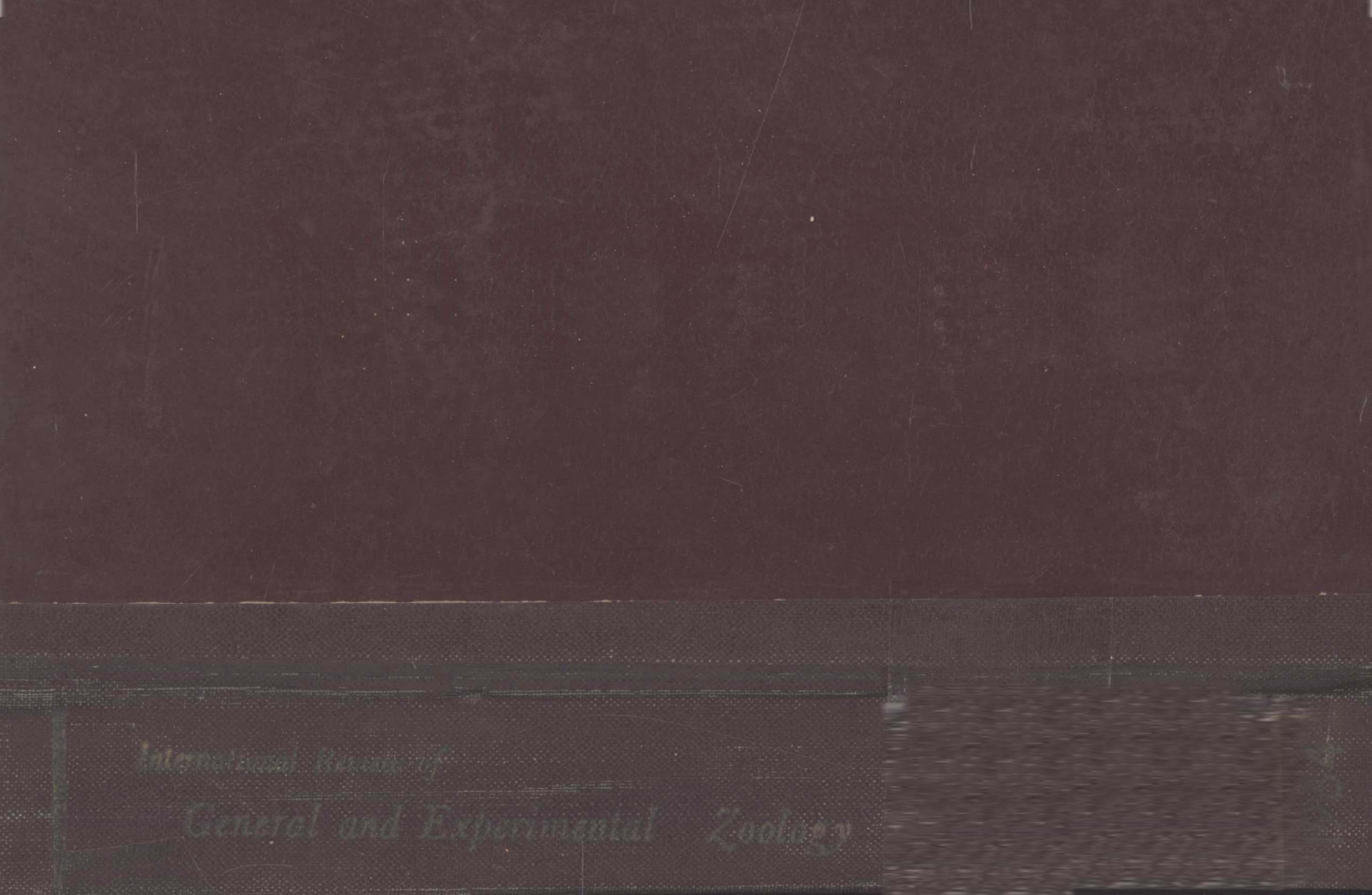
International Review of
General and Experimental Zoology

International Review of
GENERAL AND EXPERIMENTAL ZOOLOGY

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Preface

The International Review of General and Experimental Zoology has been founded on the conviction that there is a need for substantial reviews for the enlightenment of both general and specialist readers in the many classic and more recently expanding fields of zoology. The current emphasis on experimentation has led to the development of many new techniques that could well have wider application were their existence better known. Histochemistry, electron microscopy, and the application of physical methods to biological problems have widened the horizons of investigation. Animal behavior, population, and genetic studies have expanded remarkably. Comparative morphological, developmental, and frankly anatomical studies are now frequently the basis of functional interpretation and experiment. The development of rockets and satellites has enabled the study of animals, including man, under bizarre environmental conditions. Primatology and physical anthropology have become important aspects of the subject now popularly known as human biology. As a result of these expanding activities the older well-known journals are being flooded with contributions, and at least three new biological journals have appeared while this volume was in preparation. Proceedings of symposia and volumes on the deliberations of experts at special meetings abound. It is our contention there is no need to attempt to justify the appearance of a review work of this nature, adding apparently even more to the ever-expanding literature on zoological topics. To make a review of his field of activity is a salutory task for every scientist, and it helps others at all levels and in more ways than one. The reader may criticize the choice of topics, but the editors feel the scope is at least fairly embracing and indicative of the fare to be offered in the future.

October, 1964

Richard J. Harrison
William J. L. Felts

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The Biology of Foraminifera

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I. INTRODUCTION

Foraminifera are single-cell animals which extrude granuloreticulose pseudopodia and construct monothalamous or polythalamous shells (tests) of an organic, arenaceous, or calcareous nature. Such characters serve to distinguish the Foraminifera from other protozoans [*teste* Loeblich and Tappan (1961), for a suprageneric classification of the class Rhizopodea including the order Foraminiferida].

So far as is known, Foraminifera inhabit only marine and brackish waters and have done so continuously since Paleozoic times. Their abundance in fossil and recent sediments, coupled with their small size, has been exploited to great advantage by stratigraphers, with the result that a large amount of information exists on the taxonomy, morphological diversity, and distribution of the group (Ellis and Messina, 1940 *et seq.;* Glaessner, 1945; Cushman, 1948; Sigal, 1952; Pokorny, 1958; Phleger, 1960; Loeblich and Tappan, 1964). The present account, however, is concerned with the much less voluminous, but widely scattered, less familiar literature devoted to the biology of these forms, which have been estimated by Levine (1962) to constitute almost half of all named Protozoa. No attempt will be made to include reference to much of the work embodied in the textbook accounts of Foraminifera by Le Calvez (1953), Jepps (1956), and Grell (1956a). The aim of this article is to present a broad picture of what is known about foraminiferal biology, enlarging on more recent reports and condensing, at times drastically, other aspects which have been discussed elsewhere.

II. FORMS WITH TECTINOUS SHELLS

The adjectives "chitinous" and "pseudochitinous" have been commonly used to describe the organic shells of Foraminifera which neither incorporate extraneous materials to produce an arenaceous shell nor secrete inorganic components to produce a calcareous shell. As there is no convincing evidence of any foraminifer, indeed of any protozoan, secreting chitin, such naked forms—sometimes referred to as allogromoid Foraminifera—are best referred to as tectinous. Tectin is a general term implying a basic composition of glycoprotein (Hyman, 1940), and its application to the allogromoid Foraminifera is consistent with what is known of their shell composition.

Typical animals belonging to this group are *Allogromia, Gromia, Myxotheca,* and *Shepheardella* which are commonly found living among certain seaweeds and in shallow water coastal sediments. All are monothalamous, and some are capable of leaving their shells and building new ones. Although none is known as a fossil, Collinson and Schwalb (1955) indicate that there is great similarity between some of the Paleozoic Chitinozoa and *Gromia oviformis.* This has been refuted (Hedley, 1962a).

Some explanation is necessary for including *Gromia oviformis* in an account of Foraminifera. This animal does not fit nicely into any rhizopod order (Arnold, 1952; Hedley, 1958a, 1962a) and the inclusion of it in the

Testacea, where it is most frequently placed (Deflandre, 1953), is as unsuitable as its inclusion in the Foraminifera (Jepps, 1956). Enigmatic animals like *Gromia* are often useful in comparative studies, so that for the purposes of this account *G. oviformis* will be considered a foraminifer.

A. Morphological Variation

The basic morphological organization consists of a protoplasmic mass surrounded by a tectinous shell, which in some genera may be 1.5 μ thick (*Allogromia*) and in others 10 μ (*Gromia*). The shell is modified at one point, occasionally at more than one, to form an apertural or oral complex through which cytoplasm is extruded as pseudopodia (Fig. 1). So far as is known, in all forms except *Gromia oviformis*, the pseudopodia retreat back over the shell surface to form an extramural layer of cytoplasm.

Great intraspecific morphological diversity in shape and size, even for the same individual, has been described for *Allogromia laticollaris* (Arnold, 1953, 1954a), *Hippocrepinella alba* (Nyholm, 1955), and *Gromia oviformis* (Jepps, 1926; Hedley, 1962a). These accounts all indicate a highly plastic organization which is a little unexpected in forms possessing a relatively thick organic shell. The conditions under which diversification occurs are ill-defined, however, and the reports do no more than merely indicate the variation potential of these animals. Figures rarely exist for the percentage of individuals in any sample or culture which vary from the "normal"; an exception is provided by Arnold (1954a) who found that only 1.4% of 4250 individuals of *Allogromia laticollaris* taken from seven known-lineage cultures varied from the typical ovoid shape with one aperture or "mouth." An extreme example of the speed at which an allogromoid foraminifer can change form is seen in *Shepheardella taeniformis* (Fig. 2), which was observed by the present writer to transform in 50 minutes from an elongate wormlike strand with two "mouths" to a bizarre form with four "mouths."

Attempts to analyze the factors which may influence variability have been undertaken by Arnold (1953, 1954a) with *Allogromia laticollaris* and by Pierce *et al.* (1961) with *Allogromia* sp. Arnold (1953) concluded from 500 agnotobiotic culture experiments performed under a variety of laboratory environments, with normal and abnormal parents, that (a) the number of mouths or apertures does not vary with the "environment"; (b) progeny with many apertures appear in a fairly constant, though relatively low, frequency in most lineages; (c) "this variation is passed on from one generation to the next in some manner, although it, like haemophilia and colour-blindness in man, is not always expressed in each generation;" and

(d) variation in general shape simply reflects apertural or oral abnormalities, for example, forms with three mouths are triangular and those with two mouths are fusiform. In another species of *Allogromia,* the morphological state is affected by the type of culture in which the animals are grown (Pierce *et al.* 1961). Apparently when this *Allogromia* is cultured under agnotobiotic conditions the individuals are predominantly "normal" forms, that is, ovoid with one aperture, whereas when the cultural associates

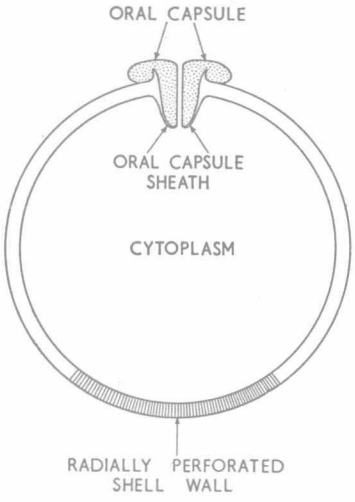

Fig. 1. A diagrammatic representation of *Gromia oviformis* showing the relationship between the shell wall, the oral capsule, and the oral capsule sheath. Pseudopodia are extruded through the aperture in the oral complex. The shell wall is perforated only in *G. oviformis* and not, so far as is known, in the allogromoid Foraminifera. (From Hedley and Bertaud, 1962.)

are restricted to *Dunaliella parva, Nitzschia acicularis,* and a number of unidentified bacteria, the typical forms undergo transformation into a mixture of morphological types resembling other allogromoid genera. Furthermore, when normal forms of *Allogromia* sp. are grown in synxenic culture, together with two bacterial species, the majority assume a form reminiscent of *Shepheardella.*

Little is known about intraspecific variation in allogromoid Foraminifera, and further understanding would seem to depend on the establishment of cultures in chemically or biologically defined media. So far this has presented real difficulty and will be discussed in a later section.

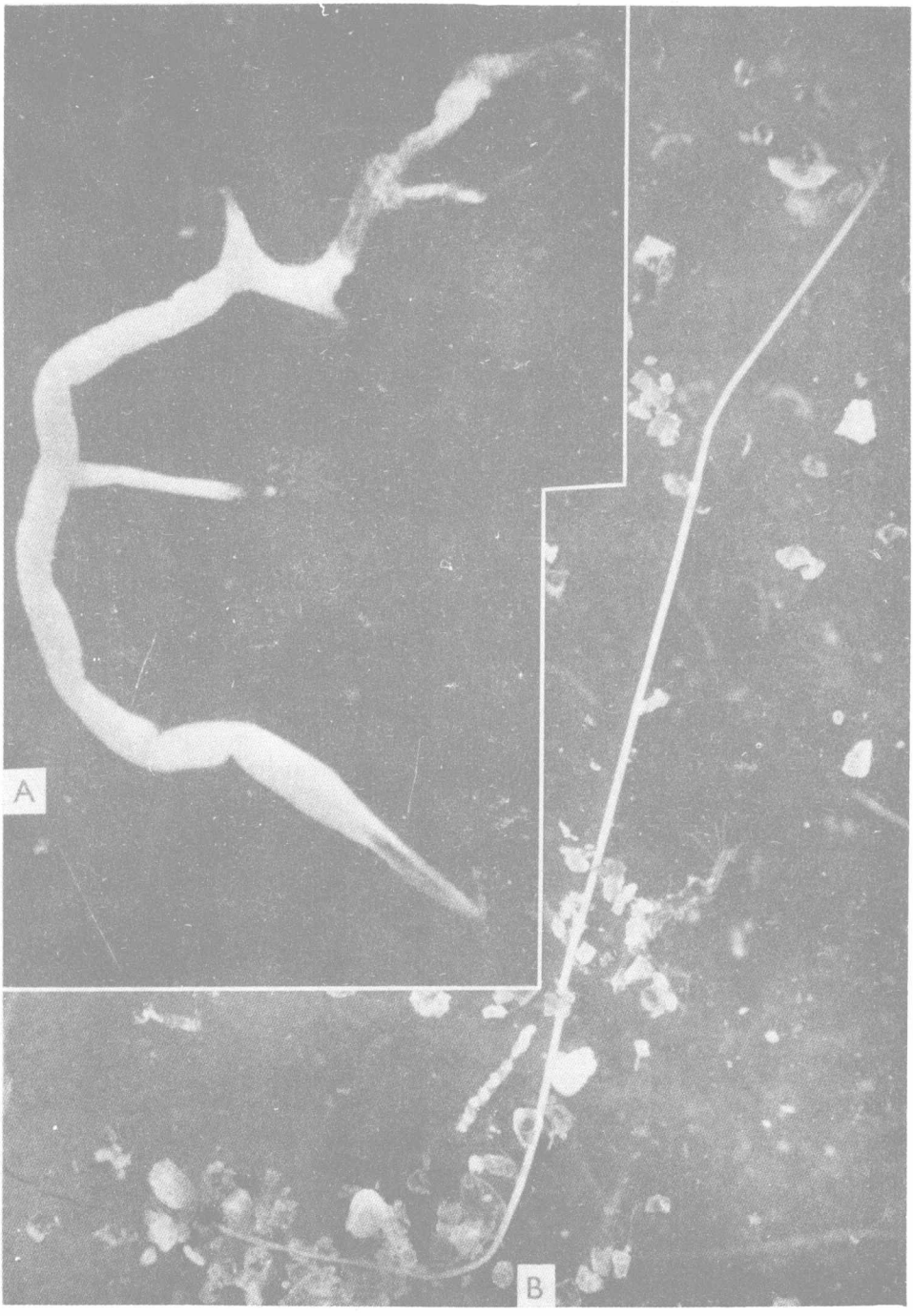

Fig. 2. Living *Shepheardella taeniformis* photographed in culture dishes; the elongate wormlike form (B) with two oral regions, one at each end, changed to a form (A) with four oral regions, from which pseudopodia were extruded, in 50 minutes. × 25. (Hedley, unpublished.)

B. Shell Structure and Composition

1. Shell Wall

Details of shell structure are virtually unknown for all tectinous forms except *Gromia oviformis,* which is atypical in having a perforate shell (so far as is known, the shells of other genera are imperforate). This may be correlated with another difference between *G. oviformis* and other allogromoid forms. In the imperforate form such as *Allogromia* (Arnold, 1948), there is a flow of protoplasm, when pseudopodia are extruded, from the oral region back and over the shell to form a surface film or extramural layer of cytoplasm. This film keeps the outer surface of the shell clean and free from settling microorganisms; in *G. oviformis,* where no such surface film is found, the cleansing operation may be carried out by extensions of the cytoplasm passing through the shell perforations to the outside surface.

The radially striated nature of the shell in *G. oviformis* noted by Jepps (1926) and de Saedeleer (1934) is seen from electron microscope studies to be due to unbranched canals going straight through an otherwise structureless shell (Hedley and Bertaud, 1962). A lack of structure has also been noted in the shell wall of *Hippocrepinella* (Nyholm, 1955). In *G. oviformis,* the shell is isotropic and composed of protein together with acid mucopolysaccharide, lipid, and organically bound ferric iron (Hedley, 1960a). The ferruginous nature of the transparent shell is reminiscent of the iron-containing sheaths, tubes, or capsules of the "iron bacteria" (Pringsheim, 1949a,b) and also of the colorless sheaths or envelopes of some "iron flagellates" (Pringsheim, 1946). It is not known whether the presence of organically bound iron in any of these structures is due to a direct reaction between the iron in the medium and certain shell components or whether the organisms themselves secrete or deposit iron in their coverings. Experiments of a histochemical nature designed to elucidate this point (Hedley, 1960a) show that when sections of *G. oviformis,* from which the iron has been removed by ethylenediaminetetraacetic acid (EDTA), are immersed in sea water reinforced with iron, the shell takes up as much iron as found in normal shells of fresh living animals only when the iron concentration of the medium is approximately 200 mg Fe per liter. It is argued that iron saturation of the shell to this concentration is attained only after immersion in a medium which has an iron concentration four hundred times as great as that of sea water (500 μg Fe per liter) and that under normal living conditions a reaction between the iron in sea water and the shell is unlikely to be responsible for its ferruginous nature. This conclusion

may be criticized on the grounds that the chemical environment in which *G. oviformis* lives is difficult to define, as the animal is found in the holdfast of kelp, on the undersurfaces of stones, and on the surface of sandy and muddy sediments. In these micro-environments there may well be large changes in oxidation-reduction potential in a very short distance. Nevertheless, whatever the physicochemical characteristics of any niche occupied by *G. oviformis*, an iron concentration greater than 500 μg Fe per liter will not be encountered. These observations support the view that the deposition of iron in the shell is a normal physiological activity. Confirmation of this could probably be obtained by experimentation involving trace element techniques in which labeled particulate food would be offered to *G. oviformis*.

It is also noted (Hedley, 1960a) that a great reduction in the amount of iron which the shell takes up from iron solutions occurs under conditions of low pH and after sections have been methylated. Under both conditions carboxyl groups are unreactive. Other acidic groups with which iron may form non-ionizing complexes—for example, phosphoric acid groups and sulfuric acid ester groups—may be involved, but the low uptake of iron with low pH and prior methylation leads to the view that most of the iron is bound through carboxyl groups. The nature of the union between the iron and shell components is seen to be similar in some ways to that found in leather, where heavy metal complexes are found. Whereas the salts of many metals can act in producing a leather, broadly defined, the best known inorganic tanning agents are the salts of chromium, aluminum, and iron. Of these, chromium is found to be the most satisfactory in so far as industrial processes are concerned, whereas in *Gromia* and perhaps elsewhere in bacterial and algal forms, ferric iron, acting as an inorganic tanning agent, may be acting as a stabilizing or tanning agent of the shell, envelope, or sheath.

In the ultrastructure of *Gromia,* Hedley and Bertaud (1962) found a "membrane system," composed of between eight and ten units, on the inner surface of the shell (Fig. 3A). Each membrane or unit consists of minute cylinders approximately 100 Å in diameter and up to 200 Å in length, organized in hexagonal array (Fig. 3B). The axes of the cylinders lie perpendicular to the membrane with a center-to-center spacing of about 210 Å. The wall thickness of the cylinders is about 30 Å and each is connected to its neighbors by septa 20–30 Å thick. So far as is known, these honeycomb membranes are unique and without homolog, and the question raised is whether they are an integral part of the shell, a shell percursor, or some form of plasma membrane. It may be noted that a conventional cell mem-

brane or standard unit membrane, such as is found in all protozoans studied so far (Grimstone, 1961), has not been recognized in *Gromia.* A superficial similarity in appearance and order of size exists between the honeycomb membranes in *Gromia* and the outer membrane of Rous sarcoma

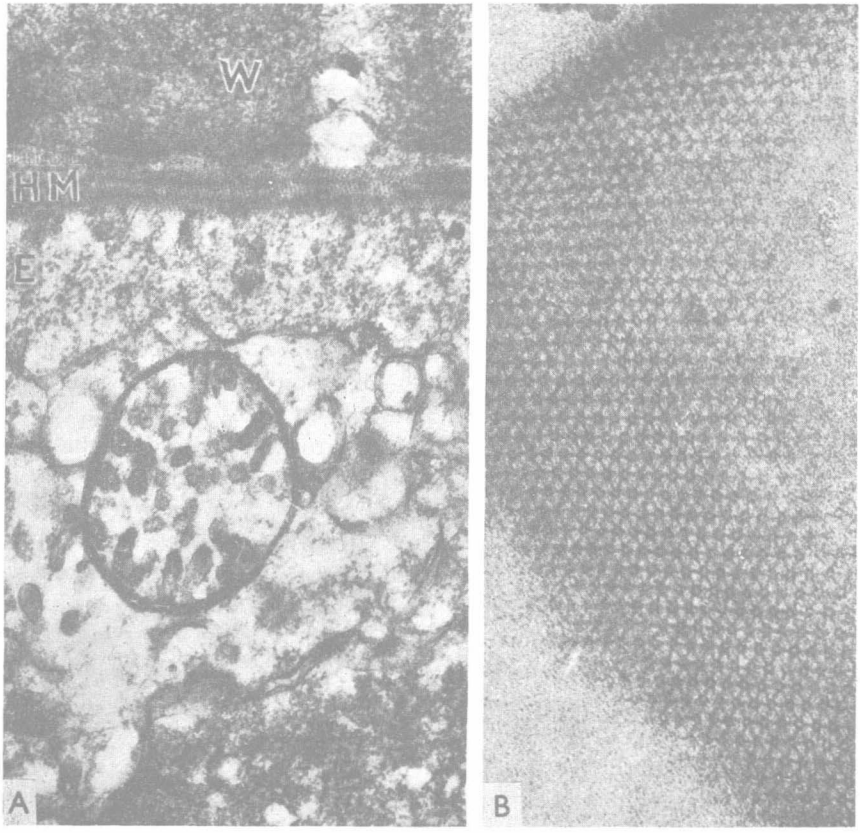

Fig. 3. A, Electron micrograph showing the honeycomb membranes (HM) between the peripheral region of the cytoplasm (E) and the shell wall (W) in *Gromia oviformis.* × 39,000. B, Oblique section of a honeycomb membrane showing the minute cylinders organized in hexagonal array. × 137,000. (From Hedley and Bertaud, 1962.)

virus, the cell membranes in chicken liver cells, and human or guinea pig erythrocyte ghosts which have been treated with saponin (Dourmashkin *et al.,* 1962). The *Gromia* structure differs from these in its center-to-center spacing and in the presence of linked septa which make it the more complex

structure. Nevertheless, the possibilty that this membrane system in *Gromia* is an unconventional plasma membrane cannot be disregarded. One would like to know if such honeycomb membrane systems were present in all tectinous Foraminifera and formed an essential component of the basic morphological organization in animals of this type; so far no comparable structure has been found in *Allogromia laticollaris,* where the cytoplasmic boundary is a conventional or standard unit membrane located right against the inside surface of the shell (Wohlfarth-Bottermann, 1961; Hedley and Bertaud, unpublished data).

2. Oral Region

The presence of a distinct apertural or oral region, also known to some authors as the entosolenion tube, stomostyle, or pharynx, has not been described for all tectinous Foraminifera (Cushman, 1948, plate 8). This, however, may reflect inadequate observation or technique and it is likely that when certain forms are rediscovered and redescribed they will be seen to conform broadly to a morphological plan which includes a distinct oral region (Fig. 1). Such structures are present in *Gromia oviformis* (Arnold, 1952; Hedley, 1960a), *Allogromia gracilis* (de Saedeleer, 1934), *A. lagenoides* (Cushman, 1948), *A. laticollaris* (Arnold, 1948), *Rhyncosaccus immigrans* (Rhumbler, 1894b), *Iridia lucida* (Le Calvez, 1936), and *I. serialis* (Le Calvez, 1935). Furthermore, if one disregards the arenaceous shell of certain arenaceous monothalamous Foraminifera, it is evident that they possess a structural organization like that of the tectinous forms with a distinct apertural region; a close relationship between the allogromoid and monothalamous arenaceous Foraminifera is thus indicated (Fig. 5). The arenaceous forms which have distinct oral regions and serve to illustrate this point are *Saccammina sphaerica* (Rhumbler, 1894b), *Pelosphaera cornuta* (Hedley, 1960b), *Saccammina alba* (Hedley, 1962b), and *Astrorhiza limicola* (*Hedley,* unpublished, see Fig. 12A and Section VI,B).

Virtually nothing is known about the detailed structure of any of these oral complexes, except that of *Gromia,* which becomes completely everted when pseudopodia are extruded (Fig. 4). The nature of the material which permits such transformation of shape is a gel, composed mainly of acid mucopolysaccharide (Hedley, 1960a), with an ultrastructure which is either tubular or fibrillar (Hedley and Bertaud, 1962). In all the oral complexes examined so far by the present author—*Allogromia, Saccammina, Pelosphaera,* and *Astrorhiza* (Fig. 11A)—a similar composition to that of *Gromia* has been found and a similar eversion when pseudopodia are extruded is forecast. The oral complex in all these forms is far from a simple