form, represented in my samples by only 7 specimens, which is hardly a significant sample to affirm the absence of a rectilinear growth following homology 1. A rectilinear growth following homology 1 is however common among specimens belonging to *S. bradyi* and *S. orbitolites*, but is rare among *S. orbiculus*, represented in only 2 specimens.

A secondarily developed rectilinear growth is present in the very last adult chambers among all the species included in group H. Rectilinear growth is extremely rare within *Androsina* and *Archaias*

(group I), but at least 3 specimens have been encountered, from each species, possessing rectilinearly arranged chambers following homology 23. About 4% of the specimens belonging to *P. protea* express a rectilinear growth following homology 23. Of the *Cyclorbiculina* species 1-4 specimens of each possessed rectilinear arciform chambers, following the arciform growth (23), and rectilinear flaring chambers following the circular chambers (homology 26). These secondarily developed rectilinear growth modes, would replicate groups H, J, and I, if they were construed as homologies.

A few specimens distinctively belonging to each species included in group D, possess 2-6 flaring chambers, arranged in a rectilinear series, following the annular chambers.

These secondarily developed rectilinear growth modes within groups H and D, can be construed as independent homologies, defining groups combinable to diagram 10, but I have reservations. The primary reason is that the specimens that possess a rectilinear growth are often extraordinarily deformed, perhaps as the result of some pathologic factor. Rather than resorting to examination of preserved specimens, a better way to inquire into the nature of the rectilinear growth would be to cultivate these species under controlled conditions. If it can be adequately determined, that the rectilinear growth modes are inherently a part of the developmental program, rather than some deformity imposed by a pathogenic or toxic agent, then these various rectilinear growth modes can be incorporated into diagram 10. If classification is the successive grouping of species, then diagram 10 is a classification, representing a hierarchical set of species groups. I will not formally name all the 15 species groups represented in diagram 10. I do however reiterate the names of the groups indicated by groups A, B, C, G, and K. As I mentioned in the introduction these groups have persisted in history, as recognizable groups, and were according to taxonomic procedures given a distinct name. An excellent reference to the synonymy of these groups is in Loeblich and Tappan (1964 and 1984), and is not repeated herein. In

addition to these classical groups, I have indicated as branching points, 10 new groups within diagram 10. History will judge these groups, and if replicated by future researchers they will eventually be named.

In diagram 10, homologies 1 and 13 are common to all species within the Soritoidea, represented as group A. Members of the Soritoidea are recognized as a distinct group from all other Miliolina subtaxa, by the planspiral lenticulate growth form, that immediately follows the embryonic stage (Hofker 1930, Cushman 1930, and 1933, Loeblich & Tappan 1964, Haynes 1981, and Glaessner 1963). The planspiral, lenticulate growth is present in all members of the Soritoidea, and defines it as a monophyletic group. This growth pattern is present in both the A and the B-form of all species, except in *M. vertebralis* and *A. hemprichii*, where the planspiral growth is only present in the B-form but suppressed in the A-form.

The ornamentation on the apertural face is similar among all members of the Soritoidea, and is confined exclusively to this group. The apertural ornamentation consists of pits, partially fused forming irregular furrows. This has not been proposed before as a homology defining the Soritoidea as a group (see for example fig. 12 and 45).

Hofker (1952 b) included the genus *Haueriina* within the Soritoidea, on the basis of a "porous" embryo with a flexostyle, possession of a cribrate aperture, and the presence of chamberlets. The development of the apertures in *Haueriina* begins with an "initial primary tooth, which later subtends a ring tooth braced to the apertural margin by secondary teethes, and which becomes a complex trematopore in adults" (Ponder 1972, p 147). I have never observed this type of apertural development within the Soritoidea. The internal skeleton in *Haueriina* consists of transverse septa that seem to be confined to lateral sides and the keel of the chamber. Further the chambers are tubular, with series of septa subdividing the tube into chamberlets, where the aperture is confined to the end of the tube (Hofker 1953). The septa in the *Haueriina* and the Soritoidea, are probably not

homologous structures, but a detailed analysis of the internal skeleton in *Haueriina* is not available.

The Alveolinidae is morphologically a well defined family. An irregular coiling of the first volitions is found in the B-form of all Alveolinidae, indicates a close relationship to the Miliolidae. In the A-form there is a direct transformation into planspiral fusiform growth (Reichel 1964). Carpenter (1861, pp. 572-573) included the Alveolinidae (=Alveolina) within the Soritoidea, assuming that the planspiral lenticulate and fusiform growth forms were homologous structures. This mistake was corrected by Brady (1884, p. 222) where the similarity in growth form among the soritids and alveolinids is referred to as an analogy. Hofker (1952 b) reports a planspiral lenticulate ("peneropline") growth stage in the B-forms of a single alveolinid species, *Alveolinella quoyi*. Hofker suggests that the lenticulate ("peneropline") growth form in the alveolinid *A. quoyi* is comparable to the typical planspiral lenticulate growth in the soritid *Archaias*. It is very difficult to assess from Hofker's figures whether the growth form in *A quoyi* is truly planspiral lenticulate rather than fusiform planspiral, a defining feature for the Alveolinidae. In contrast to Hofker, Chapmann (1908) describes the growth form of the embryo in the B form of *A quoyi* as a triloculine coiled miliolid embryo. It seems that the structural dimorphism of *A quoyi* has not been adequately determined. I will follow Reichel (1937 and 1964), and include *A. quoyi* in the Alveolinidae rather than in the Soritoidea and assume that Chapmann's assessment of the structural dimorphism in *A. quoyi* is correct.

Carpenter (1856) and Brady (1884) included within the Soritoidea the species *Orbitolites tenuissima* (= *Discospirina tenuissima*), which assumes in its adult stage a growth form of annular series. This species properly belongs to the Opthalmidiacea (Haynes 1981), which is defined by its planspiral tubular growth form, a condition which is clearly observed in the juvenile stages of *D. tenuissima*. The annular growth form in the Soritinae originates from an evolutive, planspiral, and lenticulate growth form. In this sense the

annular growth form in *Q. tenuissima* and the Soritinae is analogous, because the ontogenetic origin of the annular growth is different. Therefore, with reference to ontogeny the similar ring-formed chambers in the Soritinae and *Discospirina* are analogous (Hofker 1930, Cushman 1948, Henson 1950, Loeblich and Tappan 1964). *Q. tenuissima* also possesses an internal skeleton, remarkably similar to the septula present in the Soritinae. However, I examined 5 specimens of this rare species in the Cushman Collection at the U. S. National Museum and can affirm that the internal skeleton in *Q. tenuissima* is not homologous with the skeleton in the Soritinae. The skeleton in *Q. tenuissima* consists of transverse septa, confined to the base of the chamber, never fusing internally with the apertural face to form a apertural stolon complex. The chamberlets in each chamber are of about equal size, but do not form the hexagonal arrangement as is present in the Soritinae. There are other important differences, but the anatomy of *Q. tenuissima* is beyond the scope of this text.

The exterior of the Soritoidea test wall is covered with pits or holes which end blindly. Presumably comparable pits are also present in other milioline subgroups, but it is not adequately known how widely distributed these pits are among the milioline taxa. There are distinct pits in the adult growth stages of the species *Miliolinella subrotunda* (Lints & Pfister 1967) and *Miliolinella enoplostoma* Reuss.(Kihle and Løfaldi 1979) which are both grouped within the subfamily Miliolinellinae Vella 1957. Brady (1884) and Keijzer (1935) reported on pit-like structures in *Triloculina rupertiana* (Brady) and *Massilina agglutinans* Keijzer. Hofker (1953 and 1964) reported on pore-like structures in the embryos of genera *Hauerina* and *Alveolina*. Brönniman and Zanietti (1971) observed pore or pit-like structures in the Triassic quinqueloculine genus *Miliolipora* Occasional specimens grown in culture (ranging from one out of several hundred to thousand or more) of the species *Spiroloculina hyalina* had pit-like structures. These pits were not evenly dispersed over the test surface but coalesced with adjacent pits to produce

multilobed depressions (Arnold 1964). If these pits within the miliolids are homologous then it defines a much larger group, including the Soritoidea.

It is to be noted in this context that holes in the Soritoidea test are caused by boring organisms. Winter (1907) described in detail holes in the test of *Peneroplis* caused by organisms, which he believed to be boring bacteria. It has also been observed that boring algae attack the test and produce holes in living Soritoidea. The protoplasmic animal often extends pseudopods through these holes (Lee, personal communication).

Carpenter (1856) used the presence of perforations to separate the Rotaliina genera *Cycloclypeus* and *Heterostegina* from the Miliolina genera *Sorites* and *Archaias*. Later, in 1862, Carpenter, Parker, and Jones utilized in their classification scheme the presence and absence of pores to divide all Foraminifera into two subgroups, the Imperforata (=Miliolina) and the Perforata (=Rotaliina), where the Soritoidea were naturally placed within the Imperforata. Williamson (1858) noted that the crystal structure of the wall in the Imperforata consisted of a distinct porcellaneous type, in contrast to the Perforata, which possessed a different wall structure, termed hyaline. It seemed that the Miliolina were only characterized by the porcellaneous wall structure, without any traces of pores. Subsequently there have been conflicting reports concerning the perforated nature of the Soritoidea embryo. Either the embryos of certain members of the Soritoidea have been characterized as porous (Rhumbler 1894, Awerinzew 1903, Winter 1907, Hofker 1950-1953, Hamaoui and Brun 1974), or the embryos have been described as pitted rather than porous (Schacko 1883, Lacroix 1940 and 1941, Ersu 1983 and 1985).

The significance of a perforated embryo in the Soritoidea has an important taxonomic implication. The supposed perforated embryo has been used to argue for various perforated rotaliine ancestors for the Soritoidea, and consequently the Soritoidea has to be removed from the Miliolina and placed within the suborder Rotaliina. If that is

true then the porcellaneous nature of the Soritoidea wall has to be considered as an analogous feature evolved independently in the supposedly rotaliid Soritoidea and then again in the Miliolina. Various rotaliine ancestors have been suggested for the Soritoidea. Hofker (1971) suggested the genus *Cushmanella* as an ancestor, Galloway (1933) suggested the genus *Spirillina* and Cushman (1948) considered as ancestors some members of the Nonionidae or even the Nummulitidae. To summarize this taxonomic problem within the context of congruence analysis, there are two homologies, perforations and porcellaneous wall structure. These homologies define groups which can not be represented as branching points in the same diagram.

In the course of this study I have searched for pore-like structures in the soritid embryo. Over 200 specimens of the 18 soritid species have been examined using SEM techniques and I am now able to present a fairly detailed analysis of the wall structure of the soritid embryo. The A-form embryo of *Archaias angulatus* is described here but this structure holds true in all essentials for all members of the Soritoidea. The embryo is constructed of at least two calcite layers (fig. 64 a). The outer layer is about 8-12 µm thick and consists of loosely packed calcite needles, randomly oriented (fig. 64 b). The outer layer is distinctly pitted, where the pits are present as shallow concave depressions about 1 µm deep and 2-3 µm wide (fig. 65 a). These embryonic pits conform to the pits observed on the adult chambers. There is in addition a different kind of structure present, which I have called tubules. The tubules open to the outer surface either at the base of the pits or between the pits (fig 65 a). These tubules are about 0.5 µm wide and extend perpendicular through the outer layer (fig 65 b). Frequently, up to three tubules anastomose, forming a branching network of tubules (fig. 66 a). There is no apparent structural connection between the pits and the tubules. The inner layer is about 1-2 µm thick and consists of densely packed crystal needles (fig. 66 b). This inner layer seals off the tubules in the outer layer and forms a continuous solid lining on the inner

surface of the proloculus and the flexostyle (fig. 65 b and 66 b). The crystal structure of these two layers is identical to all other porcellaneous forms, consisting of variously oriented calcite needles.

It is interesting to note that all the presented evidence for a perforated soritid embryo are all derived from studies with a light microscope. For light microscope techniques it is essential either to prepare thin sections or to crush the specimens between glass slides in order to expose the embryo before any examination is possible. However both these procedures almost invariably dislodge the two calcite layers, such that the pitted and tubulated outer layer is examined without its proper inner counterpart. Obviously, when the outer layer is examined separately it can give the illusion of a truly perforated embryo.

There has never been evidence presented for a perforated embryo in the B-form of the Soritoidea, despite a thorough search even by such eminent microscopists as Winter and Rhumbler. I examined, using a SEM, the wall structure of the B-form embryo of *Sorites orbiculus* of the marginalis form. The B-form embryo possesses only a single layer of densely packed calcite needles. This structure has a striking similarity to the inner dense layer in the A-form embryo (fig. 66 b).

The question remains, whether the pits in the Miliolina and the pores in the Rotaliina are homologous structures. There are significant differences between the pores in the Rotaliina and the pits in the Miliolina. The Rotaliina pores are lined with an organic membrane, and the organic membrane is thickened at the base of each pore, forming a 'pore plug' or pustule. The pustule forms calcified sieve plates in lamellated forms (Banner and Williams 1973, Angell 1967). On the other hand the Miliolina pits are confined to the exterior of the test, without pore plugs and apparently without an organic lining. A biochemical and fine structure analysis on properly fixed living specimens is needed to determine if the soritid tubules and pits are covered with an organic lining. However, it is tentatively assumed here that the Miliolina pits and the Rotaliina pores are not homologous structures, but are an analogy.

It remains for future research to determine whether the tubules here described within the Soritoidea are also present in other miliolline subtaxa. It is beyond all reasonable doubt that the tubules here described for the Soritoidea and the perforations in the Rotaliina are analogous structures. There is no comparison for the anastomosing features among the soritid tubules and the perforations in the Rotaliina. Neither is there any comparable rotaliine feature similar to the soritid inner, dense calcite lining, sealing closed the tubules. Based on these conclusions, the taxonomic problem disappears, regarding the conflicting soritid relationship indicated by the presence of rotaliine "pores" versus the miliolid porcellaneous wall structure. The soritids possess a porcellaneous wall structure and in addition tubules and pits in the embryo.

Family Peneroplidae Schultze, 1854.

Subfamily Peneroplinae Schultze, 1854

All the species included in the group Peneroplinae are defined by homology 18, (aperture of an X or Y type) and by homology 15, (striations, present as pits arranged in a single row). Concerning homology 15, it seems that this trait is expressed only in a portion of the population among the species within group M, but when it is expressed it appears early on in the ontogeny, or is present throughout ontogeny along with multiple rows of pits. The Peneroplinae are further divided into 4 subgroups (groups L, M, N, and O) defined by homologies, 19, 16, 20, 21, 29, 17, and 22. Some of these subgroups have not been suggested before in the literature.

The monotypic genus *Monalysidium* was erected by Chapmann (1900) This genus was based on a rectilinear growth mode and the apertural

characteristics of a phialine, fimbriated lip. However as discussed on page (41-42) it is likely that a rectilinear growth following homology 1, is defining for group A, the whole Soritoidea. The presence of a phialine, fimbriated lip is a unique feature of the sole species of this genus, and therefore does not indicate any relationship with other species.

The genus *Spirolina* (Lamarck 1804), is based by some authors on the rectilinear growth mode (homology 30), following the planate involutive growth, a common characteristic of the species *P. arietinus*. However the type species of *Spirolina* is a fossil. I examined a topotype specimen (cat. # USNM, 433516) of *Spirolina cylindricea* from M. Eocene, Lutenian, Grignon, France, figured in Loeblich and Tappan, 1964 (p. C484, fig. 371, 2 a and b). This specimen shows a rectilinear growth, following a planspiral, evolutive growth mode, which is different from the rectilinear growth mode following the planate involutive growth. A varying proportion of the population of all the species included within group M, develop a rectilinear growth mode following homology 21, the planate involutive growth. The rectilinear growth is extremely rare in *P. antillarum*, represented by only 4 specimens out of 409 (1%). In *P. planatus*, it is represented in about 3% of the population, in *P. pertusus* about 11% and in *P. arietinus* 34% of the specimens possess a rectilinear growth. The rectilinear growth following the involutive planate growth (homology 21, is represented as homology 29.

The genus *Dendritina* (Orbigny, 1826) is based on the presence of a dendritic aperture, a feature which I have observed to be present in all species included in group L. However, a single dendritic aperture has not been used consistently to define a higher taxon, since many species possessing a single dendritic aperture have been included within the genus *Peneroplis*.

Henson (1950, p. 10) defined the Peneroplinae as undivided in the median plane, where one chamber is added one at a time to the test. This is not only defining for the Peneroplinae, but is generally true for all Foraminifera, which grow in this mode by adding one chamber

at the time to the test. Henson lumped together the Peneroplinae and the Archaiasinae, noting that the former lacks an internal skeleton but that latter possesses an internal skeleton made of pillars. However, Henson insists that the "foundations" of an internal skeleton are present in the Peneroplinae although these have never been obseved. Apparently the kinship between the Peneroplinae and the Archaiasinae is evidenced by the initial development of chambers devoid of an internal skeleton, a relation based on something that does not exist. Generally this is also true for all Foraminifera, where the initial development begins with chambers devoid of an internal skeleton. The usage of negative evidence in systematics is further discussed on page 69.

In the collection at the Smithsonian Institution, I came across specimens labeled as *Peneroplis carinatus* (cat. # 14658, Albatross station D 5159). Some of these specimens at first sight seem to possess only evenly dispersed pits, in conjunction with a single, highly dendritic aperture, and involutive, planate growth. Based on the apertural characteristics, *P. carinatus* would have to be placed within group M, which would however be in conflict with homology definition 15, indicating that the pits are arranged in a single row. With a simple stereo-microscope I did observe that at least 2 specimens, out of 7 examined, did in fact possess pits on the adult chambers, arranged in rows. If the specimens are stained to increase contrast (e. g. with a black ink) and the light is oriented such as to produce a maximal reflection of the specimens, then these faint rows of pits can be seen. If some members of the species do possess rows of pits, then it is a characteristic of the species *P. carinatus*. To conclude, *P. carinatus* naturally falls within group M, possessing homologies 15, 19, 21, and probably also 18. Further implications are that the involutive, planate growth (homology 21) is a more general feature than both homologies 16 and 20.

Some species that do not belong to the Soritoidea possess pits that are linearly arranged. One species was examined, *Triloculina rupertiana* (cat. # USNM 13794), which does possesses a peculiar

type of ornamentation. It possesses rows of pits, forming a multiple series, ranging from 1 - 35, on different parts of the test, but are evenly dispersed on the keel of the chambers. The pits seem to fall between longitudinally placed elevations or crests, which is a feature characteristic of at least some of the Quinqueloculinae forms, but is absent from the Soritoidea. It seems that the pit-rows are present only in conjunction with these crests, and that these secondarily impose the pits as to be arranged in rows. Therefore, I will not compare as a homology the linearly arranged pits within the Soritoidae and other miliolid forms without further investigation.

Peneroplis acicularis (Batsch, 1791)

Figures 41-43.

Nautilus (Lituus) acicularis BATSCH (1791),p. 3, pl. VI; fig. 16a & 16b.
Monalysidium lituus CUSHMAN (1931), pl.9; fig. 22.
Spirolina acicularis CUSHMAN (1930), p.42-43, pl. 15; fig. 1-3
Dendritina acicularia HOFKER (1951 a), p. 236-238, fig. 15 b-f, & 16 a-e.
Dendritina (Monalysidium) politum HOFKER (1951 a), p. 238-239, fig. 18 a-e.
Cribrospirolina distinctiva var *punctata* HAMAN (1976) p. 159-162. pl. 2; fig. 5-8.

No. of specimens examined, 16, (AMNH 43869 - AMNH 43887).
No. of specimens dissected, 6.
Geographical distribution, Red Sea, (samples 16, 29, 30, and 31).

Growth form.

Only A-forms were found of this species. The ontogeny of the growth form is summarized as: Embryo (proloculus + flexostyle) --- evolutive, planspiral and lenticulate growth (6-17 chambers) --- rectilinear growth.(up to 28 chambers). The general appearance of the test is illustrated in figure 41.

Aperture.

In this species the aperture remains a single opening throughout development. The last formed chamber in all the tests examined features a highly dendritic single aperture (fig. 42 g). In all the other chambers in the same test, the apertures have a much wider opening and less dendritic curvatures, as if the aperture has been secondarily changed by dissolution. However, the first 8-11 chambers possess almost a perfectly round aperture with a distinct lip (fig. 43 a). In the 9th-12th chambers a crescentic formed aperture appears (fig. 42 b). The remaining chambers (fig. 42 c-f) show a gradual transition from a round or crescentic form towards a highly dendritic aperture as is always present in the last chamber (fig. 42. g). In all the 6 specimens dissected, the characteristics of the aperture in the last chamber is very different from all the remaining chambers preceding the last chamber. This is independent of the number of chambers in the test. It is as if the apertures in the chambers preceding the last chamber are secondarily widened by dissolving away the former apertural faces. The degree of the change seems to increase, the older the chamber is. Thus the aperture in figure 42 f (the 20th. chamber) is less deformed than the aperture in figure 42 c (the 17th chamber).

Ornamentation and Sutures.

The ornamentation in the embryo consists of evenly dispersed pits, which develop in all the post-embryonic chambers into simple rows of pits. The sutures are distinct and depressed, without pits at the base of of each chamber (figure 43). The ornamentation on the apertural face consists of elongated pits or groves radially arranged around the aperture, identical to what is observed in *P acicularis* aff. (fig. 45).

Remarks

The species described by Hofker (1951 a) as *D.(Monalysidium) polita* is differentiated from *P. acicularis* on the basis of more ovate shaped chambers and the presence of striations instead of pits in *D. (Monalysidium) polita* Originally Chapmann (1900), described the ornamentation in *D.(Monalysidium) polita* as consisting of vertical rows of puncta and possessing an aperture with an "inverted or everted phialine termination." Neither of these features is apparent in Hofker's description. Further, the shape of the chambers seems to represent intraspecific variation. The ovate versus oval shape of the cross section of the chamber is a feature which is present even in the same specimen, where there is a haphazard transformation of ovate to circular and then again to ovate shape.

Upon examination of one of the paratypes of *Cribrospirolina distinctiva* var *punctata* kindly supplied to me by Dr.Haman, it became clear that these specimens possess a single, dendritic aperture, conspecific to *P. acicularis*

Peneroplis acicularis aff. (Batsch, 1791)

Figures 44-45.

Number specimens examined, 13, (AMNH 43866 - AMNH 43868).
Number of specimens dissected, 4.
Geographical distribution, Red Sea, and Marshall Islands (samples 8, 29, 30 and 31)

There were 17 specimens encountered, identical to *P. acicularis* except that the aperture develops only into an X-formed opening, and the apertural form is preserved in all chambers. Further the planspiral growth is composed of up to 26 chambers, a substantially higher number of chambers than in *P acicularis* This form is here tentatively suspected to be a different species, primarily because of the structural differences in the aperture. The species described as *Peneroplis austriaca* by Orbigny (1846) shows apertural characteristics similar to these above. I was unable to locate any specimens at the U. S. National Museum, conforming to this species. A formal decision is postponed until efforts are completed to locate the type specimen of *P. austriaca*. At present the apertural characteristics of this species are described.

Only the typical A-form embryos were encountered. In the first 11-15 chambers, the aperture is a single, round opening, provided with a distinct lip (fig. 44 a). In the 12th -16th chamber a slightly deformed aperture develops (fig. 44 b), transforming in the 13th -17th chamber into a distinct X-formed aperture, which persists throughout development. In the specimen illustrated in figures 44 e and g two chambers (the 20th and the 24th), Y-formed apertures are present.

The ornamentation of the apertural face and the lateral sides is illustrated in figure 45.

Peneroplis arietinus (Batsch, 1791)

Figures 46-49

Nautilus (*Lituus*) *arietinus* BATSCH (1791), p. 3 & 6, pl. VI; fig. 15d, 15e, & 15f.
Coscinospira (*Spirolina*) *hemprichii* EHRENBERG (1839), p.143, pl. II;fig. a-b.
Peneroplis pertusus var *arietinus* CUSHMAN (1917), p. 88, pl. 36; fig. 2.
Peneroplis arietinus HOFKER (1951 b), p. 350-356, fig.31, 32, & 35.
Spirolina arietina ERSU (1983) p. 101-102. pl. 9; fig. 1-6.
Cribrospirolina distinctiva HAMAN (1972), p. 110-113, fig. 1, 3, & 4. HAMAN (1976), p. 159-162. pl. 1; fig. 1-9, pl. 2; fig. 1-4.

Number of specimens examined, 207,.(AMNH 43873 - AMNH 43896).
Number of specimens dissected, 13.
Geographical distribution, Mediterranean Sea, Caribbean, Red Sea, and The Great Barrier Reef (samples; 5, 14, 16, 17, 20, 23, 24, 29, 30, and 31).

Growth form.

All the dissected specimens belonged to the A-form, but the B-form of this species was described by Hofker (1951 b) as possessing a single spherical prolocular embryo. The first 4-11 chambers grow in typical evolutive, planspiral, and lenticulate mode, transforming later into a completely involutive, planate chambers. In about 34% of the specimens examined the growth mode gradually transforms into a rectilinear growth mode from an involutive, planspiral growth. The rectilinear growth consists of up to 7 chambers. In about 50% of the specimens, a slightly evolutive growth form is assumed, resulting in a slightly depressed umbilici. The evolutive, umbilicated traits are

usually present in those specimens which present a rectilinear growth (fig. 46 a). The remaining specimens are all distinctly involutive, mostly specimens from a small juvenile growth stage (fig. 46 b). The growth development can be summarized as evolutive, lenticulate, and planspiral (4-11 chambers) --- involutive, lenticulate, and planspiral (up to 36 chambers) --- evolutive lenticulate planspiral (0-14 chambers) --- rectilinear growth (0-7 chambers).

Apertures.

The aperture in the first 5-7 chambers consists of a single circular opening, provided with a distinct circular lip (fig. 47 a). The next 8-13 chambers possess a single aperture, which I group into three distinct types. These are: type 1, a crescentic form (fig. 47 c); type 2, a Y-shaped form (fig. 47 d); type 3, an X-shaped form (fig.47 b). In some specimens one, two or all three of these simple apertural types are present. Further, the first ontogenetic occurrence of these three types in different specimens was observed to be from: type 1 --- type 2 --- type 3; or type 2 --- type 3 --- type 1; or type 3 --- type 1 --- type 2. The remaining three possibilities would probably have been discovered if more specimens had been dissected. Further, after the first appearance of one type, it is displayed at various later ontogenetic stages without any specific regularity.

The multiple apertures usually start with a chamber possessing 2 or 3 apertures (fig. 47 e). The apertures gradually increase in number as the chamber size increases. The maximum number of apertures present in a single chamber was 16. The apertures are always provided with a distinct lip, which only in some chambers can form slightly protruding elevations or teethes. A new type of aperture develops in the chambers possessing multiple apertures. This is an irregularly formed aperture of a dendritic type (fig. 47 f). The embryonic circular aperture and the 3 types of the juvenile apertures

all appear at times on the chambers possessing multiple apertures. In the rectilinear chambers, the apertures are arranged in a circle along the periphery of the apertural face. In some of the larger chambers randomly placed apertures appear inside the circularly arranged apertures (fig. 47 g).

It is of interest to note that in one specimen from the Red Sea, a single aperture of type 2 appeared in the 23rd chamber, where the previous 18 chambers had all possessed multiple apertures. In this species it is not uncommon to observe, a recurrence of juvenile features during ontogeny, a transformation from an adult feature (multiple apertures) into a juvenile feature (a single aperture).

Ornamentation and sutures.

In the adult chambers the ornamentation consists of deep grooves covered with pits. The pits in the grooves form multiple rows, which are usually fused and irregular in outline, except that close to the sutures these appear as round and distinct pits. The surface of the ridges are devoid of all pits (fig. 48 a). The ridges frequently anastomose, such that two or three ridges fuse, forming a fork-like structure, where the fork is usually oriented towards the apertural face (fig 49). The ornamentation on the apertural face consists of pits and elongate groves, which in some chambers are overlaid with a smooth calcareous mass (fig. 48 b).

It proved to be impossible to clean the calcareous remains of the chambers covering the embryo. Therefore no reliable information was obtained on the ornamentation in the embryo. However Hofker (1951 b) described the A-form as "porous" and his figuration indicates an evenly dispersed ornamentation. Therefore it is tentatively assumed here that the embryo in *P. arietinus* possesses evenly dispersed pits which could then either transform into a single row of pits or into a multiple row of pits.

Remarks.

In a light microscope, specimens of this species appear white and opaque, and are unusually difficult to dissect. The morphological variability within this species is well defined, such that specimes from each geographical locality are impossible to tell apart.

Peneroplis planatus (Fichtel and Moll, 1803)

Figures 56 - 59.

Nautilus planatus FICHTEL and MOLL (1803), p.91-94, pl. 16; fig. a-i.
Peneroplis planatus MONTFORT (1808), p.258-260. EHRENBERG (1839), p. 142-143, pl. 11; fig. a-d.

Number of specimens examined, 2056, (AMNH 43913 - 44018, and 43980 - 44018).
Number of specimens dissected, 26.
Geographical distribution, Hawaiian Islands, Mediterranean Sea, Red Sea, The Great Barrier Reef, British Solomon Islands, New Caledonia, and Japan (samples 1, 5, 16, 17, 20, 21, 22, 23, 24, 25, 28, 29, 30, and 31).

Growth form.

All the dissected specimens belonged to the A-form. The first 5-12 chambers grow in a planspiral, evolutive, and lenticulate mode, gradually transforming into involutive, planspiral, and lenticulate growth in the following 6-15 chambers. Up to 28 chambers of the last chambers gradually assume a flabelliform and evolutive growth mode, usually with a slightly inflated chambers. The general appearance of the whole test is very compressed and flaring (fig. 56 a

and b). Not all the specimens express in the last chambers planspiral, evolutive growth. In total 65 (3%) of the examined specimens, up to 17 of the last chambers are arranged in a rectilinear mode, with a flabelliform to cylindrically shaped chambers.

The above ontogeny is summarized as: embryo (proloculus + flexostyle) --- planspiral, evolutive, and lenticulate growth (5-12 chambers) --- involutive, planspiral and lenticulate, (6-15 chambers) --- evolutive, planspiral, and flabelliform, (up to 28 chambers), or rectilinear, cylindrical to flabelliform chambers, (0-17 chambers).

Apertures

The first 3-4 chambers possess a single circular aperture, identical to what has been described for all other Peneroplinae species. The apertures are transformed in the next 3-6 chambers into the crescentic, the X-formed, or the Y-formed apertures, apparently without any particular order of appearance. The shape of these juvenile apertures is indistinguishable from what is observed in other species within the Peneroplinae (see fig.42 a and b, fig. 44, fig. 47 a, b, c, and d, and fig. 51 a, b, and c). Multiple apertures appear in the 6th - 10th chamber (fig 57 a), which usually coincides with an expression of irregularly dendritic apertures (fig. 57 b). The apertures gradually increase in number as the size of the chambers increases. The apertures frequently form double rows. Sometimes the whole chamber possesses double rows, or only a part of the chamber (fig. 57 c), or there is exclusively a single row of apertures (fig. 57 d). Therefore there exists within the same specimen a continuous gradation from a single row towards a double row, without any apparent regularity. A few specimens possessed exclusively a single apertural row, while others possessed only a double row.

All apertures are provided with a distinct lip, which can form protruding extensions or teeths, especially in the adult chambers.

Ornamentation and sutures.

The ornamentation on the proloculus and the flexostyle consists of evenly dispersed pits (fig. 58 a). In one embryo the pits formed a distinct single row of apertures in the first 3 chambers (fig. 58 b). In other embryos the pits formed double to triple rows on the first juvenile chambers (fig. 58 a). The ornamentation on the adult chambers consists usually of a single to triple rows of pits, but more than triple rows are very rare (fig 59 a). The pits are always located in slightly depressed furrows. The apertural face is ornamented with irregularly shaped pits, fused into longitudinal furrows.

The sutures are distinct and depressed.

Remarks.

Three specimens (0.5%) from the Red Sea exhibited a juvenile, growing in a involutive, planspiral mode, transforming directly into rectilinear growth. The chambers in the rectilinear growth were almost cylindrical in cross section, and in two specimens gradually assumed a flabelliform chambers. The rectilinear growth gives the test superficial resemblance to *P. acicularis* However the apertural characteristics of the rectilinear chambers in these specimens always exhibit multiple apertures and the ornamentation of the lateral sides is identical to *P. planatus* Therefore these 3 aberrant specimens are included as a varient growth form of *P. planatus*

In samples 16, 17, 20, 21, 25, 28 and 29, some of the specimens encountered (in total about 4%) showed a strong resemblance to *P. pertusus* This resemblance stems from the partial evolutive growth mode in the adult chambers and the inflated chambers, resulting in a distinctly depressed umbilici. These specimens differ from typical *P. pertusus* in that the umbilici is always covered with a smooth chalk material, such that the surface of the chambers of the previous whorl is not visible, and there is a strong tendency to develop flabelliform chambers. The ornamentation on *P. planatus* always consists of a

simple to triple rows of distincts pits, in contrast to *P.pertusus* which possesses multiple rows of pits, sometimes partially fused.

Peneroplis pertusus (Forskål, 1775)

Figures 50-52.

Peneroplis pertusus BRADY (1884), pl. XIII, fig 17. CUSHMAN (1930), p. 35-36, pl. 12; fig. 3-5.

Number of specimens examined, 297, (AMNH 43888 - AMNH 43897).
Number of specimens dissected, 7.
Geographical distribution, Hawaiian Islands, Caribbean, British Solomon Islands, New Caledonia, Samoa Islands (USA) and Japan (samples 1, 11, 21, 22, 25, 26, and 28).

Growth form.

All the dissected specimens belonged to the A-form. The first 3-5 chambers grow in a lenticulate, evolutive and planspiral mode, then transform in most specimens into an involutive growth, similar to *P. arietinus*(fig. 46 b). The involutive growth mode dominates up to about 10 chambers, then assumes an evolutive growth which persists throughout development. As a result of the inflated form of the chambers and the evolutive growth mode, a distinctly depressed umbilicus is formed. In the umbilici the bases of the chambers in the previous $1\,1/2$ - 3 whorls are visible (fig. 50 a and b). In about 30% of the specimens up to 7 chambers begin to form slightly flattened chambers, superficially resembling *P. planatus*. Further in approximately 11% of the specimens, a rectilinear growth mode develops in the last 1-4 chambers.

Aperture.

The aperture consists of a single circular opening in the first 3-5 chambers (fig. 51 a). The next 7-11 chambers possess the three types of the juvenile aperture, an X-formed (type 3, fig. 51 b), a Y-formed (type 2,fig. 51 c), or a crescentic aperture (type 1, fig. 51 d). In the dissected specimens, the first ontogenetic appearance of these juvenile apertures was observed to be from; type 3,---type 2,---type 1, or from; type 1,---type 3,---type 2. Each of these three juvenile types can recur after its first appearance, at any developmental stage without any apparent regularity.

The apertures in all the remaining chambers exhibit as a rule multiple, dendritic apertures (fig. 51 f). The maximum number of apertures on each chamber in different specimens is variable. The average number of apertures in the last chamber for all the adult specimens is about 9, but can range from 14, to as low as 3. In those specimens that possess 1-5 apertures in the last chamber, the apertures tend to be larger and can at times assume an extremely dendritic form (fig. 51 e and f). The apertures in the rectilinear chambers are irregularly dispersed over the apertural face (fig. 51 g and 50 b), identical to the apertural arrangement observed in the chambers of the planspiral stage. However, in 3 specimens a circular arrangement of the apertures was observed in the rectilinear chambers, similar what is observed in *P acicularis* (fig 47 g). However the circularly arranged apertures in *P. pertusus* are more dendritic in comparison to *P. acicularis*.

All the apertures are provided with a distinct lip, which in the adult chambers can form slightly elevated projections (teeths).

To summarize the above it can be stated that the apertural characteristics of this species are very variable, with a strong tendency to possess irregularly shaped, dendritic apertures.

Ornamentation and sutures.

The embryo possesses evenly dispersed pits. Immediately in the second chamber the pits show a strong tendency to form striations, which partly consist of single rows, on the second chamber (fig. 52 a). In the adult chambers the ornamentation consist of shallow striations, with multiple rows of pits, sometimes partially fused.(fig. 52 b). Frequently the ridges anastomose, to form a two-pointed fork. The apertural face is ornamented with fused pits and elongated grooves, radially arranged around the apertural face (fig 52 b). The sutures are always depressed and distinct.

Remarks.

This species has frequently been confused with *P acicularis*, but is easy to distinguish from it on the basis of the ornamentation. In *P. pertusus* the striations are shallow, and the width of the ridges is about equal to the width of the striations. In contrast to *P acicularis* striations are deep, and the width of the striations is 5 to 10 times the width of the ridges (compare fig. 52 b and fig. 49). Under light microscope *P. pertusus* always appears glass-like and semi-translucent, in contrast to *P acicularis* which tests always appear opaque and white.

Peneroplis antillarum, (Orbigny, 1839)

Figures 53-55

Dentritina antillarum Orbigny (1839), p. 58-59, pl. VII, fig. 3-6

Number of specimens examined, 409, (AMNH 43898 - AMNH 43908).
Number of specimens dissected, 11.
Geographical distribution, British Solomon Islands and Japan (samples 21 and 28).

Growth form.

All the dissected specimens belonged to the A-form. The first 3-5 chambers grow in a planspiral, evolutive, and lenticulate mode. In about 88% of the specimens examined, these transform into an involutive growth, persisting throughout the development (fig. 53 a and b). However in about 12% of the specimens up to 12 of the last chambers become flabelliform, growing in a evolutive mode, creating a superficial similarity to *P. planatus*.

APERTURE

In the first 4-5 chambers the aperture consists of a single circular opening, provided with a distinct circular lip. These develop into a Y-formed aperture in the 5th - 6th. chamber and transform in the 10th - 11th chamber into an X-formed chamber. The crescentic aperture was not observed in these early juvenile chambers, but it is distinctly present in the adult chambers possessing multiple apertures (fig. 54 b and d). The order of appearance of these apertural types was identical in all the three specimens, which I was able to dissect at all developmental stages. The apertural anatomy of the juvenile apertures in *P. antillarum* is identical to what is observed in other species of the Peneroplidae (see fig.42 a and b, fig. 44, fig. 47 a, b, c, and d, and fig. 51 a, b and c). Multiple apertures develop in the 20th - 23rd chamber and transform into the irregularly dendritic type (fig 54 a). The apertures gradually increase in number as the chamber size increases, ranging from as few as 5, up to 16 apertures in adult specimens. The average is 7 apertures in adult specimens. Frequently the apertural lips form the typical teeth-like projections, especially in the adult chambers.

Ornamentation and sutures.

In the embryo the ornamentation consists of evenly dispersed pits, transforming into a row pits in all the post embryonic chambers. The pits are usually distinct, but rarely fuse into short, longitudinal furrows (fig. 55 a). These pit-rows form either single, double or triple rows of pits. The sutures are smooth and almost never depressed. The pits are never transformed into grooves as is observed for example in *P. acicularis*. The ornamentation on the apertural face consist of distinct and fused pits, sometimes forming elongated furrows radially arranged along the apertural face (fig. 55 b).

Remarks.

I did not encounter any specimens at the U. S. National Museum, which could be compared to this species. *P. antillarum* was described by Orbigny (1839) from Cuba and was reported to be rare. The excellent figures by Orbigny conform closely to the specimens that I examined, and the name is therefore tentatively assumed to be *P. antillarum*

Family Soritidae Ehrenberg, 1839

In diagram 10 (page 40), homology 12 is common to all species within the Soritidae, represented as group B. Homology 12 refers to the design of the apertures which in adult stages are multiple, of a circular, elongate, to crescentic shape.

The species, *Puteolina protea* (= *Peneroplis protea*) as originally described by Orbigny (1839) was postulated to be closely akin to the forms that are here recognized as the Peneroplinae, perhaps because Orbigny did not distinguish between the arciform and the planate-form involutive growth modes as different structural entities. In contrast, both Carpenter (1856, p. 551) and Brady (1884) noted the natural affinity of *P. protea* with the Archaiasinae forms. This was partly based on the arciform growth of the adult convolutions, present in *P. protea* as well as in all other Archaiasinae. Carpenter and Brady assumed that all the different forms of the Archaiasinae were nothing but a single species. Inspection of diagrams 1 and 2, suggests that Carpenter (1861) did join together the Archaiasinae (=Orbiculina) and Soritinae (=Orbitolites) and probably did recognized the Soritidae as a natural group. He did not formally name this group as a higher taxon, but stated concerning the Archaiasinae and Soritinae that they must be ranked "in immediate proximity to each other; and that no classification can have any claim to be considered as natural, in which they shall be widely separated" (Carpenter, 1956, p. 552). Brady's (1884) figured specimens of *P. protea* (= *Orbiculina adunca*) (pl. XIV, fig. 3 and 4) are explained as varieties of *Archaias angulatus* "analogous to the 'Spiroline' modifications of the *Peneroplis*".

Both the groups Archaiasinae and Soritinae are included within the same group (as the family Soritidae) by Loeblich and Tappan (1984), a practice that is also adopted herein.

Originally Hofker (1952 a) proposed the generic name *Puteolina* (changed from *Puteolus*, Hofker (1950)) for the all the species here included in group B in diagram 10, and designated *P. protea* as the type species. The peculiar design of the apertures by all members of this group was described by Hofker, and conforms to what I have termed as homology 12.

Hofker's argument (1950, 1952, and 1971) that the primary characteristic of the genus *Puteolina* is the presence of evenly dispersed pits, has placed him at odds with the latest taxonomic

practice. It has been customary in the literature to reject all anatomical features termed as "ornamentation", as being only of an interspecific significance and therefore invalid to define higher taxa (Loeblich and Tappan 1964, Lévy 1977, Ersu 1983). The rationale given, is to resort to an authoritarian definition of certain attributes as having some pre-specified hierarchical value. Thus, the crystal wall structure defines orders and superfamilies, but the ornamentation has merely a specific importance etc.. This procedure differs from what is adopted by me and Hofker, to some extent. All anatomical features are subject to be a part of a homology statement, and the generality of the homology is an indication of the hierarchical rank. This coincides in many cases with the traditional, or the authoritarian definitions of the higher Foraminifera taxa. Thus, the same porcellaneous crystal structure is widespread among a vast number of species, and therefore defines a higher taxon, like the Miliolina. In contrast to the current opinion, such as the fact, that the same kind of ornamentation or pits, is present among certain species within the Miliolina, also defines a higher taxa, but only as a sub-taxon of the Miliolina, and including the Soritoidea. It was also noted by Henson (1950, p 14-15) in a paper published before Hofker (1950) that species with a striated surface never possess an internal skeleton, recognized here as the Peneroplinae. In contrast Henson noted that the Soritoidea species with evenly dispersed ornamentation do usually possess an internal skeleton, but this was not utilized to demarcate the Soritidae as a monophyletic group. But the observation of the presence of pits as a homologous feature is accurate, although the distribution of this feature is underestimated.

Ersu (1985, p. 365) proposed a phylogenetic scheme for the Soritoidea, where a member of the Archaiasinae is portrayed as an ancestor of the Soritinae, and presumably warrants to include these two groups in a larger more inclusive monophyletic group, like the Soritidae. However this relationship was not reflected in the derived classification scheme in the same paper, and no formal name was proposed for a group comparable to the Soritidae.

The only apparent reason to place *P. protea* within the Peneroplinae is because it is devoid of an internal skeleton, and the Peneroplinae is commonly defined as being devoid of an internal skeleton (Loeblich and Tappan 1964, Henson 1950, Lévy 1977, Ersu 1983,). It is true that all groups based on some anatomical features do have a negative counterpart, i. e. those species that do not possess the feature. If this practise of observing default features is applied consistently, then each of the 30 homologies that I have recognized within the Soritoidea, has its negative counterpart or default group. Interestingly, these additional 30 default features, can not be utilized to define the same species groups as represented in diagram 10, with one exception. The groups B and K are defined by 3 homologies, which default features also define the groups indicated by groups B and K. All other default or negative "homologies" define groups which are non-combinable to diagram 10 as branching points.

If it is desired to search for a natural scheme, then presumably it is to be based on the homology concept, as inherited anatomical features indicative of a common ancestry. Then, the absence of a particular homology or non-feature would be interpreted to be an inherited trait indicative of a common ancestry, a curious sort of reasoning. For example there are three distinct kinds of internal skeletal elements recognized within the Soritidae, but absent from the Peneroplinae. It seems ambiguous to construe these as three default or non-homologies, inherited and indicative of a common ancestry among the Peneroplinae. In this context it seems obvious that default features do not indicate anything at all. However the usage of the absence of certain traits can be extremely useful to construct identification keys, whose sole purpose is to identify and learn with ease the names and structure of a given group of species. The erection of a natural classification and identification keys are different endeavors, but both can be used to form a basis of a classification, where the former is an attempt to elucidate a natural kinship and the latter is an artificial scheme of convenience.

Subfamily Archaiasinae Cushman 1927.

The species that are included in this taxon, have had a long precedence of being recognized as of a close kinship, although the group has not always formally received a name. Brady (1884) and Carpenter (1856) inferred that all the Archaiasinae forms were a single "genus", named as the *Orbiculina* Cushman (1927) included *P. protea* under the Peneroplinae, because it is devoid of an internal skeleton, and defined the Archaiasinae as possessing an internal skeleton.

Presently, I am reckoning 6 species within the Archaiasinae. I am limiting the discussion of these species, by describing the group as a whole, accompanied with a few selected illustrations. Five of these species, *Archaias angulatus* (Fichtel and Moll 1798), *Archaias lucasii* (Lévy 1977), *Cyclorbiculina compressa* (Orbigny, 1839) *Cyclorbiculina americana* (Lévy 1977), and *Cyclorbiculina discoidea* (Flint, 1899) all possess an internal skeleton. *Puteolina protea* (Orbigny 1839) is the only species within this group which never develops an internal skeleton, but nevertheless exhibits a close relationship to the Archaiasinae based on homologies 23, 27, and 28. Homology 23 refers to the peculiar growth form of the test, described as involutive, arciform growth (fig. 60), present in all the 6 species included in the Archaiasinae, including *P. protea* Normally the arciform growth is assumed after about 10 chambers of evolutive, lenticulate planate growth (homology 1), although this can vary in different species.

Circular series of chambers develop in all species included in group I. These circular chambers resemble the annular chambers in the Soritinae. By reference to ontogeny these are not comparable structures. The circular chambers in the C*yclorbiculina* develop from the involutive arciform growth. In contrast, the annular chambers in the Soritinae develop from a planspiral evolutive and flabelliform growth. If the whole ontogenetic transformation of the growth form

is taken to consideration then it is a fact that the circular chambers and the annular chambers have a different ontogenetic origin, and this is interpreted as indicating different kinship, represented as homologies 26 and 3. In other words I am assuming that there exists a parallelism between phylogeny and ontogeny (see further page 113-118). An objection might be raised and it argued that the circular chambers in *Cyclorbiculina* and in the Soritinae are homologous, in the sense that these are an inherited features from a common ancestor This ancestor did possess circular chambers, but the arciform growth is a later phylogenetic creation introduced at the juvenile stages before the circular chambers are developed in the *Cyclorbiculina* Granting this possibility, then the *Cyclorbiculina* should be included within group D. If this is correct then homology 23 is mistaken, or that the arciform growth within the *Archaias* and *P. proteais* an analogy of the arciform growth present within the *Cyclorbiculina* Despite a thorough search, I can not detect any significant structural difference in design of the arciform growth among any of 6 species included in group G. Therefore there is no objective justification to postulate that the arciform growth is a case of an analogy.

An internal skeleton is present in all the species included in group H. It varies among the different species when the internal skeleton develops, but commonly it is expressed in about the 5th - 19th chamber. The skeleton always first appears in the arciform growth stage, and invariably consists of distinct structural elements known as buttresses. Buttresses are present as a secondary thickening of lateral side of the chamber wall, only extending towards the center of the lumen (fig. 61).(Hamaoui and Brun, 1974). This is indicated as homology 24, and defines group H, in diagram 10. Throughout development, in the species *C. americana* and *C. discoidea*, the buttresses are the only skeletal element. The suggestion might be raised, that a comparison can be made among the duplex plan of the internal skeleton within the Soritinae (homology 10, see fig. 25 a), and the buttresses (homology 24, see fig. 61 b). By reference to

ontogeny these are not comparable structures. Considering the whole ontogenetic transformation of the internal skeleton, the duplex plan always develops from septula in contrast to the buttresses which initially appear and remain as buttresses throughout the development. To conclude, it is a fact that these two structural elements have a different developmental origin and this is reflected in diagram 10.

In the duplex plan the chamberlets form a typical hexagonal pattern (see fig. 7) and the apertures are organized in a displaced pattern, forming a apertural stolon-complex (fig. 24 e and 25). This is never the case within the *Cyclorbiculina* The apertures are confined to the central portion of the apertural face and are located independently of the position of the buttresses (fig. 61 and fig. 62 a and b). However, in the circular chambers the number of apertures in each chamber usually coincides with the number of the chamberlets, but there are frequent exceptions to this. The buttresses in each chamber are disposed independently of the position of the buttresses in the previous chamber, resulting in a chamberlet arrangement which I have termed here, an anomalous pattern to distinguish it from the hexagonal pattern characterizing the Soritinae.

There is a second type of skeletal elements known as pillars (Hofker 1952 a). This structure is present in the genus *Archaias*, *Androsina* and in *Cyclorbiculina compressa* represented as homology 25 in diagram 10. The pillars always develop after the buttresses, usually appearing about 5 - 10 chambers after the first appearance of the buttresses.

There are two distinct forms of *C. compressa* one that develops exclusively buttresses (fig. 61). This form always possesses a single to double row of apertures. The other form develops pillars in addition to the buttresses, and does also possess a broad segment of a circular to ovate apertures (fig. 63). These forms have been noted before in the literature but have always been assumed be variants of the same species despite these striking structural differences (Hofker, 1952 a and 1964, Lévy 1977).

The first expression of pillars in *C. compressa* occurs in about the 9th - 14th chamber. In some specimens of *C. compressa* the placement of pillars in the circular chambers occurs in the median space between the buttresses. This may give the false impression of septula as possessing two openings or stolons (e. g. Lévy 1977). By careful observation, it is apparent that the pillars are present as a distinct structure, always disposed independently of the position of the buttresses. In large specimens, possessing circular chambers, the pillars are placed in the center of the chamber, forming a broad segment of pillars located between the apertures (fig. 63).

There is also a pillar like skeleton present in *A. lucasii* and *A. angulatus*, identical to what is observed in *C. compressa*. The presence of pillars is represented as homology 25, defining a group of species as group J, not representable in the same diagram with homology 26, defining group I.

I have examined in total 47 specimens of the 3 Cyclorbiculina species. As a preliminary conclusion it seems that the characteristics overlap, which have been evoked in the literature to demarcate these 3 species. This results in a large portion of specimens which possess the characteristics of two or all three species. As such, these osculant forms do not necessarily prove that these 3 species are all conspecific. Such questions can only be properly answered by life-cycle experiments. However, as an inference based on test morphology, there is no clear structural difference between the 3 *Cyclorbiculina* species, and therefore no objective basis for erecting three different species. If it is correct that the 3 *Cyclorbiculina* species are merely parts of the same life-cycle, then this species does possess pillars only expressed at one stage of its life-history. Homology 25 would then define group H along with homology 24, and the problem of non-combinable groups evaporates. It would seem therefore that representing formgroups below the species level as group definitions, results in a rather chaotic production of inconsistent or non-congruent groups. Granting the possibility that the *Cyclorbiculina* genus is in fact divisible into

3 different species, then homologies 24 and 25 (and 30) are the only group definitions not simultaneously representable in diagram 10. (See further discussion on page 103-104).

Subfamily Soritinae Ehrenberg 1839.

The Soritinae group is defined by homology statements 4, 6, and 7, as defining features present in all the species included in group C. This group is divided successively into subgroups by a succession of a set of less general inclusive groups. I discussed under the Archaiasinae some of the superficial similarity of the Soritinae septula with the skeletal elements of buttresses and pillars present within the Archaiasinae. I have retained the names of the monotypic genera of *Amphisorus* and *Marginopora* to maintain nomenclatural stability. *Sorites bradyi* is removed from the Peneroplinae, where it was originally placed by Cushman (1930), based on the default character that it does not possess an internal skeleton.

Carpenter (1861) was the first author to recognize the Soritinae (=Orbitolites type) as a distinct group, although he possibly believed these to be a single species. The descriptions and the figurations of the Soritinae varieties which Carpenter recognized are accurate enough to be reinterpreted as the species which are described herein. The ontogenetic transformation of the internal skeleton, from simple septula, to the duplex plan, and finally to the complex plan is lucidly described by Carpenter (1861, p. 224, and 1883).

Brady (1884), Cushman (1917, 1930, and 1933), and Hofker 1952 b followed the tradition of Carpenter and included mostly the same species as Carpenter did within the Soritinae.

Henson (1950), divided the whole Soritoidea (=Peneroplidae) into two subgroups, the Peneroplinae and the Soritinae (= Orbitolitinae). Henson (1950, p. 19) states that the growth mode in the Soritinae takes place by the additions of numerous small, separate cells, in arcuate or annular series, and that there are no communications

between the small cells of the same cycle. This growth mode is utilized to define the Soritinae. This interpretation of the growth mode within the Soritinae is not correct. It has been amply demonstrated by the detailed studies of Kloos (1984) on the life-cycle of *Sorites orbiculus*; that it grows in steps by the addition of one annular chamber, subdivided into chamberlets. This growth mode is identical in *Amphisorus hemprichii* and *M. kudakajimensis* (Lee, personal communication). The sutures, as these are observed in preserved specimens, always form whole circles between succeeding annular chambers as is expected if one annular chamber is added as a separate growth step (see, fig. 21). There are never sutures present between the chamberlets (cells), as would be expected if each chamberlet represents a separate growth stage.

Lehmann (1961) described in detail the structure of the fossil forms of *Orbitolites*; originally described by Lamarck 1816, from Eocene at the Paris region. *Orbitolites* shows some structural affinity with the Soritinae, where the growth form consists of annular chambers. *Orbitolites* differs from the Soritinae by possessing a complicated embryo, made of a proloculus (= Hantelförmige Kammer), flexostyle (= Ausguss), and a large ring-formed chamber (= ringförmige Kammer) completely surrounding the proloculus and the flexostyle. Then several auxiliary chambers (=Auxiliarkammern) are arranged around the proloculus, flexostyle, ring-formed embryo complex, a unique feature of *Orbitolites*. It is possible that the ring-formed chamber is homologous with the vorhof in *Amphisorus* and *Marginopora*. The "hantelförmige Kammern" and the "Ausguss" are probably homologous to the proloculus and the flexostyle of the Soritoidea (see fig. 6 a). The internal skeleton in the *Orbitolites* consists of transversely oriented septum, similar and perhaps homologous to the septula present in the Soritinae. (Lehmann 1961 and Hofker 1964, p. 52-54).

Lévy (1977) and Ersu (1985) reerected the subfamily Meandropsininae and included in it a species which is herein named *Sorites orbitolitoides*. The Meandropsininae is defined on the basis of the following. "Test discoidal, very thin, beginning as planspiral, then

rapidly becoming annular. Chambers regularly divided by small, rudimentary septula. Apertures form series of pores, mostly circular at the apertural face" (Ersu 1985, p. 352, translated) All of these structural elements are present within the Soritinae, and therefore can not be utilized to define another taxon, the Meandropsininae. The fossil forms that have been included under the Meandropsiniae, Henson 1948, except *Broeckina* all seem to possess unique structures. However the Meandropsininae show some structural similarity to the Soritoidae, such as a juvenile planspiral growth stage, and also an arciform growth stage (e.g. *Fallotina*), and therefore showing a resemblance towards the Archaiasinae. The structural affinity among the Meandropsininae and recent Sortitoidea is uncertain (Loeblich and Tappan 1964 and 1984, and Hamaoui and Brun 1974).

Sorites orbiculus (Forskål 1775)

Figures 5 - 12.

Nautilus orbiculus FORSKÅL (1775), p. 125

Sorites orbiculus EHRENBERG (1839), p. 134 & 144-145, fig.II, a, b, c, & d. LEHMANN (1961), p.641-643, pl. VIII; fig. 1-8. COLE (1965) pl.6; fig. 1-5, 7 & 9, pl. 7; fig. 1-8, 10-12, pl. 8; fig. 7-9. Ersu (1985), p. 355-356, pl. IX; fig. 10-16, pl. X; fig.1-18, pl. XI; fig. 1-3, pl. XV; fig 9-11.

Sorites marginalis LEHMANN (1961), p. 643-645, pl. VIII; fig 9-10, pl. IX; fig 1-6. LÉVY (1977), p. 426-427, pl. 8; fig. 1-10. COLE (1965), pl.4; fig. 3, 7, & 9, pl. 6; fig 6, & 8. CUSHMAN (1930), p.49-50, pl.18; fig. 1-4. Ersu (1985), p. 354-355, pl. XI; fig 4-18, pl. XV; fig. 8

Orbitolites orbiculus SMOUT (1963), p. 259, pl.IV; fig. 3, & 4.

Orbitolites marginalis SMOUT (1963), p. 259-260, pl. IV, fig. 5, & 6. HOFKER (1952 b), p. 63-64, fig. 57. HOFKER (1930), p.153-155, pl. XLI, fig. 1,pl. LV, fig. 9, pl. LIX, fig. 1-6, pl. LXI, fig 1, 2, & 7,

CARPENTER (1883), p. 20-25, pl.III; fig. 1-7, pl.IV; fig. 1-5, BRADY (1884), p. 214-215, pl. XV; fig. 1-3 & 5. CUSHMAN (1917), p. 92-64, pl.38; fig 1-2.
Orbitolites hemprichii SMOUT (1963), p. 260-261.
Orbitolites carpenteri SMOUT (1963), p. 261-262.
Amphisorus hemprichii LÉVY (1977). p. 428-429. pl. 8 fig. 11-17.
Orbitolites(Amphisorus) hemprichii HOFKER (1976), p. 137, fig 131.
HOFKER (1964), p. 52-55, fig. 119-128.

Number of specimens examined, 1211, (AMNH 43816 - AMNH 43857).
Number of specimens dissected, 17.
Geographical distribution, Hawaiian Islands, Mediterranean Sea, Caribbean, Red Sea, Kanton Islands, The Samoa Islands, The British Solomon Islands, The Great Barrier Reef, French Oceanica, and Japan (samples 1, 2, 4, 5, 14, 17, 18, 19, 20, 21, 22, 23, 24, 26, 28, 29, 30, 31, and 33).

Growth form.

The A form.

This form is characterized by the presence of a globular proloculus and a flexostyle normally enrolled 360^0 around the proloculus (fig 6 a). The development is summarized as; embryo (proloculus +flexostyle) --- evolutive, planspiral, and lenticulate growth (3 to 5 chambers) --- evolutive and flabelliform growth (8 to 11 chambers) --- annular series, up to 72 chambers. This species normally forms an almost round, flat or slightly concave disk (fig. fig. 5), but less frequently it forms an irregularly fluted margin. In two rather aberrant specimens from the Red Sea, a 2-3 rectilinearly arranged chambers followed the initial planspiral growth. There is no apparent difference in the growth mode in different geographical localities.

The B form

Only five specimens of the B-form were found (0.4%), all from the Red Sea. Both belonged to the form group that is known in the literature as *S. marginalis*(fig 5 a and b). The embryo consist only of a spherical proloculus, followed by planspiral and lenticulate juvenile chambers (fig. 6). The growth pattern development is summarized as; embryo (proloculus) --- evolutive lenticulate planspiral (12 chambers) --- flabelliform evolutive (5 chambers) --- annular series (up to 32 chambers)

Internal skeleton.

The internal skeleton is identical in the A, and the B-form. It first develops in the 2nd to the 7th postembryonic chambers in the A-form but later in the B-form (in about the 10th or 14th chamber). The skeleton consists exclusively of septula dividing each chamber into chamberlets. Each septulum possesses an opening (stolon), providing a communication between all the chamberlets in the same chamber. Directly above the stolon there is always an aperture, such that each aperture opens into two chamberlets (see fig.4 and 8). Therefore, each chamberlet in the same chamber is associated with two apertures. In those chambers that possess a single row of apertures, the septula are always oriented perpendicular to the lateral side of the chamber wall. In some specimens possessing a double rows of apertures (fig. 12 b) the septula may run obliquely between the lateral sides of the chamber, but the apertures are as a rule always located above the stolons. Obliquely arranged septulum may give the false impression of randomly inserted septula (Smout (1963), p. 235 and 259) or this has been mistakenly interpreted as the duplex plan, as is present in *A. hemprichii* (Lévy 1977). Several specimens of this type in the U. S. National Museum are incorrectly labeled as *A. hemprichii* (JAC 55635, 55636, and USNM 27470), but distinctly belong to *S. orbiculus*

Normally each chamberlet is directly connected to 6 chamberlets, 2 chamberlets in the same chamber, 2 chamberlets in the previous chamber, and 2 chamberlets in the succeeding chamber. This chamberlet arrangement is here called a hexagonal arrangement (fig. 7 and 8). The apertures of each chamber always opens centrally into the lumen of the succeeding chamberlet (fig. 7 and 8).

In all specimens, some chamberlets have an auxiliary aperture opening directly into the lumen of the chamberlet (fig. 7). Those chamberlets are connected to 7 other chamberlets. The chamberlets located above the auxiliary aperture are connected to 5 other chamberlets. These chamberlets were named auxiliary chamberlets (Zusatzkammerchen) by Lehmann (1961).

Apertures.

The apertural structure in the A and the B-form is identical. The embryo has a single circular to crescentic shaped aperture. As the animal grows and the chambers get bigger, more apertures are added but the crescentic to circular apertural form persists throughout development. The apertures are arranged in a single row along the apertural face and are provided with a distinct collar lip, slightly protruding. The presence of a simple row of apertures has been used as a diagnostic feature for the *S. orbiculus* var. *marginalis* form (see fig.5 a and b), (Lehmann 1961). In the material from the Red Sea examined by me, approximately 52 specimens (18%) of the typical *S. orbiculus* var. *marginalis* possessed double rows of apertures. Five of these specimens were dissected and the double apertural rows was present in the last 2-8 chambers. At times the same chamber may possess a single row at a portion of the chamber, and the rest has double row of apertures. The pre-adult chambers all possessed the typical single apertural row. Of all the specimens of the typical *S. orbiculus* form, double apertural rows are more often observed in the adult growth stages (78%) (fig 5 c and d), but a single row of

apertures is always present in the first 4-21 pre-adult chambers. The shape of an individual aperture can vary, even on the same chamber, from a transversely elongate, to almost a circular form (fig. 9 c and d). The development of the apertures is summarized in figure 9. The apertures are always located directly above the stolon in the septula throughout development.

Ornamentation and sutures.

The ornamentation on the embryo consists of distinct pits (fig. 10) In all other chambers the ornamentation has developed into pits which are shallow in comparison to the embryo and form depressions or grooves as well as pits arranged in an irregular pattern (fig. 11). There is no difference in the ornamentation among the A and the B-forms. The ornamentation is evenly dispersed over the sutures.

The ornamentation on the apertural face consists of elongate pits or grooves arranged parallel to the margin of the apertural face and radially around the apertures (fig. 12 a and b). This type of ornamentation on the apertural face persist throughout the development. Frequently a secondary amorphous chalk material is deposited on the lateral sides of the test, covering the umbilical part.

The sutures as well as the portion of the wall that is connected to each septulum is depressed (septulumsuture). The lateral side of the surface wall extends onto the septulumsutures of the preceding chamber, giving the sutures a wave shaped form. The wave formed suture is always present in chambers, divided into chamberlets. The surface walls of the chamberlets are slightly inflated (fig. 11 and 8)

Remarks

The morphological variability within this species supplies a lavish varients of different form-groups that have been designated as

species. A persistent criteria in the literature is to distinguish among specimens possessing a single row of apertures (= *Sorites marginalis*) versus specimens possessing a double row of apertures (= *Sorites orbiculus*). This is however only related to a degree of development, where specimens of both forms can develop double apertural rows at adult stages. The shape of the chamberlets as seen in equatorial section (fig. 7) are usually more ovate in the *marginalis* form as opposed to elongate to crescentic in typical *S. orbiculus*, but both these shapes are sometimes present in the same specimen.

The main differences between those two form groups according to Lehmann.(1961) are;

1) Whole test more biplane than biconcave in *Sorites marginalis*

2) Rather than forming a flat regular disk shape, *S orbiculus* tends to become more irregular, especially in the adult and the reproductive chambers. This is related to the fact that *S. orbiculus* often grows attached and is shaped by the substrate (Kloos 1984). This form is probably the same varient growth form which has been referred to as a separate species, *Sorites variabilis* (Lacroix 1941).

3) The planspiral lenticulate stage in *S orbiculus* ranges between 5-8 chambers as opposed to about 13 in *S. marginalis*.

4) The apertures develop double rows in typical *S. orbiculus* as opposed to single rows in the *marginalis* form.

In the material that I have, all these criteria form a morphological continuum and render it impossible to discriminate decisively between the formgroups *S. marginalis* and *S. orbiculus*. It is however easy to select individual specimens of each formgroup and point out these differences as are listed above. It has been my experience that in all geographical localities, about 12-37% of specimens are impossible diagnose as either *S. marginalis* or *S. orbiculus* since these specimens could possess in any combinations the features which were used to define both these form groups. It seems that these forms are parts of the same lifecycle, representing varieties or ecotypes, and are here reduced to a subspecific rank. The

detailed studies of Kloos (1984) on the lifecycle of *S orbiculus* seemed to indicate that *S. orbiculus* and *S marginalis* are conspecific.

Amphisorus hemprichii Ehrenberg, 1839

Figures 22 -25.

Amphisorus hemprichii EHRENBERG (1839 [1840]), p.130 & 145, pl.3; fig.3. LEHMANN (1961), p. 647 - 650, fig. 39 and 40, pl.X; fig.6 -9, pl. XI; fig. 1 - 5.
Orbitolites duplex CARPENTER (1883), p. 25 - 29, pl.III; fig. 8 -14, pl.IV; fig. 6 - 10, pl. V; 1,2, and 6 - 10. BRADY (1884), pl. XVI; fig. 7. CUSHMAN (1917), p. 94 - 95, pl.38; fig. 3 & 4, pl. 39; fig 1. HOFKER (1930), p.155 - 158, pl.LX; fig. 1, 2, & 4, pl.LXII; fig. 10. SMOUT (1963), p. 262 - 263, pl.IV; fig. 3, 4, 5, & 8.
Orbitolites complanata BRADY (1884), pl. XVII; fig.3 - 5.

Number of specimens examined, 477, (AMNH 43790 - 43793, 437999 - 43815).
Number of specimens dissected, 11.
Geographical distribution, The Red Sea, Hawaiian Islands and the Caribbean, (samples; 14, 16, 22, 29, 30, and 31).

Growth form.

The A-Form.

In 3 specimens (0.6%) all from Taba (Red Sea), the vorhof is almost nonexistent (fig.22 a), but otherwise in all specimens it is a large distinct structure. The total diameter of the A-form embryo has been recorded to vary from 150µm to 340µm (Zohary et. al. 1980). The embryos illustrated by Hofker (1930 pl. LX, figure 3), and Cushman

(1917, figure 48, page 94) show a proloculus followed by a flexostyle, but without a vorhof. Despite a thorough search I have been unable to find a single A-form specimen of this species without the vorhof. Either this is an extremely rare morphotype or the illustrations by Hofker and Cushman are of another species, perhaps *S orbiculus* which can resemble *A. hemprichii* if it possesses double apertural rows. The specimens of this species form a circular and flat disc (fig. 23). The development is summarized as; embryo (proloculus + flexostyle + vorhof) --- evolutive, flabelliform growth (1 to 5 chambers) --- annular series (up to 83 chambers).

The B form.

I found three specimens of the B form (0.6%), where the embryo consists only of a proloculus (fig 22 c). The growth pattern is summarized as; embryo (proloculus) --- evolutive, lenticulate, and planspiral growth (14 chambers) --- flabelliform, evolutive growth (about 3 chambers) --- annular series evolutive (up to 72 chambers).

Apertures.

The apertures of the vorhof in the A-form form a single apertural row (fig. 24 c). A single row of apertures persist in the next 9-15 chambers (fig. 24 d). Following the single row of apertures, a double row of apertures develops. This double row of apertures forms a regular pattern of displaced apertures, such that each aperture in one row is facing the space between two apertures in the opposite row.(fig.24 e). In about 30% of the specimens from the Red Sea, Taba, additional apertures are inserted between the double marginal rows usually only on a part of the chamber, somewhat resembling the apertures in *M. kudakajimensis*, as is illustrated in figure 28 d. I observed these apertural characteristics only in the last 1-4 chambers, in very large specimens possessing over 58 chambers.

The B-form.

In the B-form, the first 9-11 chambers possess a single aperture (fig 24 a). Multiple apertures develop in the B-form in about the 10th-11th chamber, gradually increasing in number as the size of the chamber increases. The multiple apertures form a single row, persisting until about the 18th or the 21st chamber, a condition already present in the vorhof in the A-form (fig. 24 c). Then a double row of displaced apertures develop in the B-form, identical to what is present in the the A-form.

Internal skeleton.

In the B-form the skeleton develops in about the 13th chamber, but in the A-form, the skeleton develops in the first chamber following the embryo. In both forms the initial development of the skeleton always consists of a transverse septula. In those chambers possessing only a simple apertural row, the skeleton consists of simple septula dividing the chambers into series of chamberlets arranged in the typical hexagonal pattern, a condition identical to *S orbiculus* (see fig. 7 and 8). When the double rows of marginal apertures develop the structure of the septula are also transformed. The stolon is enlarged into a large opening, forming a division in the septula such that one septulum is facing the space between two septula on the opposite side of the chamber (fig. 25 a). This structure has been described before and is known as the duplex plan (Carpenter 1856 and 1883). This disjunct arrangement of the septula in the duplex plan is closely associated with the displaced arrangement of the marginal apertures, described above (fig 24 e and 25 a). The apertures in the double row are always located above the underlying septula and open directly into the centrally located annular canal (fig 24 b).

It was noted that some specimens from the Red Sea, Taba, possess traces of median apertures inserted between the double apertural

rows. Despite a thorough search I was unable to detect any traces of a median skeleton, which is always associated with the development of median apertures in *M. kudakajimensis*

Sutures and ornamentation.

The ornamentation of the lateral walls consists of pits and depressions or grooves forming an irregular pattern over the lateral surface throughout the development, evenly dispersed over the suture. The apertural face has a typical spongy appearance of irregular holes and groves arranged longitudinally along the margin of the apertural face and radially around the apertures. The sutures are shaped in the typical wavelike form, reflecting the hexagonal arrangement of the surface chamberlets. The walls of the chamberlets are inflated but depressed over the septula, forming typical septulum-sutures.

Remarks.

Carpenter (1886) designated the double rows of apertures as the diagnostic feature of *A. hemprichii* with the result that specimens of *S. orbiculus*have frequently been confused with *A. hemprichii*(e.g. Heron-Allen and Earland (1915), Levy (1977) and Cushman (1930)). However as shown here both these species can posses double rows of apertures, but clearly differ in the structural relation of the apertures to the internal skeleton. Thus, in *A. hemprichii* the double aperture form a displaced pattern, which is absent in *S. orbiculus* Also the internal skeleton in *A. hemprichii* develops into the duplex plan a condition absent in *S. orbiculus* All distribution records of *A. hemprichii*should therefore be considered with caution.

In total 175 uncataloged slides (USNM) from the Marshall Island contained a disorderly assemblage of *A. hemprichii*, *S orbiculus*, and the *marginalis*variety. The hypotype (USNM 433525) of *A. hemprichii* (Loeblich and Tappan, 1964, fig. 386,2), clearly possesses the

displaced pattern of double apertures defining this species, but it has a very reduced vorhof similar to figure 22 a.

Marginopora kudakajimensis nov sp.

Figures 26 - 30

Number of specimens examined, 654, (AMNH 43794, 43796-43798, 43801, 43808, 43813, 43917-4319, 43978-43989).
Number of specimens dissected, 12.
Geographical distribution; Japan and the Hawaiian Islands.(samples; 1, 2, 4, and 28)

Growth form.

The embryo in the A-form possesses a proloculus, flexostyle and a distinct vorhof, identical to what is observed in *A. hemprichii*. The first 1-5 chambers in the A-form, grow in a flabelliform mode, then transforming into annular series persisting throughout development. The development is summarized as; embryo (proloculus + flexostyle + vorhof) --- evolutive, flabelliform growth (1 to 5 chambers) --- annular series (up to 98 chambers). This species normally forms almost a round, and distinctly concave disk in large adult specimens (fig. 26 a and b).

Only one specimen of the B-form was found. It possessed a single proloculus, followed by 7 evolutive, planspirally arranged chambers, then transforming into about 4 flabelliform chambers. The remaining 48 chambers possessed annular series.

Apertures.

The A-form.

The embryonic vorhof possesses a simple row of apertures (fig. 28 a). A simple apertural row persists for the next 5 to 8 chambers (fig 28 b). Double apertural rows (marginal rows) develop next, persisting until about the 8th - 19th chamber (fig. 28 c). The double apertural rows form a displaced pattern, identical to *A. hemprichii* (see fig. 24 e and 25 a). Between the marginal apertural rows a number of apertures develop next, which I have called median apertures (fig. 28 d), described here for the first time. The initial development of the median apertures ranges from the 9th.- 20th chamber, often making the first appearance only on a portion of the same chamber. Large adult specimens (73% of the specimens examined) possess an extremely broad band of median apertures, illustrated in figure 24 e.

The B-form.

Only one specimen of the B-form was found and this was dissected to examine the apertural development. The first 5 chambers possessed a single circular aperture (fig. 28 f). Multiple apertures appeared in the 6th chamber (fig. 28 g) forming a single row persisting in the next 14 chambers. The double displaced rows of apertures succeed for the next 12 chambers. Last to develop are the median apertures, persisting throughout the development in the remaining 11 chambers.

Internal skeleton.

In the A-form the internal skeleton develops in the chamber immediately following the embryo, but is not expressed until about the 6th chamber in the B-form. The single row of apertures is associated with the initial appearance of simple septula. The septula

persist in the first 6-9 chambers. These septula are identical to what is described in *S orbiculus* (see fig. 7 and 8). The introduction of the double rows of marginal apertures is associated with the transformation of the internal skeleton into the duplex plan, identical to what was described under *A.hemprichii* (fig.25). The duplex skeleton is present in next 3-12 chambers following the septula.

The appearance of the median apertures is always associated with the development of the median skeleton. Located between the septula in the duplex plan, is a network of wall partitions forming an irregular pattern of pocket-like median chamberlets (fig. 27). Usually each median aperture opens directly into a single pocket chamberlet within the median skeleton. It is rare to observe the apertures associated with stolons in the median skeleton. When the median chamberlets develop there are usually on each side of the chamber, annular canals associated with the chamberlets formed by the septula, but frequently the annular canals are absorbed into the median chamberlets and can not be recognized as a distinct entity. This type of a median skeleton has not been described before in the literature, a defining characteristic of this species.

There are two pathways connecting the surface chamberlets to the other compartments of the test. First there is a large pathway connecting the surface chamberlets to the compartments formed by the median skeleton, thus forming a connection within a single annular chamber (fig. 29 b). This is different from *M. vertebralis* where this pathway is reduced to a narrow tubule (fig. 18). Secondly the surface chamberlets are always located above one of the marginal apertures in the preceding chamber (fig. 27 a and b). The marginal apertures always open directly into the compartments of the median skeleton or the annular canal if it is present (fig 27 a and b). In the adult chambers only the marginal apertures are visible from the outside when the lateral sides of the surface chamberlets are removed (fig. 29 b).

The development of the internal skeleton in the A-form is summarized as; initial simple part with septula and stolons in the

first 5 to 8 chambers, --- duplex median part with an annular canal and disjunct septula, present in the next 3 to 12 chambers, --- appearance of the median skeleton, present in the remaining chambers (fig. 29 a).

Ornamentation and sutures.

The ornamentation consists of pits as well as depressions or grooves forming an irregular pattern over the lateral surface throughout the development The ornamentation is evenly dispersed over the suture.(fig. 30 a). The apertural face has a typical spongy appearance of irregular holes and groves arranged longitudinally along the margin of the apertural face and radially around the apertures (fig. 30 b).

The sutures are shaped in the typical wavelike form, reflecting the hexagonal arrangement of the surface chamberlets. The walls of the chamberlets are inflated but depressed over the septula, forming typical septulumsutures (fig. 30 a).

Remarks

The presence of the unique kind of median skeleton is used to define a new species, along with the peculiar presence of median apertures. Specimens of *M. kudakajimensis* have frequently been confused with *Marginopora vertebralis*, but it is simple to diagnose these two species by the form of the apertures, (compare fig. 28 and 15). It seems from the descriptions of the A_1 forma of *M. vertebralis* by Hofker (1930), that he is describing specimens of *M kudakajimensis* The apertural face of Hofker's A_1 forma is illustrated on pl. LXII, fig. 5 and the internal skeleton on pl. LXII, fig. 1, both illustrating morphology similar to *M. kudakajimensis*, but the drawings are not accurate enough to make an affirmative judgment.

It is evident from the excellent drawings in Carpenter (1883, pl. VI,fig. 5), that this particular figure is of a specimen of *M. kudakajimensis*. The figure indicates presence of the simple and the duplex plan of the median skeleton in about 23 chambers, then transforming into the complex plan in the remaining 33 chambers. Carpenter describes this specimen as "sub-typical" an displaying much irregularity in the median skeleton. This is different from *M. vertebralis* which he thought he was describing, where the simple and the duplex plan are reduced to the first 4-7 chambers. The median skeleton in *M. vertebralis* consists of transverse to oblique septa, and appears "more regular", in Carpenter's words.

The photographs by Ersu (1985, pl. XIII, fig. 5-10) showed the distinct characteristics of both the apertures and the median skeleton of *M. kudakajimensis*, reported to be from Hawaii, Mokuleia.

Several slides in the U. S. National Museum, from the Miocene, Bikini, identified by Cole, labeled as *Marginopora vertebralis* but are in fact all a disorderly assemblage of *M. kudakajimensis* and *A. hemprichii* (slides * USNM. 337337 - 337340, 3373342, 337343, 337719.). In addition slides from Bikini atoll and Rongerik are labeled as *M. vertebralis* but are all of *M. kudakajimensis* (slides, JAC 48155, 48142).

Marginopora vertebralis Blainville, 1830

Figures 13 - 21.

Marginopora vertebralis BLAINVILLE (1830), p. 377. BLAINVILLE (1834), p. 412, pl. LXIX, fig 6 & 6 a-c. HOFKER (1930), p. 160-163, pl. LVII; fig. 1, pl. LXI; fig. 5, & 11, pl. LXII; fig.2, 3, 8, 9, 11,& 12. (Not forma A1). CUSHMAN (1948), p. 245, pl.24, fig. 15-17. LEHMANN (1961), p.654-655, pl. XI; fig. 6 & 7, pl. XII; fig. 1-7. ERSU (1985); p. 356-357, pl. XII; fig. 12, 13, 14, 15, 16, & 17, pl.XIII; fig. 2.

Orbitolites complanata CARPENTER (1883), p. 29-43, pl; V; fig. 11-15, & 18, pl.VI; fig. 1-4, 6, & 8-10, pl. VII; fig. 1-7, pl. VIII; fig. 1-11. BRADY (1884), pl. XVI; fig. 5 & 6. CUSHMAN (1917), p. 95 -97, pl. 39, fig. 2.

Orbitolites complanata var. *lacinatus* BRADY (1884), p. 220-221, pl. XVI; fig. 8-11.

Orbitolites vertebralis HOFKER (1971), p. 53. Smout (1963), p. 263.

Orbitolites(*Marginopora*) *vertebralis* Smout (1963), p. 266, pl. IV, fig, 6, 7, & 9.

Number specimens examined; 287, (AMNH 43769 - AMNH 43789).
Number of specimen dissected; 12.
Geographical distribution, The Great Barrier Reef, Tonga, British Solomon Islands, French Oceanica (samples, 10, 15, 20, 21, 32, 33, and 34).

Growth form.

The A form

The embryonic apparatus in this form consists of a proloculus, flexostyle and vorhof (fig. 13 b and c). The growth pattern in the A-form transforms directly into annular series following the embryo. In occasional specimens 1 or 2 chambers assume a flabelliform growth following the embryo. This is summarized as; embryo (proloculus + flexostyle + vorhof) --- flabelliform evolutive (0 - 2 chambers) --- annular series (up to 68 chambers). Usually the annular chambers form almost a perfectly round, concave disk (fig 14), but these can develop in some of the larger specimens into plicated and lacinated forms (see e. g. Carpenter (1883), pl.VII; fig. 1-7.)

The B form.

I found 4 specimens of this form (1%), where the embryo consists only of a proloculus (fig. 13 a). The growth pattern is summarized as;

embryo (proloculus) --- evolutive, lenticulate and planspiral growth (5 to 9 chambers) --- evolutive flabelliform (5 to 7 chambers) --- annular series (up to 32 chambers).

Aperures.

The A form.

The vorhof has multiple circular to ovate apertures, always forming a single row along the apertural face (fig. 15 e). The 1st to the 2nd chamber has a double marginal rows of circular apertures, opening into a single annular canal (fig 15 d). In the 2nd to 4th chamber median apertures are added between the two rows of the marginal apertures (fig. 15 f and g). The median apertures can be ovate to circular in form, in contrast to the marginal apertural rows which are always circular. All the apertures are provided with a distinct circular lip.

The B-form.

The first 8 or 9 chambers following the embryo, possess a single circular aperture (fig 15 a). In the following 8 or 11 chambers more apertures appear, arranged in a single row (fig 15 b and c), a similar arrangement as is present in the vorhof of the A-form (fig. 15 e). In about the 18th or the 21st chamber double marginal apertural rows are assumed and the median apertures in the 19th or the 22nd chamber, identical to the apertures in the A form. In total these two dissected specimens of the B-form possessed 32 and 27 chambers.

Internal skeleton.

The development of the internal skeleton follows an orderly pattern previously described by Lehmann 1961,and Hofker 1930 and1971, and Carpenter 1856 and 1883) The development of the internal skeleton is summarized as: initial simple part with septula and stolons, --- duplex median part with annular canals and disjunct septula, --- complex part with a median skeleton (fig. 16).

The A-form.

The internal skeleton develops immediately in the first chamber following the embryo. The first 4 to 7 chambers possess a simple septula usually with a single stolon forming an annular canal, but it is also common to observe two or three stolons in these early septula. The simple septula in these first chambers are associated both with marginal and median apertures. The structure of these simple stolons is identical to *S. orbiculus* (see fig. 8). The next stage of development is the formation of disjunct partitions, (the duplex form), a condition identical to *A. hemprichii* (see fig. 25). However, the disjunct partitions were not observed in all the dissected specimens, and if it was present, it was reduced to 1 of 2 chambers or only present as a part of a single chamber. In the 5th to the 8th chamber the median skeleton appears. This is associated with the division of the annular canal, such that on each side of the chamber, an annular canal is associated with the chamberlets formed by the septula. In *M vertebralis*, the annular canals always appear as a distinct entities, in contrast to *A hemprichii*. The median skeleton consists of septula, running between the annular canals on each side of the chamber. At times, two or more secondary septula anastomose, or form short walls, only running halfway between the annular canals. A few of the median apertures open directly into the chamberlets formed by the secondary septula, but most frequently the median apertures are associated with stolons in the secondary septula.

There are two pathways connecting the surface chamberlets to the other compartments of the test. First there are tubules connecting the surface chamberlets and the chamberlets formed by the median

skeleton. The tubules therefore form a connection within the single annular chamber. Secondly the surface chamberlets are always located above one of the marginal apertures in the preceding chamber. The marginal apertures always open directly into the annular canal and therefore the marginal apertures connect each surface chamberlet to the annular canal in the preceding chamber (fig 17 a and b). In the adult chambers these two openings or pathways in the surface chamberlets are clearly visible from the outside when the lateral sides are removed (fig. 18). This is a different condition from what is observed in *M. kudakajimensis*, where the "tubule" represents a wide opening (fig. 29 b).

The B-form.

In the B-form the development of the internal skeleton is delayed until the 11th or 12th chamber. The simple stolons develop first and are present in 4-5 chambers. The duplex median part develops next and is present in 3-6 chambers. The complex part develops last and persists throughout the remaining 9-13 chambers. In the B-form the simple and the duplex stages last for about 7-11 chambers, in comparison to the A-form where the simple and the duplex parts are reduced to about 5-9 chambers and the duplex part is not expressed in all the specimens. Otherwise the structure of the internal skeleton is identical in the A and the B form.

Ornamentation and sutures.

The ornamentation on the lateral sides, consists of pits as well as grooves or canals rather irregularly dispersed over the wall.(fig 19). The apertural face has a typical spongy appearance of irregular holes and canals arranged longitudinally along the margin of the apertural face and radially around the apertures (fig. 20)

The sutures are shaped in the typical wave form. The ornamentation is evenly dispersed over the sutures. The walls of the chamberlets are inflated but depressed over the septula, forming typical septulumsutures (fig.21). Frequently the central parts of the tests are covered with several layers of amorphous calcareous veneers.

Remarks

It has been a persistent mistake to confuse *M. vertebralis* with *M. kudakajimensis*. It is evident that the median skeletons in these two species are different and therefore the mere presence of a median skeleton is not a criteria to diagnose *M vertebralis*. Cole (1965) used a large suite of specimens to demonstrate development from a simple plan to a duplex plan into a complex plan to argue that his specimens were one species, by assuming that the mere presence of a median skeleton is a criteria to fuse these species together. Cole based his observations exclusively on thin sections which can be misleading since it des not reveal adequately the anatomical difference in the median skeleton among *M. kudakajimensis* from *M vertebralis*. Ersu (1985), and Hofker (1971) made the same mistake.

Brady (1884) reports the distribution of *M vertebralis* (= *Orbitolites complanata* var. *lacinatus*) from Friendly Islands (Tongatabu) and Fiji. Cushman (1917) records it from the Hawaian Islands, Hong - Kong, Cagayan, Sulu Islands and the Philippines and Ersu (1985) from Vanuatu Islands, Efate. The U. S. National Museum hosts specimens which distinctly belong to this species from the Makemo beach, (JAC 20006), Bikini atoll (USNM 337341), and Saipan Island (USNM 383766).

Sorites orbitolitoides (Hofker 1930)

Figures 31-35.

Orbitolites marginalis BRADY (1884), (part) pl.XV, fig. 4. FLINT (1897) pl.50; fig. 2, pl. 51; fig. 1.
Praesorites orbitolites HOFKER (1930), p. 149-151, pl..LV; fig. 8, 10, & 11, pl. LVIII; fig. 1-5, pl. LXI; fig 3, & 14.
Sorites marginalis CUSHMAN (1930), pl. 18; fig. 1-4.
Orbitolites crassipora HOFKER (1952 b), p. 108-109, fig. 56.
Orbitolites orbitolitoides HOFKER (1952 b), p.105-107, fig. 53 & 54.
Orbitolites(Sorites) orbitolitoides HAMAOUI & BRUN (1974) pl. 10; fig. 1-3, pl. 11; fig. 1-2.
Broeckina orbitolitoides LÉVY (1977), p. 423-425, pl. 7, fig 8-14. ERSU (1985), p. 352-353, pl. XIV; fig. 6-13.
Broeckina discoidea LÉVY (1977), pl. 7; fig. 1-7. ERSU (1985), pl. VIII; Fig. 2-17, pl. IX; fig. 1-5

Number of specimens examined, 157, (AMNH 43858 - AMNH 434864).
Number of specimens dissected, 22.
Geographical distribution, Hawaiian Islands and Caribbean, (samples, 1, 14, 19, 22, and 17).

Growth form.

The A-form in this species possesses a proloculus and a flexostyle. I did not retrieve any B-form specimens, but these are excellently figured by Hofker (1930, pl. LVII, fig. 1) showing a prolocular embryo, without a flexostyle. The ontogeny of the growth forms in the B-form, is summarized as; embryo (proloculus + flexostyle) --- evolutive, lenticulate, and planspiral growth (12-25 chambers) --- rectilinear growth (0 to 15 chambers) --- flabelliform chambers (5-

11) --- annular series (up to 28 chambers). This species forms a flat, round disk (fig. 31).

Eight specimens possessed the rectilinear growth stage, following the planspiral lenticulate stage. The specimens possessing a rectilinear growth stage are considered to be a varient groth form of this species.

Apertures.

The embryo is followed by 5-8 chambers possessing single round or ovate apertures (fig. 32 a and 34). The following 3-4 chambers possess two apertures, where either both are round or the basal aperture forms a crescentic shape (fig. 32 b). In the following chambers more apertures are added as the size of the chamber increases, forming a single apertural row throughout the development. It is extremely rare to encounter specimens which express a double row of apertures. I observed a double row of apertures on a portion of the same chamber,.only in two specimens I was unable to detect a displaced apertural pattern, comparable to what is present in *Amphisorus hemprichii*, rather an irregular row of pairs of apertures was observed, similar to what is observed in *S. bradyi* (see fig. 37 e). The form of the apertures gradually assumes an oval shape in the adult annular chambers, but the circular form of apertures along with the more frequent ovate form is present on the same chamber throughout development (fig. 32 d and e). The ovate apertures are usually oriented longitudinally along the apertural face. Transversely oriented ovate apertures as in *S. orbiculus* were rarely observed in *S. orbitolites*. The only specimen from the Hawaiian Island possesses mostly transversely oriented apertures, which is extremely rare among the specimens from the Caribbean region. All the apertures are always with a distinct circular lip.

Internal skeleton

In all the dissected B-form specimens the internal skeleton consistently develops in about the 10th-11th chamber. These always consist of simple septula, forming the typical apertural-stolon complex as is described under *S orbiculus*. The stolons remain at all developmental stages as a large openings such that the septula form ringlike ridges, located directly below each aperture (fig. 33 a and b). The chamberlets are arranged in the typical hexagonal pattern, conforming to what was described for *S orbiculus*

Ornamentation and sutures.

On the lateral sides of the wall, the ornamentation consists of distinct, evenly dispersed pits, at all developmental stages (fig. 34). The ornamentation can either be evenly dispersed over the sutures. At times the wall is smooth and without pits on the posterior part of each chamber. On the apertural face the ornamentation assumes the form of elongate grooves or pits. The groves are always oriented longitudinally along the apertural face, parallel to the apertures (fig. 35). This type of ornamentation very rarely extends onto the lateral sides of the wall.

The sutures are straight, distinct and depressed, never forming the typical wave shape as in *M. vertebralis*, *A. hemprichii*, and *S. orbiculus*. Neither are there any traces of septulumsutures, or depressions in the lateral walls over the septulum.

Remarks.

The species *Orbitolites crassipora* from Fredrickstad, Santa Cruz, was created by Hofker 1952b and distinguished from *S. orbitolites* only by the presence of larger pits. Judging from the figures given by Hofker (1952 b, p. 108, fig 56) the diameter of the pits is around 6µm.

The specimens I have from the Bahamas and clearly belong to *S. orbitolitoides* possess pits ranging in diameter from <1µm up to 8µm, even on the same specimen. It seems therefore doubtful in this instance, that the diameter of the pits has any significance to form a basis of a new species.

Sorites bradyi (Cushman, 1930)

Figures 36 - 40.

Peneroplis bradyi CUSHMAN (1930), p. 40, pl. 14; fig. 8-10. ERSU (1983), p. 97, pl.IV; fig. 15-18, pl. V; fig. 1-15. LÉVY (1977), p. 402, pl. 1; fig 10.
Puteolina bradyi HOFKER (1952a), p. 450-452, fig. 36.
Peneroplis laevigatus BRADY (1884), pl. XIII; fig. 12 & 13
Peneroplis planatus (pleisiotype USNM 17422) CUSHMAN (1921), p. 75, pl. 18, fig. 9.

Number of specimens examined, 11, (AMNH 43865).
Number of specimens dissected, 7.
Geographical distribution, Caribbean (sample 14).

Growth form.

Only the A-forms of this species were found. The growth form is summarized as; embryo (proloculus + flexostyle) --- planspiral, lenticulate and evolutive growth (up to 34 chambers) --- rectilinear growth (0 - 4 chambers). The rectilinear growth (fig.36) was observed in 3 specimens of 11 and represents a varient growth form of this species which normally retains the planspiral growth throughout development.

Apertures.

The first 9-15 chambers possess a single circular aperture provided with a distinct circular lip (fig. 37 a). In the following 11-17 chambers more apertures are added, forming a single row. As the length of the apertural face increases more apertures develop, always arranged in a single row (fig. b, c, and d). In the last chambers, possessing a single row of apertures, it is common to observe a slightly ovate transversely arranged apertures (fig 37 d). Ovate apertures, arranged longitudinally have also been described in this species (Ersu (1983) pl. IV; fig 17), although this was not observed in the few specimens that I examined. The development of rectilinear growth, is correlated with development of a double row of apertures, showing a slight tendency to form pairs, but are rather irregularily diplaced (fig. 37 e).

In the first chambers the apertural lip is well developed and distinct. In those specimens possessing rectilinear chambers and double apertural rows, the lips are poorly developed, and are expressed as a slightly elevated border around the apertures (fig. 40).

Internal skeleton.

Inside the last 2 - 4 chambers in a specimen containing rectilinearly arranged chambers, I observed traces of an internal skeleton closely resembling septula. These are slightly elevated ridges, are always confined and running transversely across the base of the chamber, never forming a thickening inside the lateral sides of the wall (fig. 38). The septula were only detected in chambers possessing double apertural rows, in the rectilinear growth stage. The septula are located between each pair of apertures of the previous chamber.

However these traces of septula are apparently not arranged in a hexagonal pattern as was described under *S orbiculus*

The septula are not readily observed in light microscope, unless the apertural face is removed and the specimen is stained, for example with alizarin red. When using a stereo-microscope and reflected light it is useful to stain the specimen with a dilute black ink.

Ornamentation and sutures.

The ornamentation on the lateral sides of the walls, consists of evenly dispersed pits, forming an oval to round or irregular outline (fig 39). The ornamentation on the apertural face consists elongated groves or ovate pits, arranged radially around the apertures (fig. 40).

The sutures are depressed and distinct throughout the development, with evenly dispersed pits over the sutures (fig 39)

Remarks.

Ersu (1983, p. 97), mentioned the presence of irregular wrinkles (plissotements) inside the chambers of *S. bradyi*, but rejects the comparative significance of this structure with the internal skeleton in both the Soritinae and the Archaiasinae. These "wrinkles" are described as confined to the base of the chamber, always running transversely across the chamber between each pair of apertures on the previous chamber. This is in essence comparable to the homology which is here referred to as a septulum, defining the Soritinae.

The holotype of this species (USNM 4840) and the paratypes conform to the specimens examined by me, but show no rectilinear chambers. According to Cushman (1930), the species is present in throughout Caribbean region. Several slides at the USNM were labeled as *Peneroplis antillarum*, (JAC 10379, 10380, 4830, 4831, 4833, 4835, 4838, 4839, and 9955), but these are all distinctly belong to *S. bradyi*. The fossil record of this species is scarcely known, the test is

extremely delicate, and not likely be preserved as fossil. However, specimen slides USNM 18149 and 17678 are reported from the Miocene, Chipola, and specimen slides USNM 62733 are reported from Middle Oligocene.

CONCLUDING PART.

As indicated in diagram 10 (page 40), I have recognized 18 groups of specimens as species, demarcated by definite anatomical differences, with no apparent intergradation of forms, except for the 3 *Cyclorbiculina* "species." I have assumed that these 18 form-groups are species, an inference that ultimately has to be settled by life-history experiments. Among those 18 species, 30 anatomical comparisons were made, each based on a structural correspondence, and referred to as homologies. The distribution of the homologues among these 18 species.is summarized in table 1 (page 39), where the presence of each homologue indicates which species are to be included in a monophyletic group. According to formula 1 there are exactly 304745 different species groups that can be erected among 18 species.

Although I recognized 30 homologies there are only 16 groups defined as monophyletic. What is even more interesting about this particular data set is that 15 out of 16 of these groups can all be represented in a single diagram as branching points. What is the significance of this congruence? For one thing this congruent data set (with one exception) is consistent with the assumptions that these homologous features originated in some common ancestor and were inherited among all of its descendants. Loss or elimination of the homologues is probably rare, appears only in one instance as the non-congruent group definitions I and J. Parallel or convergent evolution is probably always detected by anatomical scrutiny.

Of course it is possible that the distribution of these 30 homologies was the result of a random processes although that seems to be an unlikely explanation. It instructive in this context to quantify the probability that these 15 congruent groups could have been generated by chance alone? Chance or randomness is defined in this context to signify the combined outcome of three different processes 1) ancestral origin and inheritance of anatomical features in all descendants, 2) reversal or elimination of ancestral characters in

some or all of the descendant species, 3) independent origin of the "same" structures in different species. Assuming this notion of randomness it seems clear that all of the 304745 groups have some possibility of being defined by a homology hypotheses. In the absence of any evidence of the absolute rate of origin, convergence, and elimination of features, it is further assumed that all the 304745 possible groupings have an equal chance of being observed by some homology. Diagram 10 represents 15 groups as a congruent set of internested taxa. Given the analogy of a multifaced dice, what is the probability that these particular 15 groups could have been generated by chance alone. Given that these 15 groups are defined by 29 homology hypotheses, the probability to obtain such results by chance alone is $(15/304745)^{29}$, practically a zero probability, suggesting a non-random phenomenon.

The only random element in this data set is present in the groups identified as groups I and J, since these can not at the same time define branching points in the same diagram. However it is possible to choose either group I or J as a branching point within diagram 10. For practical reasons group J is preferred since it is defined by 2 homologies but group I only by 1 homology. This invites the interpretation that homology 26 (circular growth) is lost (reversed) in *A. angulatus* and *A. lucasii*. On the other hand if group I is selected as a branching point in diagram 10 then that invites the notion that homologies 25 (pillars) and 30 (multiple segment of anomalous apertures) are lost in *C. americana* and in *C. discoidea*. It is less efficient to select group I as a branching point, because then two elimination hypotheses are needed to explain the distribution of the homologues within group J. In contrast to only 1 elimination hypotheses is needed to explain the homology distribution within group I, if group J is selected as a branching point, and group J is therefore a more efficient choice.

However I suspect that this conflict among groups J and I is more apparent than real. Cyclorbiculina is probably a monotypic genus. If I

am correct then the 3 cyclorbiculines will be represented as a single tip, and homologies 25 and 30 will define group H along with homology 24, and homology 26 will be reduced to a unique feature of a single species.

Assuming that diagram 10 is a true estimate of the soritid relationship it can serve as a basis of prediction. Discovery of a new species, or new homologies poses a challenge to the scheme presented in diagram 10. It remains to be seen if such additional information creates groups combinable to the groups already present in diagram 10. For instance, the probability that the next discovered homology among these 18 species, will define a group combinable to diagram 10 is simply 38/304745, if it is assumed that the 5 species included in group H can form all the possible groups which are of less generality and representing subdivisions of group H.

Of the 30 homologies hypothesized, 28 exist as parts of 6 independent ontogenetic sequences. Some species possess up to 4 features forming an ontogenetic sequence within each individual organism, where each of these features forms a part of a homology statement. When each individual species is examined by itself, several simple ontogenetic sequences are apparent. However, if ontogeny is perceived within the conceptual framework of branching diagrams, where ontogeny is construed as a transformation of homologies among species, a different pattern emerges. Diagram 11 (p. 106) is a graphic summary of the ontogenetic transformation of the same homologies which are depicted in diagram 10. The features described in the boxes, concerning the development of the apertures and the ornamentation, refer to structures that are also present in other Miliolina as well as the Soritoidea and therefore define much vaster groups than the soritids.

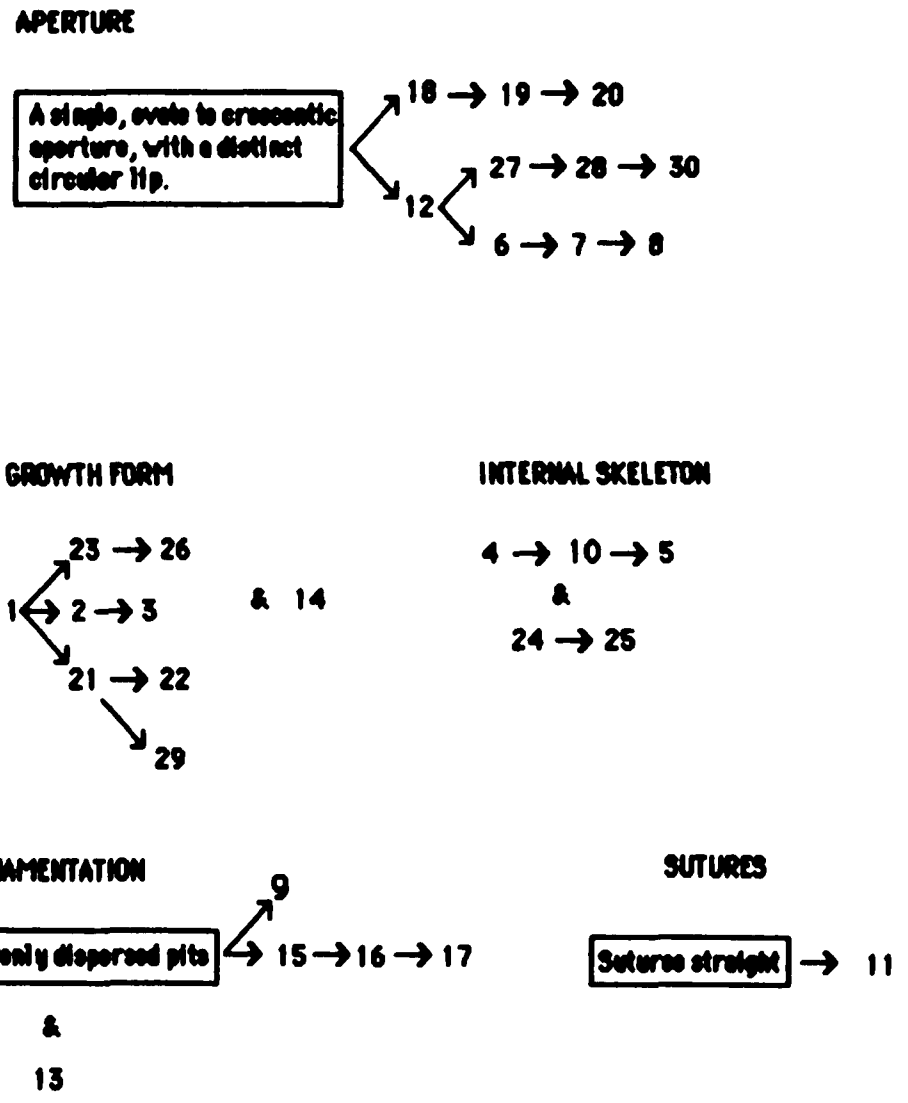


Diagram 11. A graphic summary of the ontogenetic transformations of homologous features. The numbers refer to the same homologies as are summarized in diagram 10.

The homologous structures that are inferred to be a part of the same ontogenetic sequence, do not develop intermediate forms. In a sense each homology appears abruptly during ontogeny and coexists with its preceding homology or replaces it. I assume for instance that the apertures in each organism are a transformation series of a single

anatomical structure; the apertures. When new anatomical features in the apertures are introduced, I interpret these to be transformations of the apertures in the previous chamber. Notable is the ontogeny of the internal skeleton in *A. kudakajimensis* In the A-form simple septula are present in the first 6-9 chambers. The duplex skeleton appears in the next 3-12 chambers. The appearance of the duplex skeleton replaces the skeletal structure of the septula which have disappeared. The inference is made that the septula have transformed into the duplex skeleton. Finally the complex median skeleton is expressed always after the duplex skeleton chamber. The median skeleton is placed in the center of the chamber between the skeletal elements of the duplex skeleton. The complex skeleton is therefore superimposed on the duplex skeleton and both structures coexist in the remaining chambers.

The above paragraph can be summarized as following. The internal skeleton is identified as the same structure, which is formed initially as septula, then transforming into the duplex plan and finally into the complex plan. By this I am not inferring any causal relationship, in the sense that the septula induces the duplex plan, which in turn induces the complex plan. In the case of the Soritinae I am implying that there exists a distinct anatomical unit of a special kind, referred to as the internal skeleton. If this premise is accepted then this unit structure, the internal skeleton, transforms as the organism develops.

An objection might be raised against this formulation, if it is maintained that an ontogenetic transformation can only include causally related anatomical stages, if ontogeny is to be meaningful (e. g. Albrech 1985). An ontogenetic sequence, therefore, can only contain sequence of structures where the preceding structure induces the succeeding feature. In response, it can be said that it is likely or even certain, that the internal skeleton for instance, can "cause" or induce form changes in the apertures or vice versa. However the fact that one structure can induce another structure hardly warrants the conclusion that the inducer has transformed into the induced, merely

that the presence of one or more structure affect the development of each anatomical part in the organism. Regardless of causal relationship among anatomical units which might exist, it is also a matter of fact that these anatomical units exist and develop as succession of forms. In other words the existence of the anatomical parts is independent of their causal or functional relation to other parts.

Inspection of diagram 11, suggests that most commonly ontogeny proceeds by forming a simple transformation series. This can either be as a succession from a more general general group to a less general group or alternatively as a succession of homologous forms which define the same group. This is demonstrated by the following examples. The development of the ornamentation, is given in homologies 15---16---17, proceeding within the inclusive set of grops K---M---N, respectively. There are three ontogenetic transformations observed, related to the development of apertures. Homologies 6---7---8 form an ontogenetic series within the inclusive groups C---F, where both homologies 6 and 7 define group C, and homology 8 defines group F. Homologies 27---28---30 transform within groups G---J, where both homologies 27 and 28 define group G, and homology 30 defines group J. Homologies 18---19---20 form a transformation series within the inclusive groups K---L---M, respectively. The development of the internal skeleton forms the sequence: 4---10---5, defining the inclusive groups C---F---P, respectively. The ontogeny of homologies 24---25 forms a sequence from the more general group H to the less general group J. Homologies 23---26 transform from groups G---I, and homologies 2---3 transform within group D. Finally the ontogeny of the sutures develops from a straight depressed sutures into homology 11, a wave-formed sutures defining for group E. The more general condition, straight sutures, defines a much larger group than the Soritidae.

The second mode of development as revealed in diagram 11, is that ontogeny proceeds by divergent development, from a more general group into less general but exclusive groups, or diverges within a

single group. For example homology 1 defines group A, but diverges into homologies 2, 23, and 21, each defining the less general exclusive groups D, G, and M, respectively. It is peculiar to note that homology 21 which defines group M, diverges into homologies 22 and 29, where homology 29 also defines group M, but homology 22 defines group O, inclusive to group M. In the B-form the initial development of the Soritoidea apertures is in the form of a single, ovate to crescentic aperture. This kind of an aperture is of a wide occurrence, defining a much vaster group than the Soritoidea but develops by divergence into groups K and B, defined by homologies 18 and 12, respectively. The ornamentation of the lateral sides is present in the Soritoidea embryo as evenly dispersed pits, defining a much vaster group than the Soritoidea. The evenly dispersed pits then develop by divergence into homologies 9 and 15, each defining groups E and K, respectively. Homology 12, defining for group B, diverges into homologies 27 and 6, each defining the exclusive group G and C, respectively.

The third and the last feature of the development of the Soritoidea test consists of two phenomena. The first is the disparity in the first appearance of 6 independent ontogenetic series. The second is the presence of independent homologies which are ambiguous to incorporate as parts of any of 6 ontogenetic sequences.

The ontogenetic sequences for the apertures, the growth form, and the ornamentation all begin with anatomical structures present in the embryo. Both the ontogeny of the ornamentation and the apertures define homologies defining more general groups than the Soritidae. The ontogeny of the growth form in the B-form generation begins with homology 1. The development of the internal skeleton consists of two independent ontogenies. The development of the septula and the buttresses begin in the post embryonic chambers, each defining groups C and H. The above can be summarized as following. The initial development of each of these 6 ontogenies begins by homologies which can define groups at any level of generality. There are examples of ontogenetic sequences beginning in homologies

defining larger groups and including the Soritoidea. There are also examples of ontogenies beginning with homologies which define subgroups within the Soritoidea.

There are in addition 2 independent homologies, which are ambiguous to include as a part of any of the 5 ontogenetic transformation series. These homologies are 13 and 14 defining group A and F, respectively. Group A is defined by homology 13 which refers to a peculiar type of apertural ornamentation, expressed first in the embryo, and remains unchanged throughout development. In the embryo there are then two kinds of distinct ornamentations, represented as homology 13 and the presence of evenly dispersed pits on the lateral sides of the walls. Both these kinds of ornamentations coexist in the embryo, and therefore no particular succession is observed.

Homology 14 refers to an embryonic structure, the vorhof, defining group F including only 3 species. There are indications that the vorhof develops as an outgrowth of the flexostyle, rather than as a transformed postembryonic chamber. The vorhof in *A hemprichii* and in *M. kudakajimensis* forms a bulbous extension of the flexostyle (fig. 22 b). In few specimens the vorhof is reduced to a slightly inflated swelling at the distal end of the flexostyle (fig. 22 a). The vorhof in *M. vertebralis* appears usually as a distinct structural entity, forming a separate enclosure surrounding the proloculus and the flexostyle (fig. 13 b and c). In at least 17 specimens (6%) I observed a vorhof that is identical to what is commonly observed in *A. hemprichii* and is illustrated in fig. 22 b. Similarly, I observed in at least 23% of the specimens of *A. hemprichii* a vorhof that is similar to what is illustrated in figure 13 b. These findings are assumed to indicate that the vorhof has developed as an enlargement or as an outgrowth of the distal end of the flexostyle, although it forms a distinct structural unit. It is also to be noted that the whole embryo, proloculus, flexostyle, and the vorhof are built out of a single, continuous, calcareous wall, without any traces of sutures between compartments. This may be related to the fact that the embryos are formed within the reproductive chambers of the parent test (Ross,

1972). (The studies of Kloos 1984, suggest for *S. orbiculus* that the proloculus and the flexostyle are formed in two semi-discrete growth steps with short intervals). There are then at least 2 instances of different homologies both appearing in the embryo, where homology 13 defines a group containing all the 18 species under investigation, but the other (homology 14) defines a group containing only 3 species.

The above discussion of the orderliness of ontogeny as discerned within the logic of branching diagrams can be epitomized in following statements.

1) Transforming ontogeny proceeds either by: A) a transformation of homologies defining a more general group into homologies defining any inclusive set of successively less general groups, or B) by a transformation of homologies, all defining the same group.

2) Diverging ontogeny proceeds by either, A) a transformation of a homology defining a more general group into homologies defining a any set of less general but exclusive groups, or B) by forming a divergent transformation sequence of homologies all defining the same group..

3) The ontogeny of organisms in general consists of a number of unrelated ontogenies and unique homologous structures not forming a part of any ontogenetic sequence. These can first appear at any stage of the development of the organism, and define groups at any level of generality.

It is of historical interest to note that the first two of these statements are merely a modification of von Baer's laws (1828). Von Baer formulated his laws as generalizations, concerning the ontogeny of vertebrate homologies, as represented within a dichotomous diagram, containing both exclusive and inclusive vertebrate groups (von Baer 1828, p. 225). It is beyond the scope of this text to discuss

von Baer's views on nature, but for reference his laws are here reproduced.

> "1) The commonness of the larger animal groups is formed in the embryo before the particularity."
> "2) From the most general form-conditions the less general are formed and so on, until the most special occur."
> "3) Every embryo of some definite animal form, instead of passing through other definite animal forms, rather diverges from these animal forms."
> "4) In all basis, it is not so that the embryos of the higher animal forms are like other adult animal forms, but are like the embryos." (von Baer 1828, p.224, translated)

Garstang (1922), in an influential paper, reiterated the validity of von Baer's laws, and argued for a parallelism between ontogeny and phylogeny, stated as the following:

> "Ontogeny proceeds through successive *grades of differentiation* by which layers, tissues, organs, and parts together with ordinal, family, generic, and specific characters, are more or less successively established. As differentiation increases, the combination of layers, tissues, organs, and parts, exhibited at successive stages resembles more or less distinctively the combinations characteristic of the successive *grades of evolution* represented in our scheme of phyletic classification. To that limited extent the ontogeny of a given animal is an epitome of its phylogeny, i. e. to sum it up, recall the main phases of it. This is the parallelism observed by Meckel, Von Baer, and many others expressed in evolutionary terms. It exists and is undeniable. (Garstang 1922, p. 84, italics in original).

Curiously Garstang (1922) echoes von Baer's criticism of the old recapitulation doctrine, which Meckel advocated among others . This criticism is embedded in von Baer's 3rd and 4th laws, but in Garstang's article the criticism is directed instead against Haeckel's recapitulation thesis, and his distinction among palingenetic and

cenogenetic characters. Garstang (1922) also argued that during phylogeny, all stages of an organismic lifecycle (from embryos through adults) are subject to evolutionary additions of anatomical features, transformation, and eliminations alike. To some extent, Garstang had the mistaken perception of ontogeny and homologous features, as forming a "more or less" chaotic assemblage. Different ontogenetic sequences and homologous features may seem unrelated or random, when each is examined in isolation as is exemplified in diagram 11. However when ontogeny and homologies are analyzed within the logic of branching diagrams a consistent regularity emerges, which otherwise is obscured. This is epitomized in my 3rd statement and might be referred to as Garstang's law.

The thesis that there exists a parallelism between ontogeny and phylogeny has had a long and tortuous history. It was first coherently put forward by Fritz Müller in 1864, and later elaborated on by Carl Gegenbaur. The most notorious popularizer of this notion of parallelism was Ernst Haeckel, who argued that phylogeny is the mechanical cause of ontogeny, and therefore that ontogeny recapitulates phylogeny, formally termed as the biogenetic law. Garstang (1922) also argued that ontogeny recapitulates phylogeny, but in contrast to Haeckel, because ontogeny causes (or creates) phylogeny. Regardless of idle speculations about cause and effect, the thesis of a parallelism between ontogeny and phylogeny can be restated as the following. In a given ontogenetic sequence the homologous features appear in the same order as in the course of phylogeny. In diagram 10 ontogeny always proceeds from a more general groups to a less general, never in the reverse direction. In a phylogenetic context it has been stated that the features defining the more general groups are primitive, and the less general groups are defined by derived features (Nelson and Platnick 1981, p.332). (In this context it is irrelevant that in certain instances some embryonic features can reoccur (or persist) in adults, a phenomena sometimes referred to as "atavism". The first appearance of the homologies always occurs in a definite sequence).

It has been the desire of all systematists who have dealt with the Soritoidea, to infer the phylogenetic scheme; to some it has been the ultimate end in itself. Hofker's phylogenetic scheme (diagr. 6) is an example of such an endeavor. In this scheme the branching points refer to speciation events and the length of the lines refer to the relative age of the evolving units. In this practice of inferring phylogeny, fossils have always played an essential role, to provide information on relative age of species. Traditionally fossils have in this context been utilized to restrict the number of possible speciation events. Given a complete fossil record, a younger species can never be hypothesized to be an ancestor of an older species, nor can an older fossil be an ancestor of a younger species if these never co-occur in time. All this may seem self-evident and as such the fossil record prescribes information on how the succession of phylogeny did not proceed rather than on how it did proceed, and serves merely to reduce the number of possibilities. Thus, any species observed to be older and co-occurring with any number of other species can be hypothesized as an ancestor of the younger descendants. Within these restrictions prescribed by fossils, comparative morphology and ontogeny have been interpreted to supply evidence of speciation events, as actual ancestor-descendant relations.

In comparison to what is said in the above paragraph, a slightly different approach is adopted here to interpret diagram 10. The information that is used to define branch points in diagram 10 is based on homology statements, which by definition are merely interpreted to reflect a common ancestry, not speciation events. Further, ontogeny adds the time dimension to diagram 10, where the homologous structures are observed to change in accordance with a regular transformation pattern. The combined information derived from homologies and ontogeny might invite the notion that diagram 10 is a phylogenetic scheme, where the lines indicate evolutionary linages and the branching points are speciation events, representing dichotomous splittings of species. This is not so, because the only

elements of knowledge contained in diagram 10 are summary of homologous structures present in certain species groups and the succession of these homologies as observed during ontogeny, nothing else. The fact that the distribution of homologies can be summarized in a dichotomous diagram hardly proves the conclusion that only dichotomous speciation events occurred. There do exist numerous speciation mechanisms other that dichotomous splitting, that could produce a pattern of homologies representable in a dichotomous diagram.

The thesis that there exists a parallelism between ontogeny and phylogeny (the biogenetic law), provides a basis for predicting that a complete fossil record should display the same succession of morphological forms in the sediments as is observed in ontogeny. As I discussed earlier, ontogeny can proceed either by simple transformation or by divergence. Transforming ontogeny is characterized as a succession of forms from (or within) a more general group to less general groups. Predicting the relative fossil age of species, within a set of inclusive groups is unambiguous. The species contained within the more special groups are predicted to be younger than the species only included within the more general groups. Thus, in diagram 10, the species within groups F should be younger than the species included in group E, etc.. Application of the thesis of parallelism within a set of inclusive groups makes it possible to sequence diagram 10 into species linages, indicating a prediction of the order of appearance of these species in the sediments. This is displayed in diagram 12, where individual lines indicate species linages, and the proximity of different lines merely indicates the general relation of common ancestry, as evidenced by homologous structures.

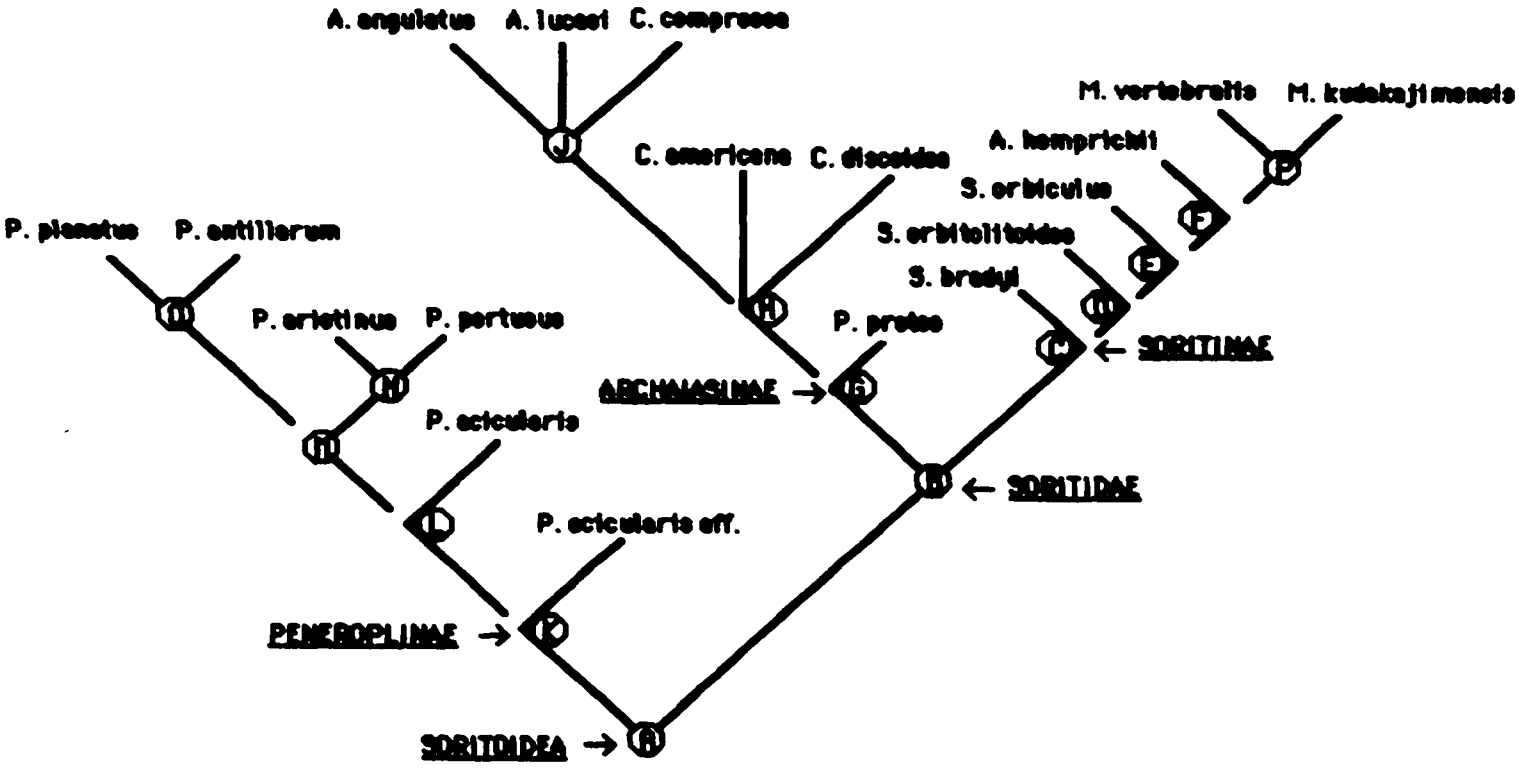


Diagram 12. A prediction of the relative fossil age of the 18 species, assuming that ontogeny and phylogeny form a parallel sequences of forms in time.

The information that can be extracted from diagram 12, is for example that *S. bradyi* is expected to appear earlier in the sediments than *S. orbitolites*, and that these share a common ancestry, an assertion that can be true even if these species do not co-occur in the sediments. As an example, this statement is concordant and independent of a discovery of a new species X which is more closely related to *S. orbitolites* than to *S. bradyi* and of an intermediate age. However if were asserted that diagram 12 indicates that *S bradyi* is the actual ancestor from which *S. orbitolites* speciated, then the discovery of a species X, would call for an emendation of the speciation scenario, which would become:
S. bradyi is the ancestor of species x, which in turn is the ancestor of *S orbitolites*. In addition to the 18 species in diagram 10, there exists a vast diversity of fossil Soritoidea forms such as the subfamily Meandropsininae and *Orbitolites*, not yet analyzed and integrated into diagram 10, producing a much more complex diagram. This renders it untenable to interpret branching points as indicating ancestor-descendant relationship, resulting in countless changes of speciation scenarios, each time a new species is described and included in diagram 10. Instead branching points are better interpreted as the more general notion of a common but unspecified ancestry, and in addition ontogeny is extrapolated to form a basis to predict succession of forms in time, devoid of all speciation assumptions.

Diverging ontogeny is characterized as transformation from (or within) a more general group to an exclusive set of less general groups. Group M includes two exclusive groups O and N. There is a divergent ontogeny within this group set, proceeding from homology 21 (group M) to homology 22 (group O) and to homology 29 (group M). This serves as a basis to predict that the species in group O occur later in the sediments than the remaining species included in group M, which are incidentally both included in group N. There is no

ontogenetic transformation proceeding from group A to the exclusive groups K,and B, and therefore no particular species age succession is defensible among the species *P. acicularis* aff., *P. protea* and *S. bradyi*. For the species contained in group P, ontogeny does not suggest any particular succession, either *M. vertebralis* precedes *M. kudakajimensis*, or vice versa. The same applies to the species in groups N, O, H, and I.

To conclude, it is to some extent possible to predict the order of the first appearance of these 18 species in the fossil record, by assuming the validity of the "biogenetic law." This inference or prediction of species age succession is unproblematic where ontogeny proceeds by simple transformation within an inclusive set of groups, from a more general to any less general group. However, in some instances there is no ontogenetic transformation detected, and therefore no objective basis to predict any particular fossil sequence.

The species in diagram 10 are all extant, and exist relatively unchanged back into the fossil record. This information on absolute (or relative) age of these species would serve as a basis for testing the concept of a parallelism between ontogeny and the order of first appearance of fossils, as forming congruent sequences. It is instructive in this context, to realize the immense number of possible fossil sequences that might be observed when the fossil record is examined. To state the question formally, for any number of N species, in how many ways can it be expected to observe the first occurrence of these N species. If it is assumed that all the N number of species are of a different age then the total number of fossil sequences (F.S.) is given in formula 3. Under these conditions F. S. = 6.4×10^{15}, if N = 18, a quantity beyond any tangible comprehension.

$$F.S. = N! \qquad \text{Formula 3}$$

Consider the possibility that some of the species can be of the same age, or that groups of 2, 3, 4, 5,....N, species are of the same age. Then

In addition to formula 3, there exist other possible fossil sequences enumerated by formula 4. N stands for the number of species and r is the portion of those N species which are of the same age. I do not know if this has been noted before.

$$F.S. = \sum_{r=2}^{N} [((N+1)-r))! (C(N,r)] \qquad \text{Formula 4.}$$

Thus, for 18 species the number of possible F. S. is increased to the order of 10^{16}, and it is still left to take into account the possibilities when there are more than one species groups, each of a different age. Given that only one fossil sequence is correct, the number of possible mistaken sequences is immense.

Regardless of this colossal number of possibilities, it is instructive to note that there exists only a limited number of fossil sequences that can be integrated or superimposed on diagram 10. In addition to the fossil succession specified in diagram 12, there are several other fossil sequences left unspecified.

1) There are two possibilities included in group P, either *M. vertebralis* is older than *M. kudakajimensis* or the reverse is true. Similar applies to the species within groups O, N, H,

2) Within group J, one of these three species is older than the other, but the remaining two should be of an equal age to be concordant with the diagram, i. e. 3 possibilities. However, assuming the validity of the ontogenetic transformation of homology 24 to 25, *C. compressa* is expected to be the youngest of the 3 species included in group I, and the remaining two species are older.

3) For the species *P. acicularis* aff., *P. protea* and *S bradyi* there is no particular fossil sequence specified. It should be noted that in general for any 3 species there are according to formula 4, 13

different possible fossil sequences, but only 6 of these possibilities can be integrated in accordance with groups A and B. In other words the structure of the diagram, which in this instance is specified by groups A and B, imposes restrictions to the number of possible fossil sequences which can be sensibly integrated into the diagram. Presently I am not able to formulate exactly these restrictions. However, considering preliminarily only those fossil sequences for N species where each species is of a different age then there exist N! possible fossil sequences. Given further that the relationship of these N species is specified in a fully resolved diagram, containing only a set of N-1 inclusive groups, then there are exactly $(2)^{N-1}$ fossil sequences which can be integrated into the diagram in accordance with the groups. In other words, there are exactly $(2)^{N-1}$ ways to draw such a diagram by using exactly N number of lines, where each line corresponds to one of the N species. Then, the probability that the age succession as specified in the fossil record can be successfully integrated into such diagrams by chance alone = $(2)^{N-1}$ / N!, practically a zero probability if N > 8. If the systematic relationship is specified by exclusive groups in conjunction with inclusive groups, then this increases the number of fossils sequences that can be integrated into the diagram. This increase seems to be inversely proportional to the reduction in the maximum level of hierarchy, as exclusive groups are introduced into the diagram. A maximum level of hierarchy for a fully resolved diagram is specified by a set of N-1 inclusive groups. A minimum level of hierarchy for a fully resolved diagram is specified by a maximum number of exclusive groups).

It is a tremendous and difficult task to determine the age of the species, as these are defined and described in diagram 10. Reliance on mere descriptions from the literature can be misleading, partly because of disparate usage of species names, and because the descriptions do not always accurately reflect the structure of the

specimens. Accurate determination of the species age should rely on examination of actual specimens from the sediments. Another concern is the integrity of the fossil record, which is a prerequisite for any sound test of the thesis of a parallel succession of forms as observed in ontogeny and in the sediments. The literature abounds in assertions of the truth or the falsity of this thesis. One source of objection of the fallacy of the concept of parallelism, has been based on the fact that embryos evolve and change (Garstang, 1922). However, as I have attempted to demonstrate, embryonic evolution does not necessarily contradict the concept of parallelism between ontogeny and fossils. I have argued that if the concept of parallelism is true, then the general features defining the larger groups are expressed early in ontogeny and will also be present in species appearing early in the fossil record. It is also true that the less general features are present at all developmental stages, both in embryos and adults, and that these features will occur in species of a more recent age. Therefore, a phylogenetic introduction of novel features in embryos does not necessarily invalidate the notion of parallelism.

The famous thesis of proterogeny, as revived by Schindewolf (1936), has been another source of objection. This notion of proterogenesis postulates that the succession of forms as observed in the sediments, is in a reverse order to what is observed in ontogeny. Schindewolf's claim relies partly on the succession of fossils, as compared with ontogeny. One line of evidence which Schindewolf utilized to support his case relied on a comparison of fossil succession and ontogeny in certain Miliolid Foraminifera. This was later criticized for relying on erroneous stratigraphy and reinterpreted in the sense of Haeckel's palingenesis, as a parallel succession of ontogenetic forms and fossils (Wood and Barnard, 1947). I can not assess this thesis of proterogenesis within the Soritidae, since I have not studied fossil material but a preliminary survey of the literature is suggestive of the validity the concept of a parallelism.

The Soritoidea are known to be hosts of a variety of symbionts, and these have lately been an intense focus of research. It has been postulated that the major force in the morphogenesis of the Soritoidea is driven by this endo-symbiotic relationship (Lee et al 1979, Leutenegger 1984, Lee and Hallock 1987). The large size and more than 98% occurrence of the A-form generation, especially within the Soritinae, suggests presumingly asexual reproduction as the most frequent mode, where the symbionts are transmitted between generations by cytoplasmic inheritance. (Lee, pers. comm.). It is interesting to note that there are three different groups of endo-symbionts found within the Soritoidea, each confined to one of the three soritid subfamilies, the Peneroplinae, the Soritinae, and the Archaiasinae (see diagr. 12). The only symbionts reported to occur among the Peneroplinae belong to Rhodophyceae (*Porphyridium purpureum*), (Kremer, et. al. 1980). The only symbionts that have been reported in association with the Archaiasinae species belong to the Chlorophyceae (*Chlamydomonas hedleyi*, and *Chlamydomonas provasolii*) (Lee, et. al. 1979). The only symbionts known from within the Soritinae belong to the Dinophyceae (*Symbiodinium microadriaticum*, *Gymnodinium obesum*, *Gymnodinium rotundum* and *Amphidinium* sp.) (Lee, et. al. 1979, and Lee and Lawrance 1989.). The systematic relationship of these diverse symbionts is still to be analyzed. It is interesting to note that *Puteolina proteа* hosts chlorophycean symbionts as the other Archaiasinae (Leutenegger, 1984), which is in agreement with the anatomical affinity of this species with the Archaiasinae, and contradicts further the placement of *P. proteа* within the Peneroplinae, based on the absence of an internal skeleton.

To conclude, there are strong indications that the distribution of similar symbionts is in agreement with the groups which are specified in diagram 10 and 12, by groups K, G, and C. This invites the interpretation that the explanation of this distribution is related to the common ancestry of these species groups.

In this last and concluding chapter I have discussed several different elements of knowledge, as derived from comparative anatomy (homology), the ontogeny of these, the geological age of species, the distribution of symbionts, and to a limited extent mentioned the geographical distribution of the Soritidae subgroups. It seems that all these diverse kinds of observations can be integrated and embraced within a single analytical expression, as structural elements of a branching diagram. The resulting diagram serves as a basis to evaluate the probability that future discoveries can be integrated into the diagram. The diagram can also be used, to some extent, to make definite predictions about future observations. Not the least the diagram serves as a basis for realizing the interconnections of all these diverse elements of knowledge, as examples of a few general relations or natural laws, which makes it possible to understand the fabric of biotic diversity.

Figures 1 - 4, schematic illustrations.

Figure 1 (p. 125).

a) A schematic drawing illustrating a test growing in a planspiral and lenticulate mode. The test is evolutive since all the chambers of the test can be viewed from the outside.
b) A schematic drawing of an involutive growth mode of the planate-type, where the chambers extend towards the umbilicus of the test in almost a single plane .

Figure 2 (p. 126).

A schematic drawing of a test in an equatorial section, illustrating development of growth forms, beginning as planspiral, then rectilinear, then flabelliform and finally annular series. Dotted lines indicate an apertural face and solid lines indicate chamber walls.

Figure 3 (p. 127).

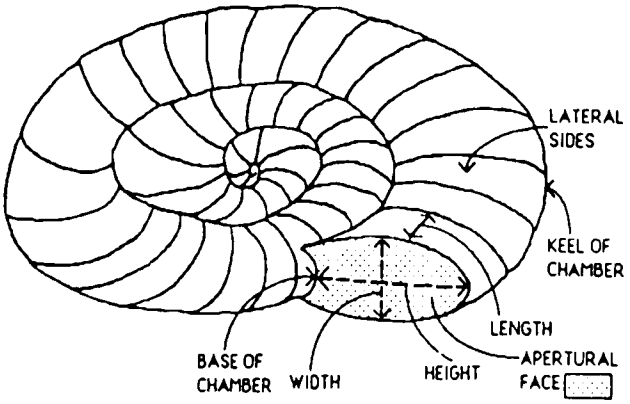
A simplified schematic illustration of pillars and buttresses. The figure shows apertural faces of two succeeding chambers, where the apertural face of the top chamber has been partially removed to show the internal skeleton of buttresses and pillars, characteristic of the Archaiasinae.

Figure 4 (127).

A simplified schematic illustration of septula, characteristic of the Soritinae (*Sorites orbiculus*). The figure shows apertural faces of two succeeding chambers, where the apertural face of the top chamber has been partially removed to show the transversely oriented septulum, located directly below the apertures. The stolon is an opening in the septula, always located directly below the aperture.

Figure 1

a


LATERAL SIDES
KEEL OF CHAMBER
LENGTH
APERTURAL FACE
BASE OF CHAMBER
WIDTH
HEIGHT

b

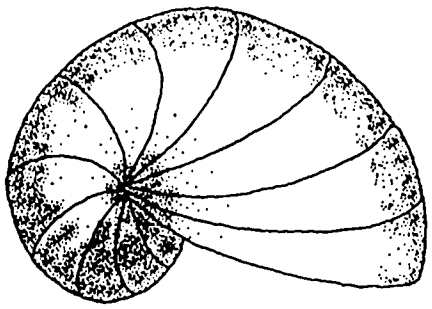


Figure 2.

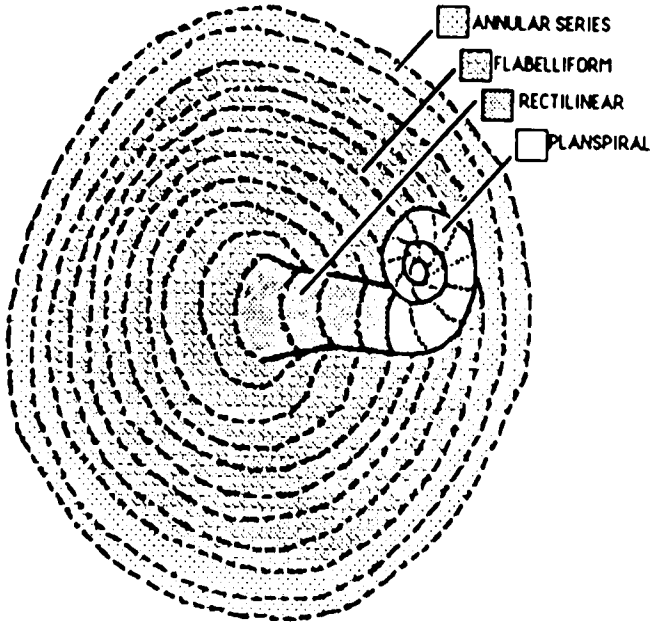


Figure 3.

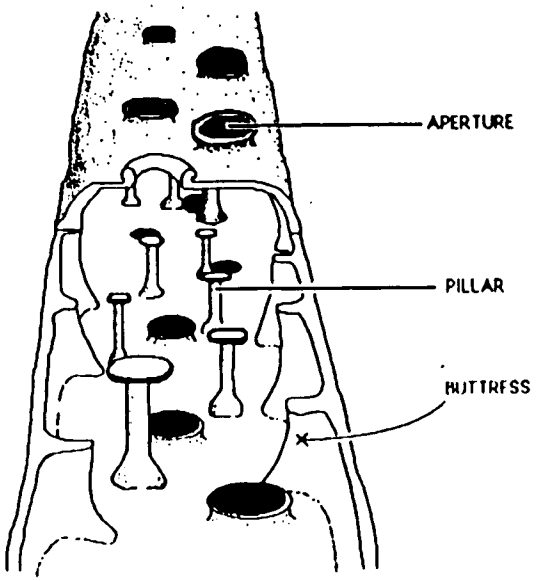
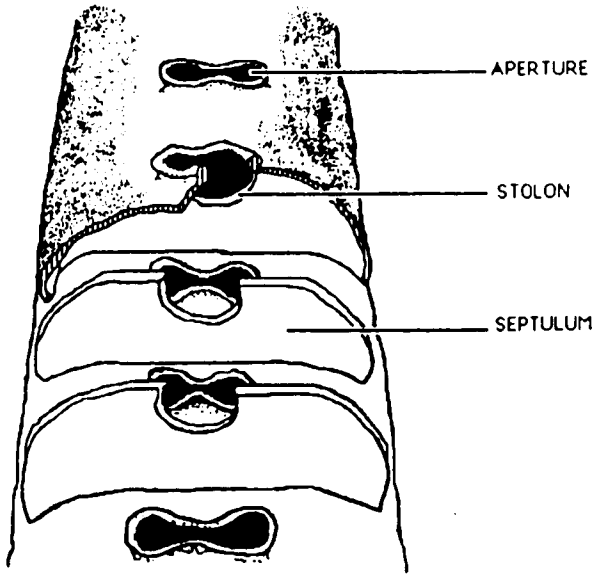


Figure 4.



Figures 5 - 12, *Sorites orbiculus*(Forskål 1775)

Figure 5 (p. 131).

General view of *Sorites orbiculus* var. *marginalis*, from Taba, Red Sea (AMNH 43826,1).
a) Lateral view.
b) Apertural view.
General view of *Sorites orbiculus*, from Taba, Red Sea (AMNH 43854). c) Lateral view.
d) Apertural view.

Figure 6 (p. 132).

a) The A-form embryo of *Sorites orbiculus* formed of a proloculus (P) and a flexostyle (F) (AMNH 43849,2).
b) The B-form of *S. orbiculus* var. *marginalis* (AMNH 43831). Proloculus and the first 13 chambers are devoid of internal skeleton, growing in a typical evolutive, lenticulate, and planspiral mode.

Figure 7 (p. 133).

An equatorial section of *S orbiculus* var. *marginalis*(AMNH 43855,1). The figure shows a part of 6 succeeding annular chambers from the adult growth stage, illustrating the typical hexagonal arrangement of the chamberlets. The septula, containing the stolons, are always located inserted directly between two apertures of the immediate preceding chamber. R is a normal hexagonal chamberlet connected to 6 other chamberlets. A is an auxiliary chamberlet connected to 5 other chamberlets. B is a chamberlet with an auxiliary aperture, connected to 7 other chamberlets.

Figure 8 (134).

An axial section of *S orbiculus* var *marginalis* (AMNH 43855,2). The figure shows 7 - 8 chambers in cross section. Because of the hexagonal arrangement of the chamberlets this section cuts through the septula of every other chamber. The septula are always located directly underneath the apertures, forming an aperture-stolon complex (see also fig. 4).

Figure 9 (p. 135).

S orbiculus var *marginalis*, from Taba, Red Sea. Figures a-d show apertural development in a single specimen of the A-form.

a) The 1st chamber following the embryo.

b) Apertures in the 10th chamber.

c) Apertures in the 17th chamber.

d) Apertures in the 24th chamber beginning to form double marginal rows. The auxiliary aperture opens directly into the lumen of the chamberlet and is not associated with a septulum.

Figure 10 (p. 136).

A dissected specimen, showing the embryo, the first, and a part of the second chamber, showing the ornamentation of the embryo and the initial form of the apertures.in *S orbiculus* var *marginalis*, from Taba, Red Sea (AMNH 43855,3).

Figure 11 (136).

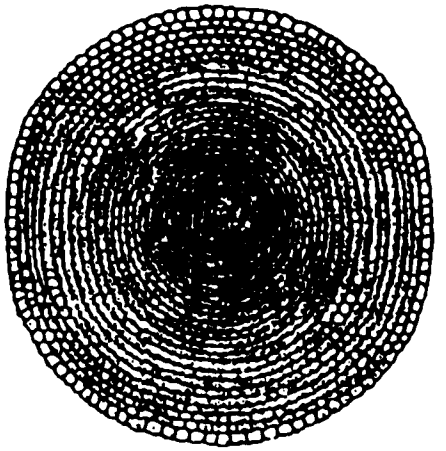
S orbiculus from Taba, Red Sea (AMNH 43854). Ornamentation of the lateral sides of adult chambers, forming a pitted surface along with irregularly fused grooves.

Figure 12 (p. 137).

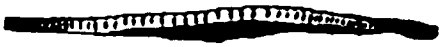
a) The ornamentation of apertural face of forming elongated and fused pits, longitudinally arranged on the apertural face. Specimen belongs to *S orbiculus* var *marginalis*, from Taba, Red Sea (AMNH 43856,1).

b) The ornamentation of the apertural face of an adult chamber, showing elongated and fused pits arranged longitudinally, and radially around the apertures. Specimen belongs to S. *orbiculus* (AMNH 43856,2),

Figure 5.



a.



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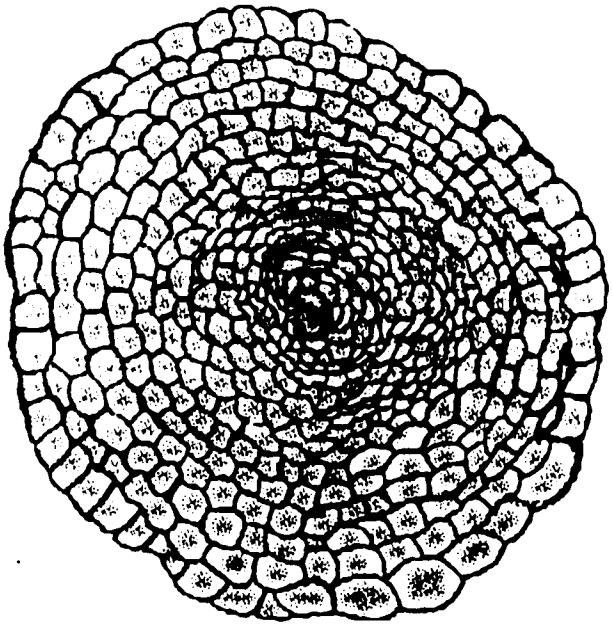

c.

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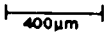
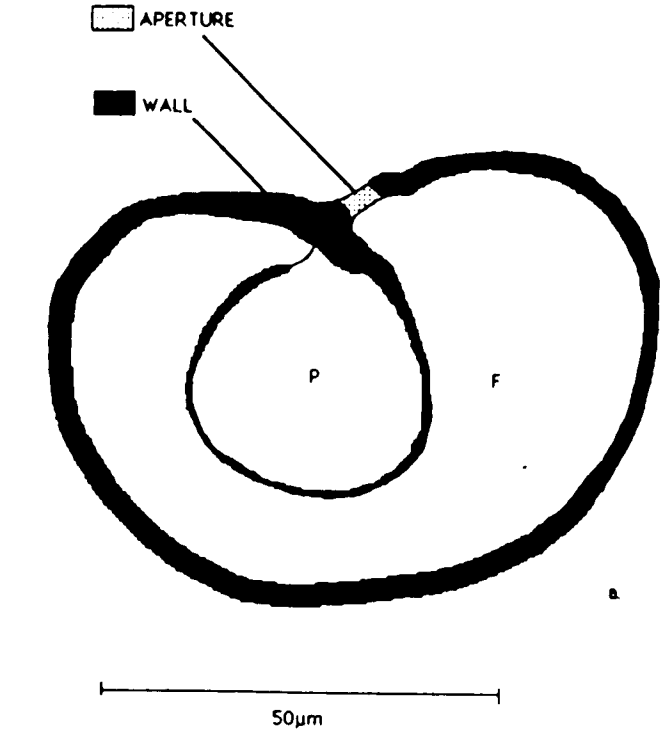


Figure 6.



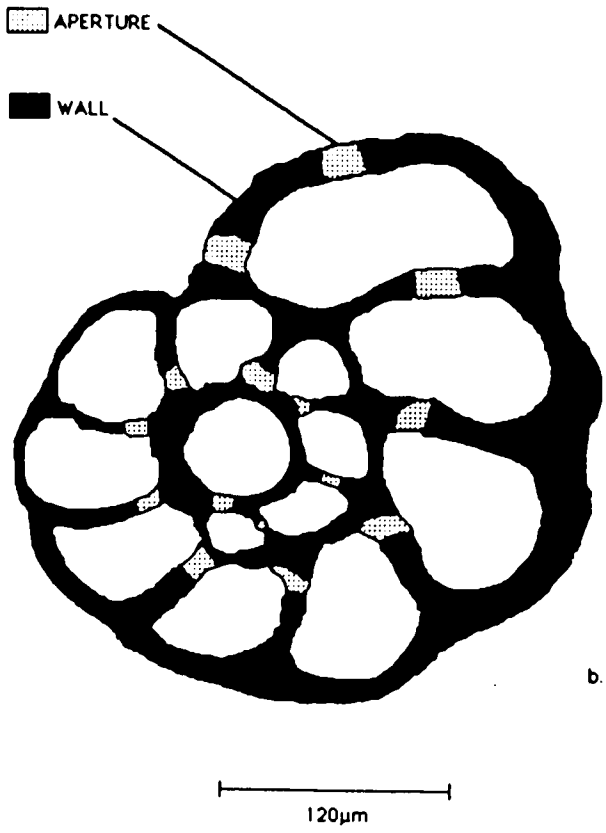


Figure 7.

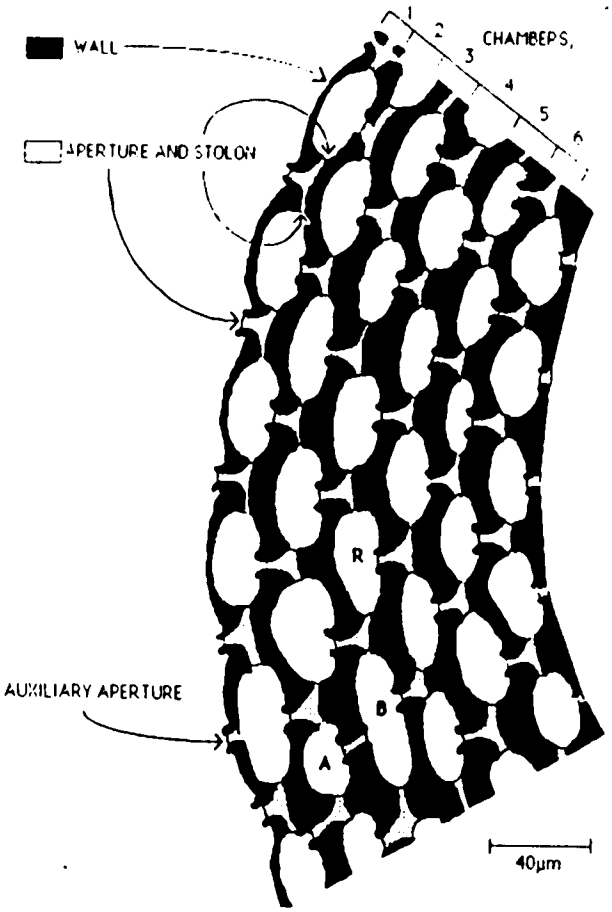

WALL
APERTURE AND STOLON
1
2
3
4
5
6
CHAMBERS
R
B
A
AUXILIARY APERTURE
40µm

Figure 8.

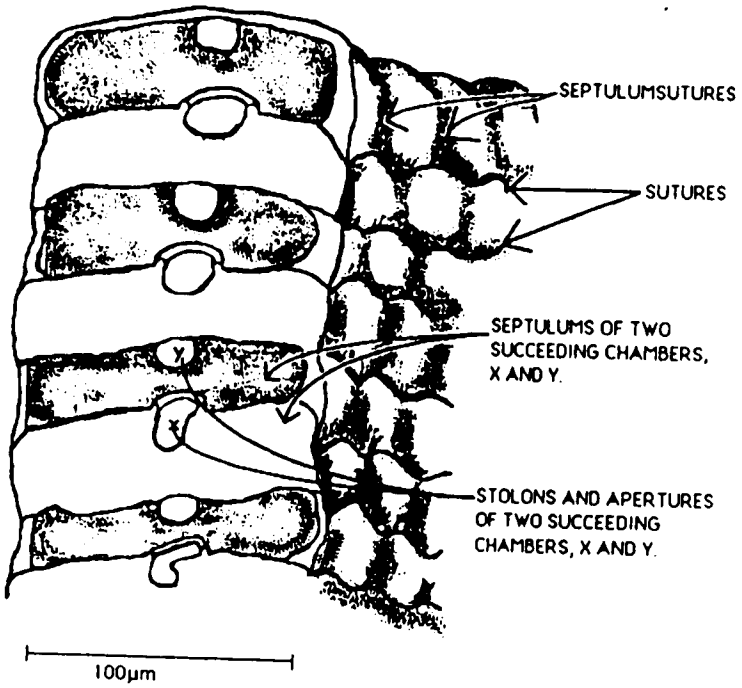

SEPTULUMSUTURES
SUTURES
SEPTULUMS OF TWO SUCCEEDING CHAMBERS, X AND Y.
STOLONS AND APERTURES OF TWO SUCCEEDING CHAMBERS, X AND Y.
100µm

Figure 9.

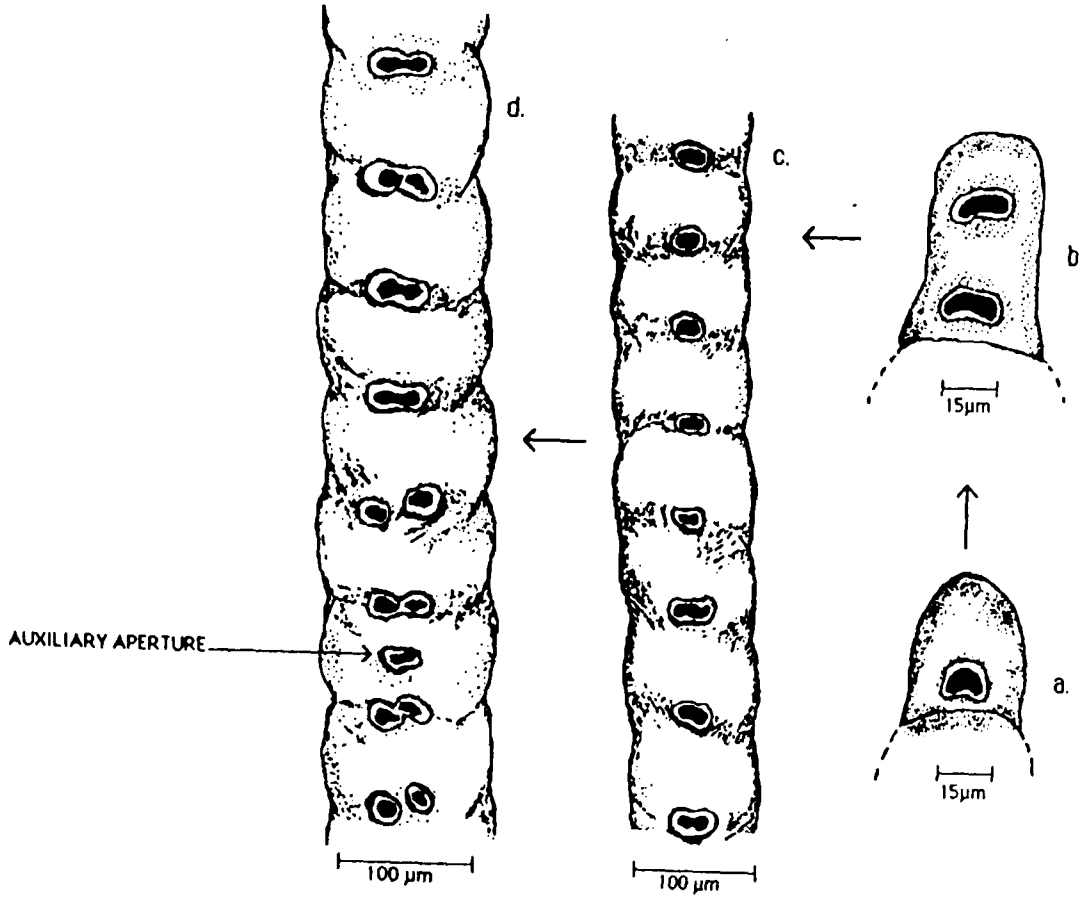


Figure 10.

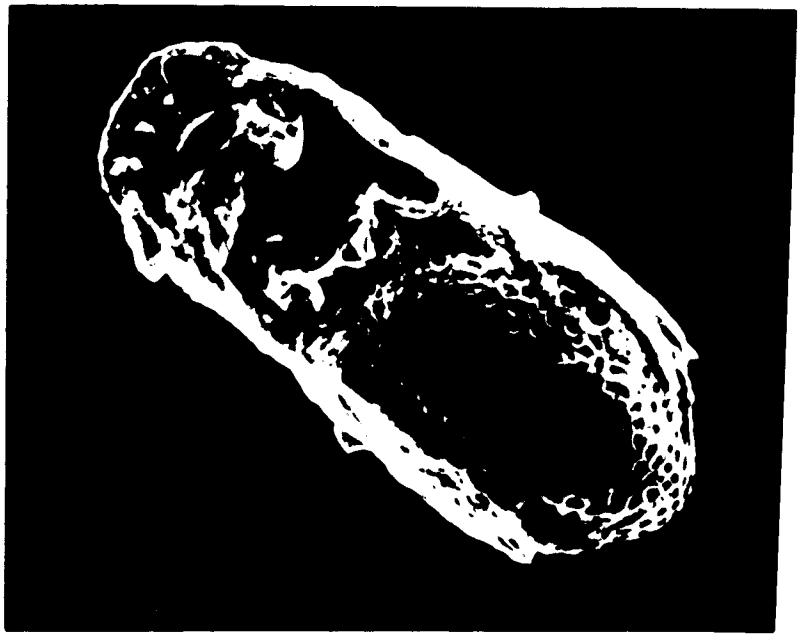


Figure 11

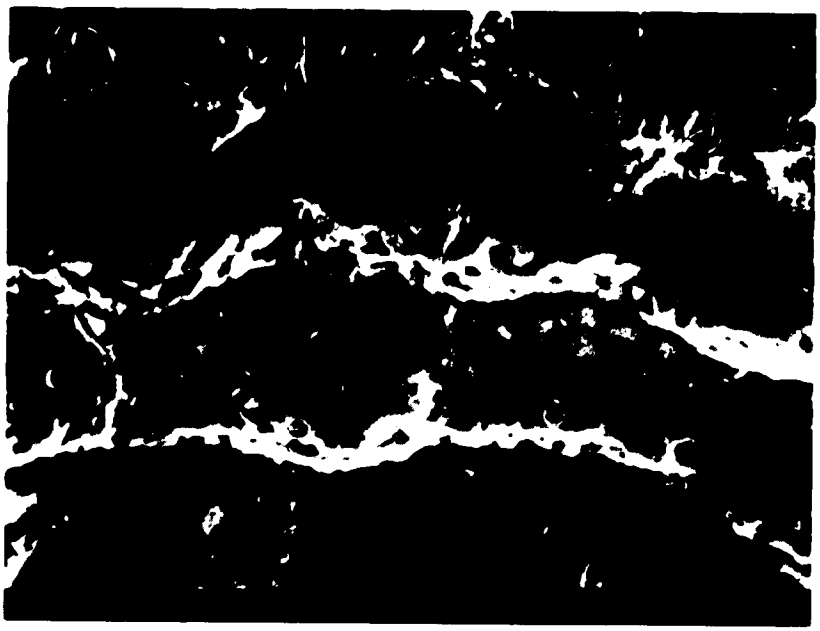
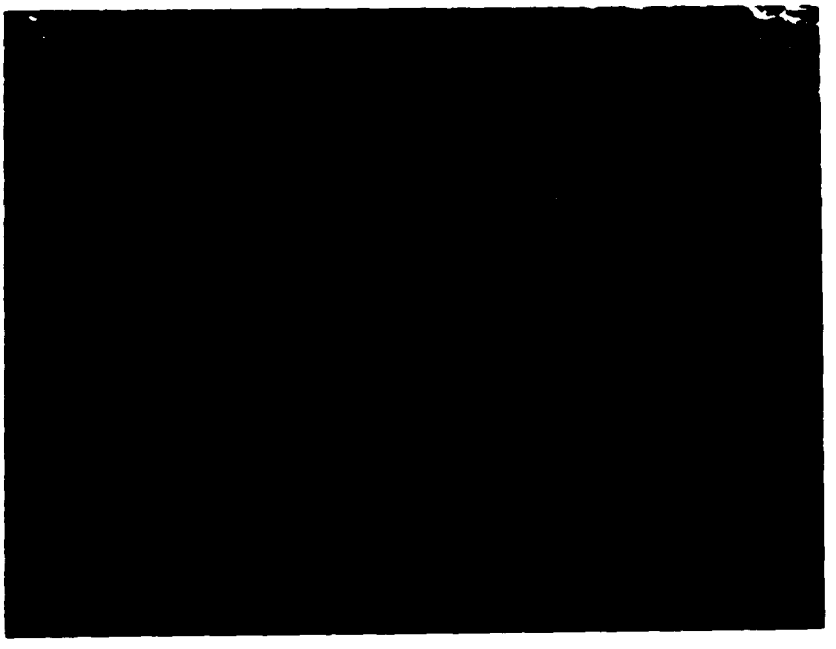


Figure 12.

a.

b.



Figures 13-21, *Marginopora vertebralis* Blainville, 1830

Figure 13 (p.141).

Embryos in horizontal and equatorial section.

a) The B-form embryo consisting only of the proloculus (P), followed by 8 chambers in a typical evolutive, planspiral, lenticulate, growth form (AMNH 43769).

b) An A-form embryo, constructed of a proloculus (P), a flexostyle (F) and a rather small vorhof (V) (AMNH 43771)

c) Another A-form embryo with a large and typical vorhof (V) (AMNH 43770).

Figure 14 (p. 142).

Marginopora vertebralis, from Heron Island, (AMNH 43772).

a) A lateral view.

b) An apertural view.

Figure 15 (p.143).

Apertural development in *M. vertebralis*. Specimens are from The Great Barrier Reef, off Heron Island. Figures a, b, and c are from a B-form specimen.

a) An aperture in the 4th chamber.

b) Apertures in the 8th chamber.

Figures e, d, f, and g are from another specimen of the A-form.

e) Apertures in the vorhof.

d) Apertures in the 2nd chamber, identical to the apertures in about the 18th to 21st chamber.of the B form.

f) Apertures in the 5th chamber, beginning to form the median apertures.

g) Apertures in about the 25. chamber, forming a broad segment of median round to ovate apertures.

Figure 16 (p. 144).

An axial section of an A-form, showing the initial development of the internal skeleton. The first 4 chambers possess a simple septulum with a single stolon, the annular canal, with the exception of the septulum shown in the 2nd chamber showing a triple stolon. The 5th and the 6th chamber show a duplex plan of disjunct partitions. In the 7th chamber and onwards the complex plan develops with the typical median skeleton.and a pair of annular canals run bilaterally (AMNH 43773).

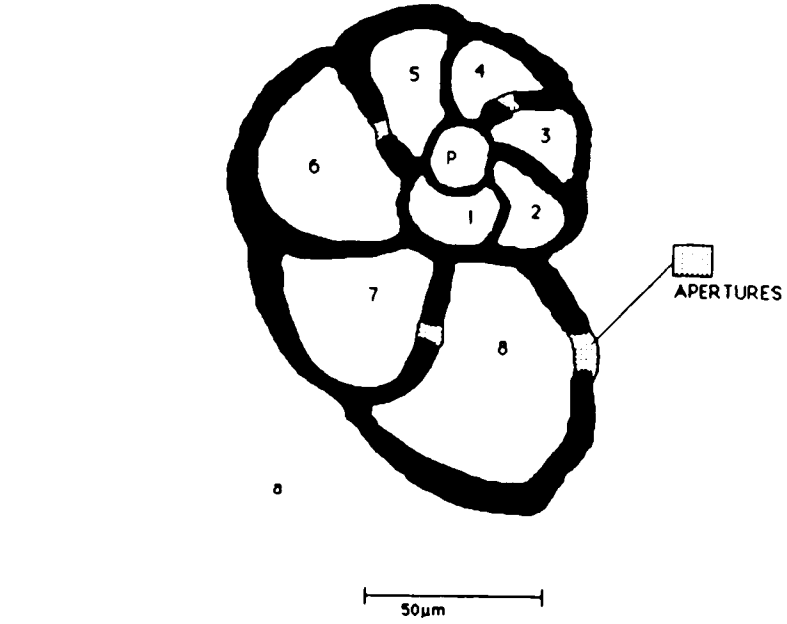
Figure 17 (p. 145).

A reconstructed image of the internal skeleton.
a) An apertural and oblique view, where the apertural face of one chamber has been partly removed to show the median skeleton which consists of transversely oriented septa, partly anastomosing. The surface chamberlets are confined to the margins of the chamber. Based on specimens AMNH 43774.
b) A reconstructed axial section of another specimen showing the internal skeleton of 10-11 adult chambers. Based on specimens AMNH 43773.

Figure 18 (p. 146).

Lateral view of the surface chamberlets, where 6 chambers have been opened to show the two pathways connecting each chamberlet to the other compartments of the test, the tubules and the marginal apertures (From the largest specimen on stub no. AMNH 43774).

Figure 13.


S
4
3
P
6
1
2
7
8
APERTURES
a
50µm

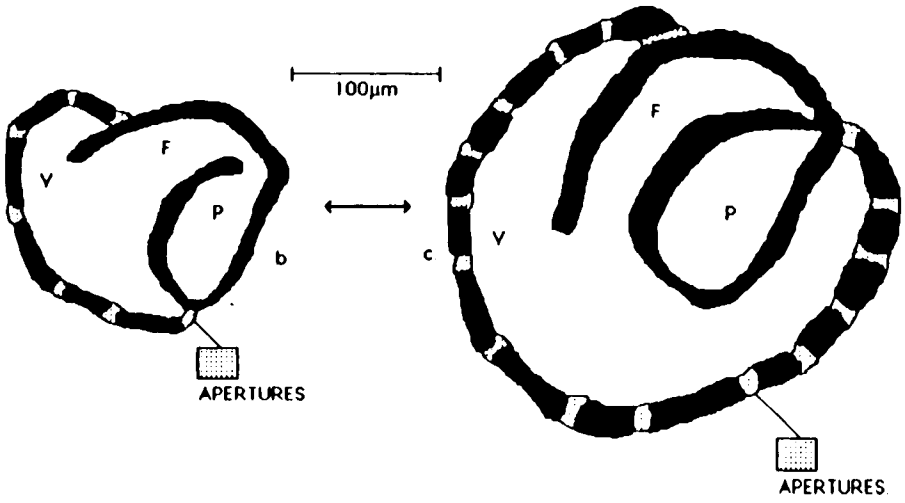

100µm
F
V
P
b
c
F
P
V
APERTURES
APERTURES

Figure 14.

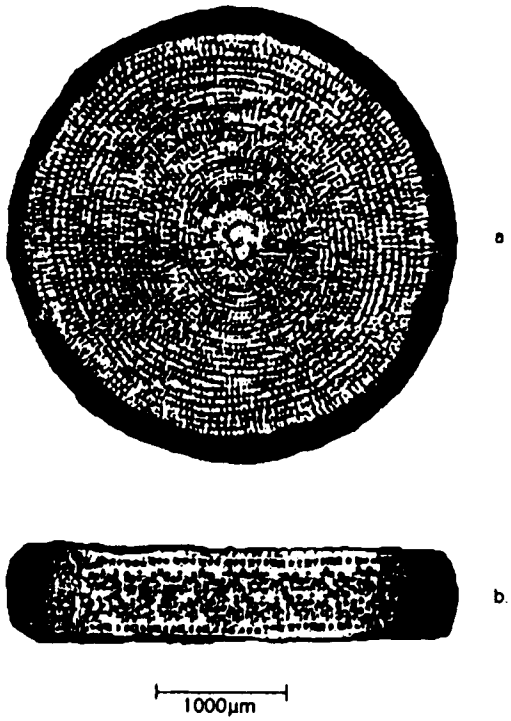


Figure 15.

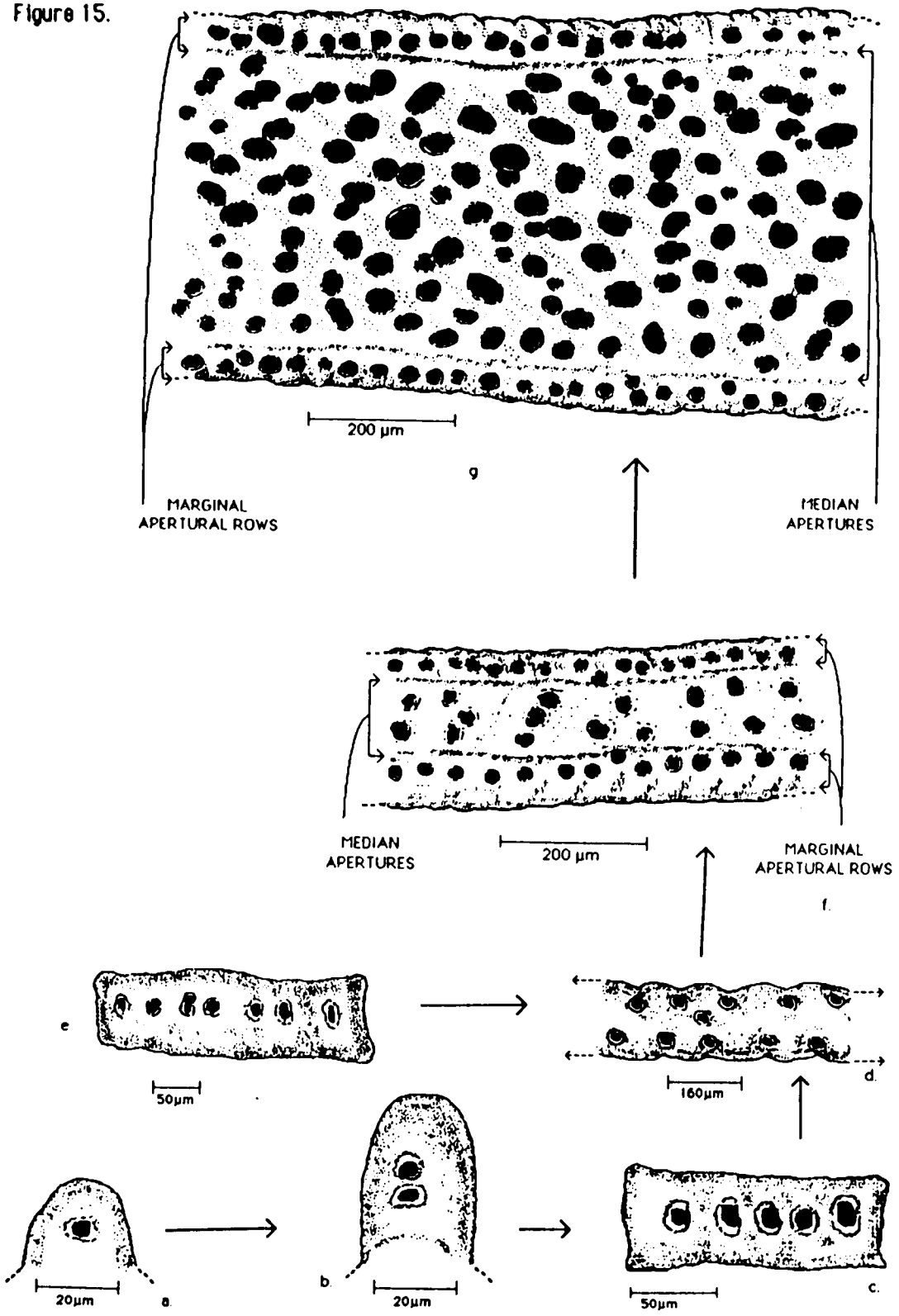

200 µm
g
MARGINAL APERTURAL ROWS
MEDIAN APERTURES
MEDIAN APERTURES
200 µm
MARGINAL APERTURAL ROWS
f.
e
50µm
160µm
d.
20µm
a.
b.
20µm
50µm
c.

Figure 16.

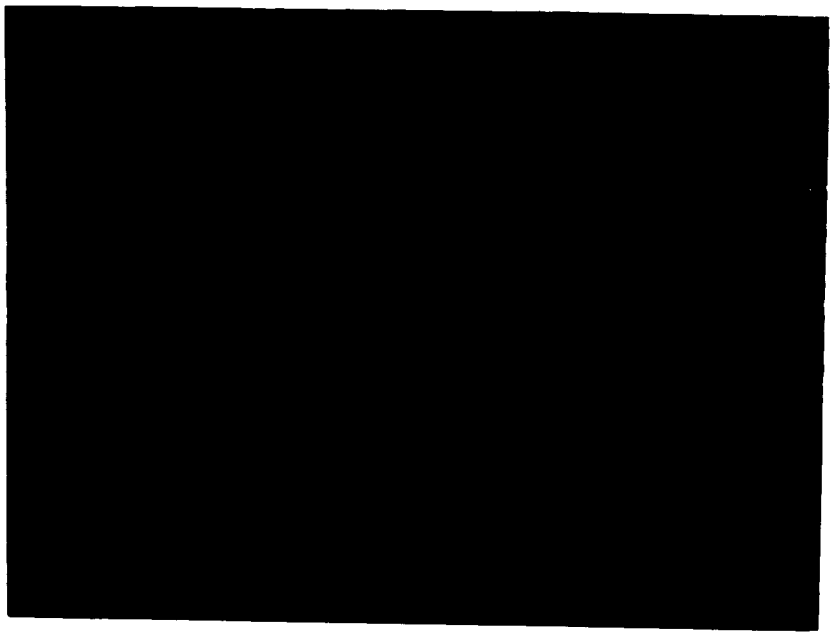


Figure 17.

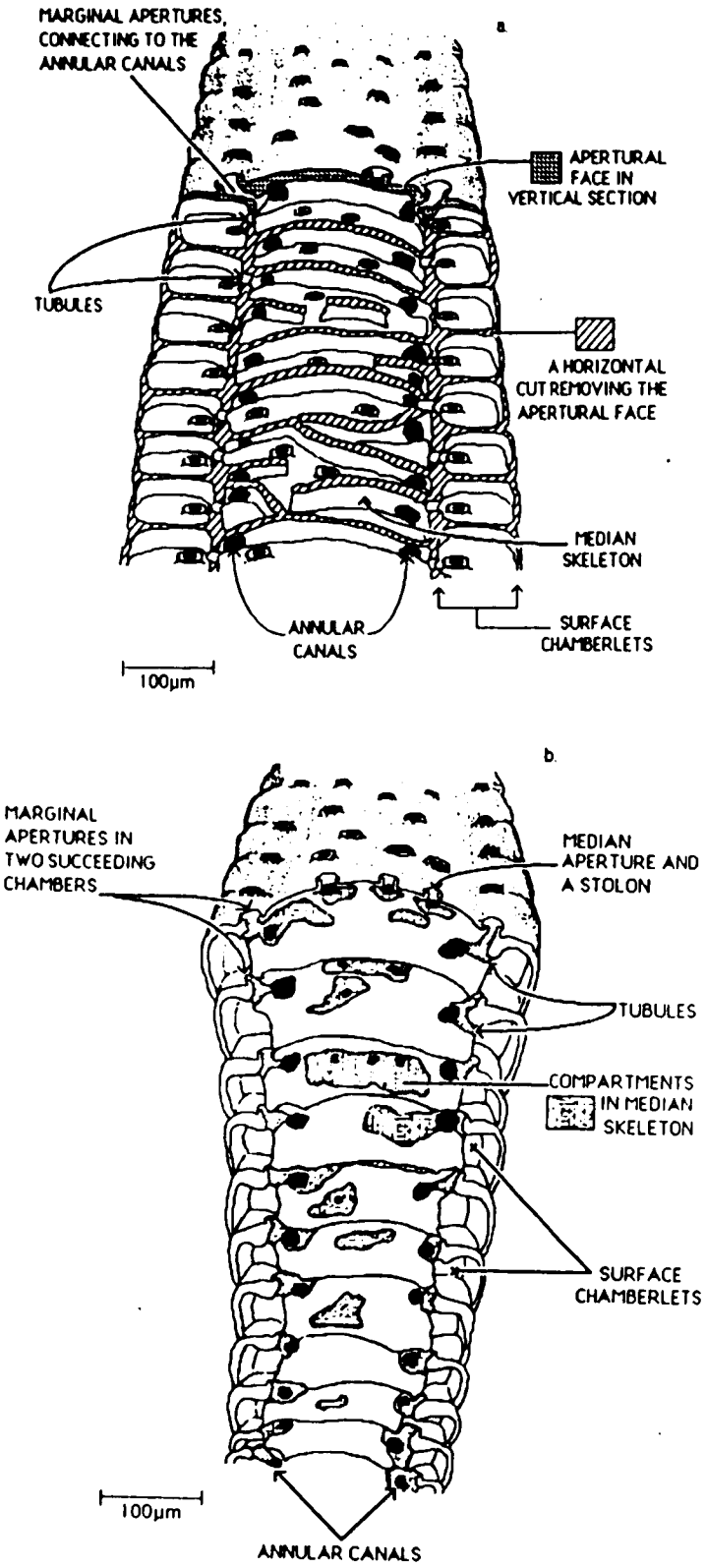

a
MARGINAL APERTURES, CONNECTING TO THE ANNULAR CANALS
APERTURAL FACE IN VERTICAL SECTION
TUBULES
A HORIZONTAL CUT REMOVING THE APERTURAL FACE
MEDIAN SKELETON
SURFACE CHAMBERLETS
ANNULAR CANALS
100µm
b.
MARGINAL APERTURES IN TWO SUCCEEDING CHAMBERS
MEDIAN APERTURE AND A STOLON
TUBULES
COMPARTMENTS IN MEDIAN SKELETON
SURFACE CHAMBERLETS
100µm
ANNULAR CANALS

Figure 18.

Figure 19.

Figure 20.

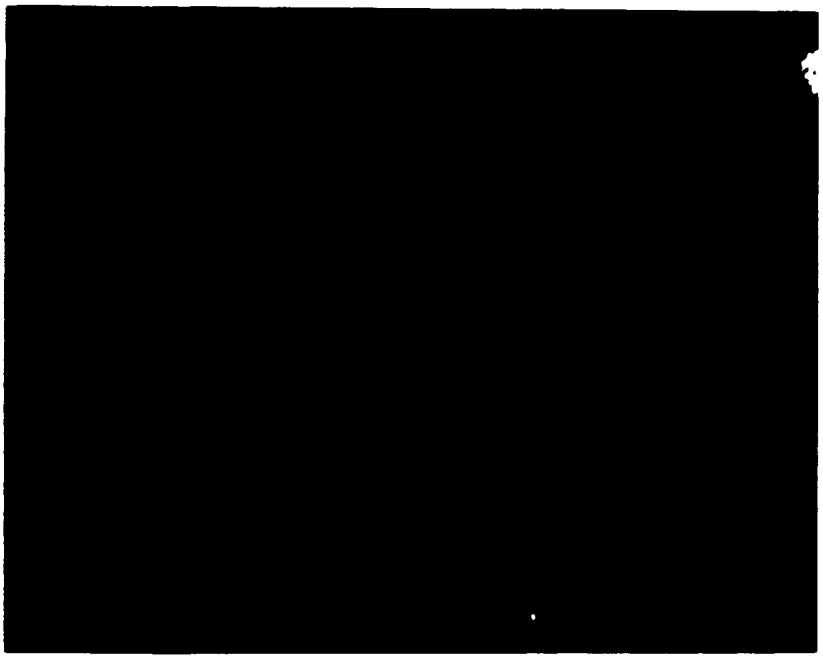
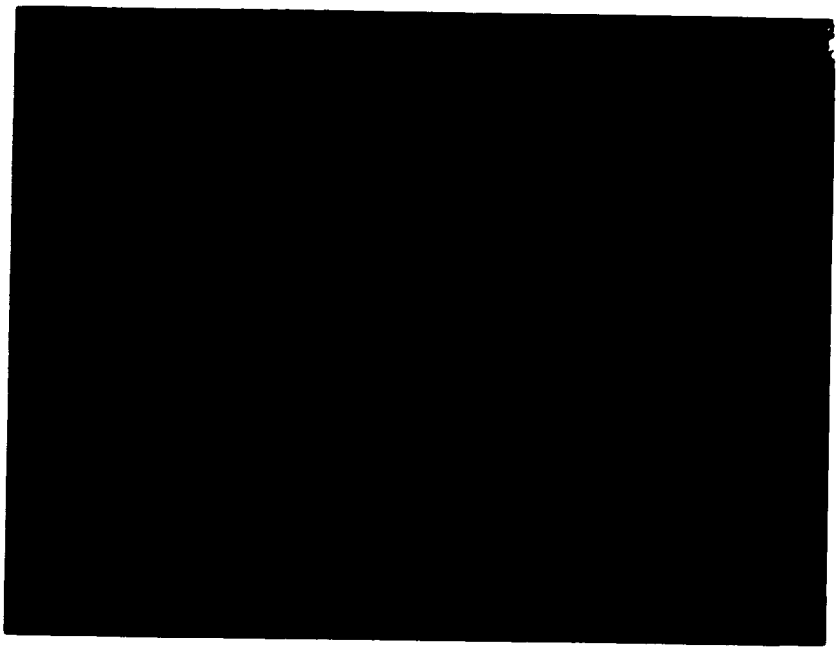


Figure 21



Figures 22 - 25, *Amphisorus hemprichii* Ehrenberg, 1839

Figure 22 (p. 150).

Embryos in horizontal and equatorial section.

a) An A-form specimen form Taba, Red Sea with a reduced vorhof,(AMNH 43791).

b) A specimen from Taba (AMNH 43792), with a typical distinct vorhof.

c) A B-form specimen from Taba (AMNH 43790), showing the embryo and the next 13 chambers, growing in a lenticulate, evolutive, and planspiral mode. In the 13th chamber the internal skeleton is formed with a single septulum. (P = proloculus, F = flexostyle, V = vorhof).

Figure 23 (p. 151).

A general view of *Amphisorus hemprichii*(AMNH 43793), from Taba, Red Sea.

a) A lateral view.

b) An apertural view.

Figure 24 (p. 152).

Figures a and b are from the same specimen of a B-form, from the Red Sea, Taba.

a) A single circular aperture in the 4th chamber following the embryo.

b) A double row of apertures in the 11th chamber.

Figures c-e are from another specimen of the A-form, from the Red Sea, Taba.

c) Apertures in the vorhof, forming a single row of circular to crescentic apertures.

d) A single row of apertures in the 4th chamber.

e) A double row of apertures in the 31st chamber. The apertures in each row are facing the space between two apertures in the opposite row, forming a displaced apertural pattern.

Figure 25(p. 153).

A reconstructed image of the duplex plan of the internal skeleton. (Based on specimens AMNH 43795).
a) An apertural and oblique view. The apertural face is partly removed to show how each septula faces the space between two septula on the opposite side of the test, forming the disjunct architecture of the duplex plan.
b) Seven chambers of the duplex plan in an axial section, illustrating the duplex skeleton.

Figure 22.

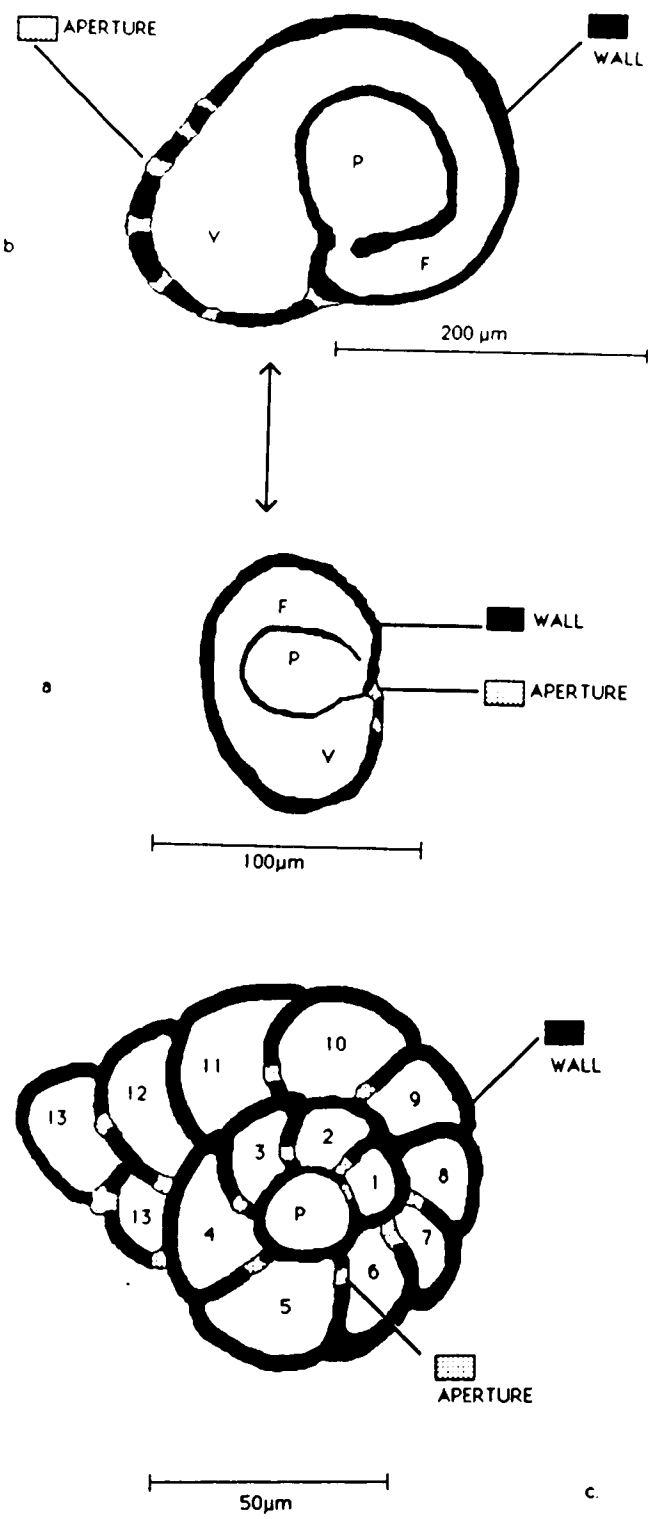

APERTURE
WALL
P
V
F
b
200 µm
F
P
V
WALL
APERTURE
a
100µm
10
11
12
13
9
2
3
1
8
13
P
4
7
6
5
WALL
APERTURE
50µm
c.

Figure 23.

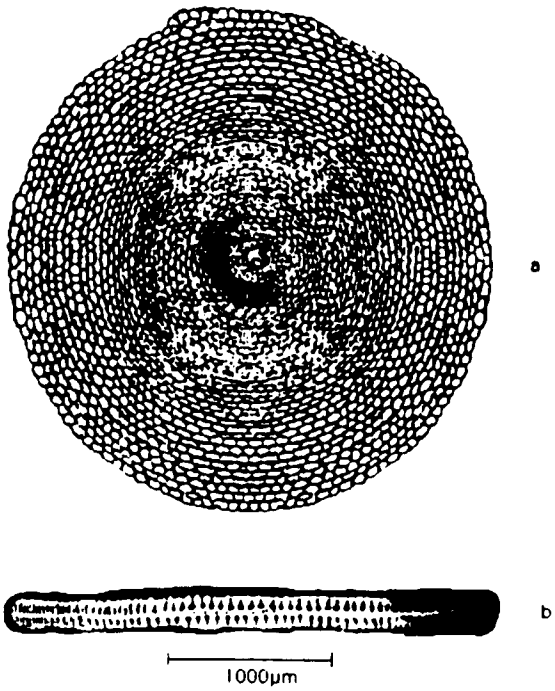


Figure 24

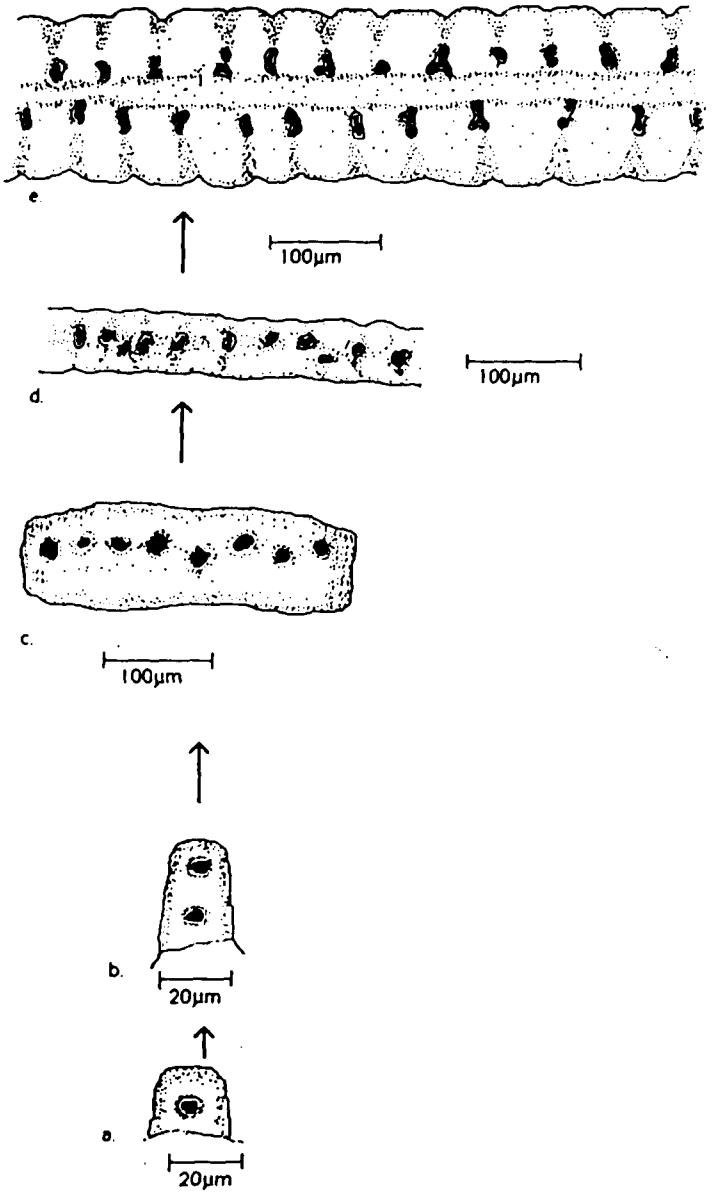
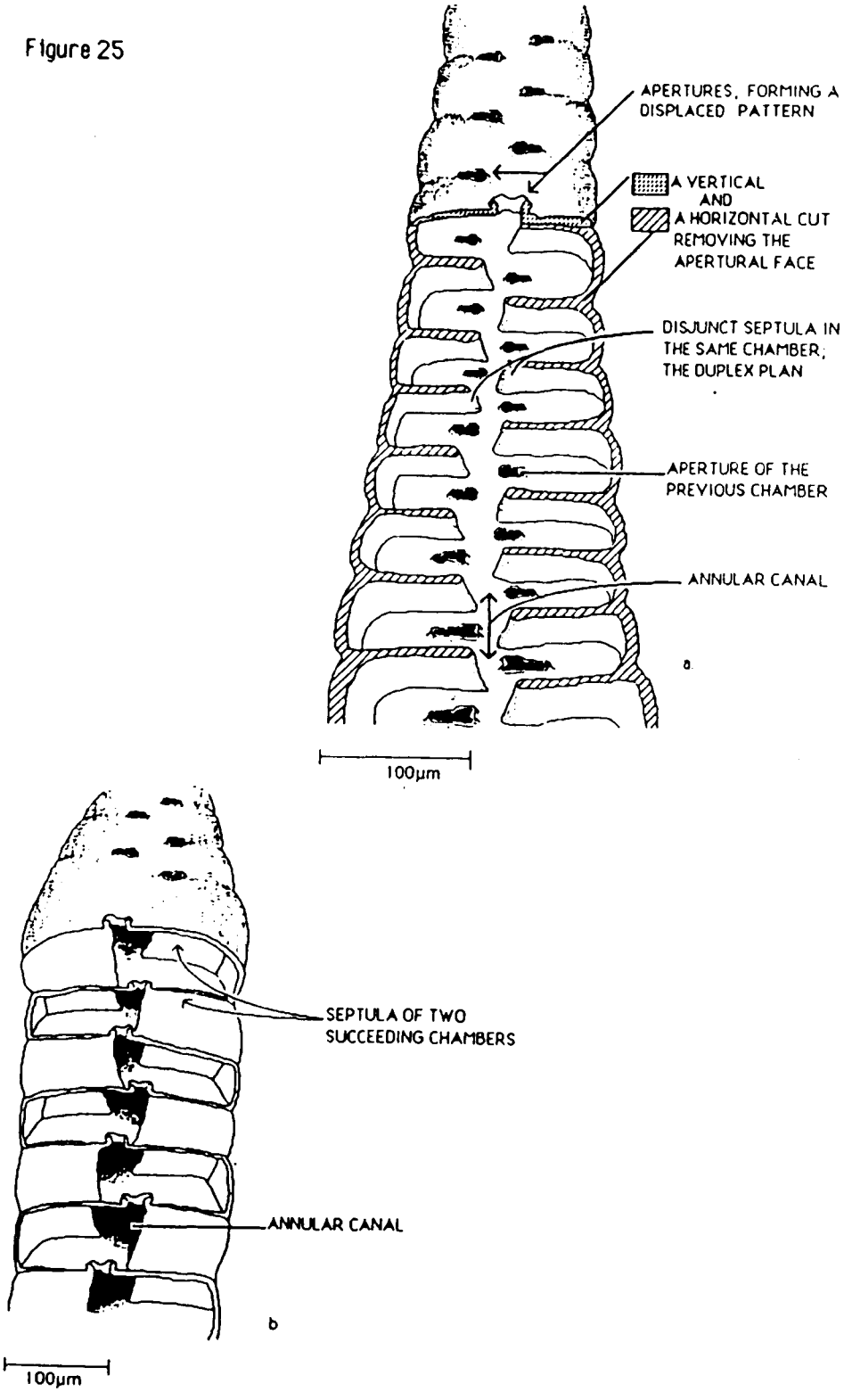


Figure 25


APERTURES, FORMING A DISPLACED PATTERN
A VERTICAL AND A HORIZONTAL CUT REMOVING THE APERTURAL FACE
DISJUNCT SEPTULA IN THE SAME CHAMBER; THE DUPLEX PLAN
APERTURE OF THE PREVIOUS CHAMBER
ANNULAR CANAL
a
100µm
SEPTULA OF TWO SUCCEEDING CHAMBERS
ANNULAR CANAL
b
100µm

Figures 26-30, *Marginopora kudakajimensis* nov. sp.

Figure 26 (p. 156).

A general view of *M. kudakajimensis*, from the Red Sea, Taba.
a) An apertural view.
b) A side view (Holotype AMNH 43917).

Figure 27 (p. 157).

A reconstructed image of the complex plan of the internal skeleton, based on specimens (AMNH 43796, 43794).
a) An apertural and oblique view, where the apertural face has been partly removed from one chamber to show the structure of the median skeleton, which forms a network of pocketlike chamberlets, located between the surface chamberlets. Note that the annular canal is not recognizable as a distinct entity.
b) 13 chambers of the same specimens as in figure a, in an axial section, where traces of the annular canals are present in some of the earlier chambers.

Figure 28 (p. 158).

Figures a - e are of the same specimen (an A - form) from Kudaka-jima.
a) Apertures in the vorhof.
b) A simple row of apertures (in the 5th chamber), beginning to form double rows.
c) A double row of marginal apertures (in the 18th chamber), forming displaced pattern, such that each aperture in one row is facing the space between two apertures in the opposite row.
d) Formation of median apertures, in the 21st chamber.
e) Apertures in the 42nd chamber, forming a broad segment of median apertures.

Figures f and g are from another specimen (B - form) from the Red Sea.

f) A single aperture in about the 4th chamber.

g) Apertures in about the 15th chamber, beginning to form a simple row.

Figure 29 (p. 159).

a) An axial section of an A-form showing the development of the internal skeleton (AMNH 43794). The 1st to about the 7th chamber possess a simple septula with a single stolon. The 8th to the 14th chamber follow the duplex plan, which in later chambers transforms into the complex plan.

b) A lateral view of the test, where the lateral sides have been removed to expose the interior of the surface chamberlets. Only the marginal apertures are seen and the compartments of median skeleton (AMNH 43815). (Compare with figure 18, of *M. vertebralis*)

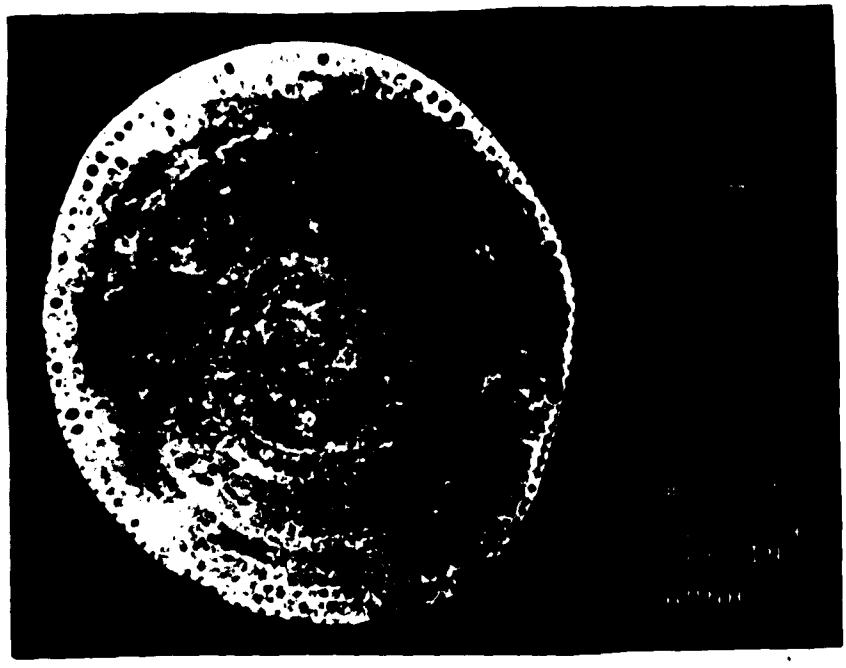
Figure 30 (p. 160).

a) The ornamentation of the lateral sides of the wall, forming an irregular pattern of pits an groves. Note the typical hexagonal arrangement of the chamberlets and the wave shaped sutures (AMNH 43798).

b) Ornamentation of the apertural face (AMNH 43798).

Figure 26.

a.



b.

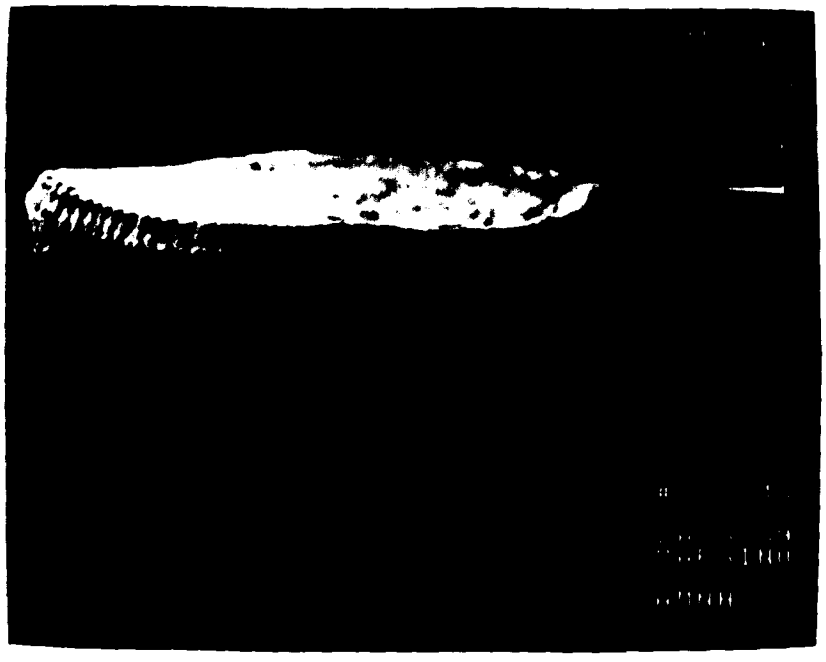


Figure 27.

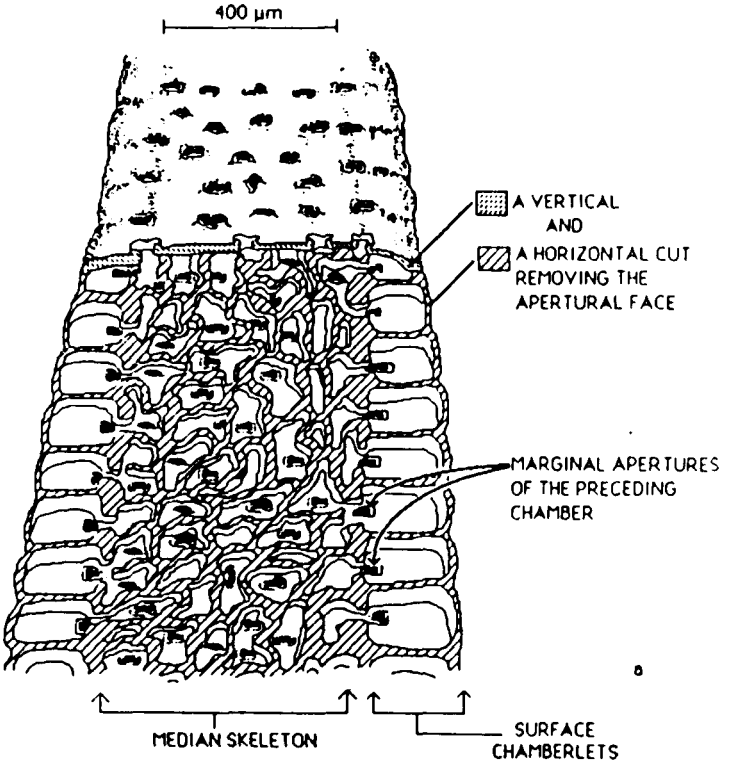

400 µm
A VERTICAL AND
A HORIZONTAL CUT REMOVING THE APERTURAL FACE
MARGINAL APERTURES OF THE PRECEDING CHAMBER
a
MEDIAN SKELETON
SURFACE CHAMBERLETS
400µm
MEDIAN APERTURE, OPENING INTO A COMPARTMENT IN THE MEDIAN SKELETON
SURFACE CHAMBERLET
COMPARTMENTS IN MEDIAN SKELETON
b

Figure 28

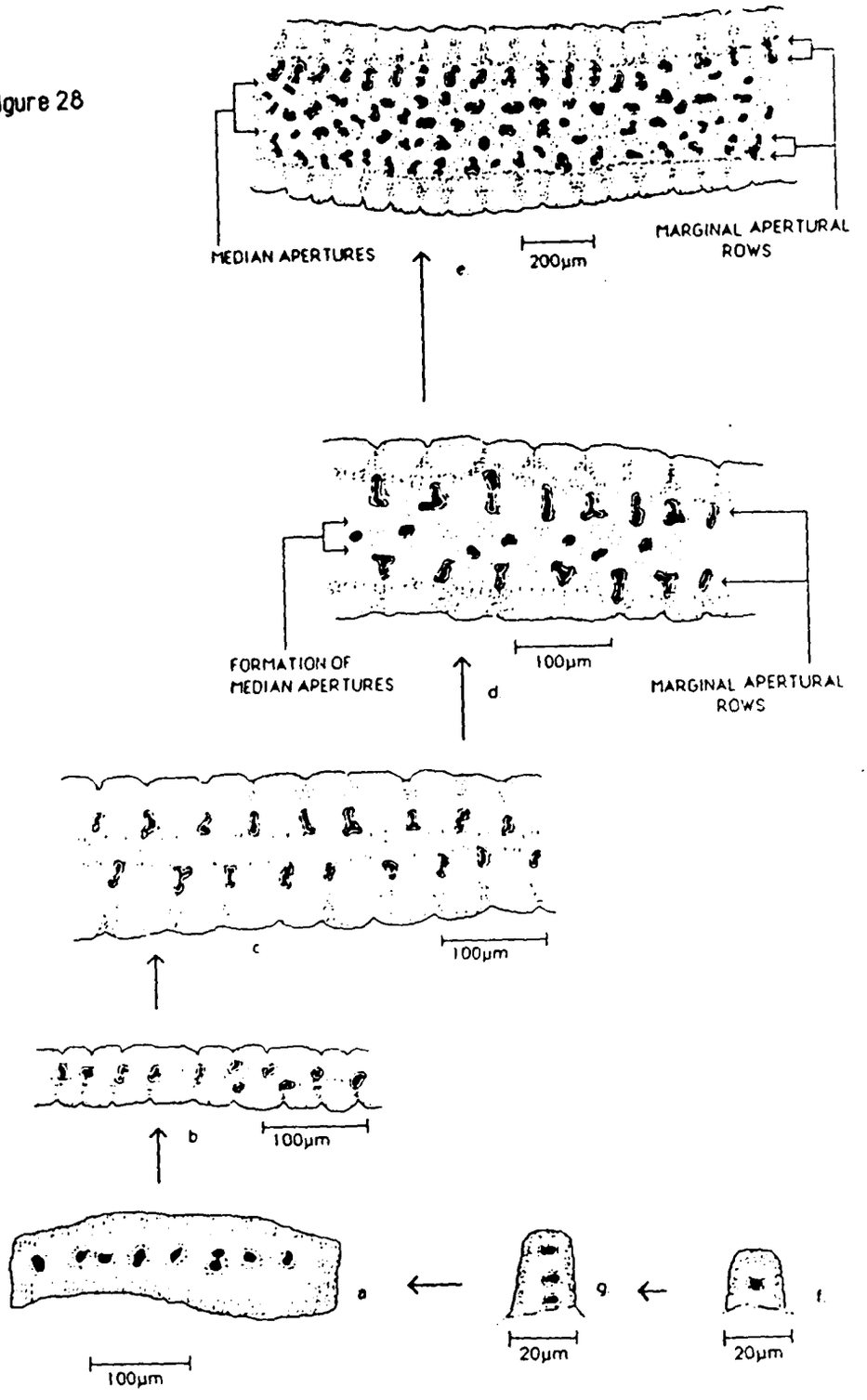

MEDIAN APERTURES
200µm
MARGINAL APERTURAL ROWS
e
FORMATION OF MEDIAN APERTURES
100µm
d
MARGINAL APERTURAL ROWS
c
100µm
b
100µm
a
100µm
g
20µm
f
20µm

Figure 29.

a.

b.

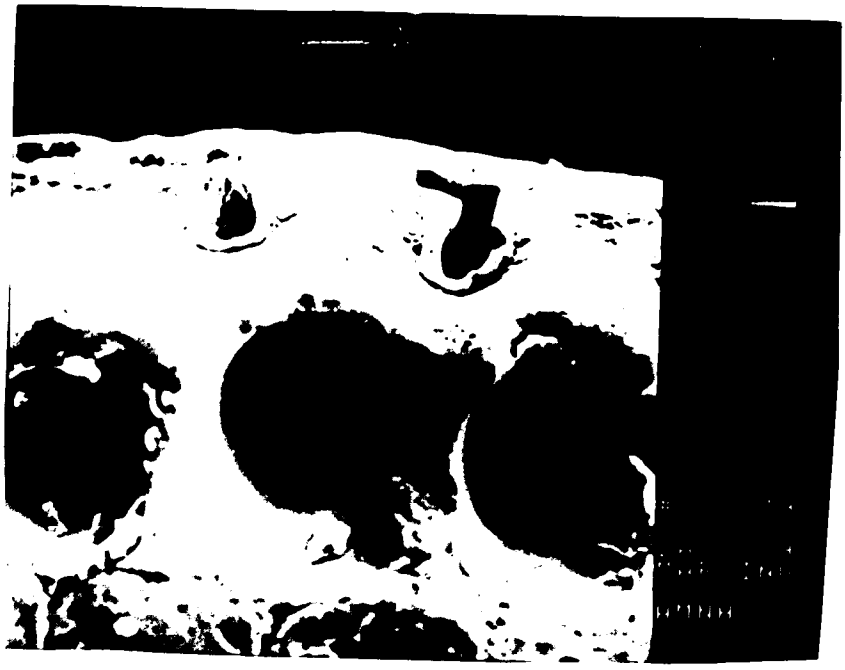
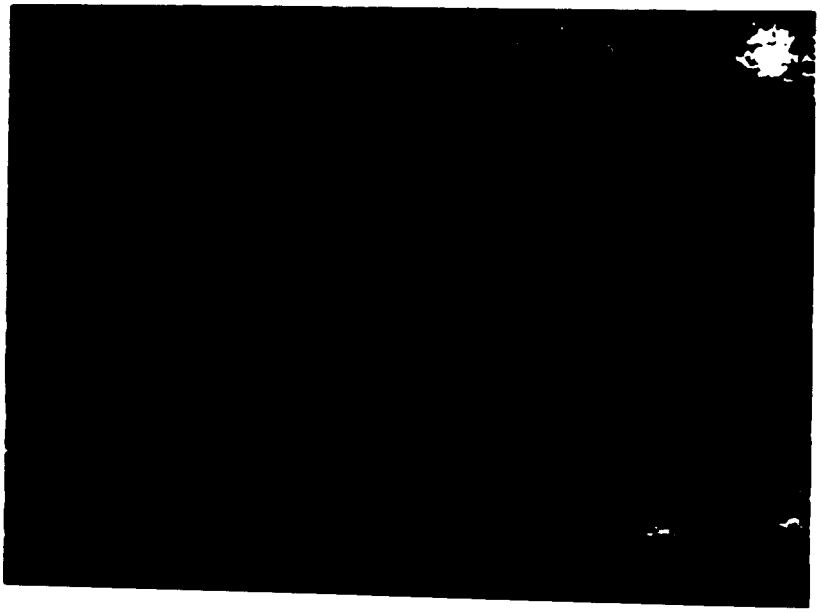


Figure 30.

a.



b.

Figures 31 - 35, *Sorites orbitolitoides* (Hofker, 1930).

Figure 31 (p. 163).

Sorites orbitolitoides; from The Bahamas, Bimini (AMNH 43863,23).

a) A side view.

b) An apertural view.

Figure 32 (p. 164).

Apertural development in a single specimen of the A-form of *S. orbitolitoides*; from Bimini.

a) A single circular aperture in the 2nd chamber attached to the 1st chamber and the globular embryo.

b) The 6th chamber with a single aperture, slightly transformed into a crescentic form.

c) Apertures on the 8th chamber where the basal aperture (closest to the test) is of a crescentic form.

d) Apertures on the 14th chamber displaying a slightly elongated to circular apertures and a basal crescentic aperture.

e) A selected part from an adult annular chamber (24th chamber), showing a single row of circular and ovate longitudinally arranged apertures. Also one or two ovate apertures are transversely arranged.

Figure 33 (p. 165).

A reconstructed image of he internal skeleton.in S. orbitolitoides. Based on specimens from Bimini, AMNH 43864,11 and 34.

a) An axial section (vertical cut) of 5-6 chambers, cutting through the septula in every other chamber, because of the hexagonal arrangement of the chamberlets.

b) A tangential (horizontal) cut and a vertical cut, demonstrating the structural relations between the apertures and the septula. Each septula is always located underneath a single aperture, forming the aperture-stolon complex.

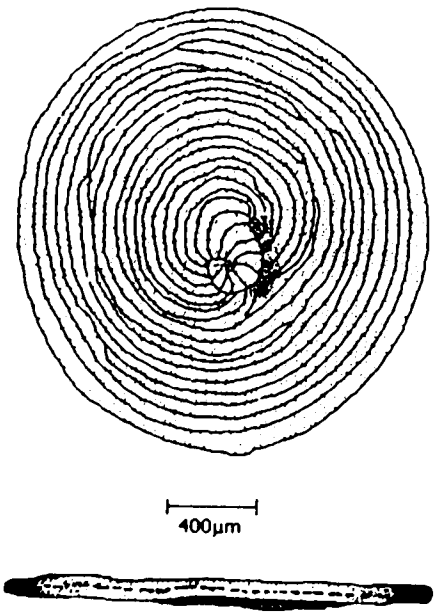
Figure 34 (p. 166).

The ornamentation of the lateral sides of the embryo and the first 3 chambers, forming evenly dispersed pits (from a dissected specimen, AMNH 43864,14).

Figure 35 (p. 166).

The ornamentation of the apertural face in an adult annular chamber, forming elongated pits or groves arranged longitudinally along the apertural face.(AMNH 43864, 34)

Figure 31.



a

b

Figure 32.

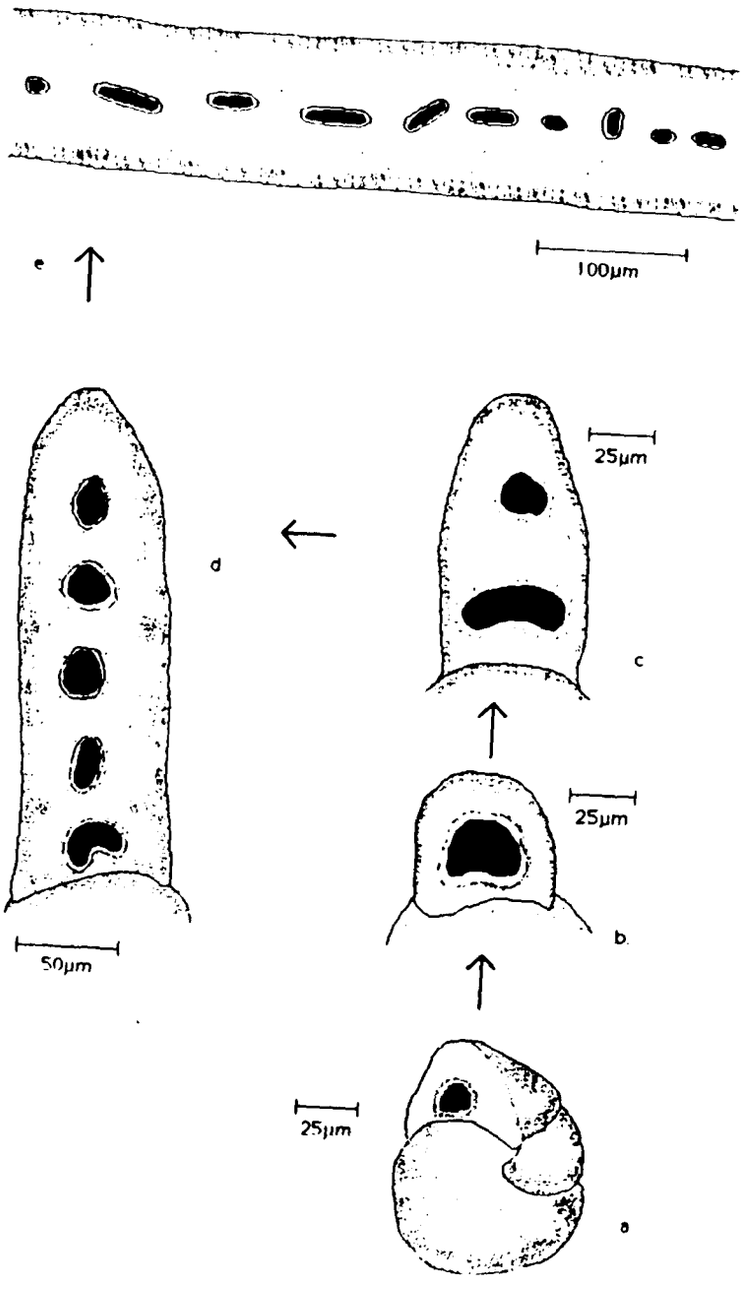


Figure 33.

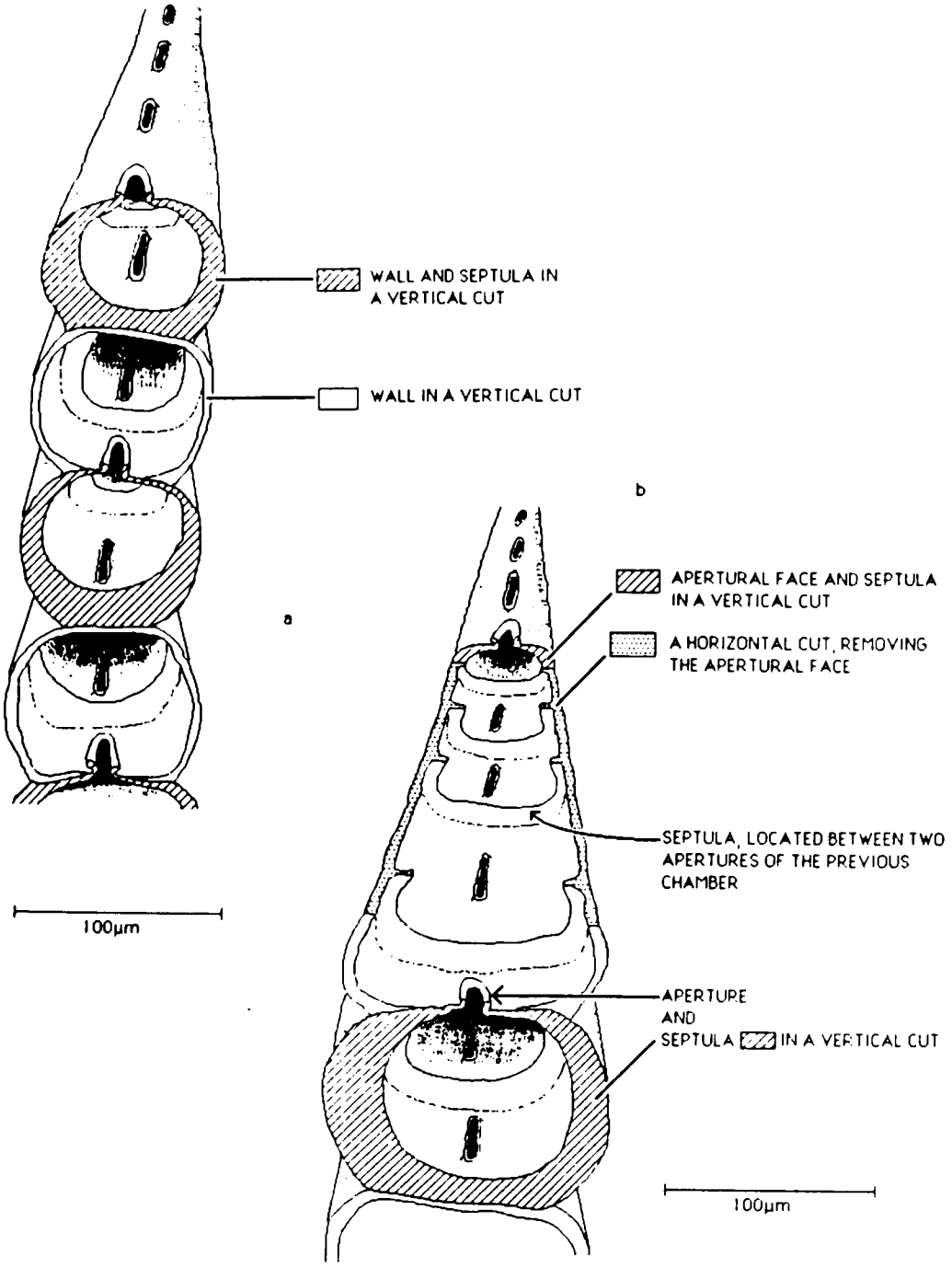

WALL AND SEPTULA IN A VERTICAL CUT
WALL IN A VERTICAL CUT
a
100µm
b
APERTURAL FACE AND SEPTULA IN A VERTICAL CUT
A HORIZONTAL CUT, REMOVING THE APERTURAL FACE
SEPTULA, LOCATED BETWEEN TWO APERTURES OF THE PREVIOUS CHAMBER
APERTURE AND SEPTULA IN A VERTICAL CUT
100µm

Figure 34.

Figure 35.

Figures 36-40, *Sorites bradyi* (Cushman 1930)

Figure 36 (p. 169).

A dissected specimen of *Sorites bradyi* from Bimini, showing a rectilinear stage in the last 4 chambers.

Figure 37 (p. 170).

Development of the apertures in a specimen from Bimini.. In total this specimen possessed 33 chambers excluding the embryo.

a) A single aperture in the 5th chamber following the embryo.

b) The 13th chamber and the first to possess multiple apertures.

c) Apertures in the 24th chamber, mostly circular in shape, forming a single row.

d) Apertures in the 28th chamber and the last in the planspiral growth stage, where most of the apertures were ovate, and tended to be transversely arranged.

e) Apertures in the 29th chamber which was the first in a sequence of 5 rectilinear chambers. All these five last rectilinear chambers possessed double apertural rows, tending to form pairs.

Figure 38 (p. 171).

An apertural view of the same specimen illustrated in figure 36. The apertural face of the last chamber has been removed. Note that the septula are confined to the base of the chamber, forming slightly elevated ridges running between the apertures of the previous chamber. The septula never extend onto the lateral walls to form thickenings inside the chambers.

Figure 36.

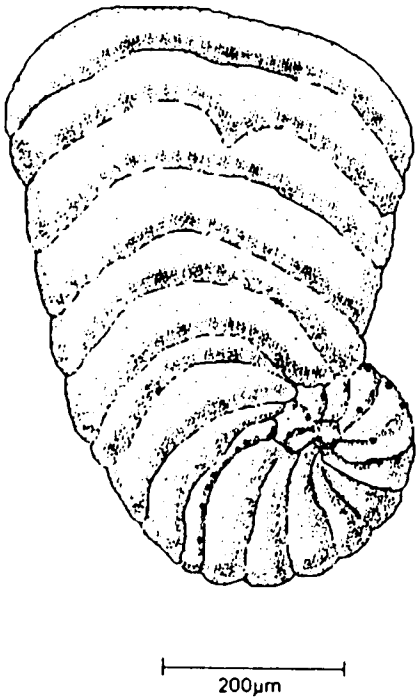


Figure 37.

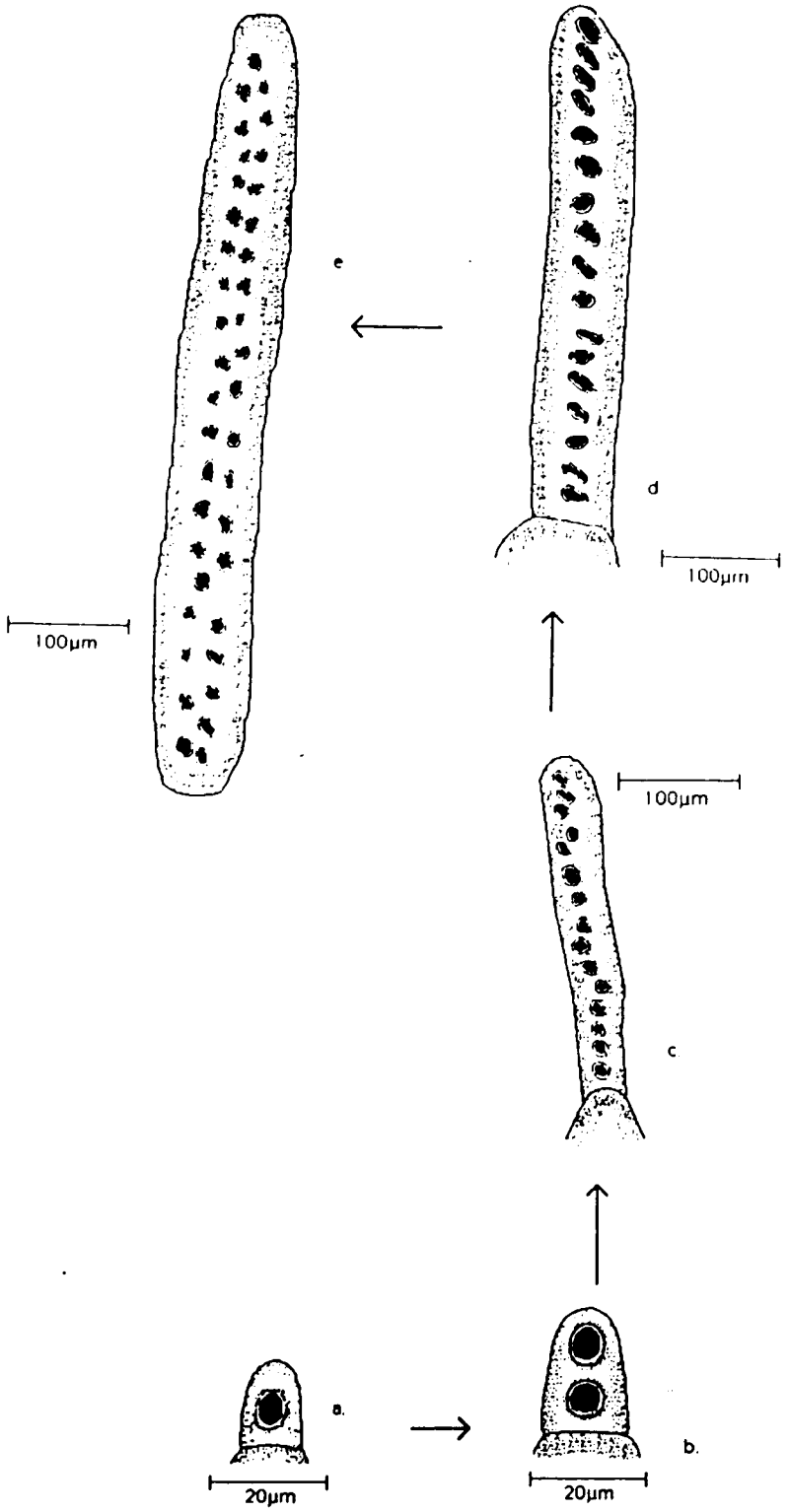


Figure38.

Figure 39

Figure 40.

Figures 41 - 43, *Peneroplis acicularis* (Batsch, 1791)

Figure 41 (p. 174).

General view of *Peneroplis acicularis* from Taba, Red Sea. This specimen possessed about 17 chambers in the initial planspiral growth, but usually these are reduced to about 10 chambers, (after a dissected specimen).

Figure 42 (p. 175).

Apertural development in a specimen from Taba, Red Sea.
a) Aperture in the 6th chamber, a single round opening with a distinct circular lip.
b) Aperture in the 9th chamber forming a crescentic shape. This is the last chamber in the planspiral growth form.
c) Aperture in the 17th chamber.
d) Aperture in the 18th chamber.
e) Aperture in the 19th chamber.
f) Aperture in the 20th chamber.
g) Aperture in the 21st an the last chamber in the test, forming the highly dendritic structure.

Figure 43 (p. 176).

The ornamentation of *P acicularis*, forming a single row of pits, discontinuous over the suture, (after a dissected specimen).

Figure 41.

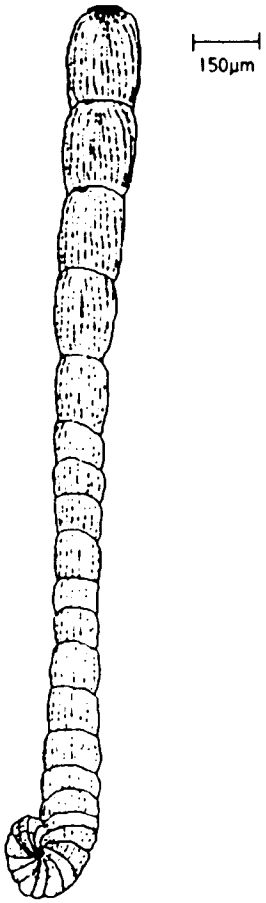


Figure 42.

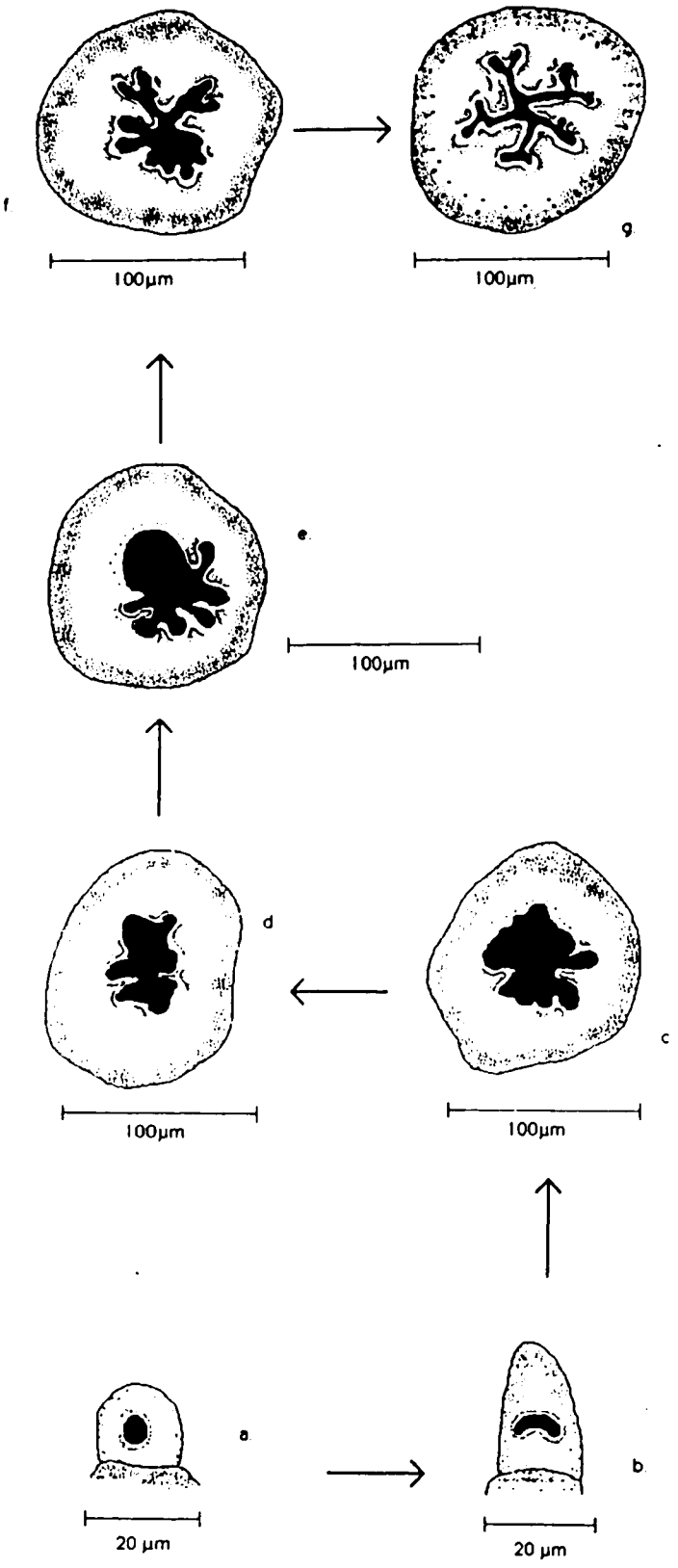


Figure 43.

Figures 44-45, *Peneroplis acicularis* aff.

Figure 44 (p. 178).

Peneroplis acicularis aff, apertural development in a specimen from Taba, Red Sea).

a) A single round aperture with a distinct lip, in the 11th chamber.

b) A slightly deformed aperture in the 16th chamber.

c) An X-formed aperture in the 17th chamber.

d) Aperture in the 18th chamber.

e) A Y-formed aperture in the 20th chamber.

f) Aperture in the 21st chamber.

g) An Y-formed aperture in the 24th chamber, inversely oriented compared to the aperture in figure e.

h) Aperture in the 27th chamber, the first chamber in the rectilinear growth mode.

i) Aperture in the 31st chamber.

Figure 45 (p. 179).

The ornamentation of the apertural face consisting of individual pits and longitudinal grooves, in contrast to the single row of pits on the lateral sides of the chamber. Note the characteristic X-formed aperture, provided with a distinct but irregularly protruding lip (after a dissected specimen, from Taba, Red Sea).

Figure 44.

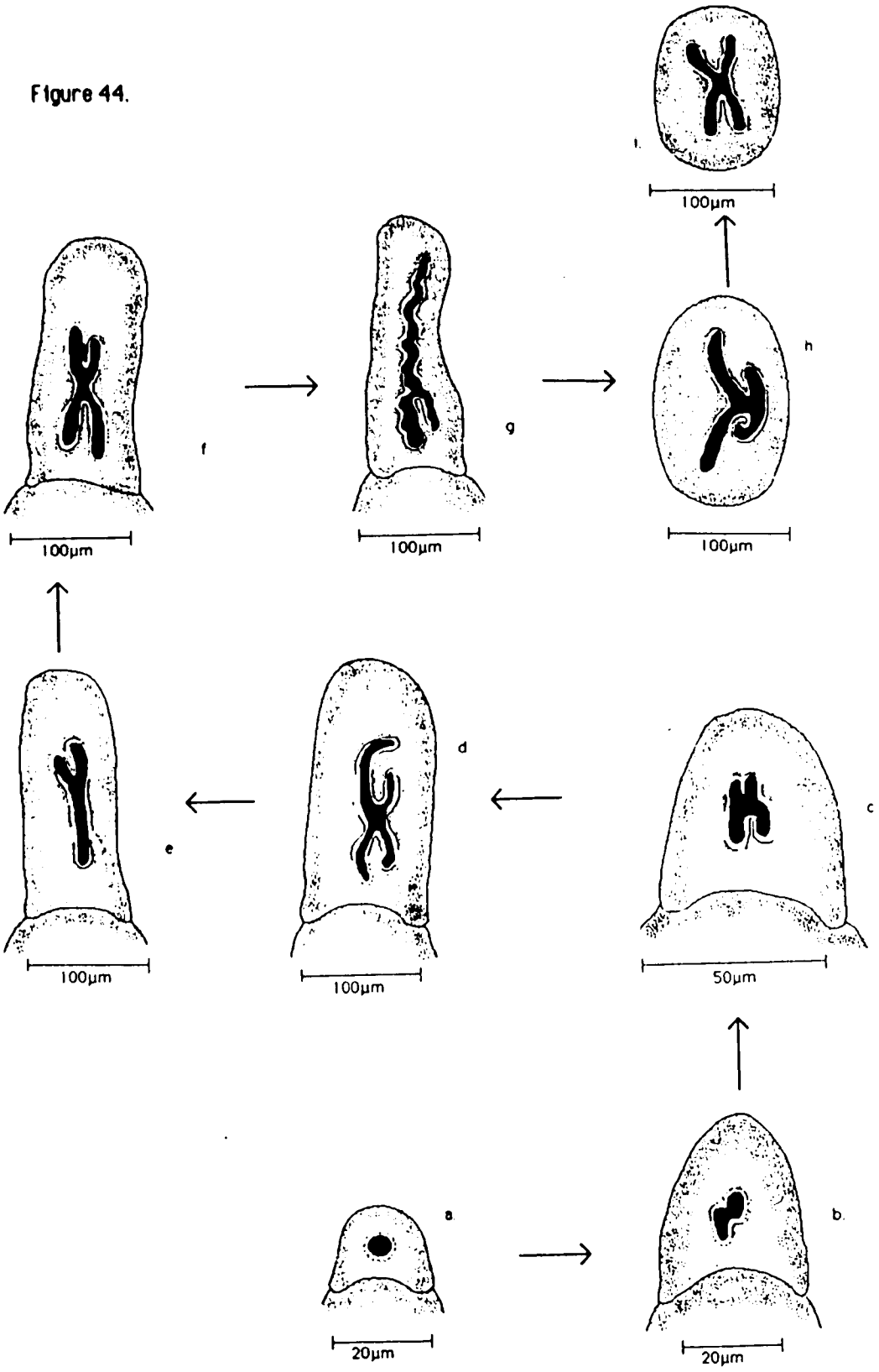

a
20µm
b
20µm
c
50µm
d
100µm
e
100µm
f
100µm
g
100µm
h
100µm
i
100µm

Figure 45.

Figures 46 - 49, *Peneroplis arietinus* (Batsch, 1791)

Figure 46 (p.182).

a) A specimen from the Red Sea.of *P. arietinus*, showing an evolutive growth in the last whorl preceding the rectilinear chambers (AMNH 43874).

b) A juvenile specimen from the Red Sea, growing in an involutive mode (AMNH 43875).

Figure 47 (p. 183).

Apertural development in a single A-form specimen of *P. arietinus*, from the Red Sea.

a) A circular aperture of the 4th chamber following the embryo.

b) The 6th chamber possessing an x-formed aperture.

c) A crescentic shaped aperture in the 7th chamber.

d) A Y-formed aperture in the 8th chamber.

e) The 14th chamber and the first to possess a multiple apertures.

f) The 24th chamber possessing multiple and highly dendritic apertures.

g) Apertures in the 33rd and the last of 5 rectilinear chambers. The apertures are elongate and are arranged in a circle along the periphery of the apertural face. There are two smaller apertures located in the center of the circle. The ridges on the lateral sides of the wall are shown as black lines reaching onto the apertural face.

Figure 48 (p.184).

a) The ornamentation of the lateral sides of an adult chamber, showing a multiple rows of pits, partially fused and irregular in outline (specimen from the Red Sea, AMNH 43873).
b) Ornamentation of the apertural face, consisting of fused longitudinal grooves and pits, partially overlaid with a calcareous mass, (from a dissected specimen).

Figure 49 (p. 185).

A young specimen from the Red Sea, showing the structural pattern formed by the ridges. The ridges frequently anastomose such that two or three fuse, forming a fork-like structure, where the fork is usually oriented in the direction of the growth, or towards the apertural face (from a specimen that was dissected).

Figure 46.

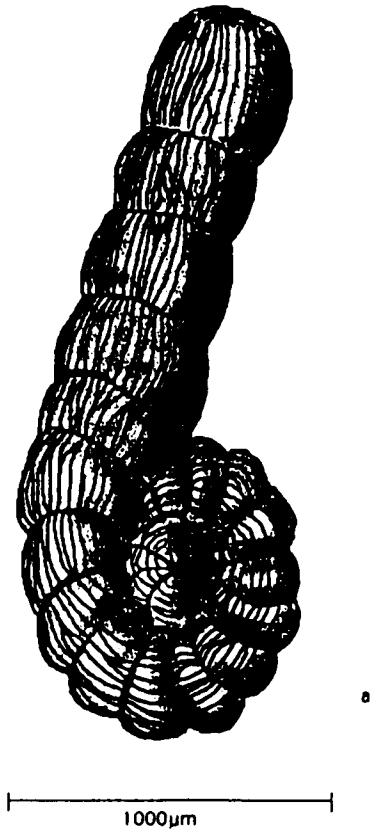


Figure 47.

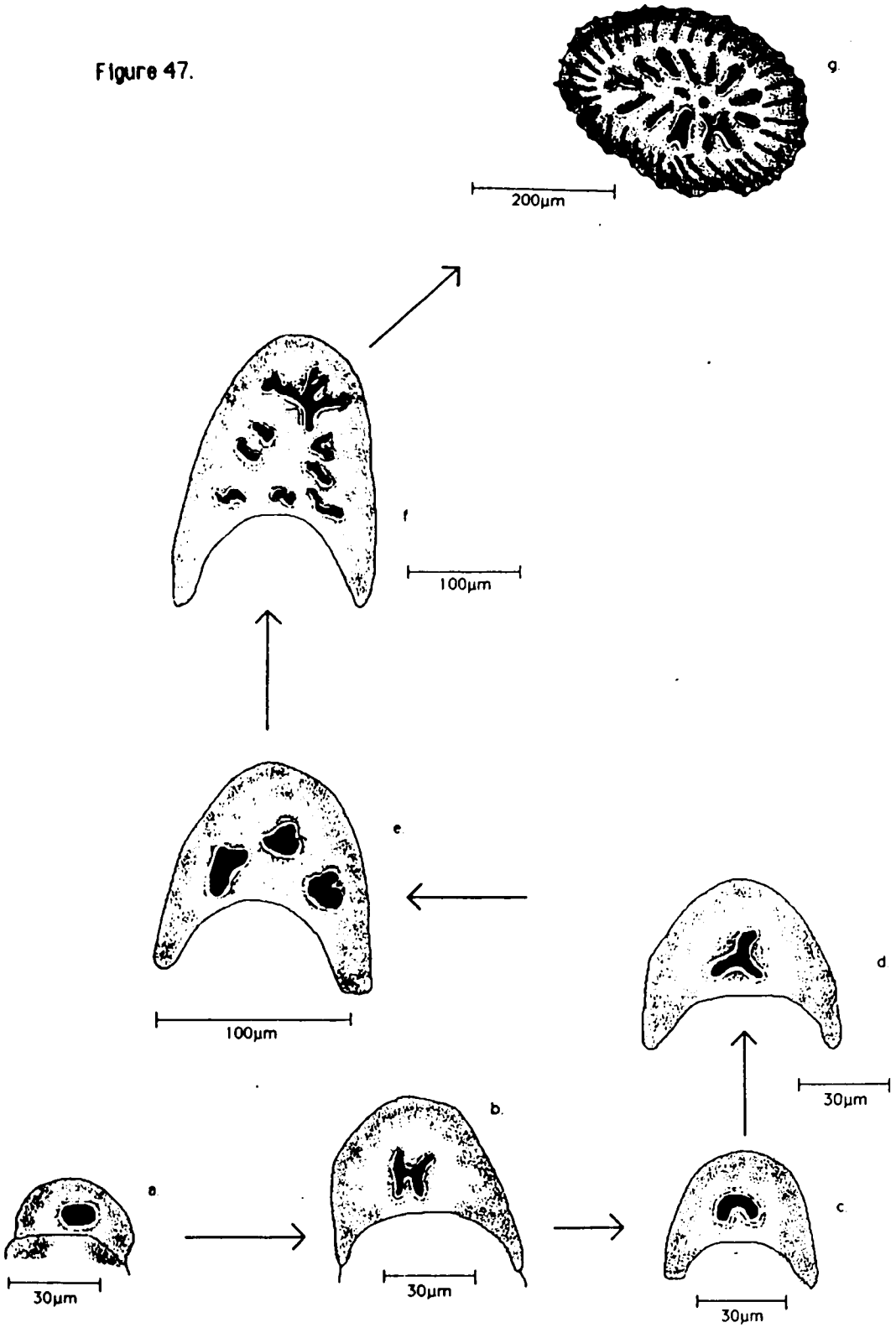
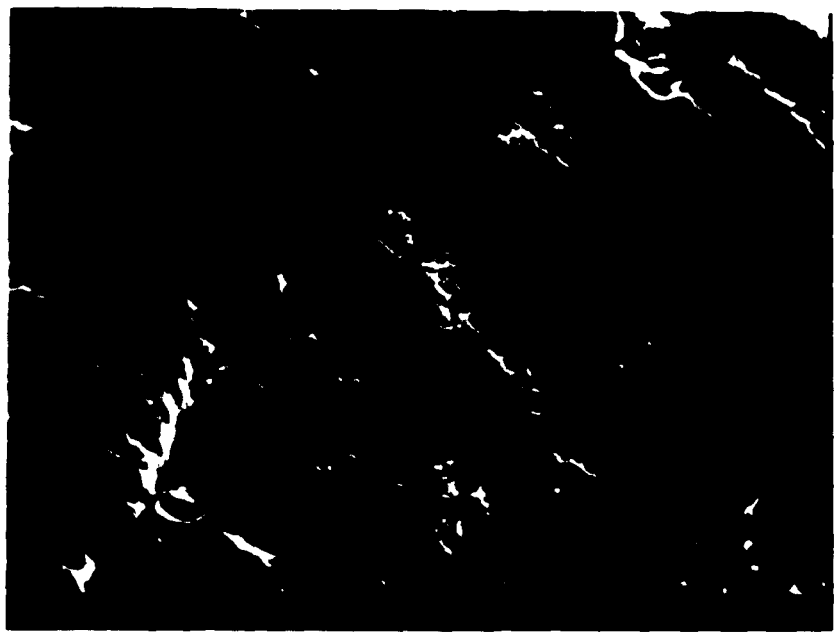


Figure 48.

a.



b.

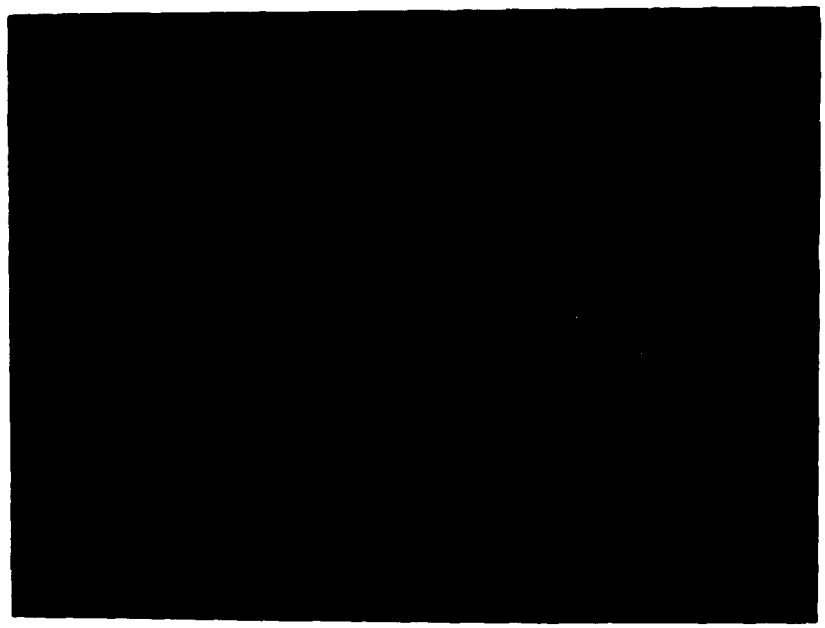
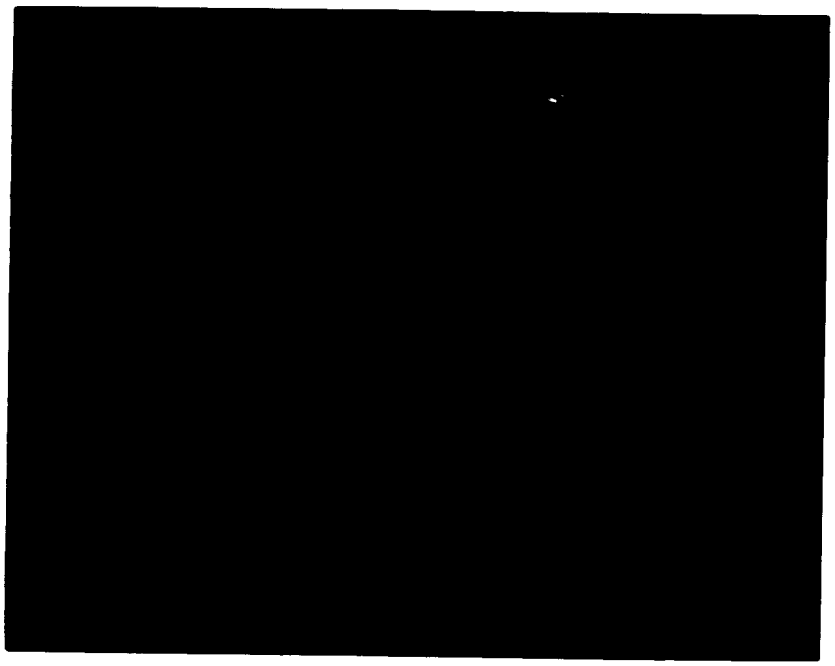


Figure 49.



Figures 50-52, *Peneroplis pertusus* (Forskål, 1775)

Figure 50 (p. 187).

A general view of P. pertusus, after a dissected a specimen from Japan, Kudaka-jima.

a) A side view.

b) An apertural view.

Figure 51 (p. 188).

Apertural development in a single specimen of the A-form, which possessed 37 chambers excluding the embryo. The specimen was from Japan, Kudaka-jima.

a) A single, circular aperture on the 3rd chamber following the embryo.

b) An X-formed aperture in the 8th chamber.

b) A Y-formed aperture first appearing on the 10th chamber.

c) A crescentic aperture, first appearing on the 11th chamber.

e) A dendritic aperture in the 12. chamber.

f) A multiple and dendritic apertures first appearing, on the 14th chamber.

g) Irregularly dispersed multiple apertures in the 36th chamber, also a part of the rectilinear growth stage.

Figure 52 (p. 189).

a) A juvenile growth stage containing an embryo and 5 chambers (dissected from an adult specimen, AMNH 43897). The embryo displays evenly dispersed pits, transforming in the 1st chamber partly into single rows, and in the 2nd to the 5th chamber, into double to triple rows of pits.

b) The ornamentation of the apertural face, showing fused pits and elongate groves, arranged radially along the apertural face. Also visible is the ornamentation in the striations, as multiple rows of slightly fused pits (AMNH 43888).

Figure 50.

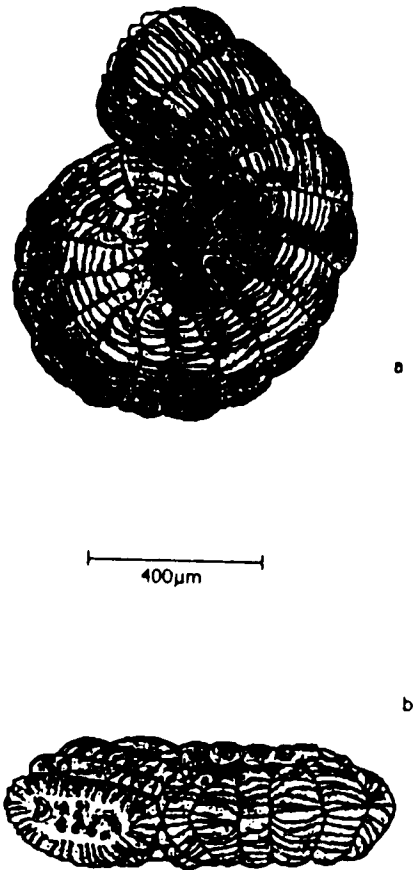


Figure 51.

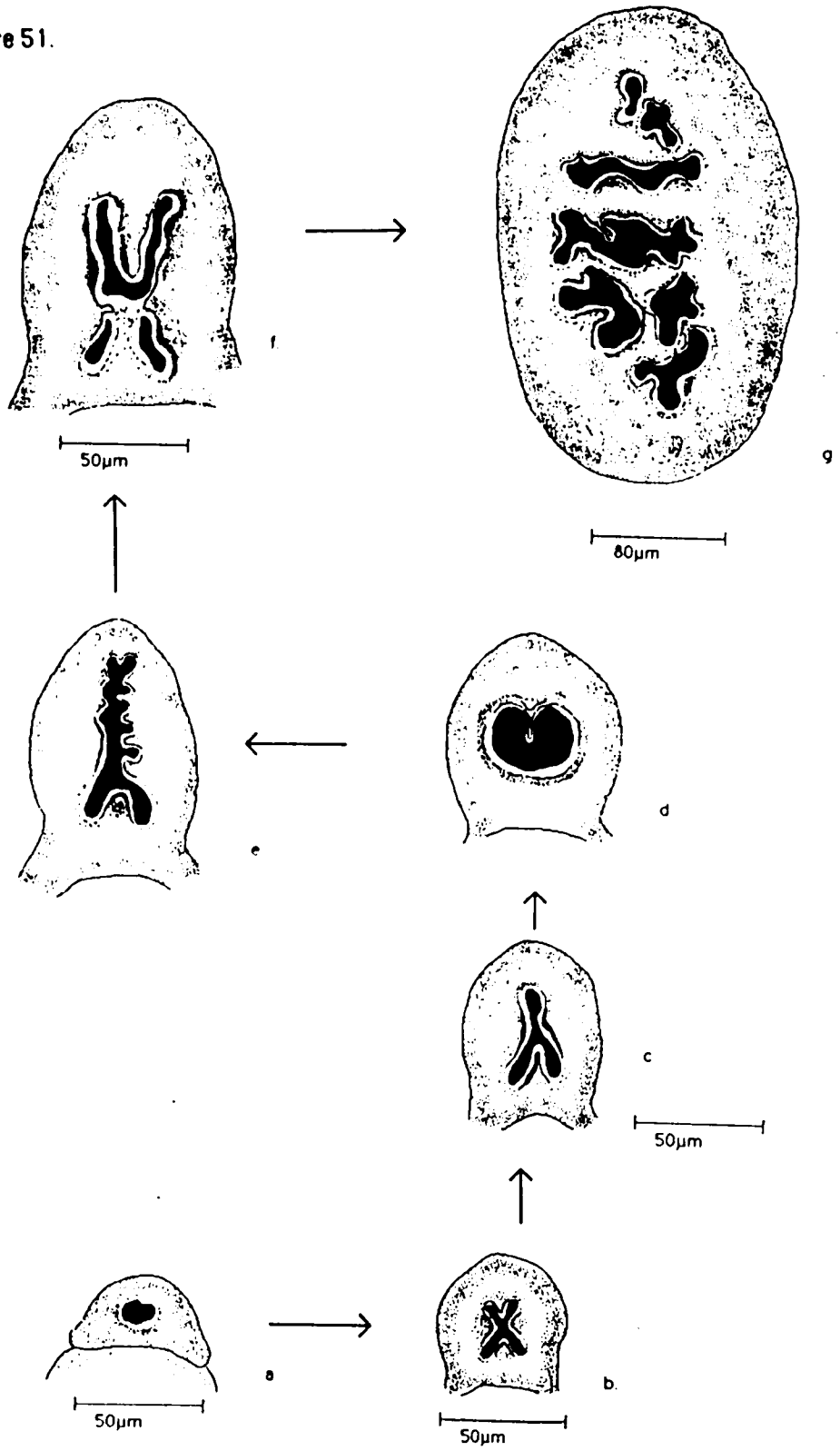
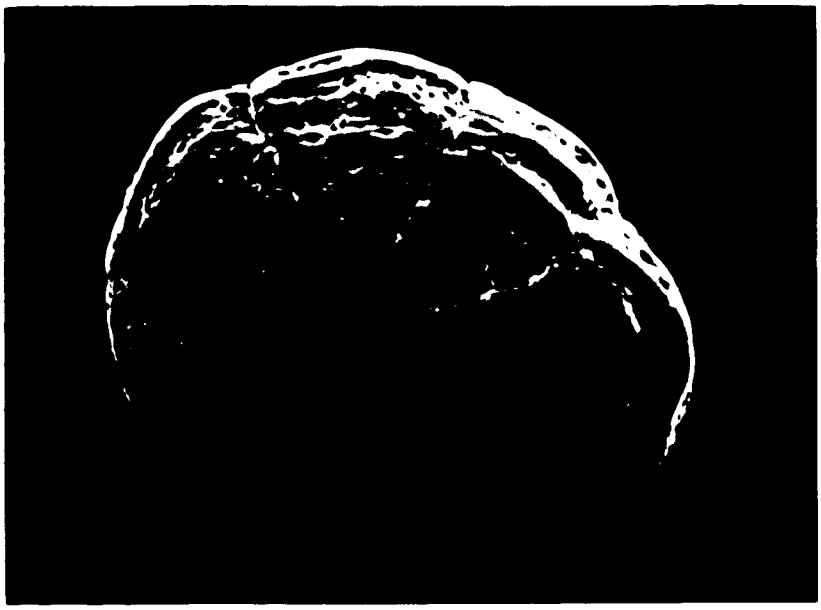


Figure 52.

a.



b.

Figures 53 - 55, *Peneroplis antillarum* (Orbigny, 1839)

Figure 53 (p. 191).

General view of *Peneroplis antillarum*. The involutive, planate, growth mode is distinctly reflected in the distribution of the apertures which extend towards the umbilicus (see also figures 54 c and d). (Specimen from Japan, Kudaka-jima, AMNH 43898).

a) A side view.

b) An apertural view.

Figure 54 (p. 192)

Apertural development in *P. antillarum*, in a specimen from Japan, Kudaka-jima.

a) The 20th chamber and the first to possess multiple apertures, displaying the dendritic shape.

b) The 28th chamber possessing both a dendritic and a crescentic formed apertures.

c) Apertures in the 33rd chamber.

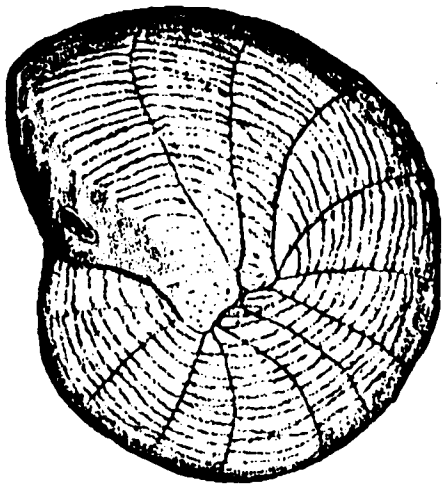
d) Apertures in the 36th and the last chamber.

Figure 55 (p. 193).

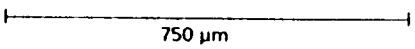
a) The ornamentation of the lateral sides of an adult chamber, showing distinct rows of pits ranging from, single to double rows, rarely fusing to form elongated furrows. The suture is smooth and undepressed.

b) Ornamentation of the apertural face, consisting of evenly dispersed pits, somewhat fused and forming elongated furrows, radially arranged along the apertural face.

Figure 53.



a



b

Figure 54.

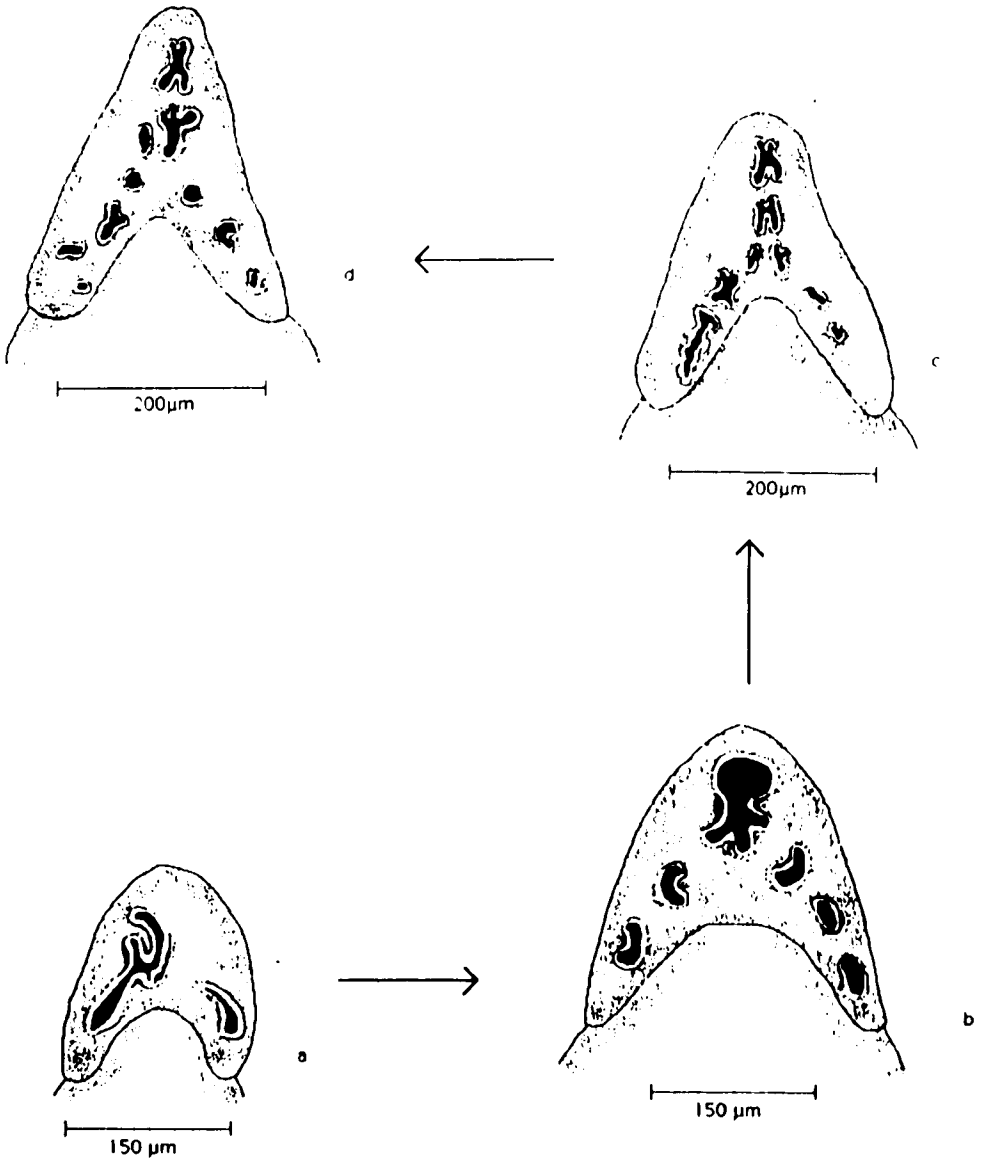
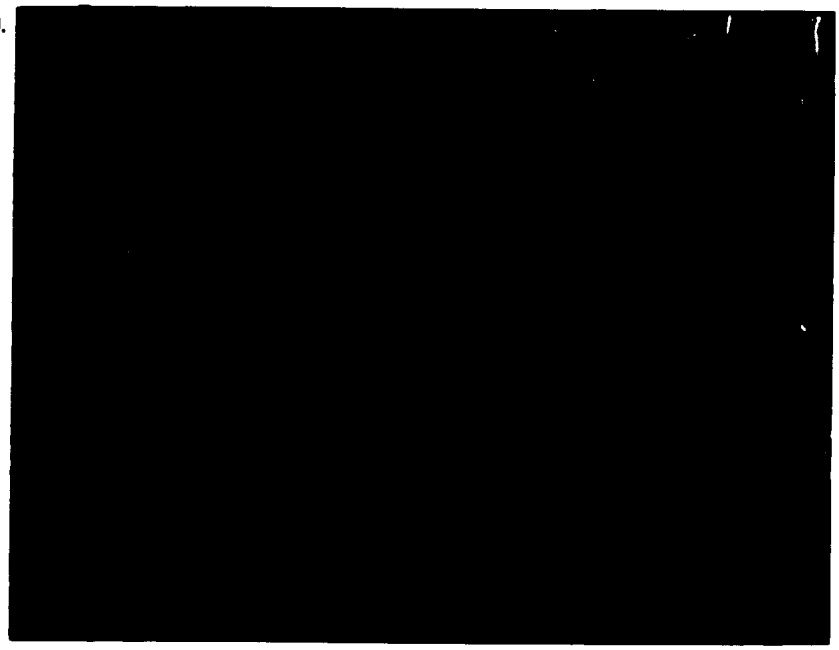


Figure 55.

a.



b.

Figures 56-59, *Peneroplis planatus* (Fichtel and Moll, 1803)

Figure 56 (p. 196).

General view of P. planatus, a specimen from Japan, Kudaka-jima.

a) A side view.

b) An apertural view (AMNH. 43913).

Figure 57 (p. 197).

Apertural development in an A-form specimen from Japan, Kudaka-jima.

a) Apertures in the 8th chamber and the first to possess multiple apertures. The apertures are of the crescentic and the X-formed type.

b) Apertures in the 13th chamber, the first to possess an irregularly dendritic aperture.

c) Apertures in the 19th chamber, possessing partly a double row of apertures at the base but a single row of apertures at the apex of the chamber.

d) Apertures in the 28th and the last chamber, consisting only of a single row of apertures.

Figure 58 (p. 198).

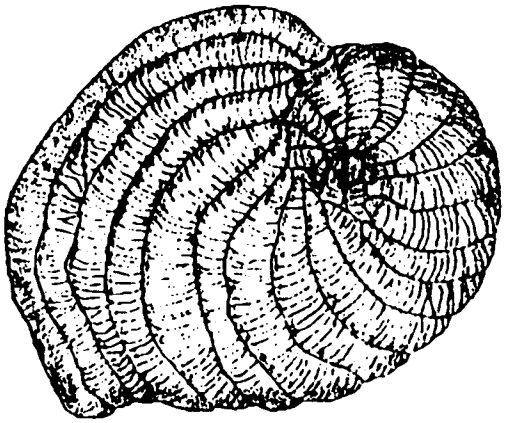
a) An A-form embryo and the two first chambers, dissected from an adult test. The ornamentation on the proloculus and the flexostyle consists of evenly dispersed pits, transforming into double to triple rows of pits on the 1st and the 2nd chamber (AMNH 43914).

b) Details of the ornamentation of the 3rd juvenile chamber, consisting of a simple row of pits later transforming into a double to triple rows on the adult chambers (AMNH 43915).

Figure 59 (p. 199).

a) Details of the ornamentation in the adult chambers, consisting of mostly of a simple to triple rows of pits, or multiple rows near the apertural face, located in slightly depressed furrows. The sutures are depressed and distinct. b) Details of the ornamentation of the apertural face (same specimen as in fig. 59 a) consisting of slightly fused pits, or elongated furrows (AMNH 43916).

Figure 56.



a

200µm

b

Figure 57.

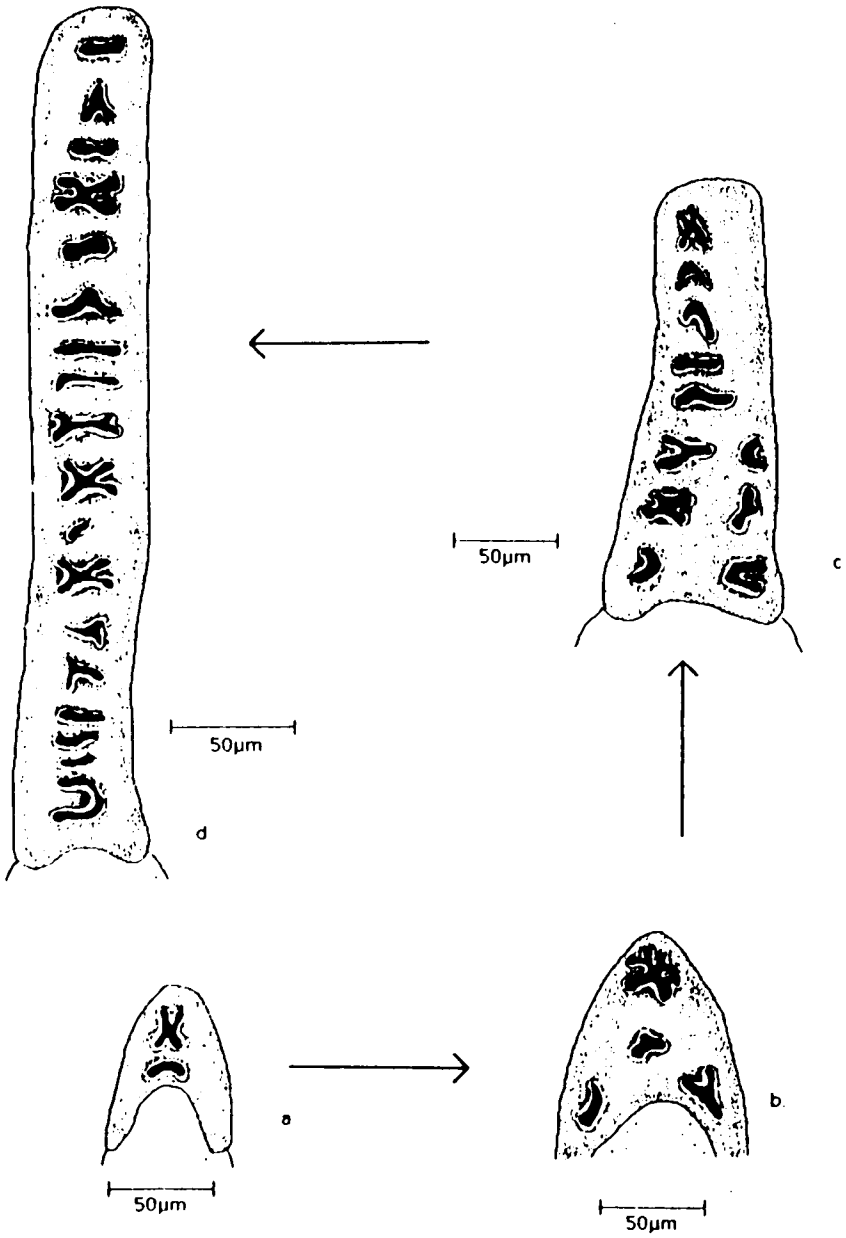
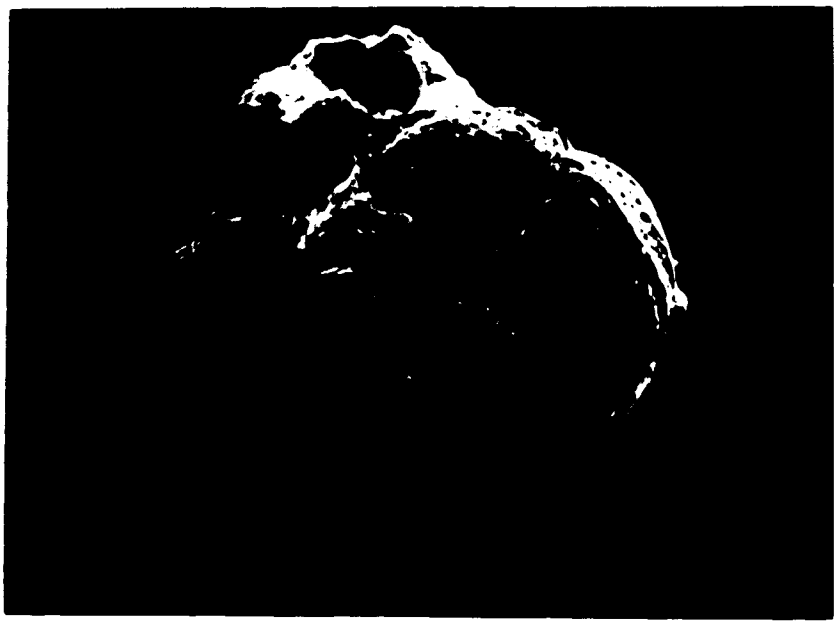


Figure 58.

a.



b.

Figure 59.

a.

b.

Figures 60 - 66, Archaiasinae Cushman, 1927

Figure 60 (p. 203).

a) An arciform growth mode, characterized by extremely curved chambers where the involutive part reaches onto the umbilici, and an evolutive part whirls around the test. Specimen of *Puteolina proteus* (AMNH, 43909).

b) A side view of a specimen of *Archaias angulatus*, illustrating the involutive growth of the arciform type, where the chambers whirl about 1.5 turns around the test in an curved plane, extending towards the umbilici of the test.

Figure 61 (p. 204).

a) A reconstructed image of a single juvenile arciformed chamber (the 11th chamber) drawn in a single plane, showing the early development of buttresses, in the arciform growth stage. The buttresses only extend towards the center of chamber lumen, and are confined to the lateral sides of the chamber wall. Note that the buttresses are absent from the chamber which covers or overlays the previous chambers of the test.

b) The organization of buttresses in one of the circular chambers in the 24th chamber. The buttresses only extend towards the center of the chamber lumen, but are now present on both the lateral sides of the chamber. (Both figures a and b are based on a single dissected specimen of *Cyclorbiculina compressa*).

Figure 62 (p. 205).

a) The arrangement of the chamberlets in *Cyclorbiculina compressa* The surface layer of the lateral side of 6

successive chambers has been removed to expose the lumen of the chamberlets (horizontal-tangential section). The chamberlets are displaced independently of the position of the chambers in the previous or the succeeding chamber, resulting in an anomalous chamberlet pattern.
b) The same 6 chambers as are illustrated in 62 a, where half of the test has been ground away (equatorial section). Note the anomalous displacement of the apertures in successive chambers. If figure a is overlaid on figure b it, is apparent that the number of apertures in figure a) do roughly coincide with the number of chamberlets in fig. b. From *Cyclorbiculina compressa*, a specimen embedded in araldite (AMNH 43910).

Figure 63 (p. 206).

A reconstructed image of the internal skeleton in a segment of the circular chambers in *Cyclorbiculina compressa*. An apertural and oblique view, where the apertural face has been partially removed. The internal skeleton consists of a broad segment of pillars placed between the apertures, and buttresses confined to the lateral sides of the chambers. (Based on specimen, AMNH 43911).

Figure 64 (p. 207).

a) An A-form embryo of *Archaias angulatus*, broken open to show the bilamellar structure of the test, the smooth inner lining and the outer layer, pitted and tubulated (AMNH 43912).
b) Details of the outer layer of the same specimen. The figure shoves loosely packed, randomly oriented calcite needles, penetrated by tubules.

Figure 65(p. 208).

a) Ornamentation of the outer surface showing both the pits, as rather large depressions and the tubules appear as smaller round openings. (AMNH 43912).

b) A fractured wall showing the bilamellar structure of the embryo (AMNH 43912).

Figure 66 (p. 209).

a) A fractured embryo showing the anastomosing or branching nature of the tubules (AMNH 43912).

b) Details of the inner layer, characterized by densely packed calcite needles, forming a solid wall structure (AMNH 43912).

Figure 60.

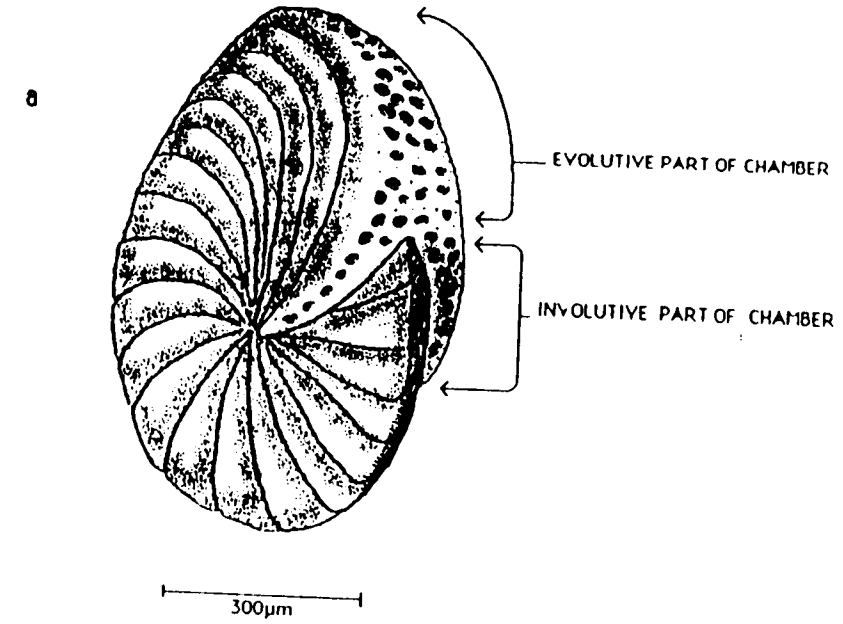

a
EVOLUTIVE PART OF CHAMBER
INVOLUTIVE PART OF CHAMBER
300µm
b

Figure 61.

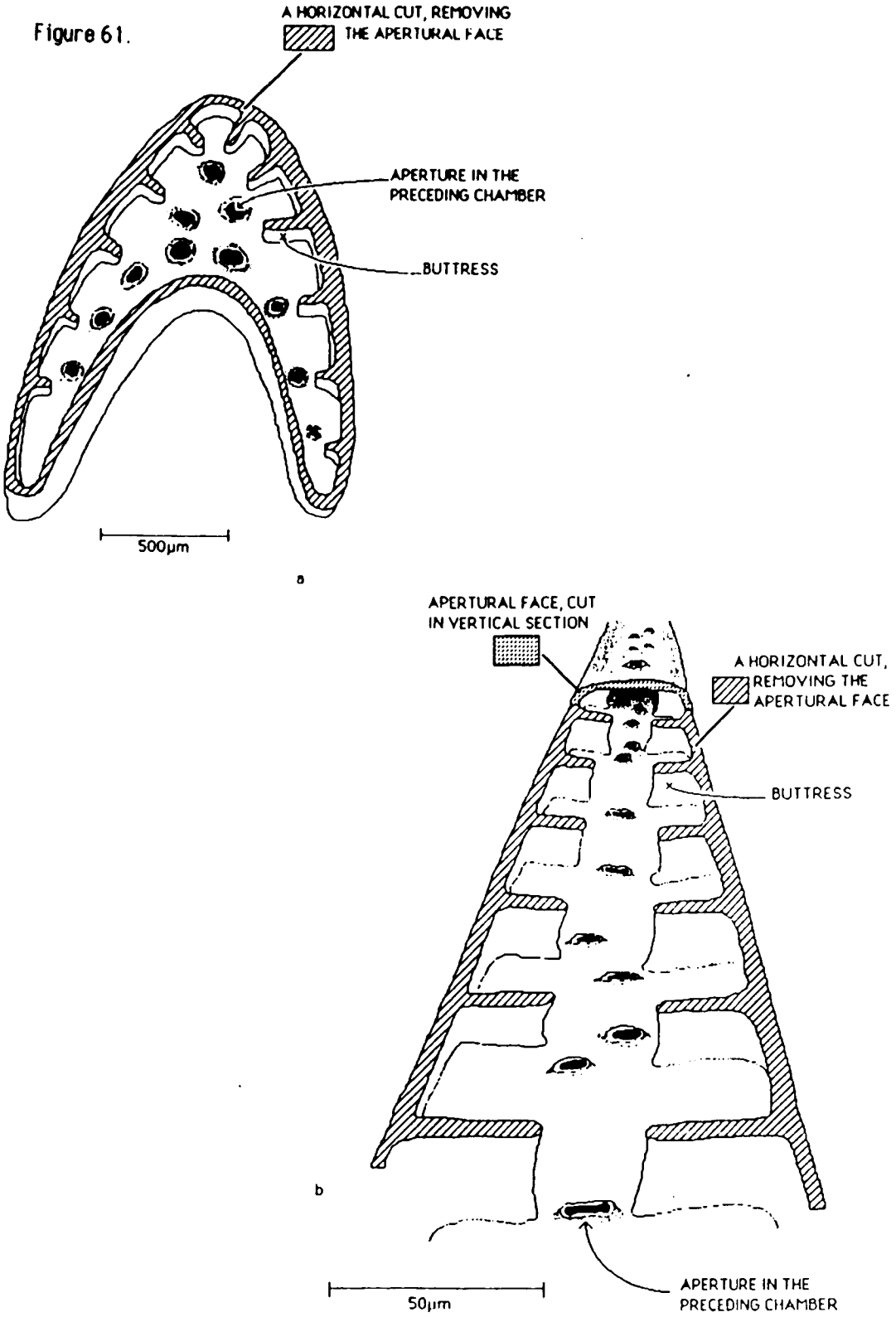
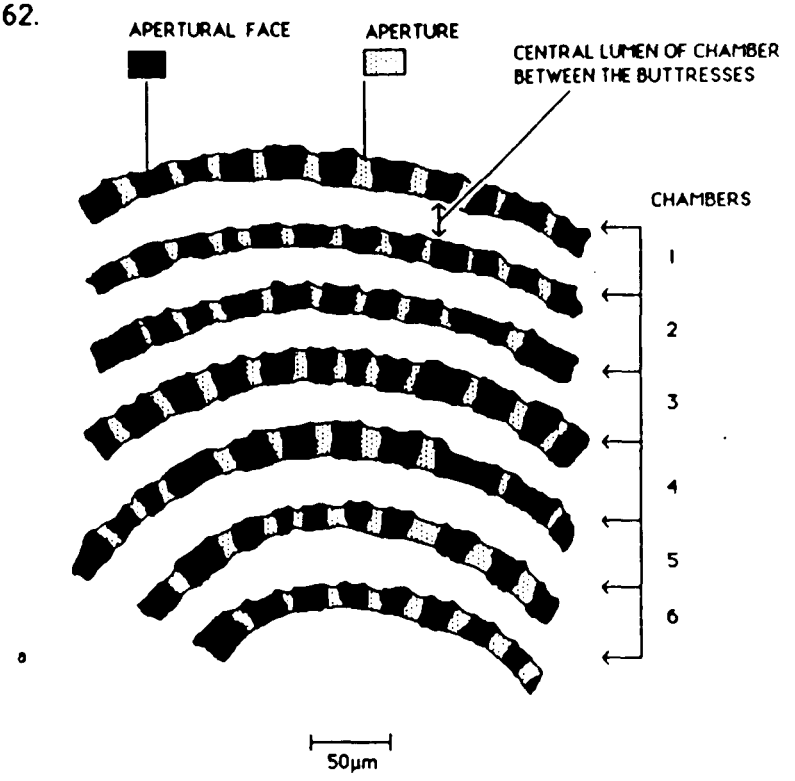

A HORIZONTAL CUT, REMOVING THE APERTURAL FACE
APERTURE IN THE PRECEDING CHAMBER
BUTTRESS
500µm
a
APERTURAL FACE, CUT IN VERTICAL SECTION
A HORIZONTAL CUT, REMOVING THE APERTURAL FACE
BUTTRESS
b
50µm
APERTURE IN THE PRECEDING CHAMBER

Figure 62.


APERTURAL FACE
APERTURE
CENTRAL LUMEN OF CHAMBER
BETWEEN THE BUTTRESSES
CHAMBERS
1
2
3
4
5
6
a
50µm

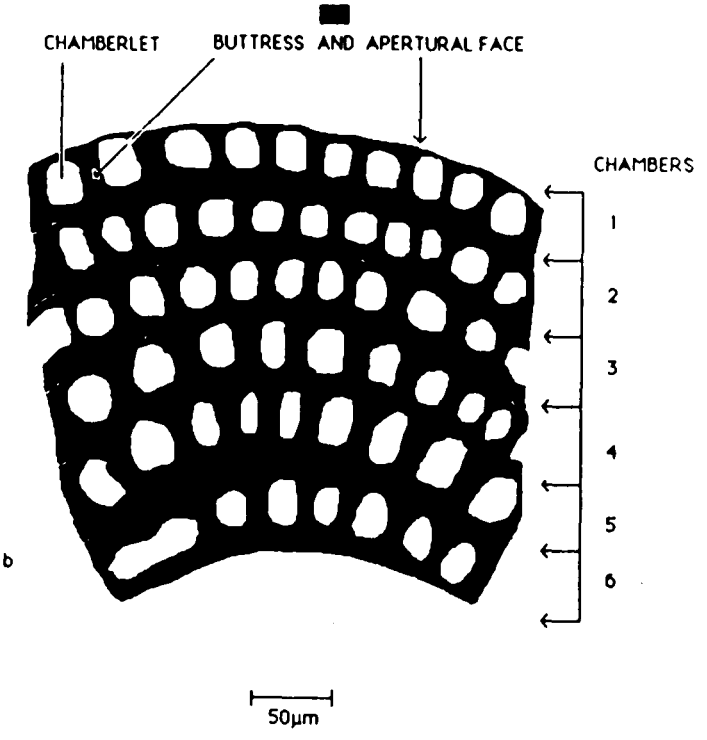

CHAMBERLET
BUTTRESS AND APERTURAL FACE
CHAMBERS
1
2
3
4
5
6
b
50µm

Figure 63.

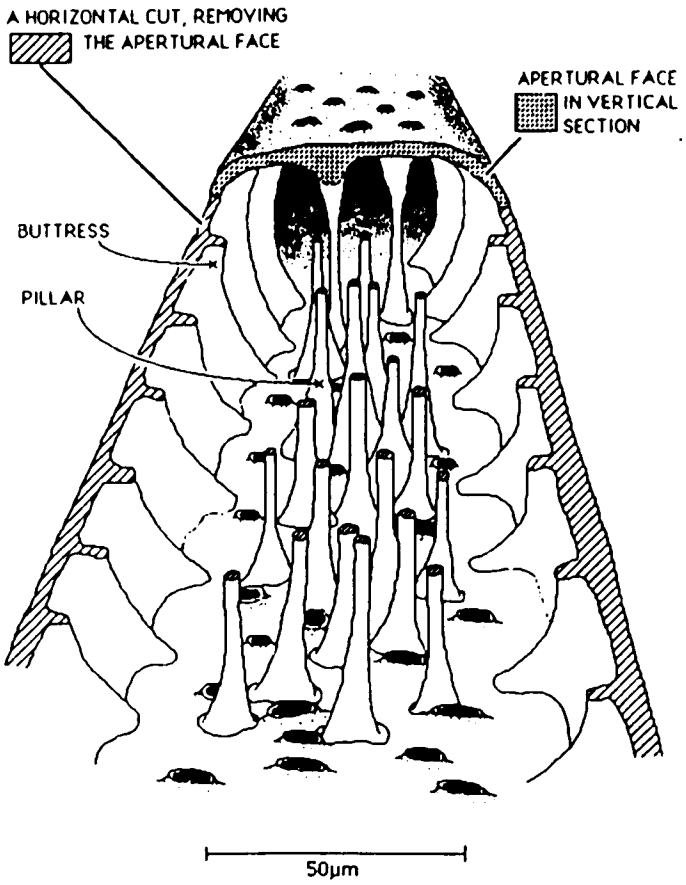
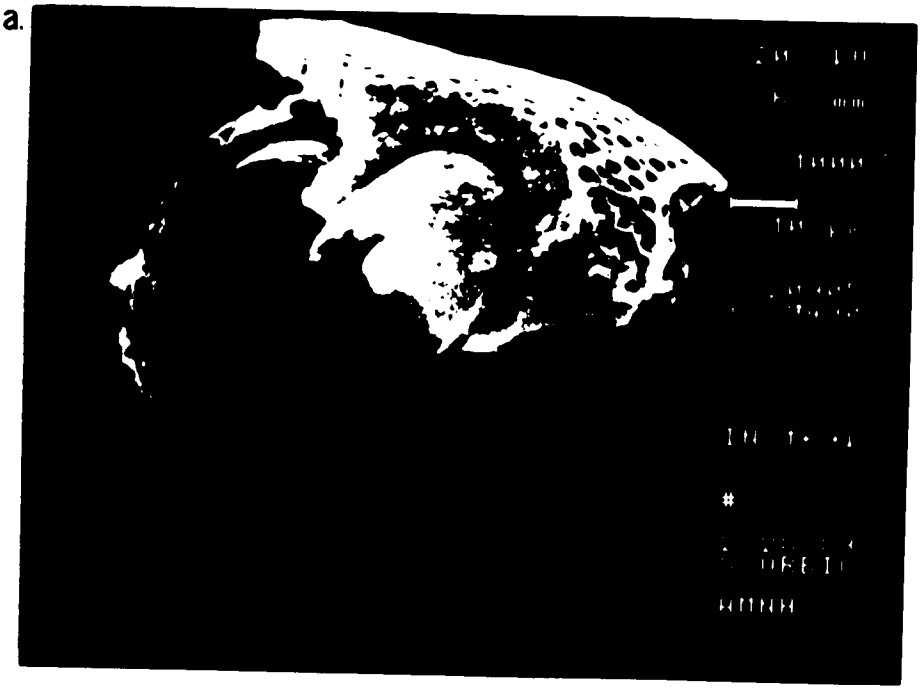

A HORIZONTAL CUT, REMOVING
THE APERTURAL FACE
APERTURAL FACE
IN VERTICAL
SECTION
BUTTRESS
PILLAR
50µm

Figure 64.

a.



b.

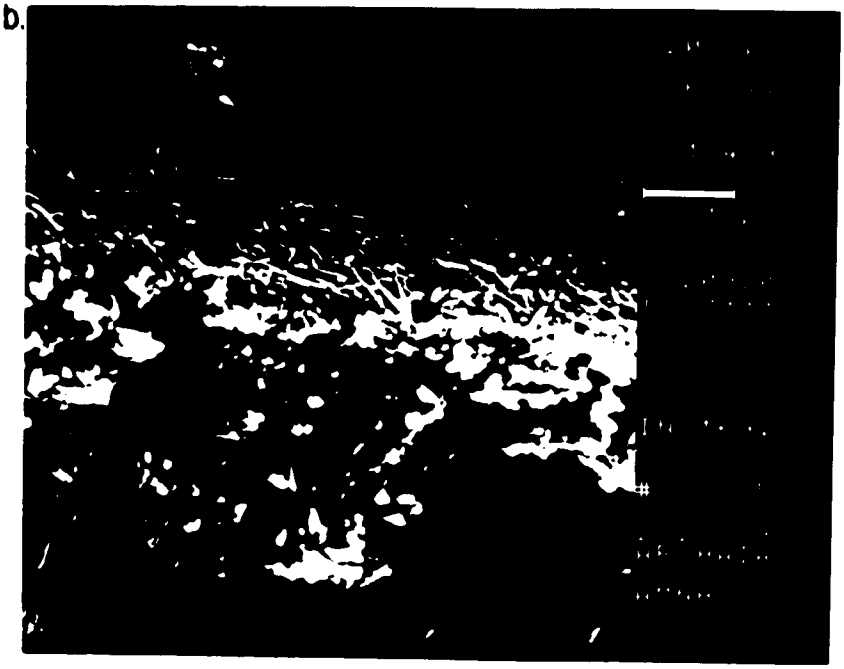
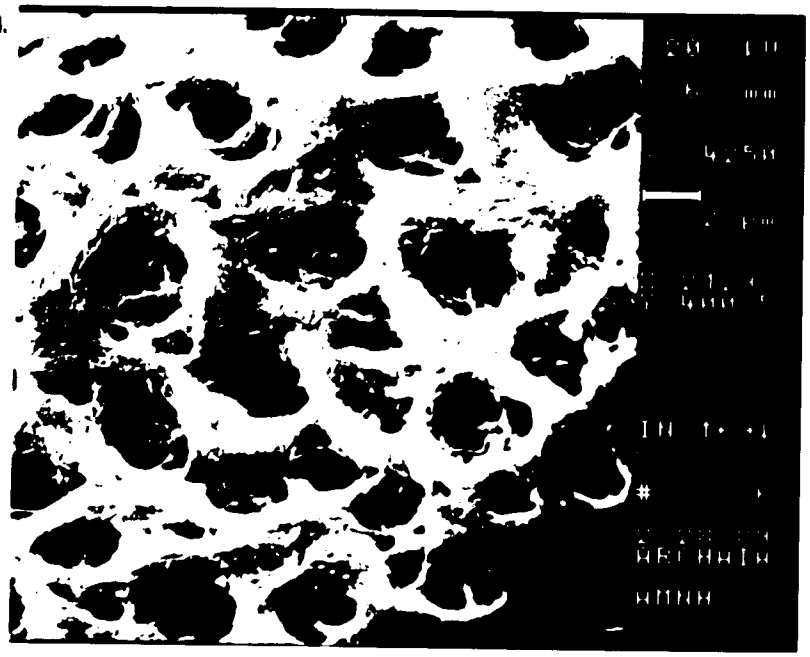


Figure 65.

a.



b.

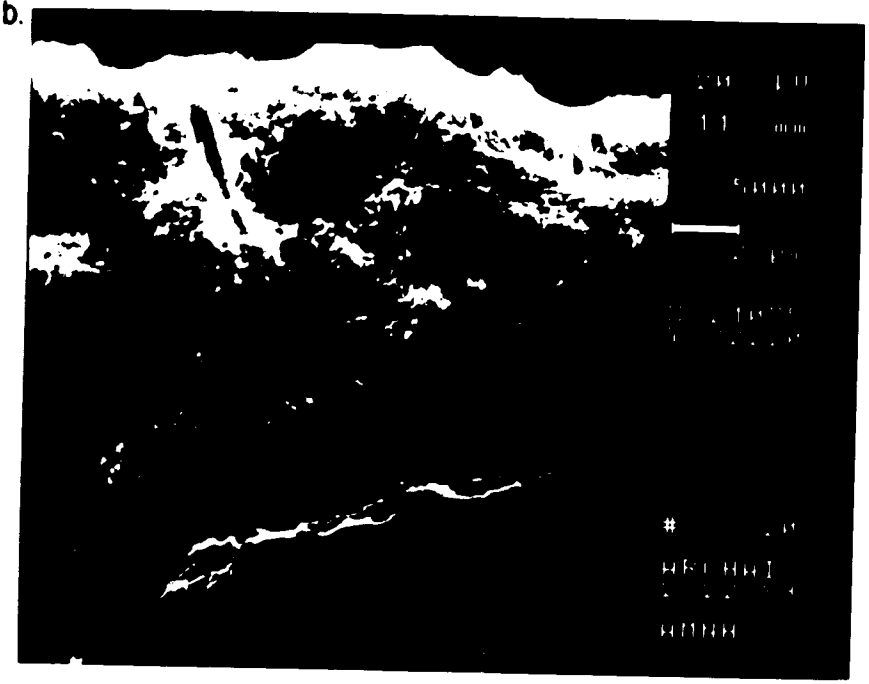
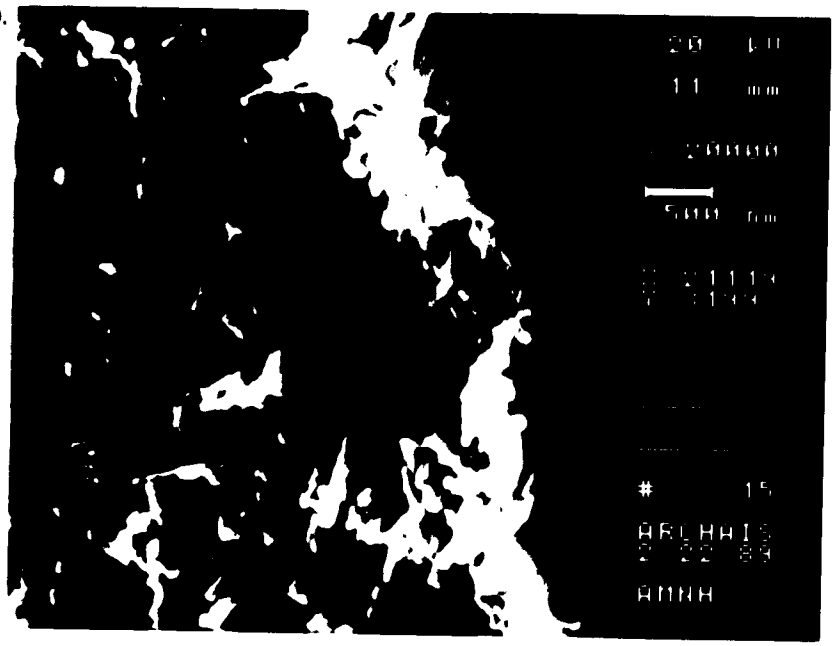


Figure 66.

a.

b.



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