UTRECHT MICROPALEONTOLOGICAL BULLETINS

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Project no. 1

DEPTH-RELATIONS OF RECENT LARGER FORAMINIFERA IN THE GULF OF AQABA-ELAT

15

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DEPTH-RELATIONS OF RECENT LARGER FORAMINIFERA IN THE GULF OF AQABA-ELAT

I.G.C.P. Project no. 1

Z. REISS, S. LEUTENEGGER, L. HOTTINGER, W. J. J. FERMONT,
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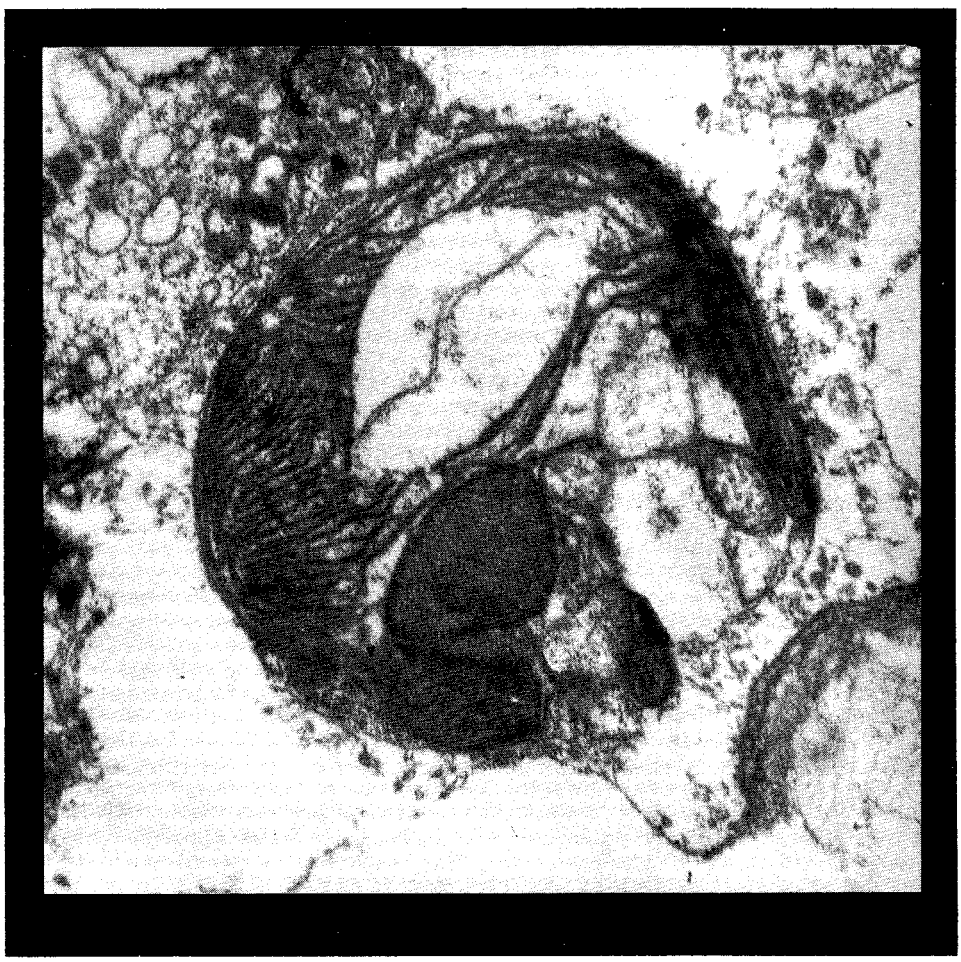

Plant-symbiont in the cytoplasm of a foraminifer — a light-dependent factor in the depth distribution of larger foraminifera?
(TEM by H.-J. Hansen of *Amphistegina lessonii* from the Gulf of Elat; x 21,830)

Intensive research on the Recent Foraminifera in the Gulf of Aqaba-Elat and their physico-chemical environment is being carried out for the last decade by groups of specialists from the Universities of Jerusalem, Basel, and Copenhagen. The results obtained hitherto indicate that this part of the northern Red Sea may represent a model-area of prime interest for a better understanding of foraminiferal distribution and, therefore, for paleontological interpretations of fossil faunas.

The involvement in the study of this model area of the Utrecht University group is based on the latter's participation in the International Geological Correlation Program, Project 73/I/1 "Accuracy in Time". Since many biostratigraphical correlations are based on the evolution of measurable parameters of larger foraminiferal species groups, an investigation of possibly environment-dependent morphological changes in living Foraminifera was urgently needed. A recently advanced theory that proloculus-size might increase at greater water-depth was one such topic.

Since the thermo-, halo-, and pycnoclines in the Gulf of Elat are rather insignificant, changes with depth in morphology and distribution of foraminiferal species must be governed by depth-related factors other than temperature, salinity or density. Direct or indirect influence of light penetration and types of substrate are thought to control in the Gulf the depth-distribution of the Soritidae and of the investigated species of *Borelis, Amphistegina, Planorbulinella, Operculina, Heterostegina,* and *Heterocylina.* Light may equally influence the intraspecific variation in several of these groups. Major changes seem to take place in the uppermost 80 meters of the depth-profiles.

For the I.G.C.P. project satisfactory estimates can be made now of the range of variation that mean values of such "evolutionary" features as proto-conch diameter and nepionic arrangement may show at one time level, as a consequence of environmental control.

The volume summarizes the present-day knowledge on the distribution and morphology of the larger Foraminifera of the Gulf, on their reproduction cycles, symbionts, and their possibly symbiont- and depth-related variability in stable oxygen-isotope ratios.

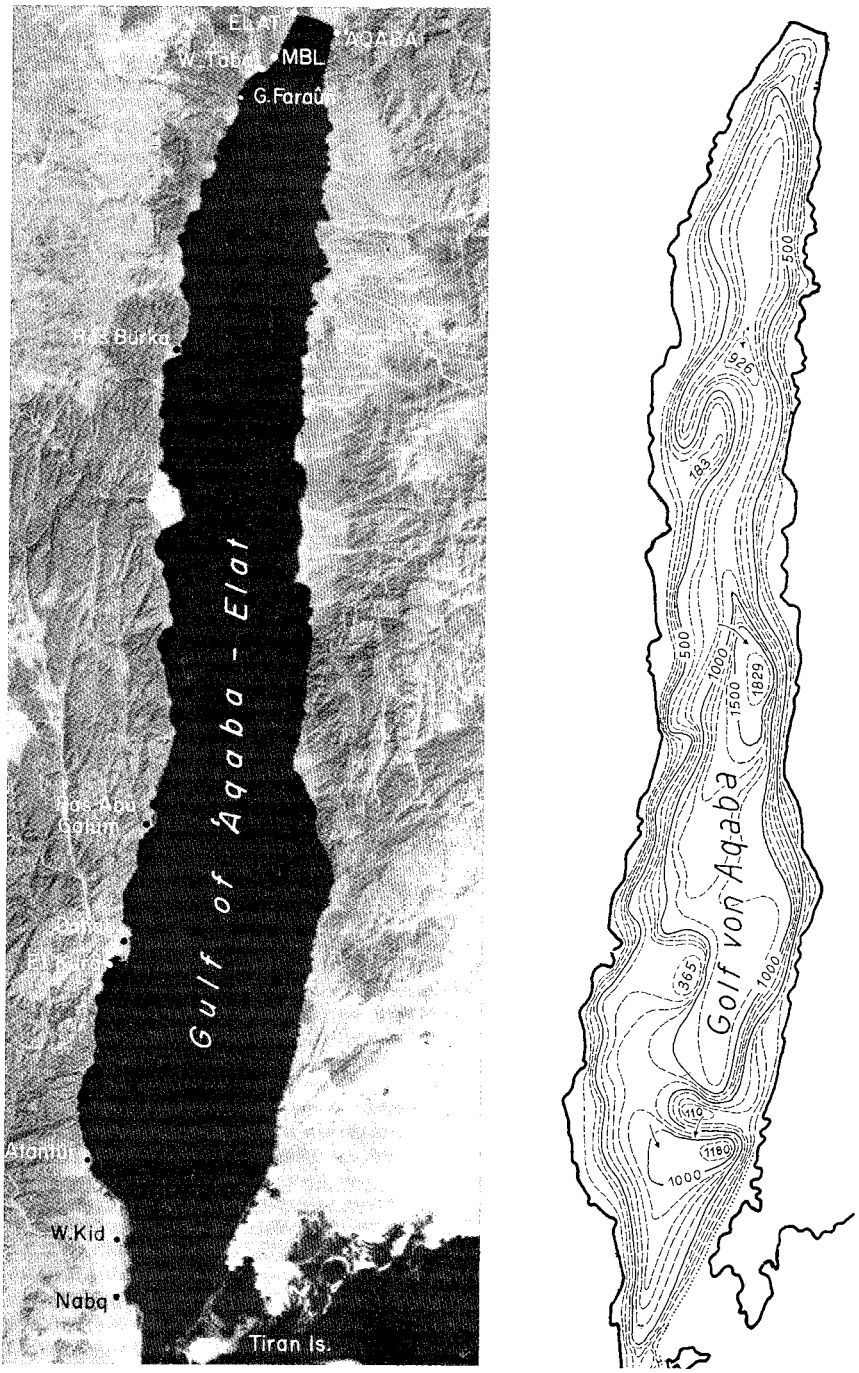

Fig. 1 Gulf of Aqaba (Elat). Location map, satellite photograph (left) and bathymetric map (right) (reproduced from M. Pfannenstiel in: Mergner and Schuhmacher, 1974).

FORAMINIFERAL RESEARCH IN THE GULF OF ELAT-ÁQABA, RED SEA – A REVIEW

Z. REISS

INTRODUCTION

The Foraminiferida are well-known indicators for the reconstruction of ancient marine environments. Physico-chemical factors of the paleoenvironments are inferred from a comparison of fossil assemblages with living populations and Recent thanatocoenoses. Since very little is known hitherto on the biology and functional test-morphology of this otherwise well-documented group of protistans, distributional patterns of living foraminifera are attributed to ecological factors mainly by empirical correlation with observed environmental characteristics of presence, absence, dominance and diversity of taxa.

Studies on the distribution of Recent foraminifera have been carried out in various places of the world and the patterns obtained have been interpreted mainly as a function of temperature, salinity, and substrate, as well as – to a lesser extent – of such factors as pH, nutrients, food requirements, and light. All distributional studies indicated for many taxa a definite depth pattern, usually interpreted as a result of temperature-, salinity- and water energy-gradients, as well as of changes in the nature of the substrate. However, in many cases, in greatly different seas from a physico-chemical point of view, bathymetric zonation boundaries occur at or around certain depths which can not be directly correlated in a simple manner with the positions of temperature, salinity or energy boundaries.

From earlier hydrographic work in the Gulf of Elat or Áqaba (for references see Oren, 1962, Klinker et al. 1977) it has been known that no significant thermocline, halocline or pycnocline are present in the warm and highly saline waters of this narrow and deep Gulf. Work by Said (1949, 1950a, b), Reiss (1950), Reiss et al. (1961), Avnimelech (1959) and Por and Segev (1966) indicated that the foraminiferal faunas in the Gulf are abundant, highly diversified, and depth-distributed. There is a wide spectrum of substrates on which foraminifera live and a variety of different, easily accessible environments are available for study.

Thus, the Gulf of Elat seemed of particular interest to studies of distributional patterns of foraminifera in tropical regions.

For these reasons and stimulated by a reconnaissance survey with W. W. Hay (University of Miami) during his visit to Israel in 1968, a research program on the Foraminiferida of the Gulf of Elat was initiated by the author in 1969. The project was soon joined by H.-J. Hansen (University of Copenhagen), L. Hottinger (University of Basel), and C. W. Drooger (University of Utrecht), as well as by Israeli and foreign graduate students, and developed rapidly into a more ramified "Micropaleontology-Ecology-Paleoecology" Program dealing, in addition to foraminifera, with pteropods, coccolithophorids, as well as with some corals and molluscs.

With regard to the foraminifera, *the major aims* of the project were outlined as follows:

1. Determination of the qualitative and quantitative distributional patterns of bio- and thanatocoenoses of benthonic and planktonic species in the Gulf, in an attempt to construct an empirical ecological model.
2. Correlation of the patterns obtained with measured ecological parameters in order to determine the major factors affecting foraminiferal distribution, both geographic and bathymetric.
3. Determining the adaptive significance of foraminiferal shell-morphology and its possible significance in evolution.
4. Determining the taxonomic levels at which comparison of Recent models with ancient analogues can be made.

In order to attain these goals the following parts of the project were initiated:

a. Sampling of living populations and of sediment assemblages by diving and by means of gear from board ship, from shoreline to great depths, in selected areas, representing different environments.

b. Qualitative study of assemblages, at generic and specific levels, involving a detailed revision of the most important species by means of various methods, like scanning- and transmission-electron microscopy and biometry.

c. Quantitative studies of assemblages including the application of multivariate analysis.

d. Measurements of physico-chemical parameters.

e. Cytological studies on selected species in order to determine nutritional patterns, especially those based on symbiosis, as well as in order to better understand relationships between protoplasm and test.

f. Laboratory experiments on living species.

In addition, an interdisciplinary Data Collecting Program in the Gulf of Elat (DCPE) is being carried out since 1974 under the author's direction,

by the Hebrew University's H. Steinitz Marine Biological Laboratory in Elat, with the participation of a number of scientists and graduate students from the Hebrew University, the Weizmann Institute of Science (Rehovoth), the Israel Oceanographic and Limnological Research Corp., Ltd. (Haifa) and from abroad. This program has provided by now important information on various physico-chemical parameters in the Gulf, such as current regime, nutrient and biomass distribution, primary production, bottom topography and subbottom structure, as well as several thousands of stratified net- and water-samples for plankton studies, carried out by various scientists and students. The foraminiferal research program and the DCPE are thus closely interrelated.

A brief summary of the results obtained hitherto from studies on the foraminifera in the Gulf of Elat is given further below and additional results are published in the present U.M. Bulletin.

In order to provide a background for the interest of the results that have become available through the investigation of the foraminifera in the Gulf of Elat, a brief summary on the general characteristics of the Gulf is deemed appropriate.

THE GULF OF ELAT

Part of the Syrian-African Rift System, the 170 km long, 14–25 km wide, and up to 1,830 m deep Gulf of Elat is a nearly enclosed segment of the Red Sea, from which it is separated by a 252 m deep, narrow sill at the Straits of Tiran. Geological and geophysical evidence indicate that the Gulf of Elat is a tectonic trough, produced by left-lateral strike-slip movement along the Jordan-Dead Sea rift and by the pulling apart of the bordering land-masses (Freund, 1965; Freund, Zak and Garfunkel, 1968; Garfunkel, 1970). The Gulf as a morpho-tectonic branch of the Red Sea has originated in Late Cenozoic times.

No true coastal plain is present, the shelf is verry narrow, while the shores and submarine slopes are extremely steep. Alluvial fans extend from the mountains to the water's edge and deltas occur in places at wadi mouths.

The bathymetry is still incompletely known, the most recent published maps being those by Allan and Morelli (1971) and by Pfannenstiel (in: Mergner and Schuhmacher, 1974), as well as – with regard to the Straits of Tiran – by the Israel Min. of Transport (1974) and by J. Hall (1976). A geophysical and bathymetric survey has been carried out recently by Z. Ben-Avraham (IOLR, Haifa and Weizmann Institute of Science), but its

results are still unpublished.

The climate of the area is arid and hot, the winds being prevailing northerlies. Evaporation is extremely high, particularly in winter, and reaches nearly 4 m per year (Assaf and Kessler, 1976), thus exceeding by far the yearly precipitation of about 25 mm on the average. No rivers flow into the Gulf, but occasionally fresh water is brought in by winter-floods.

The highly saline waters: 40.2‰ to more than 41.0‰ and even 43‰ near reefs (Oren, 1962; Emery, 1963; Friedman, 1968; and Klinker, Reiss et al., 1977) are warm throughout the year, the minimum temperature in the Gulf being 20.0°C and the seasonal and bathymetric variation not exceeding 6°C. Oxygen content is high throughout the column and ranges between 3.75 to more than 6.0 ml/l, the pH range being between 8.0 and 8.6. Tidal amplitudes are less than 1 m.

The circulation pattern has been described by Klinker, Reiss et al. (1977). Throughout the year, warm, relatively lower salinity waters from the Red Sea enter the Gulf above the sill of Tiran and flow northwards, against the prevailing winds, because of evaporative loss and because of buoyancy flux. As these waters proceed northwards, they become rapidly cooled and more concentrated and thus a return flow to the south of denser waters into the Red Sea is produced beneath the inflow. In summer (April-October) an additional, and perhaps transient, inflow of higher salinity waters from the Red Sea has been observed at sill depth beneath the main outflow. The region where the main return flow is initiated separates – from a hydrographic point of view – a northern from a southern basin in the Gulf. The inflow appears (due to Coriolis effect) to be more important on the Arabian side and the outflow more important on the Sinai side, resulting in a counterclockwise circulation pattern in horizontal plane of the upper waters. Exchange of deep waters between the Gulf and the Red Sea seems to take place only in summer and this to a small extent only. Circulation of the deep waters in a clockwise direction in vertical plane (as seen from the west) is indicated and is due to either wind-stress or to the deep inflow in summer, or to both. Wind-driven transport of surface waters mostly from north to south involves only a few decimeters (Mergner and Schuhmacher, 1974). Estimates of volume transport at the Straits of Tiran vary between 22,000 m^3/sec for the upper 150–200 m to 70,000 m^3, and residence time of the waters in the whole Gulf is estimated from winter observations to be in the order of not more than one year. Heat flow through the straits in summer is 36 W/m^2 and in winter 207 W/m^2 (Assaf in: Klinker et al., 1977).

Nutrient levels and primary production in the open waters of the Gulf are low: PO4-P between 0.10 and 0.25 μg at/l, NO3-N 0.5–2.0 μg at/l,

chlorophyll a up to 0.4 μg/l and carbon-uptake less than 1 mg C/m^3/h (Klinker, Reiss et al., in press; I. Levanon, pers. com., 1976). Biomass values are in the range of 20 to 100 ml/1,000 m^3 on the average in 65 μ net-hauls.

Illumination is very strong and – due to rather low productivity and lack of significant amounts of abiogenic material in suspension – the waters are clear and blue. Blooms of photosynthetic micro- and nannoplankton down to depths of nearly 400 m (B. Kimor, A. Winter, pers. com., 1976) indicate that light penetration is considerable.

Coral-reefs in the Gulf (the northernmost in the world) are of fringing and patch type and mangrove forests occur on the Sinai side.

The reef-environments are extremely rich and appear to represent a semi-closed system in which many animal groups (including foraminifera) rely on a symbiont-strategy of life and form specifically adapted, behavioural communities. For general descriptions of the reefs see Friedman (1968), Mergner and Schuhmacher (1974) and references therein.

Spurs and grooves dominate both on the seaward and lagoonal sides of the fringing reef, making an angle of about 25° towards the north with the reef trend, thereby enabling the coral-colonies to grow into the main direction of waves and current flow. Water movement seems to be a fundamental factor in the biophysiographic zonation of the reef. As a result of the steep slopes, fringing reef-growth is restricted to a narrow strip along the shore line. The volume of reef talus produced is insufficient to form a shallow foundation for seaward expansion. Clastic material transported from the wadis mainly by seasonal floods inhibits in places the reef growth. Prolific reef growth takes place, however, immediately outside the alluvial fans. The reef edge is generally about 130 m from the shore. Large portions of the reef are now dead, with the exception of the seaward side and of the spurs. On reef flats and on backreef areas, coralline algae are abundant.

Lowering of the erosional base-level during the last Glacial together with possible increase in precipitation and consequent intensive erosion have led to the formation of canyons down to 130 m below present sealevel. The rise in sea-level during the Holocene has caused drowning of these canyons to form deep, narrow, occasionally meandering and bifurcating embayments which are 20 to 30 m deep (so-called sharms). Newly formed fringing reefs overlie pre-existing alluvial fans and are cut by furrows across the reef flat which are due to the fluvial relief. The furrows are blocked seawards in places by coral growth and form pits and 2–3 m deep pools on the reef-flat, (G. Gvirtzman and B. Buchbinder, pers. com., 1976).

The sediments of the Gulf of Elat have been described by various authors

(see Emery, 1963; Friedman, 1968; as well as Hottinger, 1970, 1971, 1972a, b; Erez, 1972; Perelis, 1974; Zweig-Strykowski, 1973 and references). Sediments and organisms form a series of zones with increasing water depth and distance from the shore. Near the backreef zone, boulder-sized coral rubble is abundant. Carbonate sands derived from the degradation of reef builders and from autochthonous skeletal material carpet the sea bottom near reefs. The carbonate sands near reefs are less well-sorted than carbonate beach sand, because fine-grained particles which are abundant in the reef areas are winnowed by wave action from the shallow beach sand.

Abundant *Pavonia* occurs below tide level. Between the reefs and along their edges *Halophila*-meadows form important sediment traps. *Halimeda* is conspicuously absent.

In the area of the narrow shelf foraminiferal tests compose between 50 and 80% of the carbonate grains, the remainder being mainly gastropods, pelecypods, coral and algal debris. In deeper waters foraminiferal tests prevail, predominantly belonging to planktonic species. Pteropod shells occur in places in great abundance.

Detrital sediments are brought into the Gulf from the slopes on both sides and particularly from the northern Wadi Arrava, the coarsest material remaining on the beaches and progressively finer particles reaching greater depth and greater distance from the shore, where they are strongly diluted by biogenic constituents.

Grain size decreases from beach to about 50 m in both abiogenic and biogenic particles, including larger foraminifera. Deeper down grain size decreases slightly due to the dominance of biogenic particles alone and increases again down to about 100 m depth due to abundant *Operculina*. At still greater depth, grain size decreases due to the predominance of smaller foraminifera. Poorest sorting occurs where detrital and biogenic particles are about equal sediment constituents. Calcareous silts and micas are carried by currents far into open waters, being added on the sea-floor to the foraminifera-pteropod sediments to form a thick fine-grained cover, interrupted by turbidites at depth.

History of the basin, topography, current regime, and ecological zonation determine local sediment distribution.

Substrates for benthonic foraminifera vary greatly and include several main types (see also Hottinger; Perelis; Zweig-Strykowski; and Erez; opp. cit). Boulders and larger pebbles in the near shore area are inhabited by larger foraminifera. Within the areas of dense coral growth, down to depths of about 70 m depositional rates are low and biogenic sands accumulate in hollows and traps between coral patches. Mostly larger foraminifera occur

here, including *Homotrema* and Acervulinidae attached to framebuilders. Miliolids may be abundant. Generally, the coarse grained sediment between coral colonies and patches does not support perennial vegetation, although a cover of filamentous algae may develop in spring. Soft black mud, in places with considerable proportions of terrigenous, non-calcareous material, is widespread from the shore of sheltered bays and the rim of mangroves down to depths of about 80 m. Interstitial spaces in the mud are small and although there is infauna, pyrite and H_2S start 1–2 cm below surface, due to microbial activity. The black sediments are covered by *Halophila*-meadows between 10 and 70 m, the plants representing an important type of substrate for both larger and smaller foraminifera. At about 70–80 m the colour of the sediment changes to reddish-brown. Terrigenous material is restricted to the pelitic fraction. Foraminifera of different types, particularly *Amphistegina* and Nummulitidae are abundant and their shells form more than half of the sediment volume. *Turritella,* as well as small pectinids and cardiids are frequent between 80 and 120 m depth. At these depths brown algae grow in small clumps. Transitional types of substrate occur in front of inactive deltas and at the foot of the low fringing reef, at 5 to 25 m depth. Below 80 to 100 m, down to depths greater than 800 m, the sediments are brownish-yellow muds in which smaller foraminifera, both benthonic and planktonic form the bulk of the sediment, accompanied in places by abundant pteropods.

Much of the pelitic fraction is winnowed out by waves and currents in the nearshore areas and the reef-regions, with the exception of sheltered bays and lagoons, and of hollows and pools within the reef itself. Currents seem, however, not to be strong enough to lift heavy foraminiferal shells from the bottom together with the pelitic grains, although in the surface zone, between 0 and 6 m, considerable displacement by wave action and currents does take place, resulting in transport of foraminiferal tests over some distance.

Transport of grains is also caused by filamentous algae. Clouds of such algae contain mostly foraminiferal shells produced between 20 and 50 m depth and are carried by currents over great distances. Some of the clouds are caught by corals and others sink into deep waters far from shore. Below 50 m this mechanism of transport seems of no importance (Hottinger, 1972). The regular and persistent pattern of qualitative and quantitative distribution of foraminiferal species and genera with depth seems to indicate that downslope mass movement is less important than it would be expected from the steepness of the submarine slopes. Displacement of depth-zonation boundaries, occurrence of sporadic specimens of shallow water foraminifera

in deeper water sediments, obvious displacement in submarine canyons, as well as detailed analysis by biometric methods of some species (this U.M. Bull.) indicate that minor across-the-slope movement does in fact take place. There is good evidence from the foraminiferal assemblages that long-shore transport both by drag and suspension takes place from north to south, possibly down to a depth of 200 m.

BENTHONIC FORAMINIFERA

A large number of bottom samples for foraminiferal studies were collected in the Gulf of Elat since 1969, partly by diving (down to 70 m depth) and partly by Petersen grab and Willemoes three-point chandelier down to depths of 800 m. Samples were collected by L. Hottinger, R. Reber, S. Leutenegger (Basel), H.-J. Hansen, A. R. Larsen (Copenhagen), Z. Reiss, A. Almogi-Labin, Y. Erez, H. Frankel, E. Halicz, L. Perelis, S. Rothmann, A. Zmiri, M. Zweig-Strykowski (Jerusalem) assisted by the staff of the H. Steinitz Marine Biology Laboratory in Elat, which also provided the services of the vessels "Nizzan" and "Arnona".

Living specimens were collected at various occasions for laboratory experiments and for cytological studies.

Direct observations under water were made mainly by Hottinger and his collaborators.

The most intensively studied areas are up to now the northern Bay of Elat, particularly the Coral Island (Geziret el Faraoûn) area and Wadi Taba, and farther south Ras Burka, Ras abu Galum, Dahab and the bay of El Kura, Ras et Tantur, Wadi Kid, and Nabek (see map fig. 1).

For distinguishing living specimens, a modified Rose Bengal staining technique was employed, although the distinction is not fully reliable. For quantitative assemblage studies, water-washed and dried samples (200 mesh screen) were split by means of a Von Daniels splitter.

Some problems of sampling and under-water observation are discussed by Hottinger in this U.M. Bulletin.

All results of the qualitative and quantitative studies on the sediment assemblages, as well as on living faunas (Reiss, Frankel and Zweig, 1970, unpubl.; Hottinger, 1970, 1971, 1972a, b; Erez, 1972; Perelis, 1974; Zweig-Strykowski, 1973) indicated that the distribution of foraminifera shows *a distinct depth-zonation* in spite of the practically homogeneous – with regard to temperature, salinity, density, and oxygen – water column.

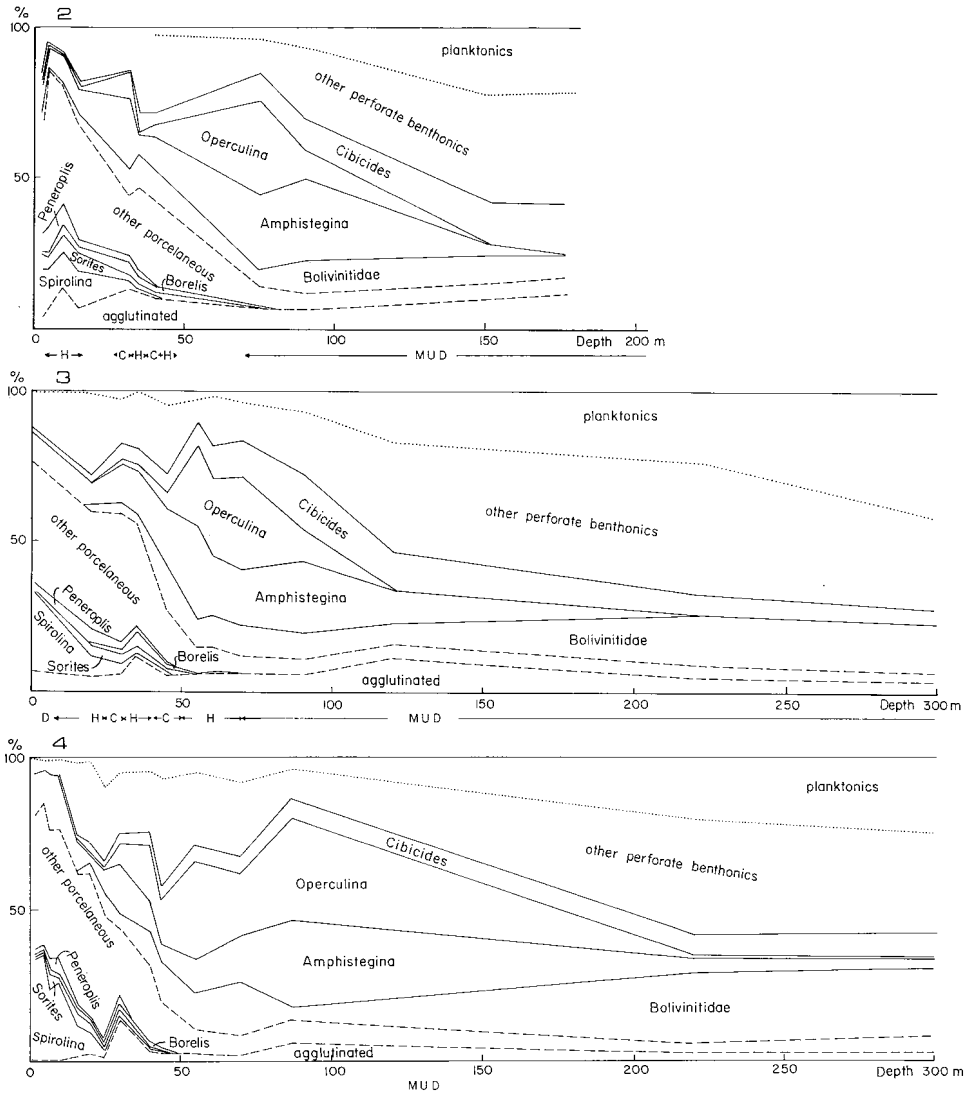

Fig. 2–4 Cumulative percentage distribution of foraminiferal genera and groups of genera in sediments of the Gulf of Elat.

2–3 W – E traverse in Coral Island region (Collected by Hansen, Hottinger, Reiss and Zweig-Strykowski. Analyzed by Zweig-Strykowski 1973).

4 N – S traverse between northern tip of Gulf (Sea Star Hotel) and off Wadi Taba (Collected by Reiss and Frankel. Analyzed by Reiss, Almogi-Labin and Zweig-Strykowski, 1972).

D – *Diplantera* bottom; H – *Halophila* meadow; C – Coral carpet.

Generally, the shallow water assemblages, down to about 50 m, are dominated by porcelaneous foraminifera, particularly *Borelis, Sorites, Amphisorus, Spirolina* and *Peneroplis,* accompanied by species of perforate genera, mainly *Amphistegina, Planorbulina, Planorbulinella, Acervulina, Miniacina, Rosalina, Ammonia, Pararotalia, Epistomaroides,* various Bolivinitidae and Cibicididae, as well as some Textulariidae.

Down to a depth of about 150 m *Amphistegina* and *Operculina* dominate the assemblages. They are accompanied by a greater variety of perforate foraminifera, including about 10% planktonic specimens per total count.

Below 150 m smaller benthonics are dominant and include *Cassidulina, Lamarckina, Stomatorbina, Gyroidina, Uvigerina,* etc., with planktonic specimens becoming rapidly abundant.

Not only are the overall *ranges* of the different *genera* fairly similar in the various areas sampled, but also their relative *abundance* follows a rather constant depth-pattern (figs. 2–4). The depth-zonation of foraminifera is also clearly shown on a *specific level* (Hottinger, 1972; Larsen, 1976; and see Hansen and Buchardt, this U.M. Bulletin) with definite, biometrically distinguishable interspecific and intraspecific depth-related variability of external and internal shell features, e.g. in *Operculina, Heterocyclina, Amphistegina,* and *Planorbulinella* (see articles in this U.M. Bull.).

The depth-zonation observed seems to be independent of substrate in many cases, except on very mobile sediments, like at wadi-mouths, where foraminifera may be absent altogether (Perelis, 1974). Within the respective depth-ranges, however, the presence, absence, and abundance patterns of various genera seem to be influenced by the type of substrate. Hottinger (opp. cit. and this U.M. Bull.) emphasizes that foraminifera with canal systems, like *Operculina, Heterocyclina* and *Heterostegina* are usually not found on plants, but live on coarse and fine sediment. On the other hand, in some places where such sediments are present, these genera may be extremely rare or absent (Erez, 1972).

Frankel (1974) reports living *Amphistegina* on plants and rocks, but did not observe them on sediment. Living specimens of *Ammonia, Elphidium, Nonion,* Textulariidae and Buliminidae are more frequent on sediment than on either plants or rocks. Obviously, such genera as *Acervulina* or *Miniacina* are restricted to hard, stable substrates (Erez, 1972).

A seasonal pattern in living foraminifera has been observed by Hottinger, by Larsen, and by Hansen (op. cit. and this Bulletin), particularly in *Amphisorus, Amphistegina, Operculina,* and *Heterocyclina.* The possibility that the seasonal pattern of at least some of the epiphytic species is related to the bloom-periods of the plants forming the substrate has been raised

by Hottinger (1972). It must be emphasized that any comparison between biocoenoses and thanatocoenoses must also take into account the (local) abiogenic sedimentation rates which vary from place to place and which determine the degree of "dilution" of the foraminiferal assemblages (Hansen and Buchardt, this U.M. Bull.).

As pointed out above, no *large-scale* transport of foraminiferal shells from biotope to biotope across the slope takes place, at least below the surface zone of 6 m or so, a fact borne out also by plankton/benthos ratios and by size-analysis of both benthonic and planktonic specimens from sediment assemblages (Reiss, Halicz and Perelis, 1974; Reiss and Halicz, 1976; Perelis, 1974). Local displacement and winnowing has been proven (Reiss et al., 1974; Zweig-Strykowski, 1973; and see articles in this U.M. Bull.). Generally, it seems that downslope movement is more important across the weak north-south slope than across the much steeper (30° and more) west-east slope (see fig. 4). Thus, longshore transport and flotation on algal clouds may be more important than drag and sliding across the steep slopes.

Multivariate analysis of sediment assemblages carried out by Erez (1972) indicated good correlation between depth-zonation of foraminiferal assemblages and observed environmental zonation in the Ras Burka area. This study suggests that all distinctive information for environmental discrimination is contained in the assemblage of foraminifera, that the response to environmental changes is dinstinct at *generic* level, and that crude presence-absence data are sufficient for association analysis in environmental classification of foraminiferal assemblages (Erez and Gill, 1977).

It is, therefore, apparent that the sediment assemblages largely reflect the overall, yearly biocoenoses, the depth-distribution of which is ecologically determined.

Considering the hydrographic setting of the Gulf of Elat, it was suggested that *light-penetration* (intensity and wave-length), as the only factor with a significant gradient in the Gulf, may be the major one affecting the depth-distribution at least of part of the foraminiferal genera and species, with substrate being of additional importance (Erez, Hottinger, Larsen, opp. cit. and this U.M. Bull.).

It has been shown (Hansen, unpubl.; Hansen and Buchardt; and Leutenegger this Bull.; Hottinger, 1972; Hottinger and Dreher, 1974; Leutenegger, 1977), that all porcelaneous and perforate larger foraminifera in the Gulf of Elat, as well as such smaller genera as *Peneroplis, Spirolina* and *Pararotalia* possess light-assimilating symbionts which at least in some forms are concentrated in the outer regions of the intralocular cytoplasm (including the pore-"cups" of *Amphistegina* shown by Hansen (1972), by Hansen and

Reiss (1972) and by Hansen and Buchardt in this Bulletin.

Larsen (1976) relates thickness/diameter ratios in species of *Amphistegina* and their changes with depth to light requirements of symbionts and similar relationships in the morphology of *Operculina* is suggested by Hottinger (1972). The different phototactic (and thermotactic) responses of different species of *Amphistegina* (Zmiri et al., 1972, 1974) further emphasize the importance of light to these foraminifera.

On the other hand, many of the species of Foraminifera which are distinctly depth-distributed in the Gulf of Elat apparently do not possess symbionts. Thus, it may not be simple to explain depth-distribution by way of light requirements of symbionts only. Moreover, different types of unicellular plants occur according to Hansen (this Bull.) in the same species at different times of the year and there is as yet no information on the identity, physiology or light requirements of these plants. Little is known as yet on the precise nature of the assumed symbiontic relationship, particularly when the evidence of possible digestion of these plants in the foraminiferal host is considered (Hansen and Buchardt, this U.M. Bull.). On the other hand, possible influence of symbionts on the oxygen isotope fractionation in foraminiferal shells is put in evidence by Hansen and Buchardt herein.

Nevertheless, considering the environmental parameters in the Gulf of Elat, it is still extremely tempting to regard *light as a major factor* determining the depth distribution of foraminifera, particularly in the illuminated zone which in the Gulf seems at least as deep as 150 m and probably more. The influence of light on the foraminiferal depth-distribution may act through the requirements of symbionts or by way of light-tolerance levels of the foraminifera themselves. Even the amount of reflected light from different types of bottom may be of importance (Hottinger, 1972, and this U.M. Bull.).

If light is indeed the major factor determining depth-distribution of foraminifera, this distribution becomes an indicator for relative depth. Absolute depth may, of course, change from place to place, with latitudinal position, cloudiness, suspended matter in the waters, primary production levels, and other local factors influencing light penetration.

It is of great interest in this connection, that some internal features of larger foraminifera seem to change with depth (see articles by Fermont and by Thomas in this Bulletin). A possible relationship of reproduction-cycles with depth is suggested by Leutenegger (this Bull.). The result obtained from these studies are of considerable significance to a better understanding of evolutionary trends in such groups as *Operculina* and *Planorbulinella* in particular and in larger foraminifera in general.

Hottinger (this U.M. Bull.) suggests a possible relationship between test-porosity and light in benthonic foraminifera. Such a relationship in planktonic species has also been suggested by Reiss et al. (1974).

Concurrently with the investigation of the distribution of benthonic foraminifera in the Gulf of Elat, systematic studies on various groups have been published or have been completed and will be published shortly, viz. Cibicididae (Perelis and Reiss, 1975), Bolivinitidae (Zweig-Strykowski and Reiss, 1975), Amphisteginidae (Larsen, 1976; Hansen, 1972, Hansen and Reiss, 1971, 1972a, b), Nummulitidae, Soritinae, Alveolinidae (Hottinger, 1972a, b and this Bull.; Reiss and Gvirtzman, 1966), Rotaliidae and Elphidiidae (Hansen and Reiss, 1971, 1972a, b; Hansen and Anderson, in press), Textulariidae (Halicz, in prep.).

PLANKTONIC FORAMINIFERA

The planktonic foraminifera from the Gulf of Elat have been described by Reiss, Halicz and Perelis (1974) and by Reiss and Halicz (1976). Remarks on the structure of some of the species are found in Hansen and Reiss (1972b).

The distribution of the planktonic foraminifera in sediment samples down to a depth of 600 m was studied by Reiss, Halicz and Perelis (1974).

The assemblage is a tropical, low-diversity one, dominated by shallow-water, spinose species and lacking any species of true *Globorotalia,* of *Globoquadrina, Pulleniatina* or *Sphaeroidinella.* It is identical with the assemblage known from the northernmost Red Sea, but differs from those in the southern Red Sea and in the Gulf of Aden. The Elat assemblage is directly comparable with tropical-subtropical faunas in the southernmost North Atlantic (Sargasso Sea) and in the NW Pacific Central Water Masses, while the main Red Sea and Gulf of Aden assemblages are comparable to those of the marginal and equatorial current systems (compare also Kimor, 1973). There is a definite change in dominance with depth, viz. from a *Globigerinoides sacculifer*-dominated, shallow water assemblage down to about 200 m to a deeper, *Globigerina quinqueloba*-dominated one.

An empirical correlation of the assemblages with the ecological parameters in the various areas mentioned, strongly suggests that temperature, salinity, or density can not be regarded as the major factors controlling the composition, relative frequency, and depth-distribution of the planktonic species. It was suggested (Reiss, Halicz and Parelis, 1974) that fertility of the water masses, hence *light-penetration* coupled with *feeding habits* of the different

species (symbiont-dependent, omnivore, or specific, multiple food requirements) may be the major factors in determining planktonic foraminiferal distribution.

This may account for the absence of deeper-water and probably less euryphotic species in tropical gyre-centers of the ocean and in the Gulf of Elat, environments which are quite dissimilar in their physico-chemical characteristics, but which have in common clear, blue waters, with strong light-penetration, because of low productivity and little suspended matter from the continent. It may be noteworthy in this connection that a study of pteropods from the Gulf of Elat (Almogi-Labin and Reiss, in press) shows their assemblage to be equally similar to those of the southern Sargasso Sea, hence of low diversity and comprising epi- and shallow meso-pelagic species only.

A study of stratified, vertical plankton hauls between surface and 600 m depth from the DCPE stations in the Gulf, carried out currently by A. Almogi-Labin and the author, indicates that the composition of the foraminiferal sediment assemblages reflects closely the overall, yearly populations in the water column.

The plankton/benthos ratio in foraminiferal sediment assemblages is shown to be independent of distance from the shore (or run-off from the continent) and to be mainly a function of the light-dependent decrease with depth of species and specimens of benthonic foraminifera, as well as of the increasing abundance of planktonic specimens, because of the deepening of the water column (Reiss, Halicz and Perelis, 1974).

The problem of symbiotic relationship between plants and planktonic foraminifera remains still to be investigated in detail. Hansen (1975) showed planktonic foraminifera from Elat to contain in their cytoplasm various types of algae and chloroplasts, which are vacuolated and in various stages of decomposition. Hansen, therefore, doubted the true symbiotic relationship between plants and planktonic foraminifera. Another type of symbiotic relationship is discussed by Hansen and Buchardt in this U.M. Bulletin with regard to benthonic species and may well apply to planktonic ones as well. A study of oxygen isotope fractionation in the shells of living and dead planktonic foraminifera from the Gulf of Elat is currently being carried out by B. Luz (Jerusalem).

A study of the depth-distribution in the Gulf of Elat of particular phenotypes (*G. ruber* with kummerform chambers and *G. sacculifer* with sac-like chambers, as well as asymmetrical forms of *G. siphonifera*) has been made by Reiss and Halicz (1976). It was shown, that despite the lack of any significant thermocline, halocline, or pycnocline ratios of normalform/kum-

merform *G. ruber* and of specimens with sac-like chambers vs. such with no such chambers in *G. sacculifer* change with depth, like in other seas. No trends in the ratios symmetrical/asymmetrical types of *G. siphonifera* were found.

The plotting of the data obtained from Elat on published regression-lines relating phenotype ratios to isotopic, as well as in situ temperatures, gives reasonable results for *G. ruber,* but would indicate for the phenotype-ratio of *G. sacculifer* a temperature between 13 and 18°C, which is far below the actual minimum temperature in the Gulf.

It seems, therefore, that phenotype ratios in planktonic foraminifera can not be correlated in a simple manner with temperature and the latter can not be regarded to be the major factor in determining the ratio changes with depth. It was suggested that kummerform/normalform ratios in *G. ruber* may be correlative with productivity of the sea and that lack of food may be the ecological stress-factor inducing kummerform growth. No explanation is offered, however, for the frequency of individuals with sac-like chambers in *G. sacculifer* (which are not necessarily a "terminal" growth feature).

It appears from the study of the planktonic foraminifera from the Gulf of Elat that density of the water can not be regarded either as a major factor in determining the distribution of species or the relative frequency of specimens with such features as kummerform or sac-like chambers. The ranges of sigma-t values published and claimed as characteristic for such species as *G. ruber* and *G. sacculifer* and their phenotypes are far below the actual density of the waters in the Gulf of Elat. In contrast the sigma-t ranges given as characteristic for various species of *Globorotalia* are in fact found in the Gulf, but the species concerned are absent.

The diel-migration of planktonic foraminifera is another light-dependent aspect of interest, on which little is known hitherto. It has been emphasized by Reiss, Halicz and Perelis (1974) that most of the species present in the Gulf of Elat have reportedly insignificant diel migration ranges, while those absent in the Gulf are reported to have considerably greater ranges. It may be noteworthy in this connection that Hansen (1975) suggested for the so-called vesicular reticulum in planktonic species a possible role in a buoyancy mechanism involving a light-triggered ion-exchange.

Again, it seems that light-penetration plays a major role in determining the distribution of planktonic foraminifera.

CONCLUSIONS

The Gulf of Elat represents a unique, "natural laboratory" for foraminiferal studies, where some of the most important ecological parameters like temperature and salinity, hence density, do not show any considerable gradient with depth or season.

As far as the larger foraminifera are concerned, the Gulf of Elat is so far the only model-area in which a complete sequence of Recent species and genera occurs from shallow waters down to depths of more than 150 m, below the photic zone. Distributional studies indicate up to now that depth-distribution of benthonic foraminifera may be largely determined by light penetration, acting either directly on the animals or through the requirements of symbiontic plants, or both, as well as – in some cases at least – by nature of substrate (which in itself may be depth- and light-dependent).

Assumed correlations of planktonic foraminiferal depth-distribution with either temperature or density is conclusively proven in the Gulf of Elat not to be generally valid.

Light penetration and nutritional patterns may be the major factors in the distribution of planktonic foraminifera as well.

With more information becoming available, the Gulf of Elat may well serve as an important model for the interpretation of ancient tropical environments, both with regard to reef-facies and to gyre-centers of the oceans, as based on foraminifera. Morphological and biometrical studies on foraminifera carried out in the particular setting of the Gulf may well provide a better insight in the evolutionary changes in stratigraphically important groups.

The articles in the present U.M. Bulletin are an important step in this direction.

It is hoped that the investigations of the Foraminiferida in the Gulf of Elat will continue, with more emphasis being placed on seasonality in benthonic populations, on feeding patterns and symbiosis, as well as on measurable parameters of shell-morphology changing with ecological factors.

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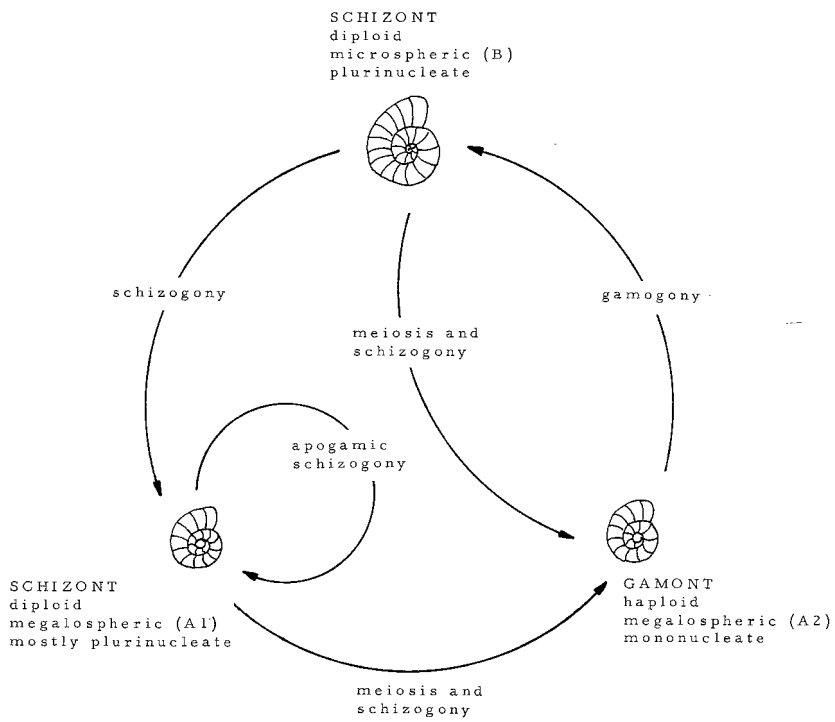


Fig. 1 Paratrimorphic life cycle, as supposed to occur in soritid and nummulitid foraminifera (after Leutenegger, 1977).

REPRODUCTION CYCLES OF LARGER FORAMINIFERA AND DEPTH DISTRIBUTION OF GENERATIONS

S. LEUTENEGGER

ABSTRACT

Cytological, morphological and distributional studies of *Amphisorus hemprichii* and *Sorites orbiculus* from the Gulf of Elat indicate that apogamic schizogony within a paratrimorphic cycle is the predominant form of reproduction in these species. In *Heterostegina depressa* a paratrimorphic cycle occurs with apogamic schizogony of the A1-forms predominant. Asexually reproducing individuals are mononucleate and megalospheric, although biologically they are schizonts. The lifecycles of *Operculina ammonoides* and *Heterocyclina tuberculata* are believed to be similar to that in *Heterostegina.* Difficulties are encountered in simple correlation between "biological" and "morphological" trimorphism. A1 – and A2 forms appear to have unequal depth-distribution. The relative number of microspheric individuals of *O. ammonoides* and *H. depressa* increases generally with depth down to 100 m, but is extremely small between 30–50 meters depth, indicating that sexual reproduction is limited to certain ecological zones, determined by such factors as light, nutritional setting, and vegetal growth.

Modes of reproduction

Studies on living foraminifera have demonstrated an alternation of sexual and asexual generations. In the simplest case, a sexually reproducing generation (gamont) alternates with an asexually reproducing generation (agamont or schizont). The haploid gamont, which produces gametes, is always mononucleate, whereas the diploid schizont, which reproduces by multiple fission, is mostly plurinucleate. Such a biphasic cycle is typical of *Iridia lucida, Discorbis patelliformis, Patellina corrugata, Myxotheca arenilega, Rotaliella heterocaryotica* and many other foraminifera (J. le Calvez, see Arnold, 1956; Grell, 1967).

In polythalamous foraminifera with flagellate gametes, the two modes of reproduction are associated with variations of the test morphology affecting the prolocular size and the proportions of the adult test. In these cases, the schizonts derived from the zygote are usually microspheric (B-forms), the gamonts megalospheric (A-forms). The life cycle (A-B-A-. . .) is then called dimorphic. The initial chambers of the two generations are of unequal size because the young gamonts, the products of multiple fission, are larger than the zygotes formed by the fusion of gametes.

Some foraminifera introduce to the cycle a third generation. If chromo-

some reduction (meiosis) fails to occur prior to asexual reproduction of the microspheric schizont (B), diploid, megalospheric schizonts (A1) rather than haploid, megalospheric gamonts (A2) are produced (fig. 1). These A1-forms reproduce by multiple fission as their parent (B), but are morphologically identical with gamonts (A2) since they have large proloculi. Such a holotrimorphic cycle (B-A1-A2-B . . .) has been demonstrated for *Ammonia beccarii* (J. le Calvez, 1938).

A complex cycle of the paratrimorphic type (fig. 1) characterizes *Planorbulina mediterranensis* and *Elphidium crispum* (Le Calvez, 1938). In many foraminifera such as *Heterostegina depressa* (Röttger, 1974; Röttger & Schmaljohann, 1976), *Marginopora vertebralis* (Ross, 1972) and *Rosalina globularis* (Sliter, 1965), a succession of A1-generations is the predominant form of reproduction ("apogamic schizogony"). It explains the fact that, in recent and fossil assemblages, megalospheric individuals of many species are much more abundant than microspheric ones.

The loss of sexual reproduction has progressed to an extreme degree in *Discorbina orbicularis,* which reproduces exclusively by multiple fission (apogamic cycle, Le Calvez, 1938).

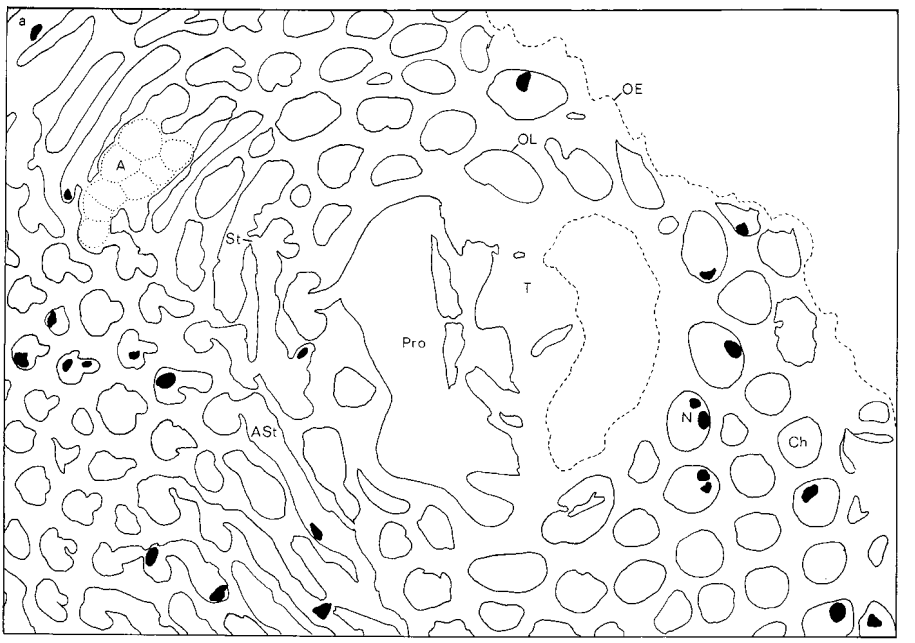
Nuclei and reproduction cycle of *Amphisorus hemprichii* and *Sorites orbiculus*

Ultrastructural studies of living *Amphisorus hemprichii* and *Sorites orbiculus* (for details see Leutenegger, 1977) have demonstrated that adult individuals are plurinucleate. The ameboid, vegetative nuclei are randomly distributed throughout the chamber cytoplasm of the inner part of the test (fig. 2a). They are characterized by an electron-light caryoplasm containing peripherally arranged, dense nucleoles (fig. 3d). Different types of nuclei have been observed in megalospheric *S. orbiculus* preparing for reproduction: vegetative nuclei as described above, nuclei with electron-dense caryoplasm and numerous micronuclei (figs. 2b, 3a-c). The latter are supposed to represent stages of differentiating gamete nuclei. In size and structure, they are well comparable with the gamete nuclei of *Myxotheca arenilega*

Fig. 2 Schematic drawings of equatorial, slightly oblique thin sections showing distribution of nuclei within chamber cytoplasm. ASt: annular stolo, Ch: chamber, OE: organic envelope covering outer shell surface, OL: organic lining covering inner shell surfaces, Pro: proloculus, St: radial stolo, T: mineralized test.

a Vegetative nuclei (N) of adult *Amphisorus hemprichii.* A: parasitic alga. x 170.

b Vegetative nuclei (N1), dense nuclei (N2) and approximate position of micronuclei (MN) in a reproductive stage of *Sorites orbiculus,* x 220.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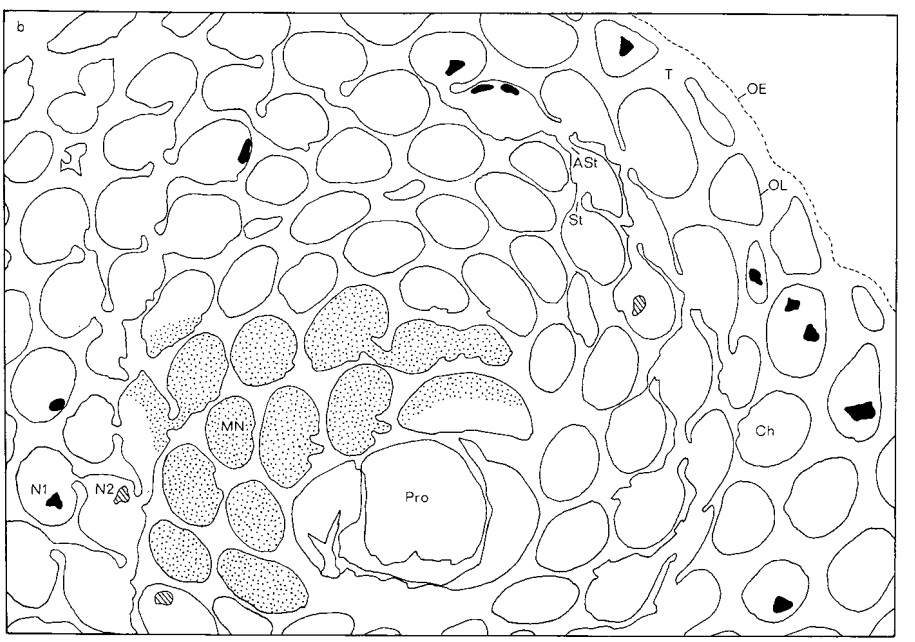
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(Angell, 1971) and *Allogromia laticollaris* (Schwab, 1976). I suggest that the micronuclei have generated from the larger, dense, "reproductive" nuclei, the vegetative nuclei being destined to disintegrate ("Zerfall-Nukleus": Föyn, 1936). However, the exact proceedings of nuclear divisions and associated cytoplasmic differentiation leading to reproduction are not yet known.

The microspheric, as well as the megalospheric individuals of *Amphisorus hemprichii* and *Sorites orbiculus* investigated are plurinucleate. Many authors have shown that schizonts are plurinucleate and gamonts mononucleate (Le Calvez, see Arnold, 1956; Grell, 1967; Schwab, 1969). Thus we may interpret our megalospheric forms as schizonts (A1-forms) and consequently infer a trimorphic life cycle consisting of plurinucleate B- and A1-schizonts and mononucleate A2-gamonts. The assumption that the gamonts are mononucleate seems to be inconsistent with the fact that the reproducing specimens described above contain numerous vegetative nuclei. However, these vegetative nuclei may have been formed only during gametogenesis, or shortly before, young gamonts being actually mononucleate. The fact that the number of megalospheric forms is much higher than that of microspheric forms in the sediments of the Gulf of Elat, indicates that apogamic schizogony within a paratrimorphic cycle is the predominant form of reproduction in *Amphisorus hemprichii* and *Sorites orbiculus* (fig. 1).

Conditions in nummulitid foraminifera

Heterostegina depressa is known to reproduce mainly by multiple fission, at least in laboratory cultures (Röttger, 1974). Gamogony is greatly reduced. We know further that, in the Gulf of Elat, microspheric individuals are rare as compared with megalospheric forms. Thus, we may assume that a life cycle of the paratrimorphic type occurs in *H. depressa,* apogamic schizogony of A1-forms predominating. In contrast to megalospheric schizonts of *Amphisorus hemprichii* and *Sorites orbiculus,* those of *Heterostegina de-*

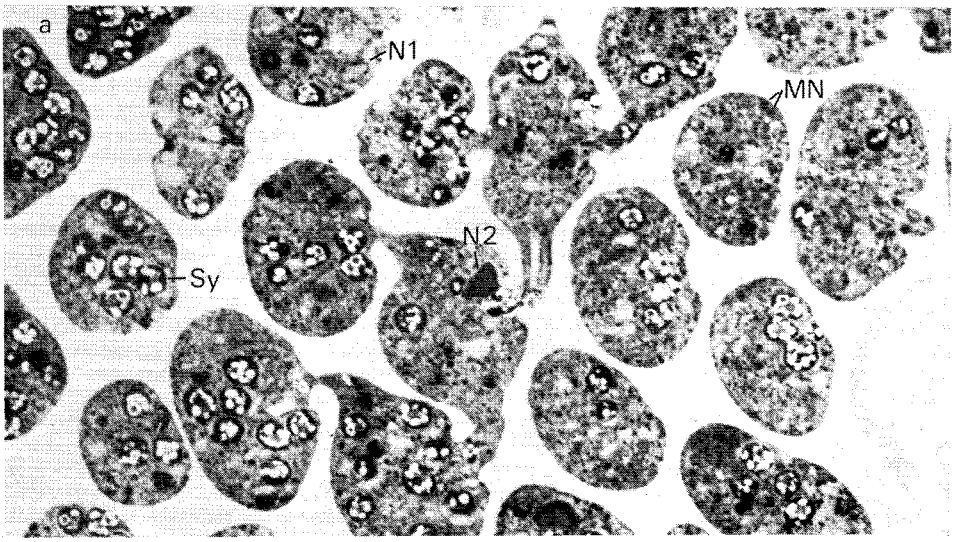
Fig. 3 Nuclei of adult *Sorites orbiculus*

a Megalospheric individual in reproductive stage. Chamber cytoplasm containing vegetative nuclei (N1), dense, reproductive nuclei (N2) and numerous micronuclei (MN, see also fig. 2a). Sy: symbionts. Light microscope, x 500.

b Detail of vegetative nucleus. Electron microscope, x 4,400.

c Detail of large, dense reproductive nucleus. Electron microscope, x 10,500.

d Detail of micronuclei. Electron microscope, x 5,100.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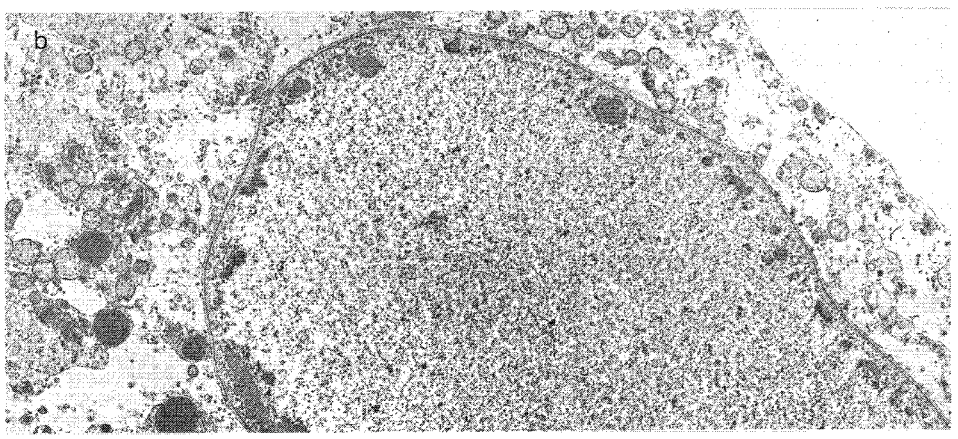
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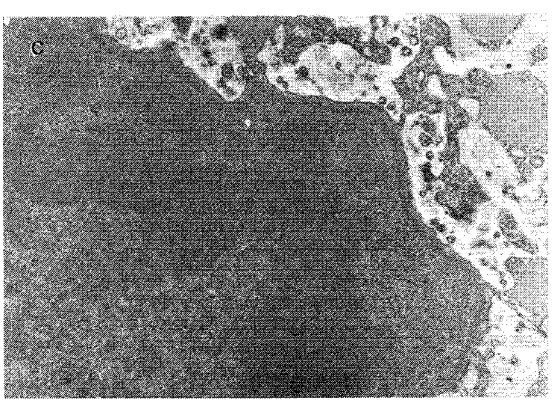
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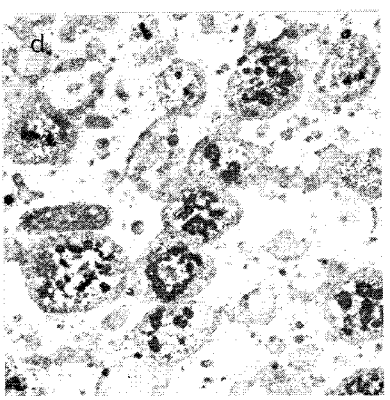
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pressa are mononucleate (Spindler, 1976, see Röttger & Schmaljohann, 1976). Hottinger and Dreher (1974) too have found only one vegetative nucleus in *H. depressa.* The megalospheric individuals reproducing by multiple fission have been interpreted as gamonts (Röttger, 1974; Röttger & Schmaljohann, 1976). This is incorrect in my opinion, since the term "gamont" defines individuals which produce gametes (Le Calvez, 1953; Loeblich & Tappan, 1964). Thus, though the asexually reproducing individuals of *H. depressa* are mononucleate and megalospheric as gamonts, they are biologically spoken schizonts.

The life cycles of *Operculina ammonoides* and *Cycloclypeus tuberculatus* (= *Heterocyclina tuberculata,* see Hottinger, 1977) are not known. Nevertheless, we have reason to believe that a similar cycle occurs as in *Heterostegina depressa*: In *O. ammonoides,* microspheric individuals are even more seldom than in *H. depressa,* whereas microspheric individuals of *C. tuberculatus* have not been found at all. The megalospheric schizonts of *O. ammonoides* and *C. tuberculatus* seem to be mononucleate as in *H. depressa.* Nuclei must be rare at least, since none was found by investigating the cytoplasmic ultrastructure of several individuals (Leutenegger, 1977).

Impact on morphology

Only few studies have been made to clarify whether a "biological" trimorphism (diploid, microspheric schizont – diploid, megalospheric schizont – haploid, megalospheric gamont) is linked with a "morphological" trimorphism (three different test forms) or not. The findings are opposite: Whereas, for example, the megalospheric schizonts (A1) and the megalospheric gamonts (A2) of *Planorbulina mediterranensis* are identical by means of the prolocular size and the test proportions (Le Calvez, 1938), those of *Choffatella decipiens* can be morphologically separated (Sigal, 1959). No morphological trimorphism is known in soritids and nummulitids. Still, it is quite possible that differences of nuclear development and differences in the chromosomal number (A1 = diploid, A2 = haploid) are expressed by the prolocular size or by other variables reflected by the shell morphology. Suggesting such morphological parameters of A1- and A2-forms are different, but only to a low degree, it will not be easy to discover them by means of a statistical analysis only, since the morphological variability of a species in dependance of ecologic factors may be considerable (Arnold, 1954; Schnitker, 1967 and 1974; Lutze, 1964; Sliter, 1970). It must also be taken into account that A1-forms are much more abundant than A2-forms, at least in

larger foraminifera reproducing mainly by multiple fission. Further we should consider that A1- and A2-forms may have an unequal depth distribution, as has been found to occur by comparing the distribution of microspheric *Heterostegina depressa* and *Operculina ammonoides* with that of megalospheric specimens (see below). Certainly, three different morphologic forms could be determined at best by investigating cultured specimens whose biological nature (gamont or schizont) is known. At the moment however, such investigations would encounter with difficulties, since sexual reproduction is generally suppressed in larger foraminifera cultured in the laboratory (*Heterostegina depressa,* see Röttger, 1974; personal observations on *Operculina ammonoides, Sorites orbiculus* and *Amphisorus hemprichii*).

Environmental control of reproductive cycles?

The relative number of microspheric *Operculina ammonoides* and *Heterostegina depressa* increases with depth, reaching in the Gulf of Elat a maximum at 80–100 m (*O. ammonoides*) or 60–70 m (*H. depressa*). In 30–50 m, B-forms are rare or even absent. This unequal distribution pattern indicates that sexual reproduction is limited to certain ecologic zones (Hottinger, 1977). We might suggest that in greater depths a biphasic alternation of sexual and asexual reproducing generations (A-B-A . . .) predominates, whereas apogamic schizogony (A-A-A . . .) takes rather place in shallower water. If this is true, we would expect to find megalospheric gamonts (A2-forms) in deeper water, together with microspheric forms. We must further conclude that the life cycle of these foraminifera is variable in dependance on the environment. It can not be exclusively controlled by endogenous factors as in foraminifera with an obligatory succession of sexual and asexual generations. But which are the exogenous factors causing the formation of gamonts? We do not know. Temperature and salinity seem to exercise some influence on the mode of reproduction in *Rosalina globularis* (Sliter, 1965). However, the distribution of the microspheric *H. depressa* and *O. ammonoides* rather points to depth as such a factor. The major physical factor known in the Gulf of Elat which changes with depth is light intensity. Since light intensity is related to vegetal growth, we might suggest that factors inducing sexual reproduction are nutritional and/or depend on a specific, physico-chemical and biological composition of the substrate.

To explain the unequal distribution of A- and B-forms we might also postulate that sexual as well as asexual reproduction take preferentially place at greater depths, megalospheric schizonts migrating upwards. The

distribution of megalospheric gamonts would then be similar to that of microspheric schizonts.

A third explanation is possible. On the supposition that sexual reproduction is not limited to certain ecologic zones, the high number of B-forms at greater depth could be the result of a downward migration (or passive transport) of the flagellate gametes. In this case, we would expect to find megalospheric gamonts in any water depth.

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DISTRIBUTION OF LARGER PENEROPLIDAE, BORELIS AND NUMMULITIDAE IN THE GULF OF ELAT, RED SEA

L. HOTTINGER

ABSTRACT

Distribution patterns of larger foraminifera as observed in situ by skin diving are primarily controlled by substrate and water depth. *Amphisorus hemprichii* and *Sorites orbiculus* are epiphytes living mainly on *Halophila* and various algae from 0–20 m depth; *Sorites orbitolitoides* occurs also on hard bottom and is frequent down to about 50 m. *Borelis schlumbergeri,* independent of substrate, reaches its highest frequencies between 25 and 35 m. *Heterostegina compressa* is limited to hard bottom between 20 and 70 m depth forming up tot 50% of the larger foraminiferal assemblage between 40 and 60 m. *Operculina ammonoides* living directly on soft bottom ranges from 30–150 m. *Heterocyclina tuberculata* occurs on soft bottom between 70 and 150 m. The most conspicuous response of intraspecific variation to depth in shell morphology of *O. ammonoides* and *H. depressa* acts on the adult growth spiral: variants from shallow water (30–60 m) are more involute, thicker and have a higher spiral than specimens from 60–150 m. *O. ammonoides* from shallow environments have higher densities of pores in the ultimate or penultimate chambers than forms of deep water.

INTRODUCTION

The distribution pattern of marine organisms in recent seas permits to recognize relationships between organisms and environmental factors, if the distribution pattern of the particular organism and of a particular environmental factor can be geometrically correlated. This empirical method shows the existence of the relationships, it does not explain them. Such relationships observed in recent seas are often used by the paleontologist to interpret environments in fossil marine deposits on the basis of fossils occurring in these deposits. In most cases, however, the fossil organisms are morphologically and taxonomically not identical with the ones living today and used for the actualistic model. Although there might exist close relatives of fossil forms in recent seas, the question remains open whether taxonomic relations reflect the relationships to particular environmental factors. In other words, we do not know if the taxonomically closest relatives of recent organisms played the same or similiar ecological parts millions of years ago as their recent successors do today. This idea is supported by the fact that neighbouring species of the same genus of larger foraminifera living in the Red Sea have different habitats: *Sorites orbitolitoides* lives independent of substrate in depths from 10 to 60 m, *Sorites*

orbiculus in 0–30 m depth as an epiphyte.

A second method used by paleontologists to reconstruct paleoecology of fossil marine deposits consists in comparing sedimentological features of fossil with recent marine deposits (Harms et al. 1975). The physical and physico-chemical laws controlling distribution, composition, textures and structures of sediments and of stratification sequences have not changed during geological times so that sedimentology of recent and fossil sediments may be safely compared and interpreted on the basis of actualism. Particular sedimentological features, however, may be generated independently in different environments: Sedimentology has not yet produced a detailed bathymetry. If fossils in sediment bodies are mapped and their distribution is plotted against the distribution of features characterizing their sedimentary environment, we may again observe the existence of relationships between fossils and sedimentological features without understanding their meaning. Therefore, the fossils will not help to choose between different actualistic interpretations of sedimentological features.

In order to advance significantly in paleoecology integrating paleobiology to sedimentology, we must try to understand the biological meaning of ecological relationships in living marine organisms. In particular, if we want to understand the biological meaning of structures in shell morphology generated independent of taxonomic relationships as features of adaptation to environmental factors, we may use such structures as indicators for such factors in paleoecology. If, for instance, we can show and understand relations between foraminiferal shell shapes and depth of their habitat, we may use shell shapes in paleoecology as an indicator for depth. As all morphogenetic processes are complex, reflecting phylogenetic, ontogenetic and adaptational factors, a first step approaching the problem must consist of finding relationships between environmental factors and shell morphology. This must be done by empirical field methods, mapping distribution patterns of factors and of organisms in nature. If relationships are found between particular morphological features of organisms and environmental factors, the meaning of the relationship must be investigated simultaneously by phylogenetic studies of the fossil record and with biological methods experimenting with living organisms. The phylogenetic study must show that the investigated morphologic feature represents an adaptation to environmental factors being generated independently of taxonomic relationships. The biological experiment must furnish our understanding of the biological function of the particular morphologic feature to be used as paleoecologic indicator. If, for exemple, we accept as hypothesis that the relation of equatorial

to axial diameter in nummulitic shells reflects water depth (the flatter the shell, the deeper its habitat), we have to show first the relation of this morphological feature with depth in nature. Next we have to show that this feature is generated repeatedly and independently of taxonomic relationships during phylogeny and last we will have to explain, why this could be so: Flatter forms have larger lateral surfaces and thus may catch more light for their symbionts. If this hypothesis would find support with these three methods of investigation, we could use this morphological feature as an indicator for depth in paleoecology.

The present paper illustrates a first, small step in the direction outlined above. It tries to characterize the distribution of larger foraminifera in the Gulf of Elat, and to match their distribution pattern to those of some environmental factors. The Gulf of Elat is the nearest tropical sea accessible to european workers. It has furnished representatives of the genera *Amphisorus, Sorites, Borelis,* and three species of nummulitids discussed in this paper. Many other larger forms (amphisteginids, planorbulinids, gypsinids) and many smaller benthic and planktonic species have been collected and will be discussed in other papers of this book or in later publications.

CHOOSING METHODS OF INVESTIGATION

Distribution of organisms in recent seas can be studied in many ways. Many choices have to be made to achieve results in reasonable time and with restricted funds. Organisms have to be selected because there are too many to be studied all together, the season for fieldwork has to be chosen and the area of investigation has to be restricted so as to serve as a significant example or model for much larger areas (Schopf, 1972).

Each benthic species of the neritic realm has its own distribution pattern. The different patterns are overlapping and together they form a mosaic of a higher order of complexity which characterizes the distribution of communities. Particular environmental factors may condition the distribution pattern of particular species or of communities. In this paper, the distribution patterns of selected species are discussed in order to find relations between species and environmental factors. The species are selected according to particular morphologic features such as presence or absence of a canal system or a stolon system.

Evaluation of the model's size

There is a major difficulty in comparing distributions of benthic organisms in recent and fossil occurrences. No fossil bed surface is ever made accessible by erosion to the same extent as the present time sea bottom is accessible to the diver. Distributions of fossil organisms have to be studied in series of naturally eroded sections through a sedimentary sequence (Ferrer et al. 1973). Samples corresponding to one bedding plane are therefore always rather distant. On the other hand, distributional models worked out in recent seas often lack any dimension of time as the succession of sediments is difficult to study under water in continuous sections. In order to use recent, specific distribution patterns as a model for the interpretation of fossil environments, the size of the model area must be sufficiently large to reflect the same kind of environmental changes which can be distinguished in fossil marine deposits by changes of the fossil species assemblages. Significant changes of fauna (and of sedimentary features) in comparable tertiary sedimentary basins occur in distances varying from several hundred meters to several kilometers (Luterbacher 1973). A distribution model in recent seas must be based therefore on a surface of similar dimensions.

Dimensions of the model

Distribution patterns can be presented in one dimension (curves), in two-dimensional (maps) or in three-dimensional graphs (bloc-diagrams). In a linear model, the distribution of organisms can be compared with the distribution of one ecological factor. In a two-dimensional model, the distribution pattern can be simultaneously matched to two factors. With the next higher dimension, one more factor can be integrated in the model. As in the Gulf of Elat two main factors (depth and substrate) seemed to control the distribution of larger foraminifera, a twodimensional model (mapping) was chosen. In order to check the results of the model in other areas, linear sampling along profiles vertical to the shore line was sufficient if the two factors, depth and substrate, were noted.

Integration of seasonal changes

In order to be comparable with the distribution of fossils, a model based on distribution patterns of recent organisms must integrate seasonal changes because such changes cannot be recognized in fossil occurrences. During field work in Elat, we were much impressed by the extent of seasonal changes in the underwater flora and in the larger foraminiferal faunas (fig. 1). The model requires therefore collecting techniques integrating seasonal changes. Such an integration would be the distribution of dead shells on the sea floor, in the uppermost sedimentary layer, reflecting the distribution of living animals during several seasons. But the distribution of dead shells on the sea floor can be used as a model only, if the transport of dead shells on the sea floor is insignificant.

The use of dead shell distribution in our model has another, important advantage. There is, at present, no reliable method to distinguish quantitatively living from dead larger foraminifera. The widely used method of staining foraminifera with rose bengale does not give satisfactory results, and Walker's (et al., 1974) experiments with Sudan Black B stain must be extended to natural bottom samples to be conclusive. Many dead shells are inhabited by other, living microorganisms which are stained as easily as the protoplasm of living foraminifera, and many living foraminifera do not stain at all.

The distribution of environmental factors to be matched to the distribution pattern of organisms must also be integrated over the whole year. The most difficult factor in this respect is the movement of watermasses in space (laminar and turbulent currents) summarized by the sedimentologist under the term "water energy".

Reasons to choose larger foraminifera as model organisms

Larger foraminifera are by far the most abundant macrofossils in mesozoic and tertiary neritic sediments. They are equally abundant in recent, tropical seas. The distribution of fossils shows clearly the existence of close relationship between taxonomic units and sedimentary features indicating changing ambient environments. Their size permits to observe them directly in the field and also under water, whereas the distribution of smaller hard-shelled organisms like ostracods or smaller foraminifera must be mapped by sampling statistically, with blind "hit or miss" methods. The considerable size of the dead shells of adult larger foraminifera limits transportation by currents,

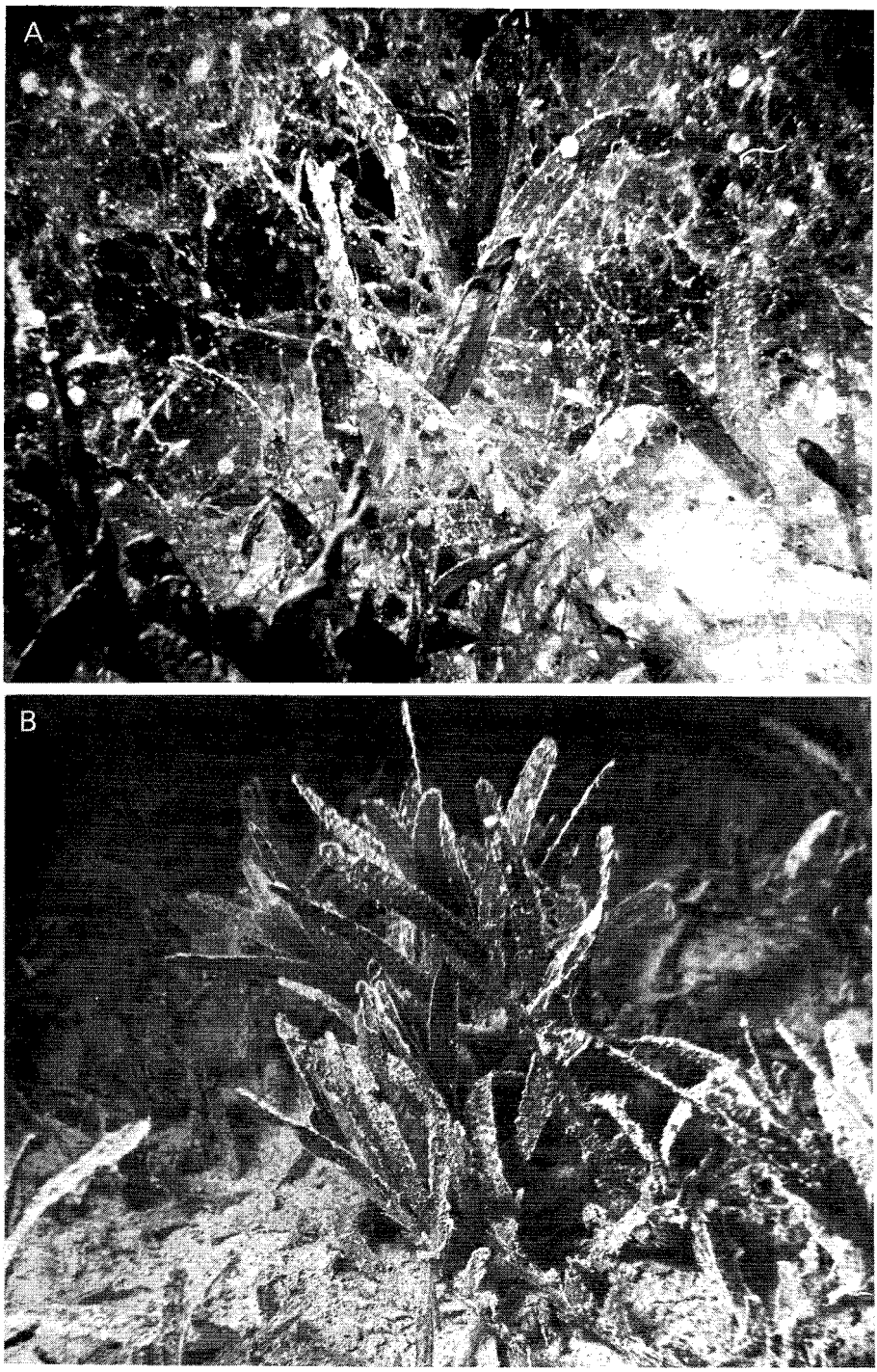
whereas larger mollusc shells are all inhabited by hermit crabs or other vagile animals. The amount of transport of mollusc shells by secondary inhabitants is impossible to estimate at present.

The evolutionary history of larger foraminifera, particularly during tertiary times, is comparatively much better known than in any other group of marine animals with a similar morphological complexity. Their ways of rapid radiation and adaptation have been studied extensively (Drooger, 1956, von Koenigswald et al. 1963). Many close relatives of tertiary larger foraminifera exist today. The morphology of larger foraminiferal shells is sufficiently differentiated to permit the use of comparative anatomy as a method to evaluate degrees of genetic relationship between fossil and recent taxonomic units. Taxonomy based on larger foraminiferal shell morphology has therefore more biological meaning than in many other groups of fossil organisms.

Mapping the distribution of larger foraminifera

Registering larger foraminifera under water, by sight, for mapping involves a considerable bias. Young and broken specimens of small size and small species (*Borelis schlumbergeri* for instance) are not conspicuous enough to be registered. On the other hand, large, microspheric forms are noticed even when they occur as single specimens at the site of sampling. Usually, specimens registered by sight are too numerous to be counted under water. However, the general impression of the composition of the fauna of larger foraminifera noted by the experienced diver corresponds to reality in all cases verified by counting foraminifera in sediment samples, when the conspicuous specimens are abundant. In one particular environment (coral reefs without vegetation between 2 and 30 m depth producing much sediment), larger foraminifera are too rare to be registered by sight at all. Therefore, the maps of distribution presented in fig. 15 are based on a combination of direct observation under water and of partly quantitative, partly qualitative evaluation of the sediment samples collected.

Fig. 1 Seasonal change in *Halophila* meadows.
A: *Amphisorus hemprichii* and smaller foraminifera on *Halophila* leaves and filamentous green algae in April 1971 (site 041, Geziret Faraoûn).
B: *Halophila* without larger foraminifera in October 1971 (site 194, Dahab). Height of *Halophila* plants 10–15 cm.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Under water mapping

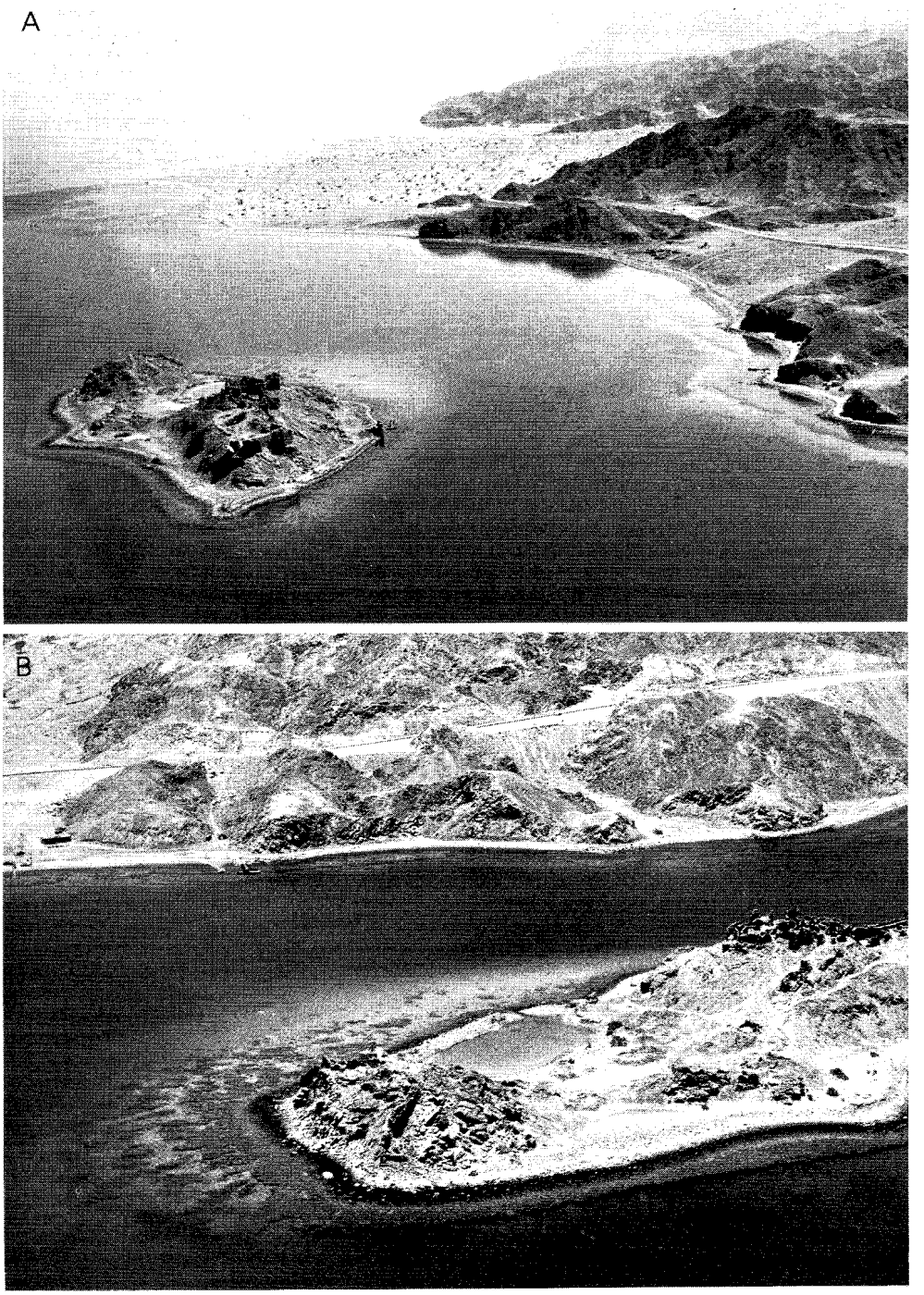
Direct observation by skin diving between 0 and 70 m depth during 4 weeks in March-April 1971 and in September-October 1971 and 1973 permitted to choose a model-area to be mapped (fig. 2, 14) around Geziret Faraoûn ("Coral Island"), South of Elat. This area was chosen because of its relatively flat underwater topography. Two small active deltas and the island called Geziret Faraoûn confer on this area a relatively important topographical variety.

A detailed map of soundings in the Geziret Faraoûn anchorage published by the British Admiralty (Hydrographic Office, Plan 3595, 1969 edition) was corrected and extended to a surface of about 8 km² by sitometer triangulation from the boat and by some registered echo sounder traverses. Depth was measured with diving depth meters and echosounders. Depth indications are accurate to 1 m from 5–20 m depth, to 2 m from 20–70 m depth and to 5 m below 70 m depth. The accuracy of the horizontal position of the samples in the model area is around 20 m in 5–20 m depth, around 50 m between 20 and 60 m depth and around 100 m below 60 m depth. Topography on land was taken over from the Admiralty map cited above. The position of the coastal road, constructed after 1967, was drawn according to air photographs taken at oblique angles.

About 45 skin dives were carried out to take samples by hand, and to register by sight the occurrence of larger foraminifera and the kind of substrate. Observations were marked on the map after each dive. Depth and other measurements were noted under water on a plastic notebook. Direct observation was complemented by sediment sampling with a grab, particularly in depths below 60 meters. Core samples of 30 cm length were taken by hand to document the most important bottom types. After induration with Araldite, oriented thin sections were made to study sediment texture.

North of Geziret Faraoûn, a series of sections of steep shores between the Nature Reserve Area S of Elat and Wadi Taba were investigated in order

Fig. 2 Aerial oblique views of Geziret Faraoûn Anchorage ("Coral Island", compare Cohen 1975, p. 42) from the North (A) and the South-East (B). Photographs by D. Masry.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B

to check the distribution model worked out in detail in the Geziret Faraoûn area. To the South of this area, Dahab Bay, Sharm el Sheikh and (in 1973) Tiran were investigated to check whether higher "water energy" in the Southern part of the Gulf of Elat influences the distribution of larger foraminifera (fig. 16, 19). Observations in Tiran will not be discussed in this paper.

In spring 1971 most dives were made from shore. In the autumns of 1971 and 1973, we used a large rubber boat with an outboard-motor to reach the diving spots. Most of the diving equipment used were Scubapro products. Photographs of the substrate were taken by R. Reber with a Rollei Marine underwater camera on 6 x 6 negatives, usually with flash lights. Grab samples and a few of the echo soundings were taken from the motorboat belonging to the Marine Biological Laboratory in Elat. A portative echosounder Seafarer Mark II was used on the rubber boat. All equipment was transported in a car from Basel, using the ferryboat from Genua or Marseille to Haifa to cross the mediterranean. Access to the Red Sea shore is made easy by the new coastal road from Elat to Sharm el Sheikh.

Sampling techniques

Foraminiferal samples taken by the diver were collected with a sweeping movement of his gloved hand over the surface of the substrate covering an area of 500–1000 cm^2. About 150–250 gr (after drying) sediment were thus collected with each sample (fig. 3). Dennison and Hay (1967) developed a model for estimation of the sampling area needed in subaquatic ecologic studies. According to their model, the surface examined with this sampling technique would guarantee with a probability of 99% the detection of the presence of a foraminiferal species with a relative abundance between approximately 1 to 0.5% if the density of specimens on the sea floor is not less than one per 1 cm^2.

Collecting surface samples on hard, uneven substrates or on larger plants is much more difficult than on soft, flat surfaces. In between the coral colonies, there were usually enough small sandy patches free of coral growth to collect a representative fauna of larger foraminifera with their substrate

Fig. 3 A: Collecting foraminifera on sandy patch in "coral-carpet" substrate, site 71/203, Lighthouse South of Elat, 45 m. Note mound cast up by burrowing organism.
B: Vertical thin-section of sediment core from same site, with *Heterostegina depressa* (H), x 10.


A
H
B

of coarse coral sand, of biogenous rubble or loose calcareous "algal" balls. On this kind of substrate, it is impossible to measure the sampled surface effectively, but since we used the same sweeping technique for sampling covering a similar area as on soft surfaces, the real surface of the uneven substrate covered by the sample is considerably larger and fulfills the requirements for an adequate sampling surface even better than the surface sampled on soft sediments.

As a consequence of the sampling methods used in this study and discussed above, relative percentages of larger foraminifera in the samples can be used as a significant measure for distribution of dead shells. The samples cannot be used for determination of population density, as there are no methods at present to measure the surface of uneven substrates.

Living foraminifera have the tendency to cluster. A very useful quantitative model of smaller foraminiferal clustering has been published by Lutze (1968) from the western Baltic Sea. Similar clustering occurs in the distribution of larger foraminifera in the Red Sea, under tropical conditions, during the blossom period in early spring (fig. 1). Clusters have a diameter of about 1–5 m^2. We do not know at present, whether the specimens belonging to a cluster represent the descendants of one individual or of more than one. In some cases, we could observe a clearly predominant size in the individuals of one cluster indicating a similar ontogenetic age of the specimens. Whatever the significance of the clustering might be, a significant sampling of living larger foraminifera in the framework of our Red Sea distribution model would have to take into account this important phenomenon. Reconsidering the requirements of significant sampling areas according to the model of Dennison and Hay (1967), we would have to consider a cluster of larger living foraminifera as an individual with a size of about 1–5 m^2. The sampling area needed in each spot would then be 90–450 m^2 to detect a cluster of more than 5% abundance proportion with a probability of 99%. Such large areas can be covered only by direct observation under water, never by sampling. For comparison with distribution models of fossils however, the clustering of living forms is irrelevant.

Morphologic units of larger foraminifera used for mapping

A short description of systematic units of larger foraminifera used for this study is given in the final chapter of this paper. Here, we will enumerate shortly the morphologic units which can be recognized under water and determined without sectioning the shell in quantitative countings of sedi-

ment samples. These morphologic units do not always correspond to taxonomical units. For mapping in particular, 5 units have been distinguished: 1. Larger peneroplids represented by three discoidal species; 2. fusiform *Borelis*; 3. discoidal to lenticular *Operculina* characterized by simple, unfolded septa; 4. discoidal to lenticular *Heterostegina* with supplementary, secondary septa and 5. discoidal, paper-thin *Heterocyclina tuberculata* with secondary septa and annular adult growth stages. Groups 3–5 have a marginal cord and are therefore nummulitids.

The genus *Sorites* defined by a single row of 8-shaped marginal apertures is represented in the Gulf of Elat by two species, *S. orbiculus* Ehrenberg, 1839 emend. Lehmann, 1961 and *S. orbitolitoides* (Hofker), 1930. The two species have a different but overlapping distribution. They are rather difficult to distinguish without sectioning their shells in order to compare the embryonic chambers. The adult chamberlets in *S. orbiculus* are larger than the chamberlets in *S. orbitolitoides*. In the counts of larger foraminiferal shells, the two species have not been distinguished. For mapping both species have been recorded together with *Amphisorus hemprichii* forming one morphologically homogeneous group of discoidal larger peneroplids.

The genus *Amphisorus* occurs in Elat with a single species, *A. hemprichii* Ehrenberg, 1839 emend. Lehmann, 1961. *A. hemprichii* must be distinguished from soritids by its double row of marginal apertures and by its large embryonic apparatus. Microspheric forms have usually undulated margins.

The genus *Borelis* is represented in Elat by *B. schlumbergeri* (Reichel), 1937. *B. schlumbergeri* shells from Elat are particularly variable in shape; many of them are shorter and more ovoid than the topotypes from Mayotte Island, North of Madagascar. *B. schlumbergeri* is very difficult to recognize under water because of its relatively small size. Its distribution map is based mainly on its recognition in sediment samples.

The genus *Operculina* is represented by involute, thickly lenticular to evolute, flat forms, all presenting the same structural type (absence of trabeculae). No morphological criteria have been found to define a clearcut distinction between involute and evolute forms. Microspheric forms seem to be evolute. All involute forms prepared so as to show their early growth spiral are megalospheric. They are therefore grouped together under one specific name *O. ammonoides* (Gronovius), 1781. Involute *O. ammonoides* are distinguished from involute "*Operculinella*" *cumingii* (Carpenter) occurring in the Eastern Indian Ocean by the absence of trabeculae (Hottinger, 1977). *O. ammonoides* is the only representative of the Nummulitidae with simple septa.

Representatives of the genus *Heterostegina* are involute or evolute in their

last 1–2 shell whorls in the same way as *O. ammonoides,* but their microspheric forms are involute or evolute and are much more frequent than in *O. ammonoides.* No specific distinction can be made between thick and flat forms, both included in *H. depressa* d'Orbigny, 1826. *H. depressa* is easily distinguished from *O. ammonoides* by its secondary septa.

The name *Heterocyclina tuberculata* (Möbius), 1880 is used here to designate extremely flat and thin-walled nummulitids with a long, heterosteginid juvenile growth stage which has up to 30 spiral main septa. The adult growth stage consists of annular chambers. Only megalospheric forms are known at present in this species. It needs some experience to distinguish small spiral juveniles of *H. tuberculata* from juvenile *H. depressa* having a narrower spiral with less secondary septa per chamber.

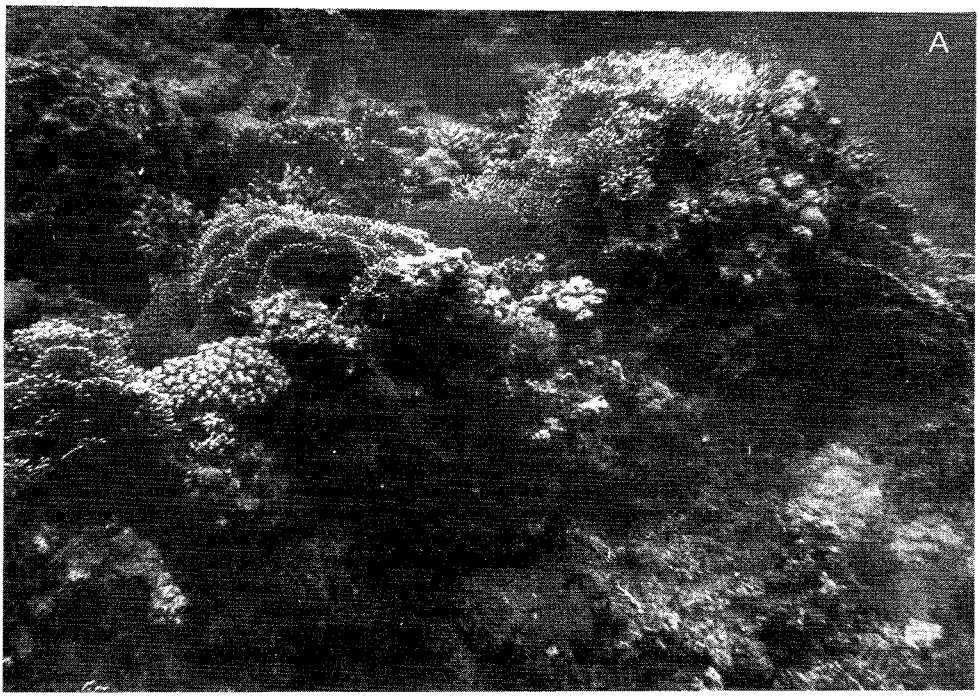
Counting larger foraminifera

Washed sediment samples were mixed, spread on a sheet of paper and split by hand into small portions of approximately 0.5 g. Usually, up to 300 larger peneroplids, *Borelis* and nummulitids were picked out. Broken specimens with their proloculus and regenerated specimens were picked, fragments without embryonic chambers were disregarded. Operator errors in picking are systematic. Regularly 10% of the specimens in the residues, mostly young specimens or fragments, were missed. Differences between percentages of foraminifera counted in the first, the second and the third successive picking of the same residue did not exceed 10%. Therefore, the effective operator error in picking is 1% maximum with regard to percentages of foraminifera in the sample.

Picked specimens were controlled as to their determination and counted. Operating errors in counting and identification of the morphologic groups cited above were insignificant compared with the picking error.

No systematic research was carried out to determine errors caused by the loss of parts of the finest sediment fractions during sampling under water and by destruction during transport and washing. This kind of error is related to total sample size, to the distribution of grain sizes in the sample and to the nature of the grains. Such research is only worthwhile to carry out when we will know more about the destruction of shells in their natural environment.

Fig. 4 A: Young fringing reef growing on coarse rock fragments deposited probably during the destruction of the medieval "Black Tower" on Coral Island, site 142, 5–10 m depth. Height of reef about 3 m.
B: Coral carpet North of Coral Island, site 140, 40 m depth. Sand patch filling depression about 2 m wide.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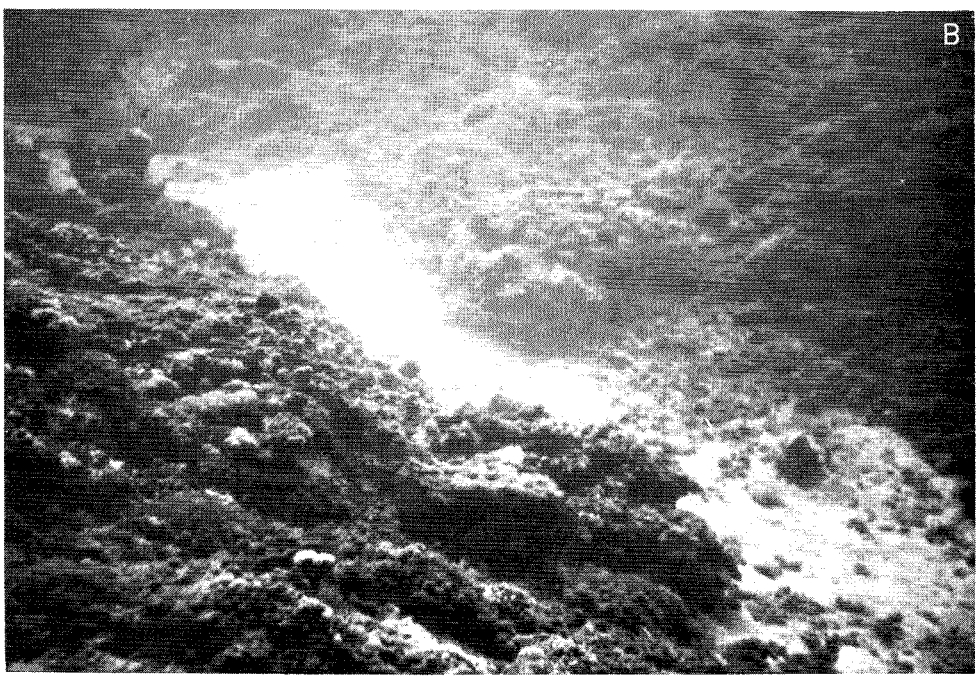
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Substrates

Mappable substrates should be perennial and express themselves in the sediment in order to be comparable to fossil distribution models. The diver in the Gulf of Elat encounters two fundamentally different types of substrate fulfilling these prerequisites. Large, continuous areas are covered with coral growth (fringing reefs, fig. 4A and coral "carpets", figs. 3, 4B, 5B). Other areas are covered with *Halophila* meadows (figs. 8B, 12).

Sediments in the coral covered areas are absent (no deposition on hard substrate, hard bottoms), or represented by coarse, well aerated sands which are white down to 50 cm depth (fig. 3B, 7).

Sediments overgrown by *Halophila* meadows (figs. 8B, 9B, 10B, 11, 13) are finer grained, often muddy, with an oxygenated, white surface layer of

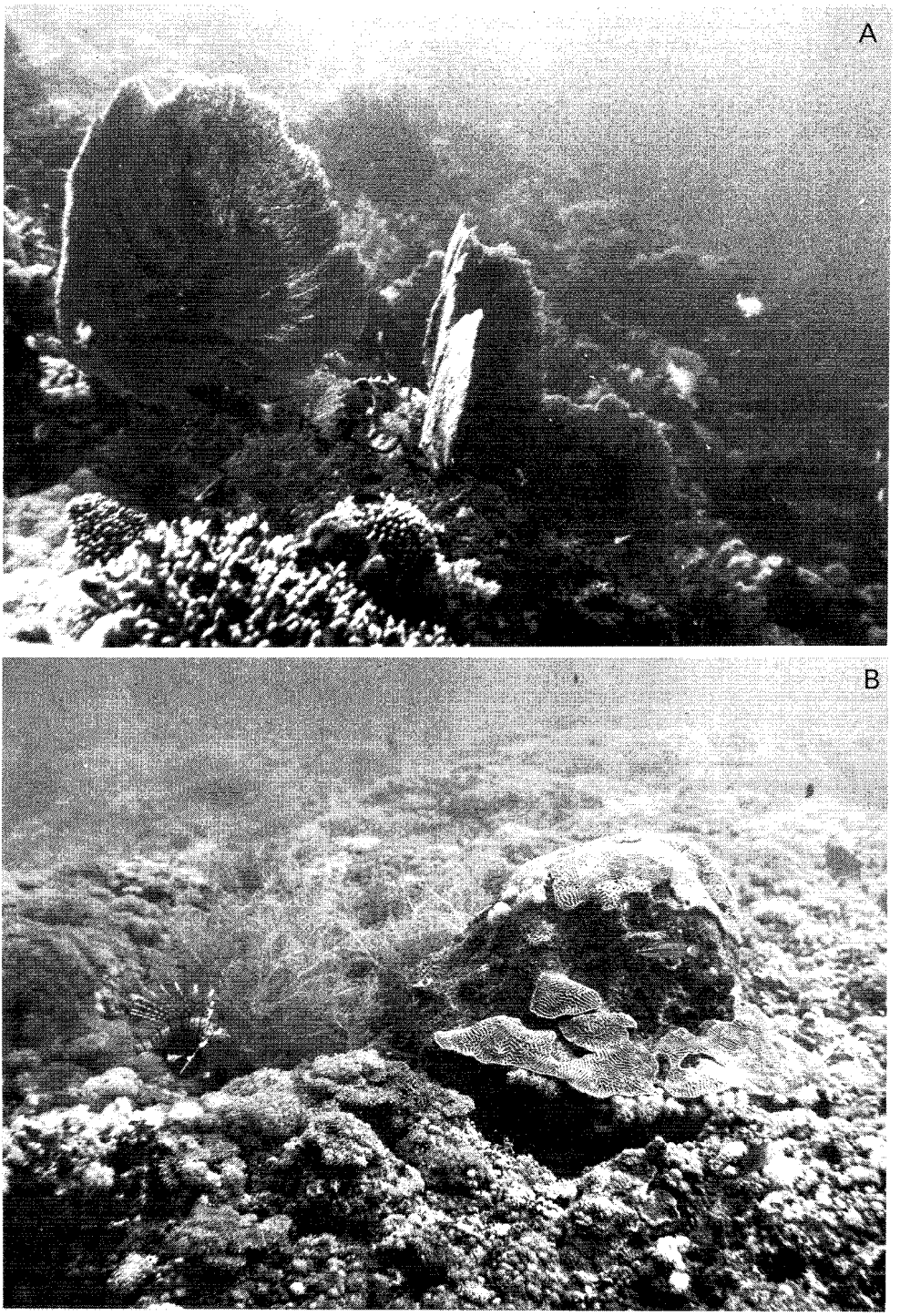
Fig. 5 A: Reef edge with belt of 2 m high gorgonian corals characteristic for exposed reef parts in 20 m depth. Marset el At, near site 126.
B: Coral carpet, near site 203, Lighthouse South of Elat, 35 m depth.

Fig. 6 Lower limit of coral growth in front of Marine Biological Laboratory, Elat, site 206, 70 m depth. This particular environment is characterized by small coral patches (A), whip-like gorgonian corals of 1–2 m height and the first brown algae forming a very thin vegetation cover (B) on the soft bottom substrate below 70 m depth. Note intensive burrowing reflected by clear patches on sediment surface.

Fig. 7 Vertical thin section of sediment core from site 206, 70 m. x 10. Note absence of stratification and orientation of the particularly numerous shells of *Operculina ammonoides, Heterostegina depressa* and *Amphistegina* sp.

Fig. 8 A: Bare strip of moving sand at wave base, at foot of fringing reef. Dahab, site 391, 10 m.
B: *Halophila* meadows growing in between and on mounds (about 1 m high) cast up by burrowing organisms. Geziret Faraoûn, site 028, 8–10 m.

Fig. 9 A: Horizontal thin section of sediment core (x 10) corresponding to environment illustrated by fig. 8A, from Geziret Faraoûn, site 146, 3–4 m, with *Peneroplis* sp., fragments of *Sorites orbiculus,* thick *Amphistegina* specimens and fresh fecal pellets deeply coloured by Rose Bengale.
B: Horizontal thin section of sediment core (x 10) corresponding to environment illustrated by fig. 8B, from Geziret Faraoûn, site 145, 8 m, with numerous Miliolids, *Sorites* sp., *Amphisorus hemprichii* and *Borelis schlumbergeri.*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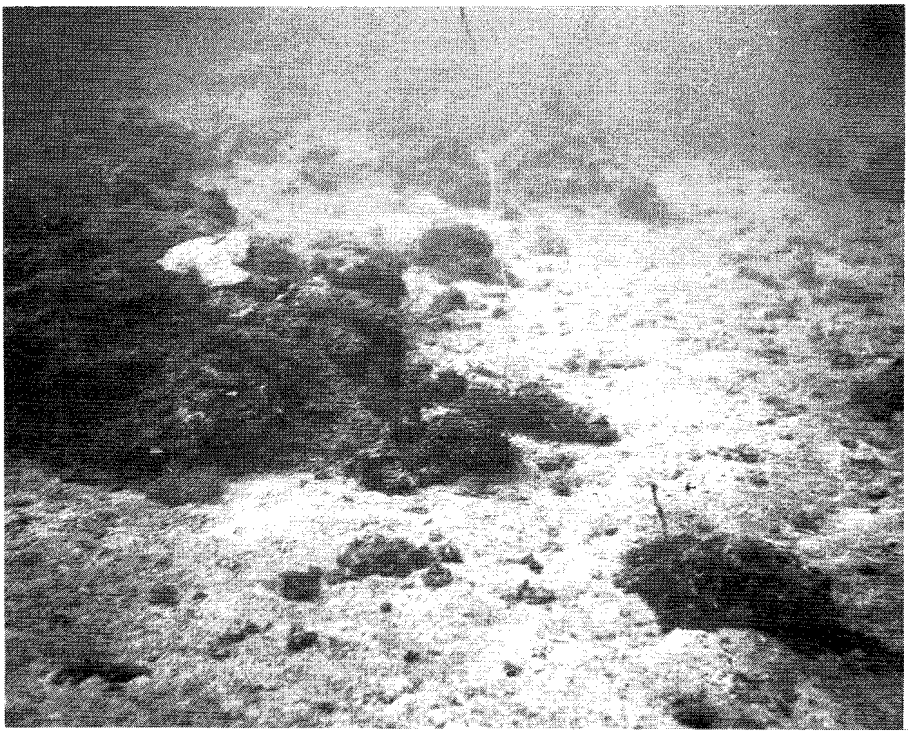

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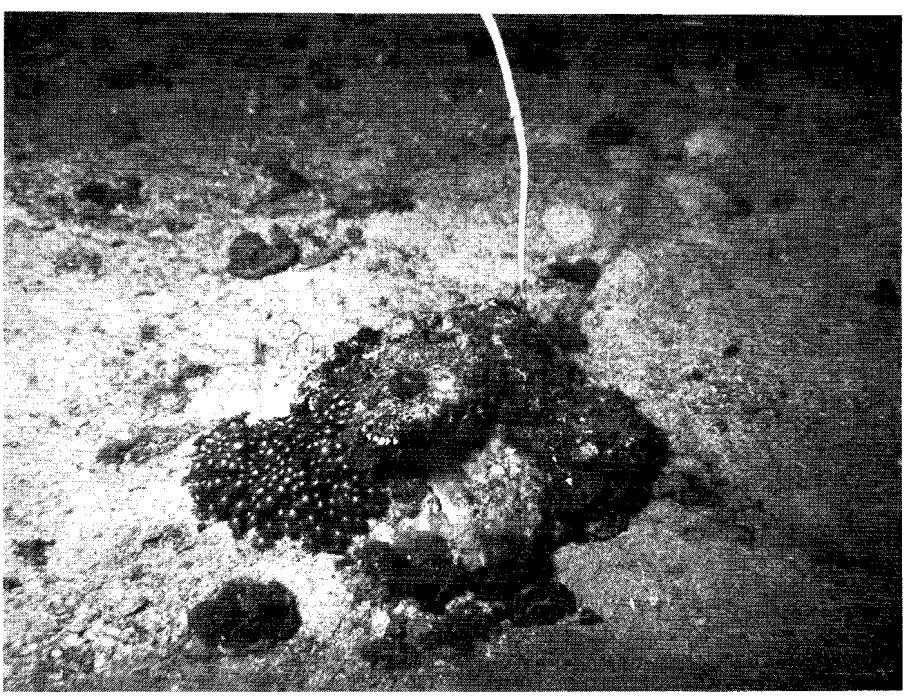

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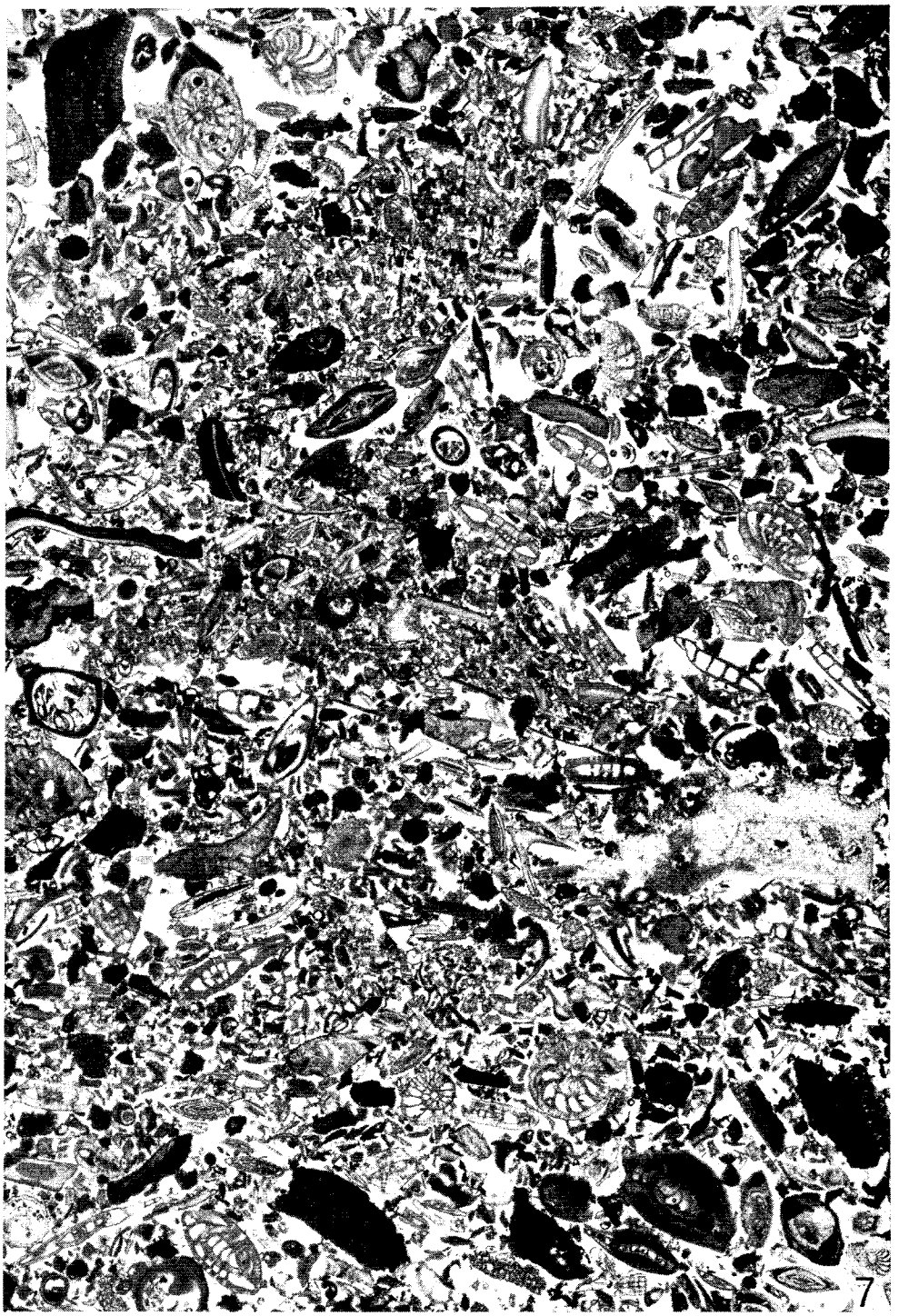
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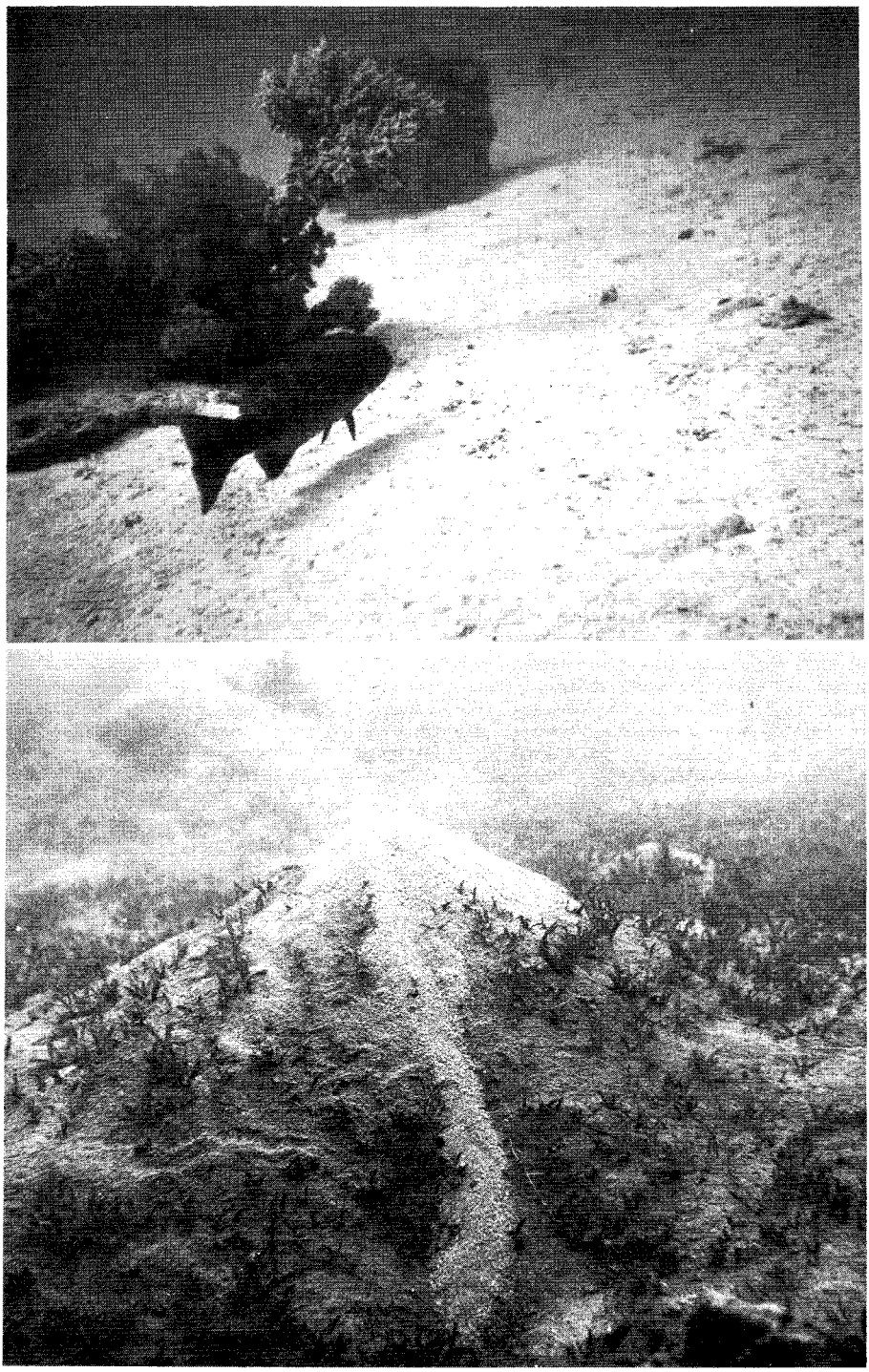

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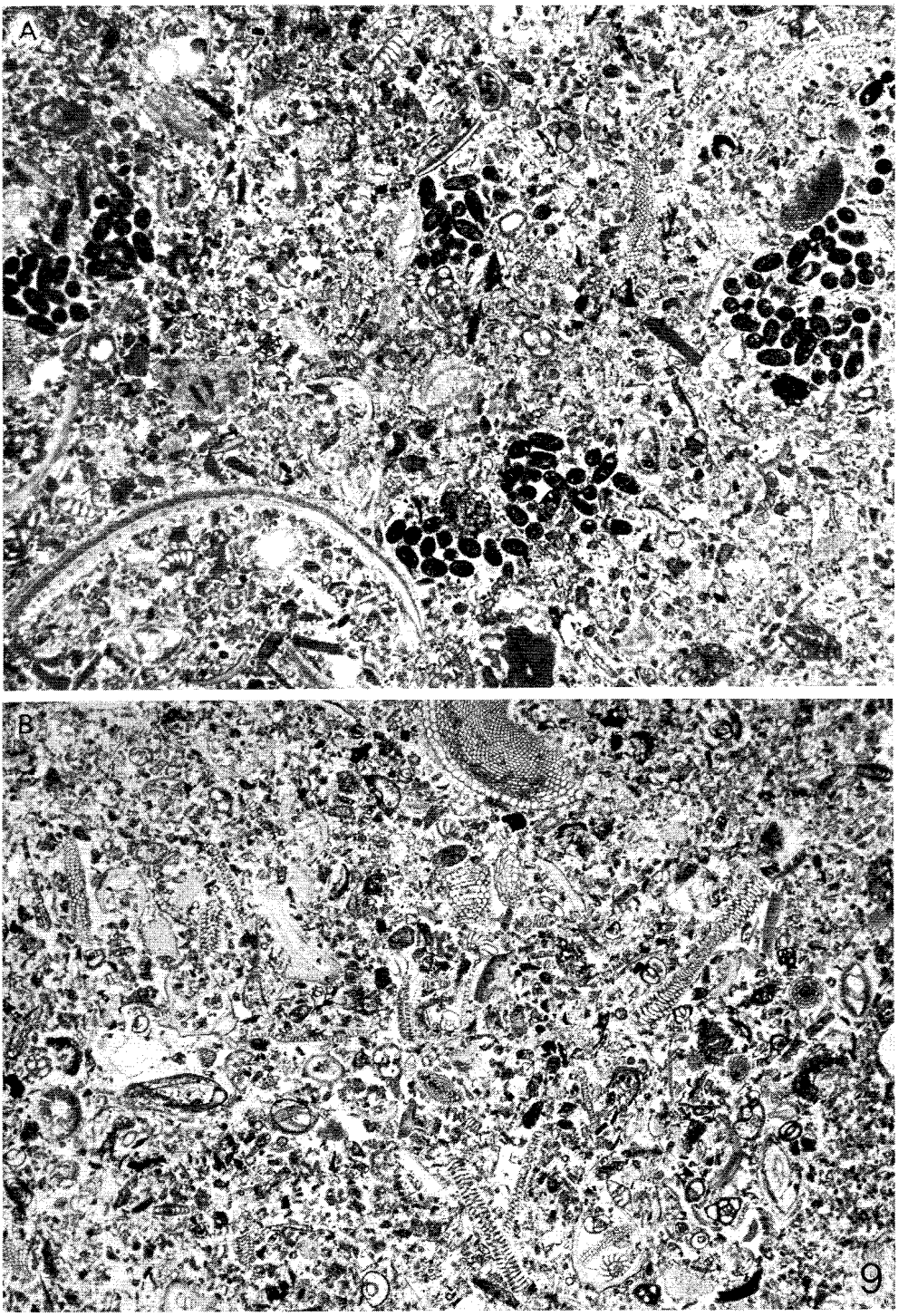
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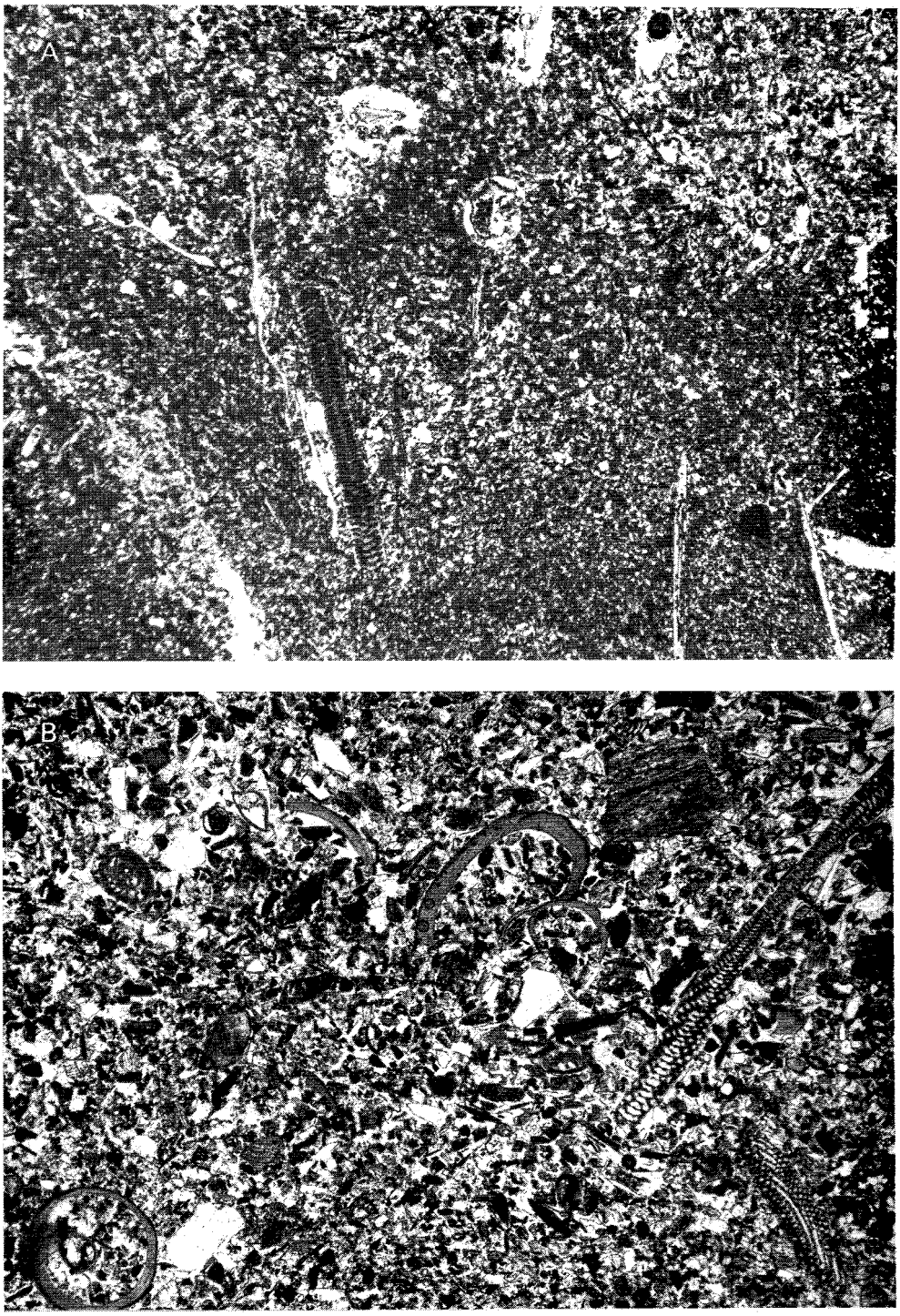

A
B

some millimeters thickness. Below the surface, sediments are dark grey to black for at least 50 cm. The dark sediments are deficient in oxygen; bacterial activity develops H_2S. Some shells of larger foraminifera and of other organisms get pyritized.

No type of sediment occurring in the model area of Geziret Faraoûn down to 60 m depth is layered. All layering has been destroyed by intensive burrowing (figs. 7, 13).

Below the divers' easy access to the sea bottom, at more than 70 m, the grab samples show the presence of a third, major type of substrate. The sediment is very fine-grained and muddy, reddish brown or grayish brown in colour. The colour reflects a progressive change of bacterial activity. This sediment covers the topographic platform extending between 70 and 200 m depth (fig. 14). All grains coarser than 0.5 mm are biogenous and seem to be generated *in situ* by benthic life or to have fallen down from the planktonic realm. For security reasons, this type of substrate has been studied by skin diving North of our model area, in front of the Marine Biological Laboratory of Elat, below the coral reefs in 68–72 m depth. Its upper limit shows a gradual thinning of the coral growth. In spring and in autumn, there is a scarce vegetation of brown algae on a very flat mud-surface in a desert-like landscape (fig. 6, 7). At the foot of the coral carpet, the biogenous sediment is still very coarse (fig. 7).

There are some additional but minor types of substrate in the area of Geziret Faraoûn

1. Sabkha sediments in a small, artificial lagoon on Geziret Faraoûn Island with temporary deposits of gypsum (sites 029 and 360).

2. Shallow lagoons on the top of the fringing reefs, 1–2 m deep, with coarse, sandy sediments where *Diplanthera uninervis* forms more or less dense meadows (fig. 10A, sites 047, 353, 355). *Diplanthera* occurs also on the shallowest subtidal part of active deltas, mixes gradually between 5 and 10 m depth with *Halophila* and is replaced entirely by *Halophila* (site 177) below 15 m.

3. Nearshore, bare, sandy spaces between 0 and 10 m depth often extend along the foot of smaller fringing reefs, corresponding to the main wave base platform (figs. 8A, 9A; sites 146, 362). This biotope is not covered with

Fig. 10 A: Vertical thin section of sediment core (x 10) in *Diplanthera* environment from Geziret Faraoûn, site 047, 1 m depth; with *Amphisorus hemprichii* and numerous plant remains. B: Coarse grained *Halophila* substrate, vertical section of core (x 10) from Marset el At, site 119, 8–10 m; with *A. hemprichii,* thick *Amphistegina* and coarse debris of mollusc shells.

vegetation and the sand is moved parallel to the fringing reefs by the weak longshore currents.

4. *Cymodocea* occurs exceptionally in the Geziret Faraoûn area where "water energy" is high, on patches of moving sand. Much larger areas are covered by this deeply rooted plant at Ras Burka in the wave base zone and in the lagoons of Ras Muhammed.

5. Mixed environments where *Halophila* grows between living coral heads and small patch reefs. Such environments are generated in front of deltas with small activity and in the shelter of moving sands of the wave base zone.

The map (fig. 14) clearly shows a relation of the distribution of substrates to the main current pattern in the area and to the prevailing winds from the North-East. Interaction of currents with underwater topography, with the supply of terrigenous sediments from the more or less active deltas on the North and the South border of the mapped area, and with the production of biogenous sediments *in situ* determine the major substrates. The limit between the substrates above and that below 70 m corresponds to a topographical break coinciding with the approximate lower limit of the depth range of hermatypic corals.

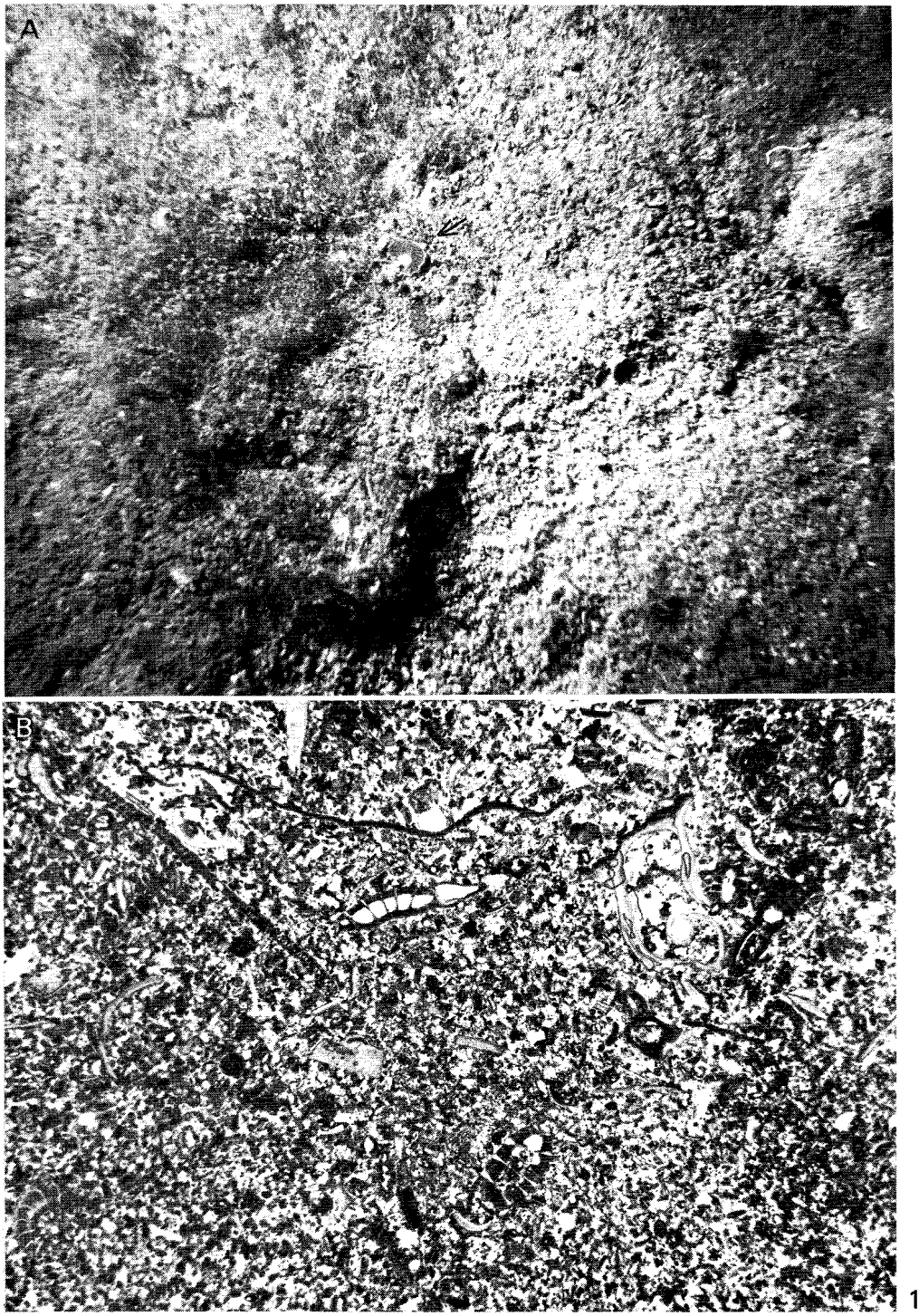
Seawater medium

One of the most striking particular conditions in the Gulf of Elat is the relative homogeneity of the seawater medium (Klinker et al. 1977). Nearshore, in the vicinity of the reefs, the temperature measured between 5 and 70 m depth did not change more than half a degree C (26°C in September 1971). Water chemistry was not known in detail, but as temperature does not change with depth, no stratification of water masses is to be expected

Fig. 11 A: *Halophila* shoots, and, mostly dead, larger foraminifera from Geziret Faraoûn, site 134, covering the floor in between *Halophila* shoots. Wadi Taba, site 059, April 1971. Arrow points to a large, living microspheric specimen of *O. ammonoides* (ca. 8 mm largest diameter).
B: Horizontal thin section of sediment core (x 10) from same site as A, with *O. ammonoides* and *Sorites orbitolitoides.*

Fig. 12 A: *Halophila* shoots, and, mostly dead, larger foraminifera from Geziret Faraoûn, sit 134, 40 m.
B: Living *Operculina ammonoides* forming local bloom between *Halophila* shoots from site 173, 35 m.

Fig. 13 *Halophila* substrate from site 352, 30 m. Vertical thin section of core (x 10) showing burrows, *Sorites orbitolitoides, Borelis schlumbergeri* and numerous smaller foraminifera.



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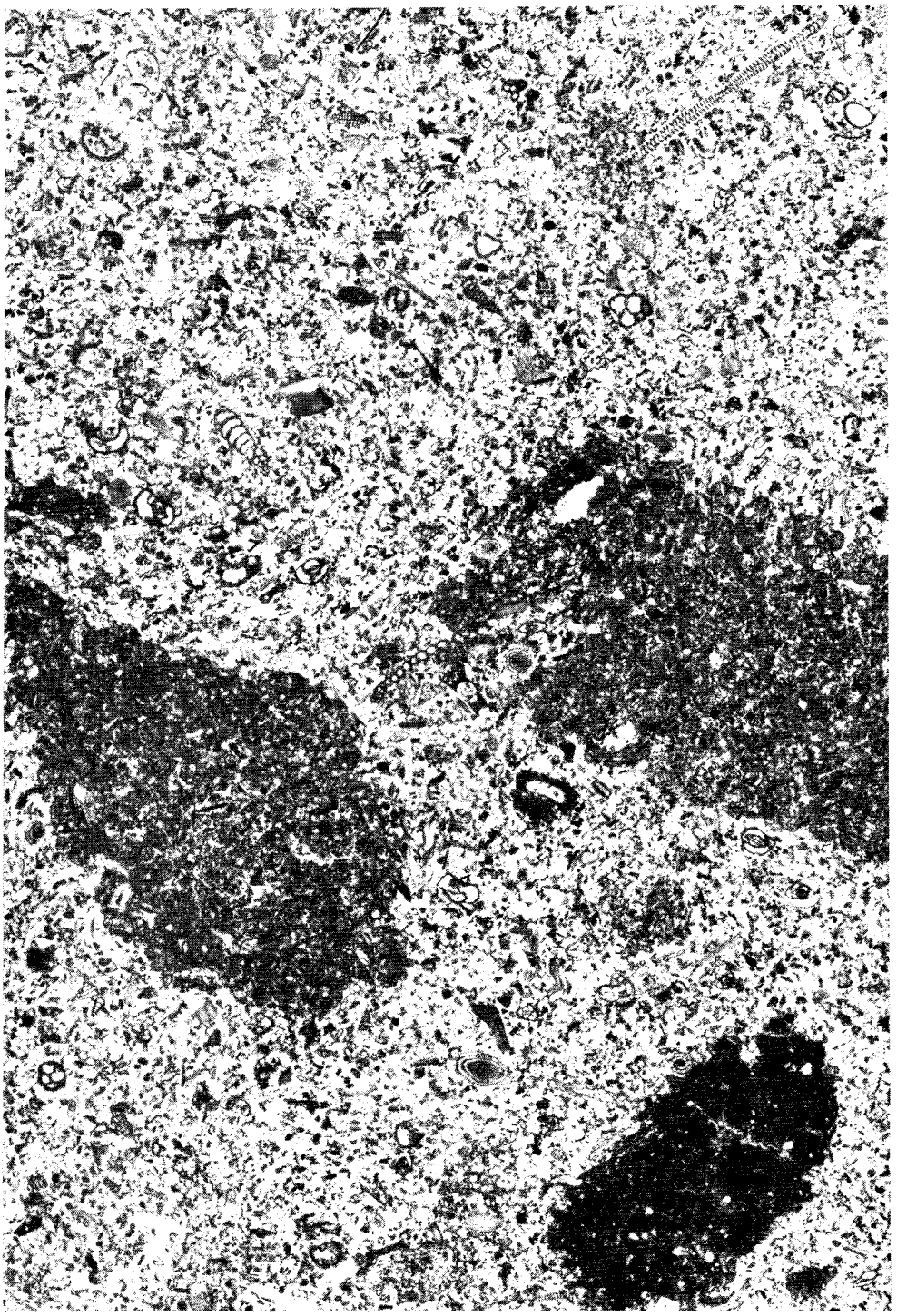

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and therefore chemical properties are supposed to be very uniform. The pH value (8.3 measured in situ in September 1971) did not change between 0 and 25 m depth, not even a few mm above the sediment-water interface.

The only important gradient of the medium conditioning this ecological model is the quantity of light reaching the bottom. This gradient has the same directional trend as water-depth so that depth values must be expected to reflect the effective influence of light on bottom communities. There is, however, one important additional factor to be considered: white coral sands without a vegetation cover are a considerable source of light energy by reverberation. Coral sand environments of a particular depth may thus correspond to much shallower environments covered with *Halophila.*

Turbulence is highest in the uppermost 10 m of the water column, where wave action takes place. The wave base as observed by the diver by rhythmic back-and-forth movement is not more than 6–10 m deep, the prevailing winds from the land having not more than 15 km searoom to put up the waves. The predominant laminar current running roughly parallel to the coast from N to S is strong until about 20 m depth and gets gradually weaker downwards. This was observed near shore between profiles 2 and 6, south of Elat. Its influence on turbulence and on the growth of coral carpets far below the fringing reefs will be studied later when appropriate measurement methods will be available. The Geziret Faraoûn Area, however, between the Island and the shoreline, seems to be located outside the main current regime because the weak longshore current directed from North to South during "normal", nice weather is reverted when the winds are blowing from the South.

The quantity of light reaching the bottom is influenced by turbidity, and to an even larger extent by the variable amount of plankton developing in the surface layer. Here again, quantitative data are not yet available.

Turbidity is highest during rare thunderstorms in late autumn to early spring. Winds blowing out of the desert from SW to NE are turning the longshore current in opposite direction. In spring 1971, we observed a sudden discharge of terrestrial sediment swept into the sea from the delta on the southern border of Geziret Faraoûn map. The coastal area up to the northern border of the map and down to at least 20 m depth was covered with a thin, yellow pelitic film killing most of the corals exposed to the turbid current. Such catastrophic events seem not to influence overall ecologic distributions in the Geziret Faraoûn area, its conspicuous effects disappearing after some days of "normal" weather with winds from the North-East.

Geziret Faraoûn Area

Underwater mapping of the distribution of larger foraminifera and of the main substrates shows geometric coincidence of distributional limits with depth contour lines and/or with the mapped limits of the main substrates. We postulate therefore the existence of ecologic relationships between larger foraminifera and substrate and/or water depth. Representatives of different genera show different relationships with substrate, all larger foraminifera show relationships with water depth (fig. 14–15).

The combined distribution of *Sorites orbiculus, Sorites orbitolitoides* and *Amphisorus hemprichii* (fig. 15A) is limited approximately by the water surface and the depth contour of 40 m. Laterally, the distribution is restricted to soft bottom environments with *Halophila* or *Diplanthera. Amphisorus hemprichii* and *Sorites orbiculus* are living almost exclusively as epiphytes on larger plants whereas contorted *Sorites orbitolitoides* shells are found also in comparatively small numbers on dead coral or mollusc shells in the coralligenous facies.

Borelis schlumbergeri (fig. 15B) occurs between 20 and 45 m depth. The highest numbers of shells are found in 30–35 m depth. The map shows no dependence on substrate. As this species is comparatively small, the shells are difficult to observe directly under water. Thus, we do not yet know, if their epiphytic way of life observed sometimes on *Halophila* leaves or on filamentous green algae is exclusive or not.

Heterostegina depressa (fig. 15C): The distribution of this species shows an upper limit parallel to the 40 m depth contour and a lower limit parallel to the 75 m contour. Lateral limits coincide rather strictly with the limits of coral growth (hard bottom substrate). Microspheric forms are most frequent in the deepest part of the distribution area, between 60 and 75 m depth, where the megalospheric forms are flattest.

The vertical distribution of *Operculina ammonoides* (fig. 15D) is limited along the depth contours of 35 and 150 m. The lateral limits correspond roughly to the limits of soft bottom environments. Relatively small numbers of involute *O. ammonoides* are present also in the hard bottom environments. Flattened megalospheric forms and microspheric forms are most frequent between 60 and 120 m depth on soft bottom.

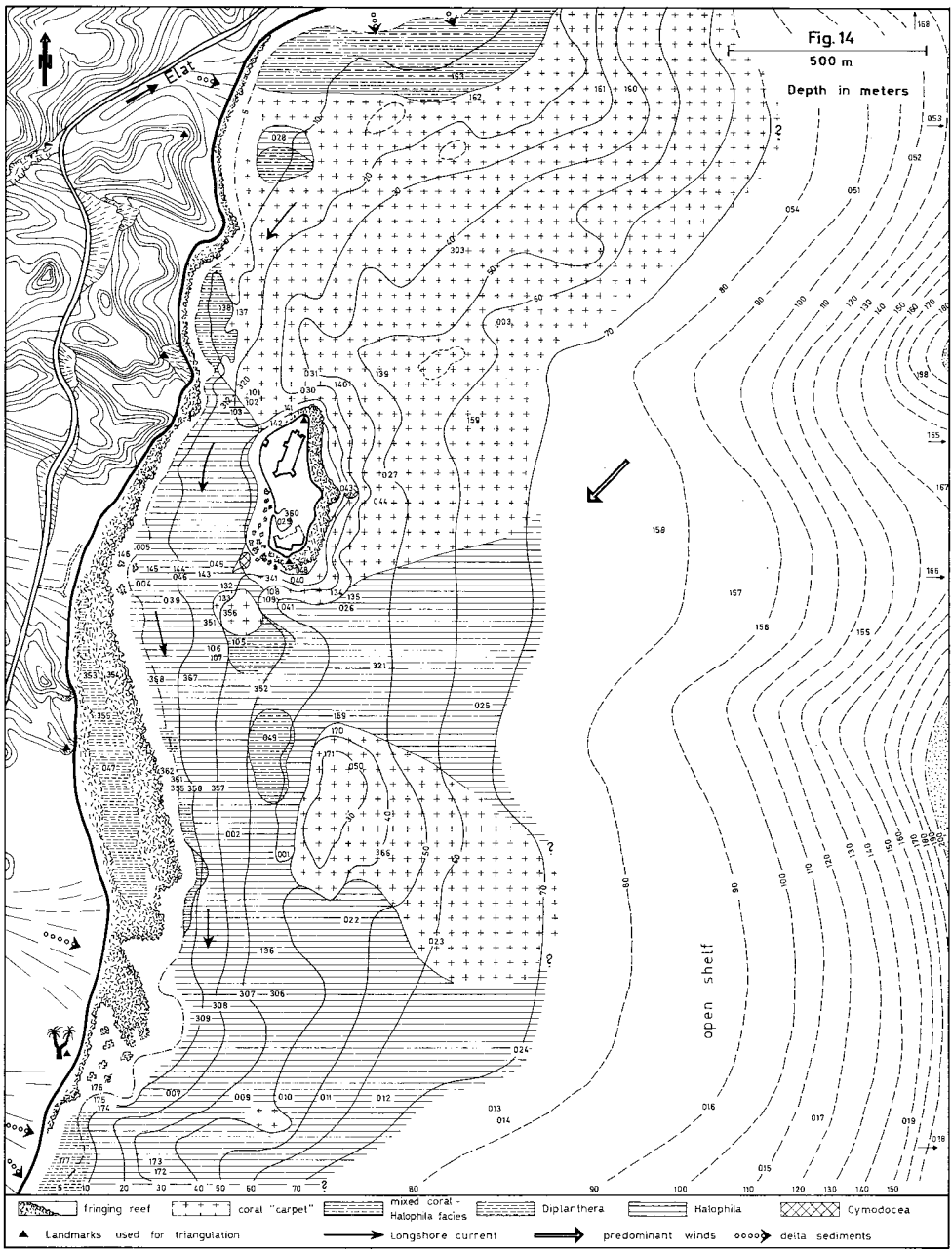


Fig. 14 Distribution of main substrates in Geziret Faraoûn area, Gulf of Elat.

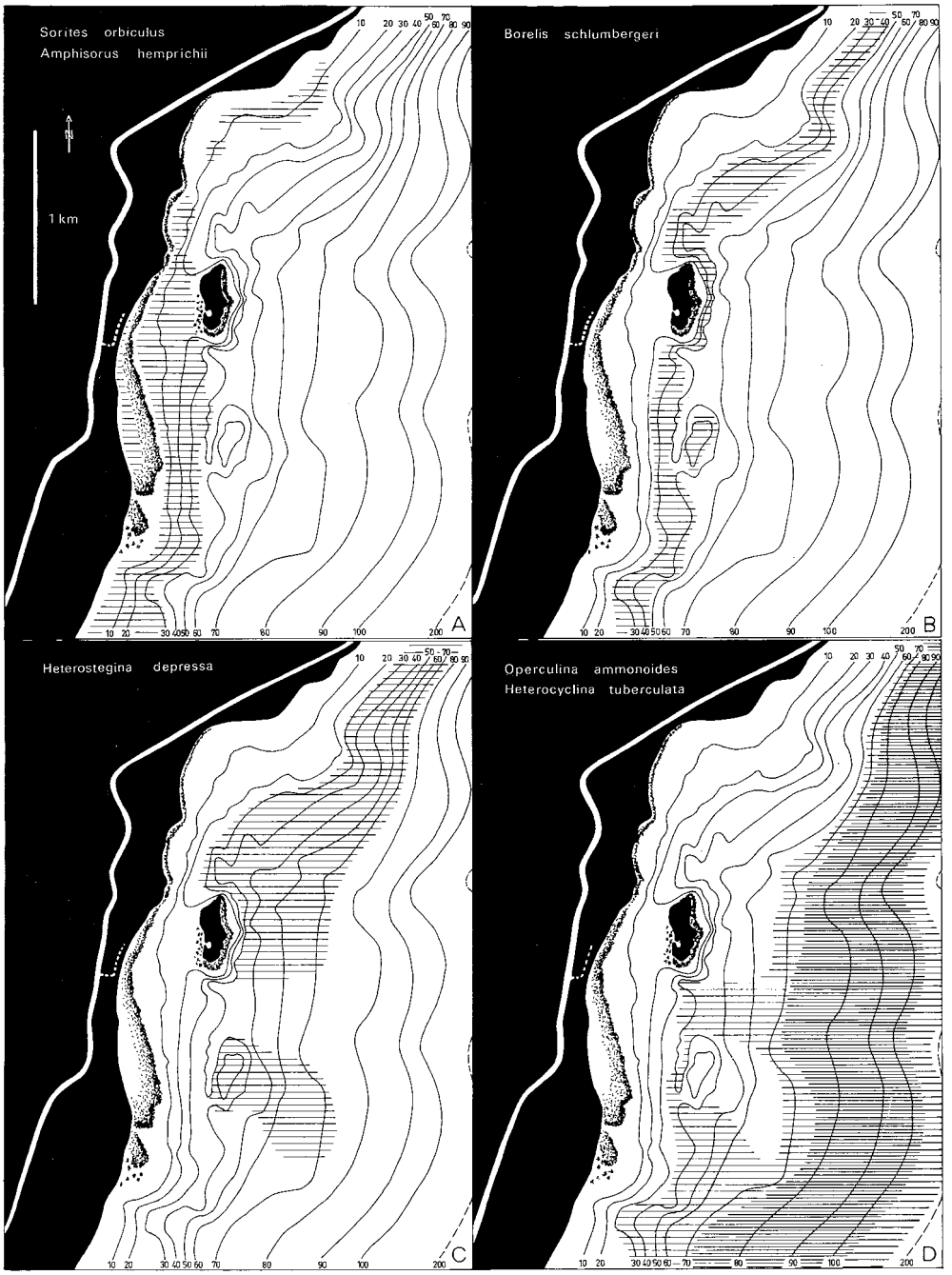


Fig. 15 Main distribution of *Amphisorus hemprichii* and *Sorites orbiculus* (A), *Borelis schlumbergeri* (B), *Heterostegina depressa* (C), *Operculina ammonoides* and *Heterocyclina tuberculata* (D) in Geziret Faraoûn.

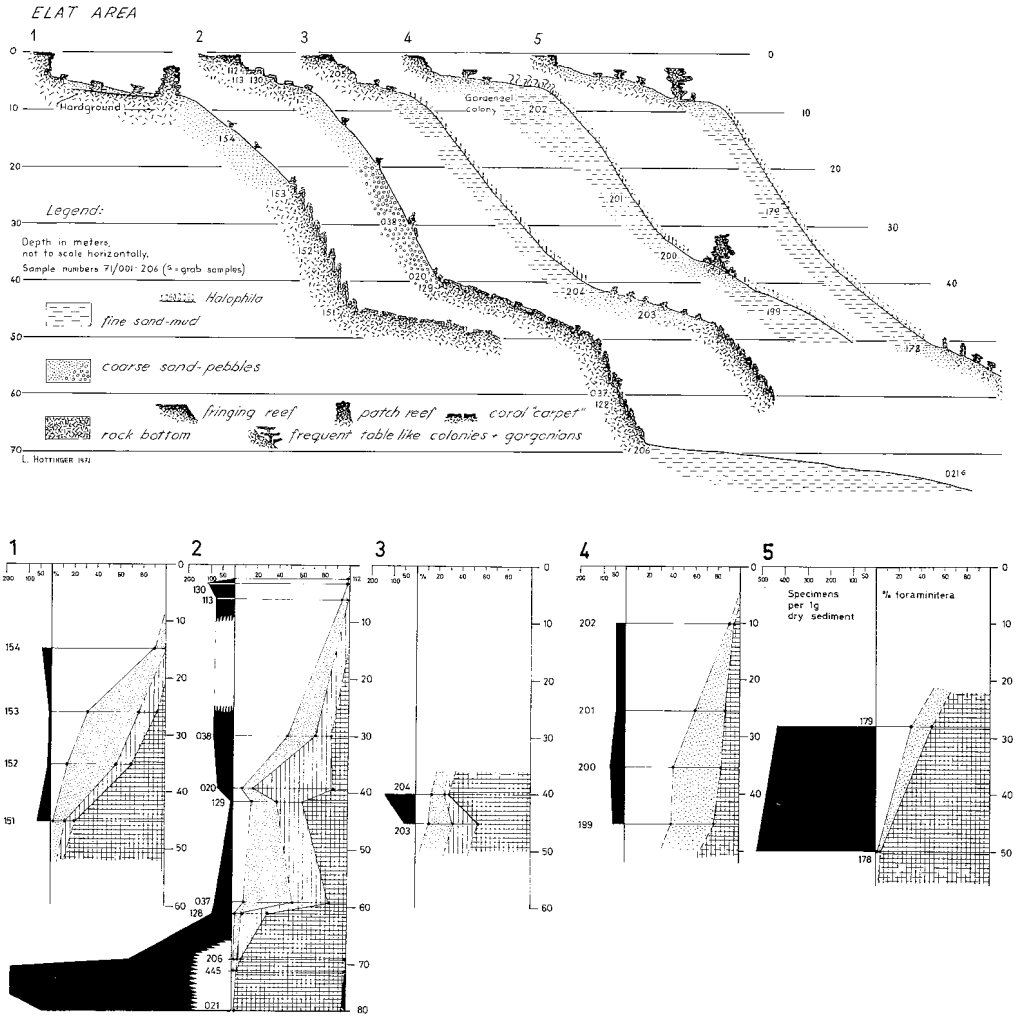
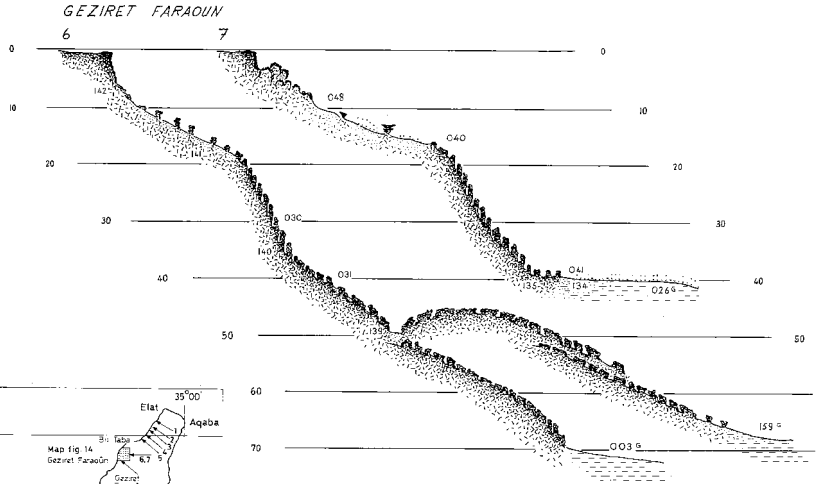


Fig. 16 Profiles vertical to the shore line between the town of Elat and Geziret Faraoûn, Northern Gulf of Elat. Above: Physiography of the sea bottom, nature of substrate and position of samples. Below: Percentage of larger foraminifera and number of larger foraminifera per one gram of dry sediment, for each profile. Position of Geziret Faraoûn South – profile between site 177 and 019, see map fig. 14. For topographic details compare Cohen, 1975. Physiographic classification see fig. 19.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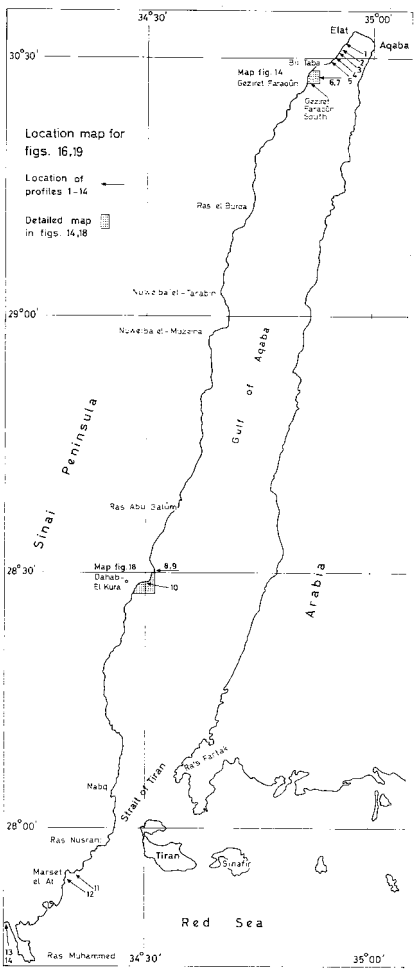
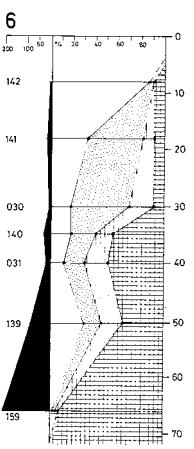

Location map for figs. 16,19
Location of profiles 1-14
Detailed map in figs. 14,18
Eilat
Aqaba
Map fig. 14 Geziret Faraoûn
Geziret Faraoûn South
Ras el Burqa
Nuweiba el-Tarabin
Nuweiba el-Mazena
Gulf of Aqaba
Sinai Peninsula
Ras Abu Galûm
Map fig. 18
Dahab
El Kura
Arabia
Nabq
Strait of Tiran
Ras Farâsh
Ras Nusrani
Marset el At
Tiran
Sinafir
Red Sea
Ras Muhammed
34°30'
35°00'
30°30'
29°00'
28°30'
28°00'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142
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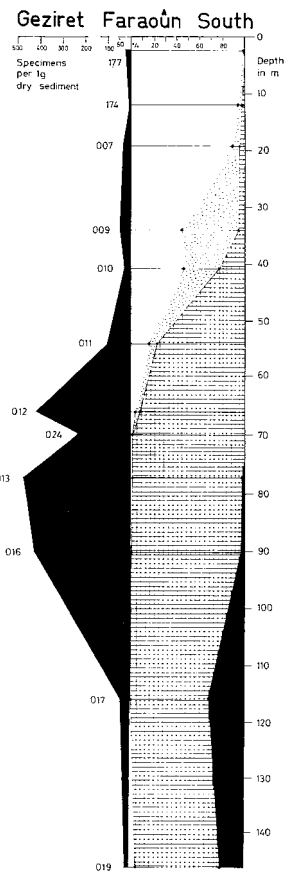

Geziret Faraoûn South
Specimens per 1g dry sediment
Depth in m
177
174
007
009
010
011
012
024
013
016
017
019

Heterocyclina tuberculata (fig. 15D, stippled area) occurs only below the zone of coral and *Halophila* growth on soft bottom. No transitional forms between flat *Heterostegina depressa* and *H. tuberculata* are found in the samples from the areas where the distributions of the two species show overlap, at the lower limits of coral growth. Microspheric forms of *H. tuberculata* have not yet been found. The number of megalospheric specimens is always very small compared with the number of *O. ammonoides* shells present in the same samples. The lower limit of *H. tuberculata* is not precisely known. It must be drawn between 150 and 170 m. Grab samples are probably not quite adequate to define this limit with precision, *H. tuberculata* being relatively large and scarce. The few samples taken by hand in 70 m depth in front of the Marine Biological Laboratory of Elat contained a higher percentage of *H. tuberculata* than grab samples taken at approximately the same spot.

Counting larger foraminifera in selected sediment samples in the Geziret Faraoûn area confirms the visual impression registered by the diver. Samples taken in a profile vertical to the coast, parallel to the southern margin of the map (fig. 15), on a homogeneous soft substrate covered with vegetation show successively the dominance of larger peneroplids from 0–20 m depth, the maximum frequency of *Borelis* in 25–35 m depth and the maximum frequency of *O. ammonoides* in 50–90 m depth (fig. 16). The high percentages of *O. ammonoides* below 70 m are due to very high numbers of young specimens. Very few of these young specimens were coloured by symbionts when the samples were taken. From this we conclude that most of these young specimens were dead. The important mortality of juveniles restricted to the deeper part of the distribution area of the species is difficult to understand. In my opinion, they are not accumulated by selective transport from shallower habitats because their frequency seems to be independent of grain size of the sediment. Microspheric adult forms are unusually frequent in the deeper part of the species distribution area, but young microspheric forms with less than two whorls cannot be recognized without cutting the shell in the median plane. Microspheric forms have therefore not been counted separately. There might be, however, a relation between the high mortality rate of young specimens and the frequency of microspheric forms instigating future systematic research on the life cycle of operculinids.

The frequency of larger foraminiferal shells per g dry sediment (fig. 16) in this profile of the Geziret Faraoûn area reflects clearly diminishing abiogenic sedimentation rates from shallow to deep parts of the delta. The overall-density of the foraminiferal population registered by sight did not

show conspicuous differences in different parts of the delta. The successively smaller foraminiferal frequencies registered towards the lower part of the open shelf terrace between 100 and 200 m depth, are due to an important production of shells, mostly benthic molluscs, to an increasing sedimentation of shells of planktonic organisms, but probably also to a true reduction of foraminiferal productivity towards the lower limit of the euphotic zone.

On substrates with coral growth, on the dead basal parts of coral heads and on patches of coarse coral sand between coral heads, the foraminiferal faunas between 30 and 70 m depth are dominated by *Heterostegina depressa.* They are particularly frequent where small green algae grow on coral debris. *Operculina ammonoides* occur on this substrate in rather high percentages as well. As they are less conspicuous than the larger *H. depressa,* the countings of larger foraminifera from the sediment samples reflect reality better than visual registration for mapping. Shell frequency on this substrate is low as compared to soft bottom out of the immediate influence of delta sedimentation, because the production of coarse coral and mollusc debris is relatively high.

Fig. 17 Aerial oblique view of Kura bay, Dahab area, from the East. Note large fringing reef in the foreground and large intertidal area around the inner bay of Kura. Compare with map fig. 18.

Dahab and other investigated areas

Dahab area (fig. 17) was mapped in autumn 1971 and 1973 in less detail (fig. 18, 19) than Geziret Faraoûn area, in order to check whether depth range of larger foraminifera and their relation to substrate were similar to the observed ranges in Geziret Faraoûn. Dahab represents an area with higher "water energy" than Geziret Faraoûn: The winds and waves have a much longer sea-room and produce more water-movement. The wave base is in 15–20 m depth during "normal" weather. This is reflected by the higher and longer fringing reefs, by the development of gorgonian growth forming a particular belt in 20 m depth (fig. 5A) and by a relatively high sedimentation rate of calcareous pelitic sediments trapped in the inner Dahab bay and suppressing growth of corals. The luxuriant coral platform of particular beauty in the sheltered zone of outer Dahab bay (fig. 20), below 30 m depth may be due to the return flow in the general current pattern of the gulf (see Klinker et al., 1977). The distribution of larger foraminifera in this area corresponds exactly to the distribution observed in Geziret Faraoûn. Larger foraminifera occur on the same substrates. The location of the lower limit of coral carpets or *Halophila* meadows and the nature of the sediments on the open shelf has not been investigated because of the lack of appropriate boats resisting the windy weather.

The bay of Marset el At, North of Sharm el Sheikh furnishes again similar distribution patterns. A particular environment was observed in the lagoons behind the fringing reefs on the west side of Ras Muhammad (fig. 19). The water in these lagoons is about 2–5 m deep and very turbulent. The sedimentation rate is high and favours dense growth of *Cymodocea*. The particular character of this environment is reflected by the presence of numerous *Calcarina calcar* which I have never found in the Northern part of the Gulf of Elat. The larger peneroplids, however, are present as usual growing as frequently on *Cymodocea* as on *Halophila* and resisting the higher turbulence.

Notes on shell transport and destruction

From direct observation in situ, only one mechanism for transport of larger foraminifera from one biotope to another could be observed. In spring, large clouds of filamentous green algae are transported by currents parallel to the coast. Some of these clouds are caught by corals (fig. 21), others are transported over great distances. Many of them contain a large

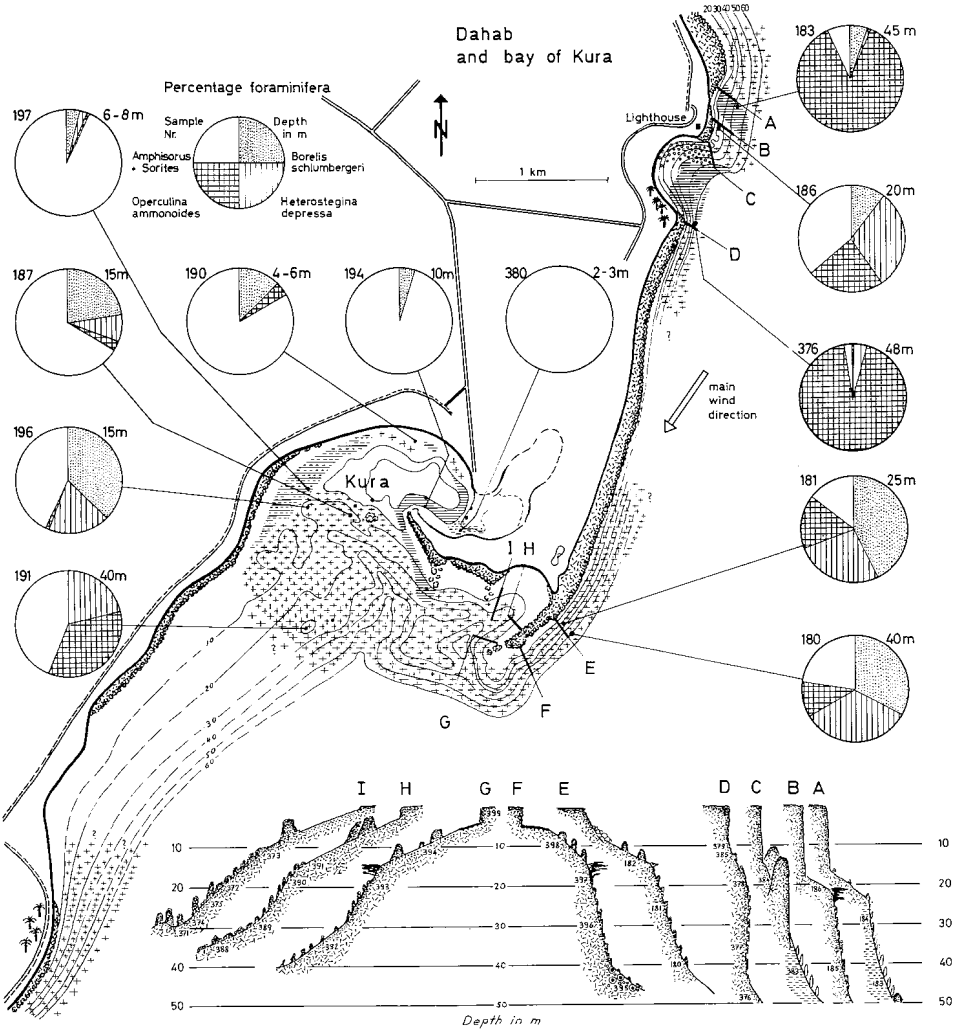


Fig. 18 Distribution of main substrates in Dahab area and Kura bay. Percentages of larger foraminifera in representative samples and physiography of main reef. Legend as in fig. 14.

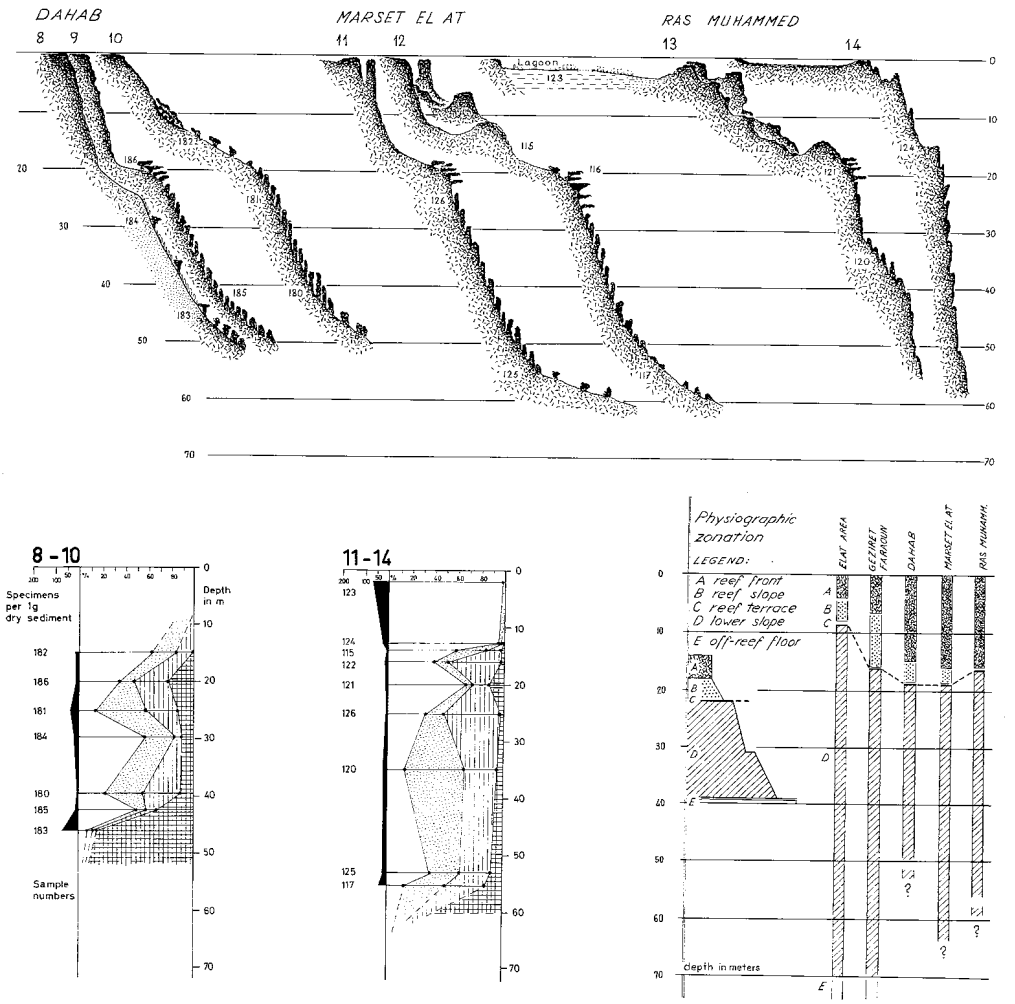
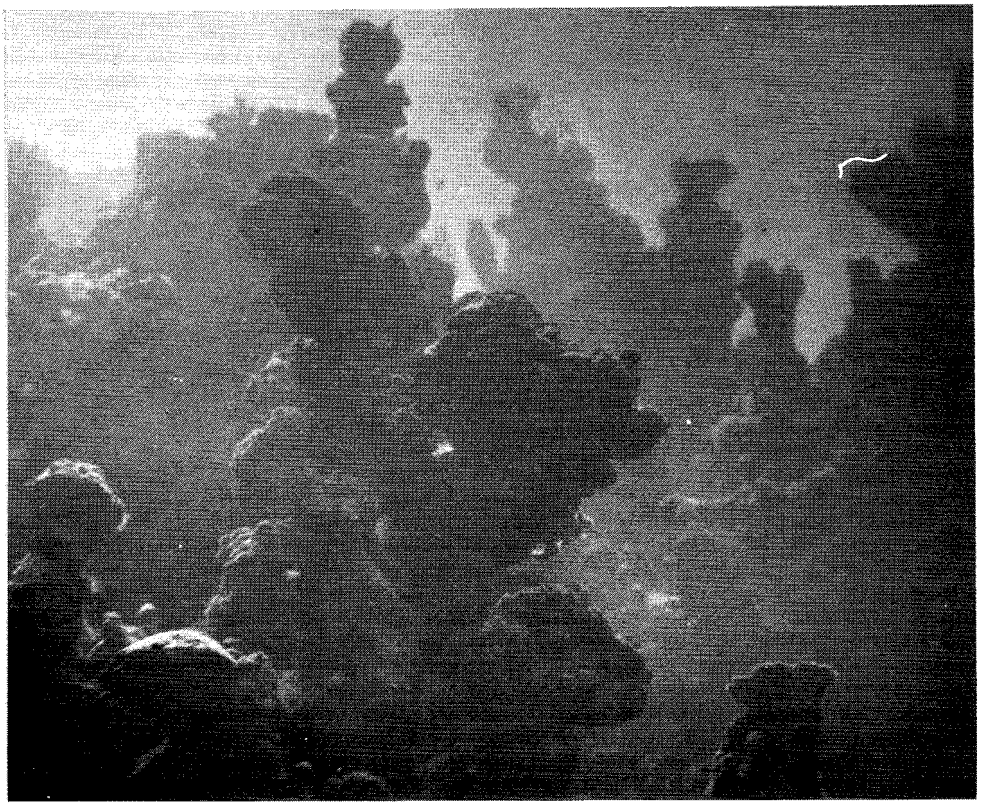
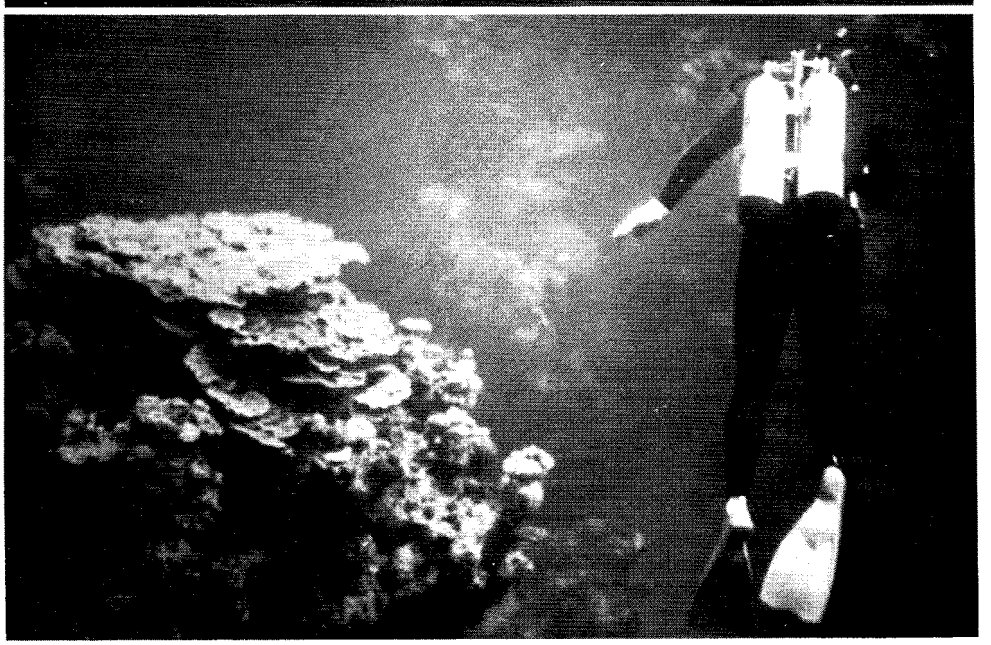


Fig. 19 Profiles vertical to shore line in Dahab and Ras Muhammed areas, Southern Gulf of Elat. Physiography of the sea bottom, percentages of larger foraminifera and number of larger foraminifera per one gram of dry sediment. Physiographic zonation of all profiles figured.

Fig. 20 Luxuriant coral growth in outer Kura bay. At site 191, the continuous coral carpet at 30 m depth is interrupted by a 30–50 m wide, elliptical hole framed by high coral towers (A) and with a sandy bottom (B) at 42 m depth. The coral carpet in outer Kura bay therefore must be at least 12 m thick.





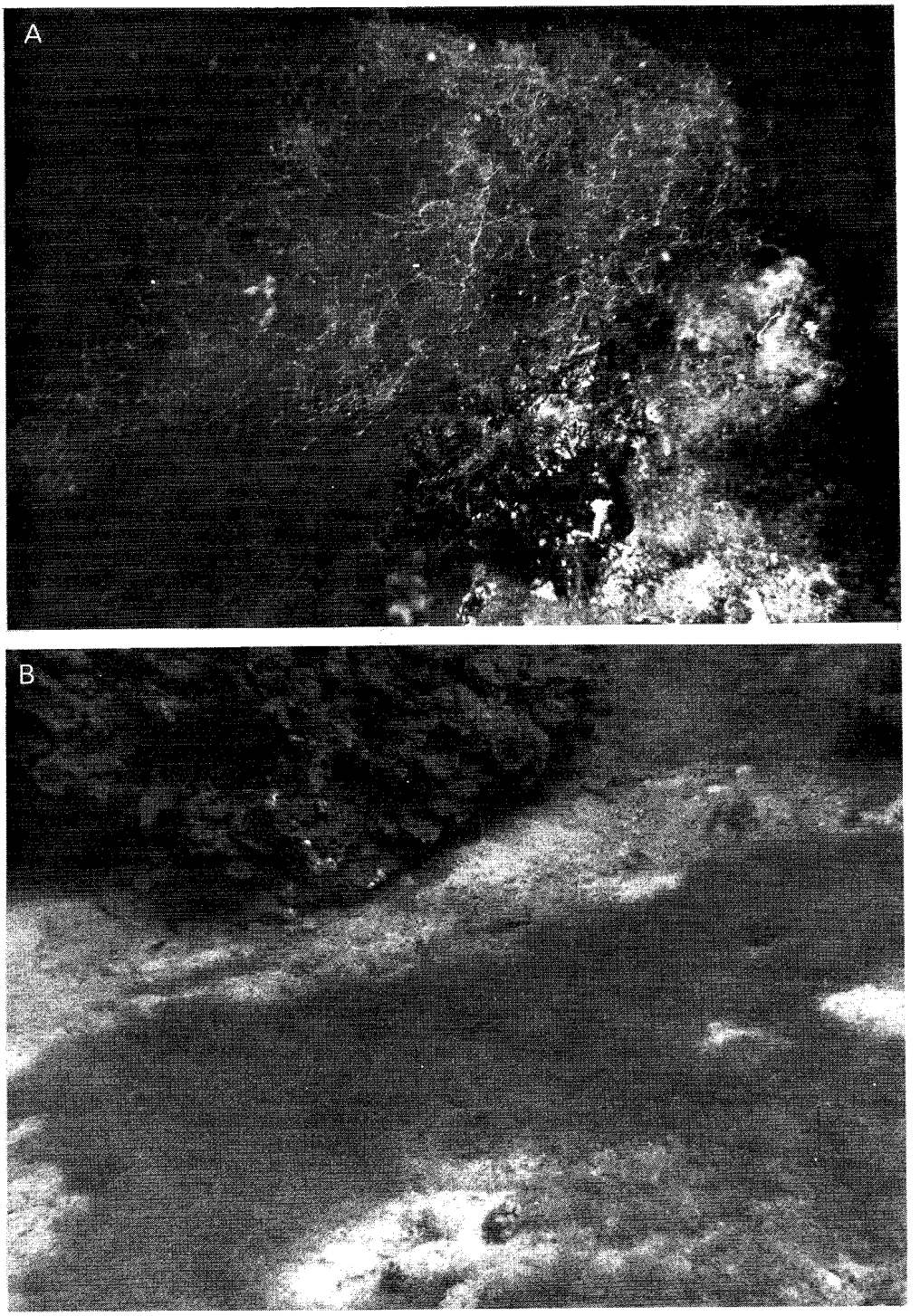
number of amphisteginids, smaller benthic foraminifera and also some of the larger foraminifera produced between 20 and 50 m depth. Farther down, below 50 m depth, this mechanism does not play an important part, because clouds of filamentous green algae were never observed.

Other kinds of passive transport have not been noticed. In particular, the winnowing of sediments by currents is not strong enough to lift the comparatively heavy shells from the bottom together with the pelitic fraction. In the surf zone, between 0–10 m depth, where a considerable amount of sand is displaced by wave action and longshore-currents, larger foraminiferal shells may be transported over a considerable distance parallel to the shore line. In these moving sands, the rate of destruction by abrasion must be very high as the shells are relatively rare (usually far below 10 specimens per 1 g. of dry sediment) and as most of the shells are broken and abraded.

Vertical movement of sediments coarser than the pelitic fraction has not been observed in the Geziret Faraoûn area, not even on the steep slopes of Geziret Faraoûn Island where the sediment is trapped by corals growing on the slope. A narrow zone not more than 50 m wide of vertical migration of coarse sand into the pelitic deposits on the outer shelf was observed at the foot of the reef slope between 70 and 80 m depth in front of the Marine Biological Laboratory of Elat.

Estimates of quantities in larger foraminiferal transport is not possible as long as we cannot measure their population density, and as long as we know nothing about reproduction rates and juvenile mortality in nature. There are natural processes of shell destruction and dissolution which we suppose to be quantitatively much more important than passive transport. The following experiment illustrates the importance of this phenomenon. 20 living specimens of *Heterostegina depressa* (3 microspheric and 17 megalospheric) were placed in a cylindrical cage made of nylon stockings (fig. 22). A second cage contained 20 megalospheric specimens of *Operculina ammonoides,* a third 10 specimens of large, evolute *O. ammonoides* and 10 of *Heterocyclina tuberculata* and a fourth 10 specimens of larger peneroplids. The cages were suspended on nylon wire 10–15 cm above the bottom in two aquaria in which the respective natural habitats of soft bottom environment with *Halophila* from 10 m depth, and of hard bottom environment with "algal"

Fig. 21 Transport of foraminifera. Filamentous green algae produced in early spring on the sand patches between coral heads (B, coral head about 60 cm large) are transported by currents with their foraminiferal fauna until they are caught by coral heads (A, about 20 cm large, current from right to left). Geziret Faraoûn, near site 028, 10 m.


A
B

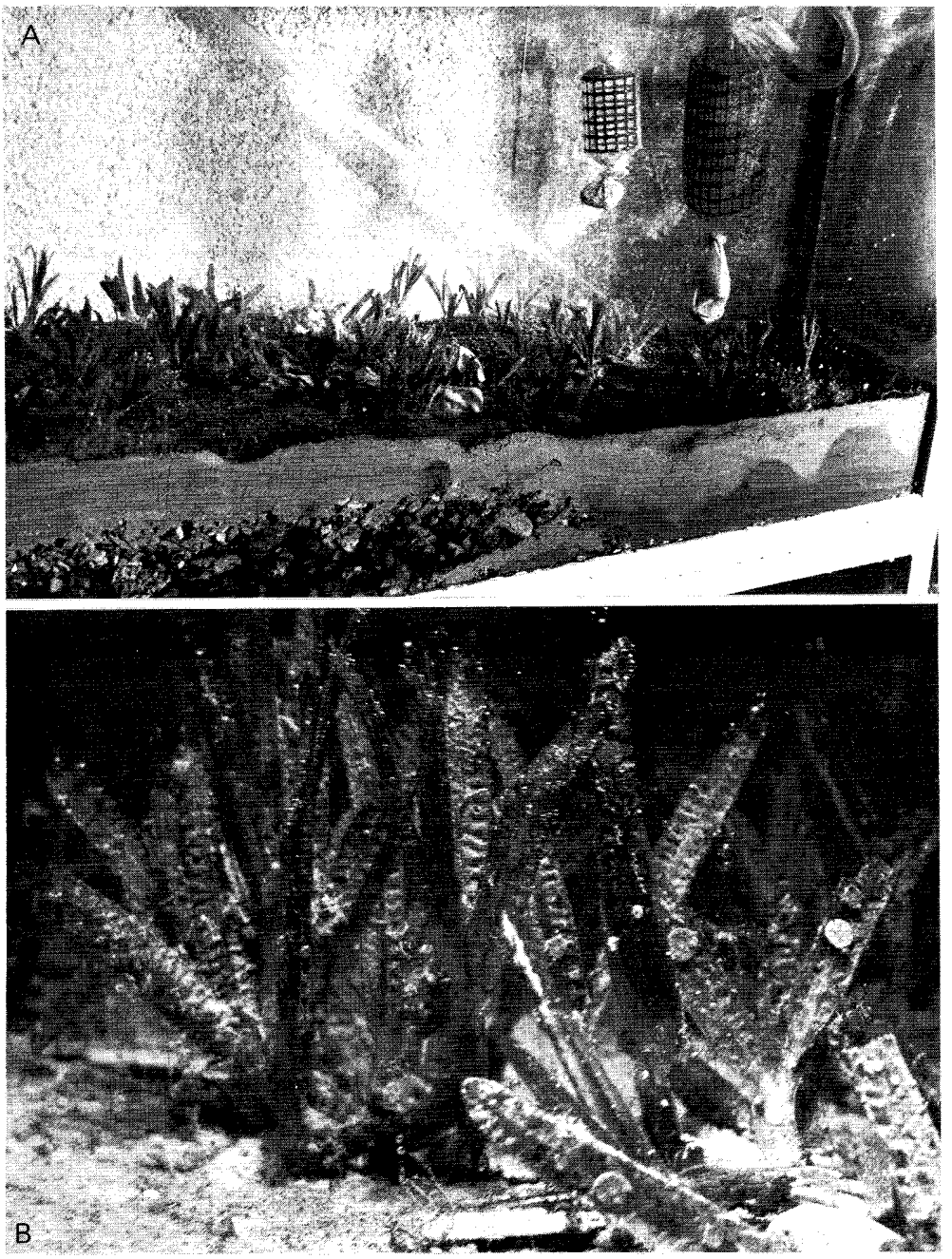
balls from 40 m depth, had been reconstructed with plants and animals from the respective sites. In the aquaria, fresh sea water from the laboratory's pumping system was circulated. From 10.4 to 15.6.1971 the environments had been stable, the foraminifera and the plants regularly growing. One month later, Z. Reiss opened the cages. Two of them were bitten open by unknown animals. The two others, in which *O. ammonoides* and *H. tuberculata* had been placed, were absolutely intact. The large foraminiferal shells had all disappeared, but some smaller benthic foraminifera inhabited the cages. This hints to the existence of biological or chemical factors destroying shells of foraminifera in shallow water, factors which must be investigated before beginning extensive and detailed quantitative research on the distribution of foraminifera.

RELATIONS BETWEEN LARGER FORAMINIFERA AND SUBSTRATES AS OBSERVED UNDER WATER

The larger peneroplids represented by *Sorites* and *Amphisorus* are living usually as epiphytes on the leaves of *Halophila, Cymodocea, Diplanthera* or other plants (fig. 22B). There is apparently no specific relation between particular kinds of plants and particular species of larger foraminifera. *Sorites orbitolitoides* in particular occurs outside dense vegetation covers as well; it is found on dead coral branches, empty mollusc shells, "algal" balls and on rounded rock pebbles. *A. hemprichii* and *S. orbiculus* are temporarily fixed to their plant substrate by some organic glue secreted by their pseudopods extruding from their marginal apertures, whereas *S. orbitolitoides* is often definitively sessile and encrusting, adapting its shell to uneven hard substrates during growth. Such shells are often grotesquely contorted and stick to the substrate after the death of the animal.

Larger peneroplids show no particular orientation towards light and may occur on vertical leaves or lower sides of leaves as well as on exposed upper sides. Some large, microspheric *A. hemprichii* were observed on the bottom, in between *Halophila* plants, shortly after a heavy spring thunderstorm. They were recognized as living because the storm had produced a yellowish sediment film covering the entire area. Only the larger peneroplids had cleaned themselves and appeared gleaming white on the sediment film. A few days later, they had all disappeared from the bottom, probably having crawled

Fig. 22 Aquarium with cages for larger foraminifera (A) suspended above *Halophila* plants with epiphytic *Amphisorus hemprichii* (B).


A
B

back to their preferred substrate. In the aquarium, where *Halophila* had been planted on its original substrate, *A. hemprichii* found its way back to the leaves in two days (fig. 22B).

Larger foraminifera with a canal system, *Operculina, Heterostegina* and *Heterocyclina,* have not been observed on leaves of *Halophila* or on other plants during the periods of observation in spring and autumn. The nummulitids lived on the bare bottom, usually flat on one of their sides, or with their equatorial plane inclined at a low angle towards the surface of the bottom (figs. 11A, 12B). *Operculina* shells are often found sticking in great numbers to roots of *Halophila.* These shells were all colorless and seemed to be dead. At present, I have no explanation for this phenomenon. The thicker, involute *Heterostegina* living on coarse sediment and at the foot of coral colonies, are less obviously oriented to light than their flatter relatives living on soft bottom.

Operculina seems to feed on a slimy, brown film covering the bottom surface and consisting of a mixture of diatoms, many unidentified microorganisms, moulds and organic debris, probably consisting of decomposing algal material.

Borelis schlumbergeri, too small to be observed directly under water, has been found in some samples on *Halophila* leaves or in clouds of filamentous green algae. Its distribution in the sediment hints to its living on all kinds of substrate. Living *Borelis* were rather rare in spring and absent in autumn. I have never observed patches with dense populations of *Borelis* covering the substrate as in larger peneroplids, operculinids or heterosteginids.

RELATIONS OF LARGER FORAMINIFERA TO THE MEDIUM

Distribution patterns of larger foraminifera show relationships with depth. In the Gulf of Elat, water depth reflects primarily the ecological gradients of pressure and light.

As living foraminifera collected by grab at various occasions in about 100 m depth resisted the rapid release of pressure without any apparent damage, pressure seems not to be an autecological factor of main importance, at least for the periods of a foraminifer's vegetative life. Bradshaw's experiments (1961) support this assumption but nothing is known about possible relationships between pressure and reproduction.

We assume that the quantity or the quality of light available to bottom

dwellers is the most important factor regulating the distribution of the larger foraminifera on a particular substrate parallel to depth contour lines. This assumption is supported by similar direct observations on *Heterostegina depressa* by Röttger, 1976 and by the fact that all larger foraminifera studied so far by transmission electron microscopy have algal symbionts needing light for assimilation (Hottinger and Dreher, 1974; Leutenegger, 1977). Every species studied so far by Leutenegger has its particular symbionts, either dinoflagellates or diatoms, which can be distinguished by the morphology of their chromatophores. Little is known about the specific requirements of symbionts regarding light intensity and wave length. Röttger and Berger (1972) have shown that *Heterostegina depressa* grows more rapidly and more regularly in cultures at 300 lux than it does in cultures at 600 lux; but Röttger (1975) found an inverse relationship. Neither symbionts alone nor larger foraminifera with their symbionts have yet been cultured successfully enough for systematic experiments. The presence of the symbionts, however, is a strong argument in favor of an autecological relationship between the foraminifer and light.

The quantity of nutrients available for benthic algae representing a great part of the autochthonous primary production is another autecologic factor in the medium. This factor varies primarily with time (seasonal factor) but possibly also with depth. Measurements of nutrients in the Gulf of Elat by Klinker et al. (1977) show extremely low values in shallow water throughout the year. Circumstancial evidence from direct observation on the impact of nutrients on the life of foraminifera is that there is a striking correspondence between short-lived algal growth and foraminiferan blooms. In early spring, dense foraminiferal populations develop on short-lived green algae. They all had disappeared in autumn. In the deeper environments, below 60 m depth, living operculinids were still rather frequent in the grab samples collected in autumn, whereas in shallower zones, the number of living forms per sample was extremely low or nil compared to the spring samples. Consistent quantitative data to support this observation are not available and difficult to produce anyway because living populations cluster in space as discussed above. The correspondence in time between short-lived algal growth and foraminiferal blooms indicates that the increase of nutrients in the medium during early spring is used either directly by the foraminifer to feed its symbionts or indirectly to feed its food organisms, particularly diatoms. The latter possibility is supported by the nutrient measurements in the open waters (Klinker et al., 1977) and by in situ observations in autumn, when restricted areas of short-lived algal growth appeared in shallow environments on hard substrates, whereas in neighbouring *Halophila* meadows

no such algal growth was observed. These algal blooms in autumn are too local to be generated by an increase of nutrients in the free seawater medium. As the algal blooms produce dense local populations of larger foraminifera, sometimes in "abnormal" depths the foraminiferal growth cannot be directly controlled by nutrients.

MORPHOLOGIC MODIFICATIONS IN NUMMULITID SHELLS RELATED TO WATER DEPTH

Shell shape

The visual impression from the observations of living *O. ammonoides* and *H. depressa* populations in situ clearly hints to intraspecific variation of shells in environments of different depths. In both species, involute, thick forms inhabit shallower waters, whereas evolute, thin forms are found in deeper environments. This trend is parallel to the one described by Larsen (1976) in *Amphistegina.* The same trend is also observed in closely related species (*Amphistegina,* Larsen, 1976) or genera (*Heterostegina, Heterocyclina*), which replace one another towards depth.

There must be relationships between the degree of involuteness of the chambers (Hottinger, 1977), the height of the adult growth spiral in the equatorial plane and the thickness of subsequent outer lamellae reflected by the solidity of the shell. Involute forms have narrower growth spirals and thicker walls than evolute forms. There must be also a reciprocal relationship between the thickness of outer lamellae and the height of the ornament ("interseptal pillars", see below) on lateral chamber walls. The number of secondary septa in *H. depressa* and the degree of curvature in primary septa of both species depend apparently on the radius of the growth spiral. Scott (1974) is certainly right to demand emphatically multivariate biostatistics of such features, but he may have underestimated the technical difficulties of measuring techniques. Consistent measuring of the axial shell diameter for instance must be executed on the rare specimens with their last chamber conserved (or exclusively on living material) in order to relate correctly the axial diameter to the true equatorial diameter of the shell. This is necessary because the outer lamella of the last chamber envelops the rest of the shell and adds to shell thickness in axial direction (at least according to current views on shell structure in perforate foraminifera by the lamellar theory (see Hansen and Reiss, 1971), but nobody has ever mapped the lateral extension of an ultimate lamella). In order to cor-

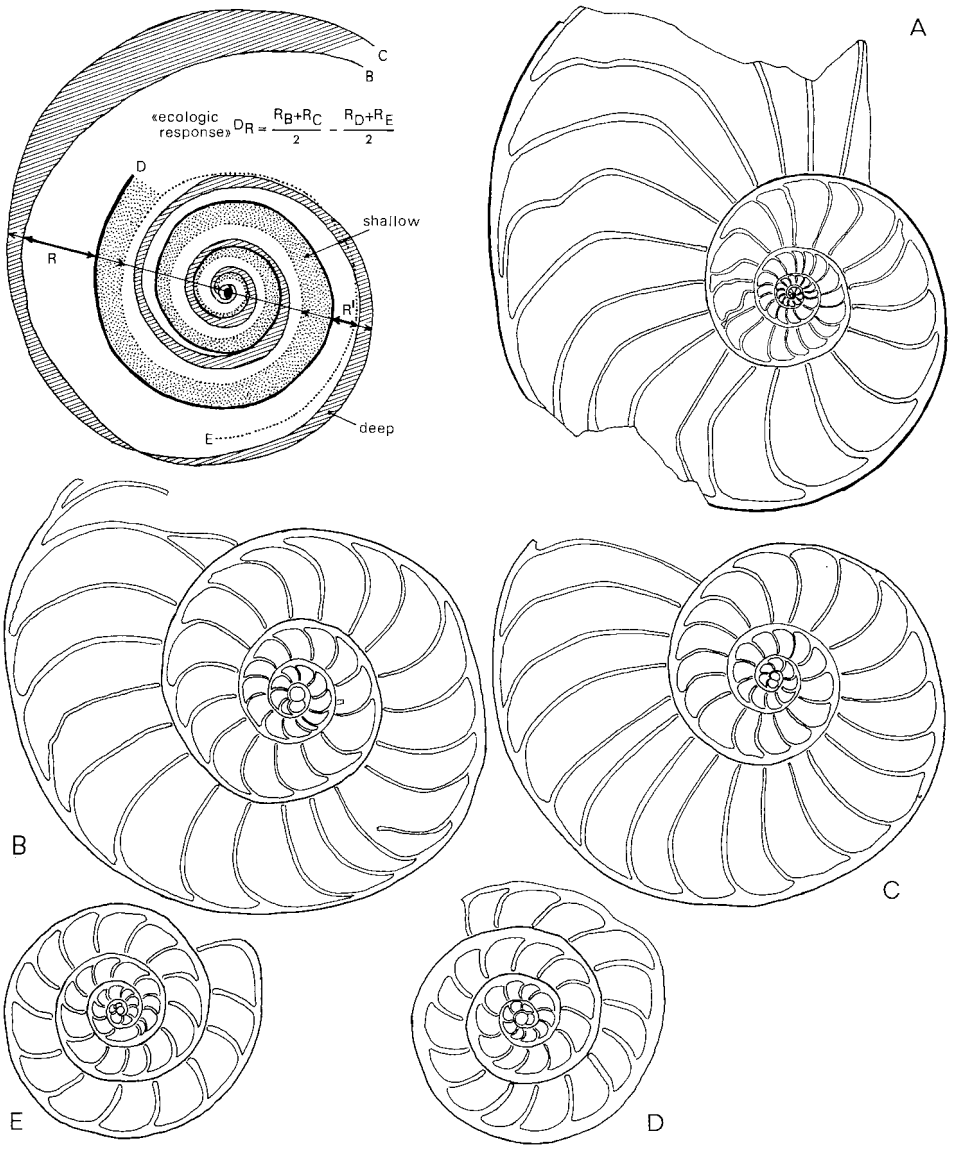
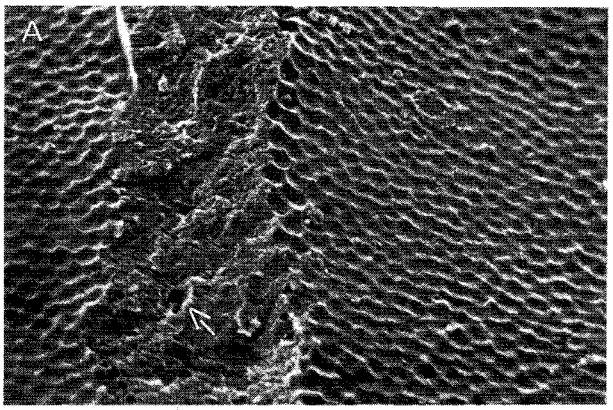


Fig. 23 Variation in spiral growth in *Operculina ammonoides*. Equatorial sections, camera lucida drawings, x 20.
A: Microspheric specimen from Elat, site 021, 77 m.
B: Megalospheric specimen, wide adult spiral, wide juvenile spiral. From site 021, 77 m.
C: Megalospheric specimen, wide adult spiral, narrow juvenile spiral. From site 021, 77 m.
D: Megalospheric specimen, narrow adult spiral, wide juvenile spiral. From Geziret Faraoûn, site 044, 45 m.
E: Megalospheric specimen, narrow adult spiral, narrow juvenile spiral. From site 044, 45 m.

relate the equatorial diameter with the number of growth stages in the shell, we would have to section the same specimen in equatorial direction without loosing the fragile ultimate chambers. The degree of involuteness (Hottinger, 1977) can be measured only in axial sections as outer spiral sutures are covered and thickened by subsequent outer lamellae. Therefore it is impossible to locate the polar chamber extensions with accuracy on the external shell surface. It is very difficult to section the same specimen simultaneously in equatorial and axial directions. Although in nummulitids it is possible to break in axial direction half a specimen split previously in equatorial direction, this procedure works only in relatively thick and large specimens and is impossible to apply to larger samples of randomly selected specimens, where all specimens of the sample would have to be prepared in order to avoid heavy bias. Other foraminiferal groups having no marginal cord cannot be split. Their shells must be cut with rock-thin-section techniques. Statistical measurements of their morphology are therefore always restricted to two dimensions.

The equatorial spiral of nummulitids reveals more morphologic data than any other plane of sectioning. The complete ontogeny of the shell, at least in two dimensions, is conserved. Intraspecific variation in nummulitid shells with loosely coiled last whorls reaches its highest amplitude in the latest growth stages (fig. 23). The same phenomenon is known particularly in *Peneroplis* representing an extreme case and in most larger foraminifera (compare Scott, 1974, fig. 24, 26). Early whorls in nummulitid shells have a smaller variability in their spiral diameter but depend on the size of the proloculus for simple reasons of growth mechanics. As the

Fig. 24 Distinct perforation of lateral chamber walls in nummulitic genera from Elat. Scanning electron micrographs (SEM).
A: *Operculina ammonoides*. Internal surface of lateral chamber wall showing regular perforation of inner lining; pores covered by organic lining; septum broken away. Geziret Faraoûn, site 013, 75 m, x 1000.
B, C, E: *Heterostegina depressa*. Megalospheric specimen from Elat, site 206, 70 m. B: Perforation on external surface of ultimate (x.) chamber. Note scale pattern around pores typical for ultimate and penultimate chambers in thin-walled *Heterostegina*; x 1000. C: Perforation on external surface of (x-10). chamber; x 1000. E: lateral view of entire specimen; x 20.
D: *Heterostegina depressa*. Microsphere and early whorls broken in equatorial direction. Note 25 operculinid early septa, the incomplete fold of second septulum and the regularity of perforation on internal lateral chamber walls. Specimen from Elat, site 020, 40 m, x 200.
F, G: *Heterocyclina tuberculata*. Geziret Faraoûn, site 016, 90 m. Perforation of external surface in (x-10). chamber with large "interseptal pillar". x 1000 (F) and detail x 5000 (G).
Arrows in A – F designate sutural canals or sutural apertures of intraseptal canal system.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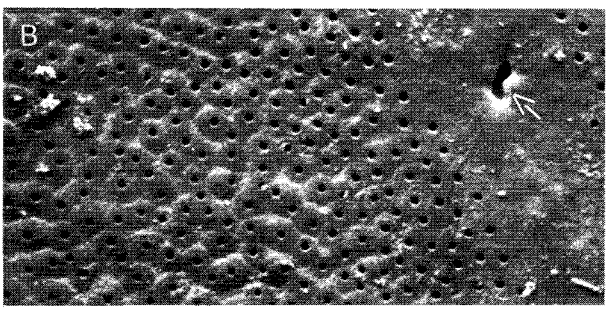
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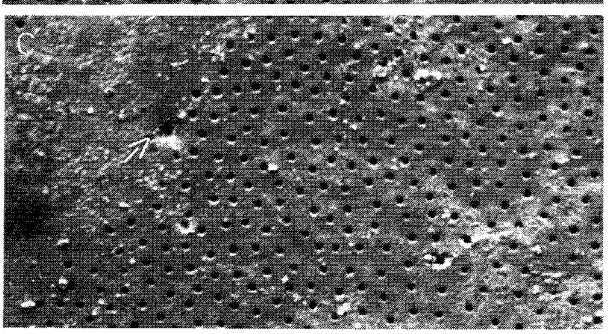
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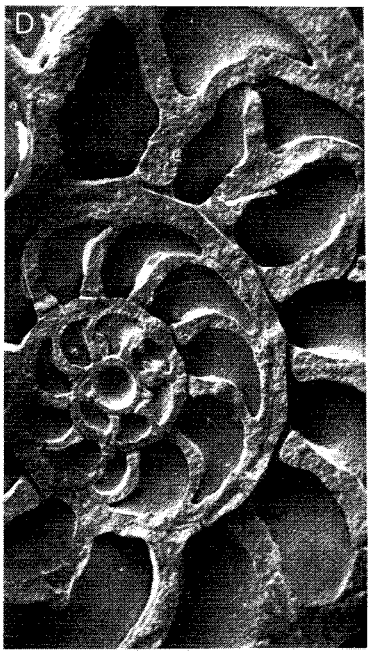
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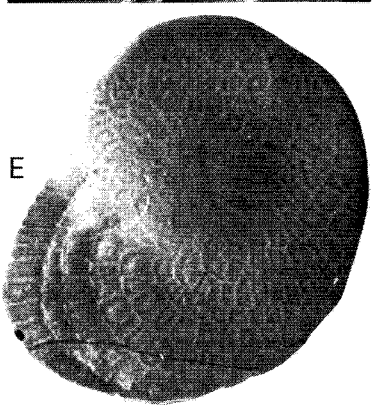
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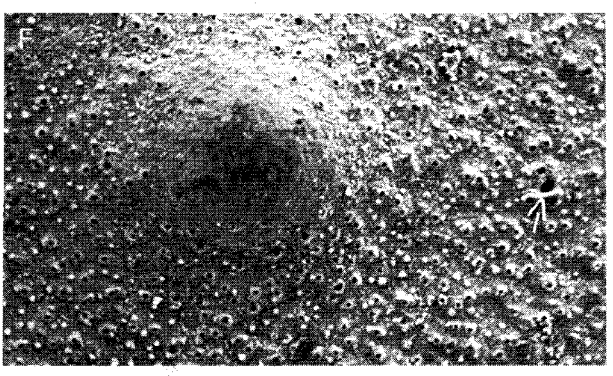
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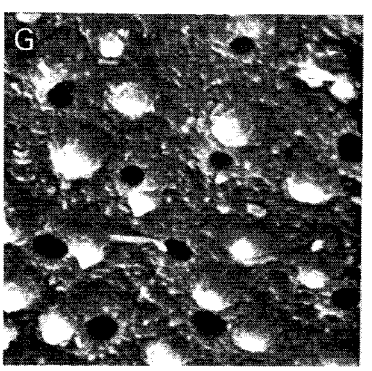
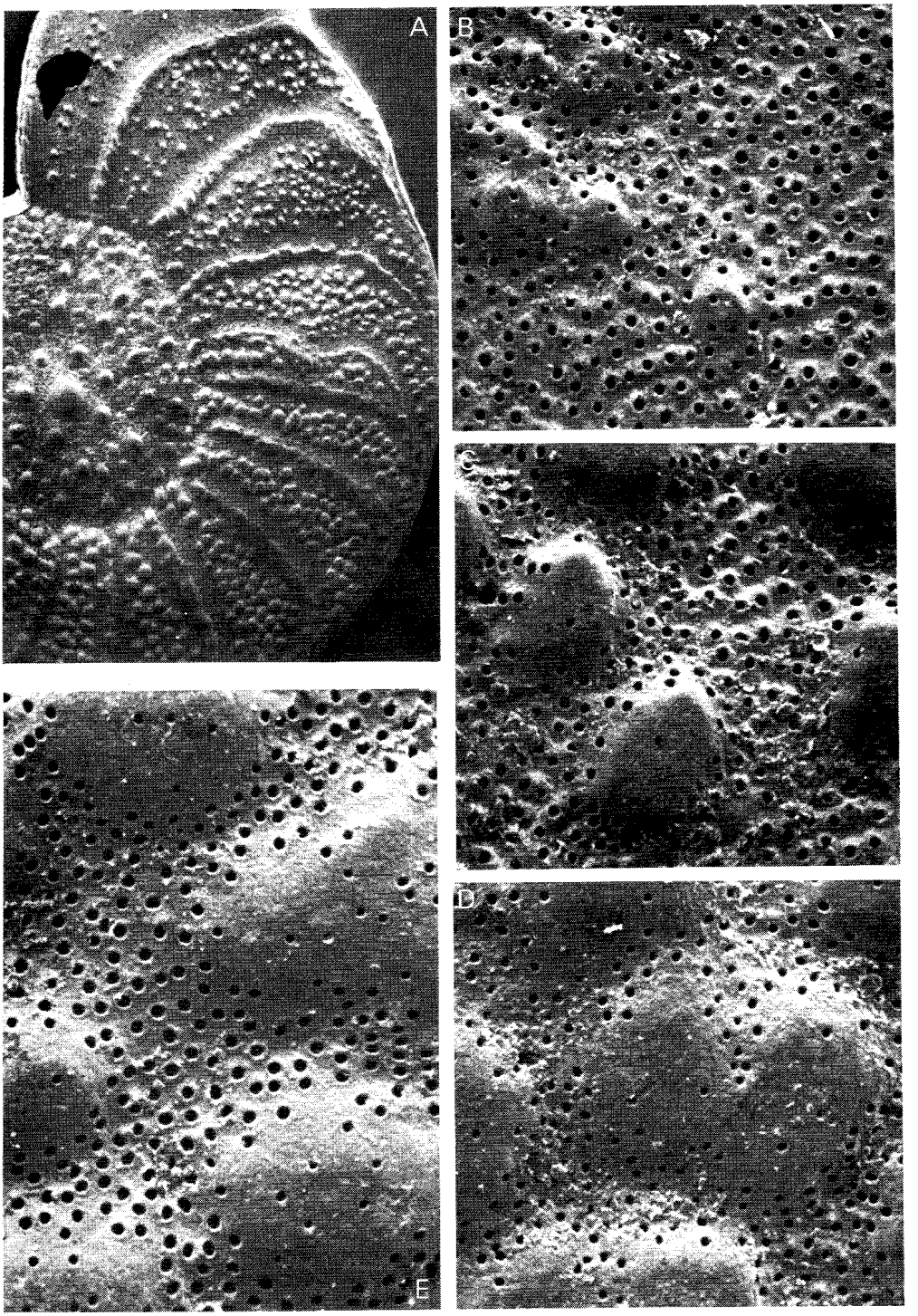

G

first spiral chambers are growing by accretion, their spiral base must follow the preexisting surface of the proloculus. As we know from dimorphism and from the fact that the amplitude of dimorphism augments during phylogeny as a trend parallel to the augmentation of the adult shell size of microspheric forms (Hottinger, 1963), the diameter of the megalosphere primarily reflects reproductive processes. The variability of adult shell shape in nummulitids seems to be linked in the Gulf of Elat to water depth and may reflect therefore autecological relations. The characteristics of the growth spiral may thus reflect at least two independent influences separately at the beginning and at the end of ontogeny. It is not known whether and where interference between the two influences appears during ontogeny and how they are reflected in the growth spiral. However, quantitative longitudinal data from nummulitid growth spirals are expected to be non-linear (compare Scott, 1974, p. 111).

Perforation

The internal lateral surface of all nummulitid chambers is covered by regular polygonal depressions each one containing one pore (fig. 24A). The distances between the pores are uniform. The outer lateral surface is covered by rounded pore openings. The distribution of the external pore mouths is not uniform but generates patterns. On the lateral walls of the ultimate and penultimate chambers the patterns are indistinct, sometimes absent (figs. 25), but earlier chambers covered by many subsequent outer lamellae, show regular patterns of pore distribution. Pore distribution patterns are thus appearing during ontogeny by subsequent outer lamellas amplifying minute divergences of pore axes laid out in each primary (first) outer lamella of the lateral wall's median zone. The phylogeny of operculinids teaches that pore distribution patterns are characteristic for nummulitid phyla (Hottinger, 1977). The patterns must be therefore fixed genetically. This is supported by the fact that the presence or absence of pore patterns in the median zone of operculinid lateral chamber walls is independent of the very variable thickness of subsequent outer lamellae; they merely amplify a preexisting pattern.

Fig. 25 Ontogeny of pore distribution patterns on outer surface of lateral chamber walls in *Operculina ammonoides* from Geziret Faraoûn, site 014, 79 m.
A: Lateral view of megalospheric specimen, SEM, x 50.
B: Perforation on outer surface of penultimate, (x-1). chamber, x 1000;
C: (x-4). chamber, x 1000;
D: (x-7). chamber, x 1000;
E: (x-10). chamber.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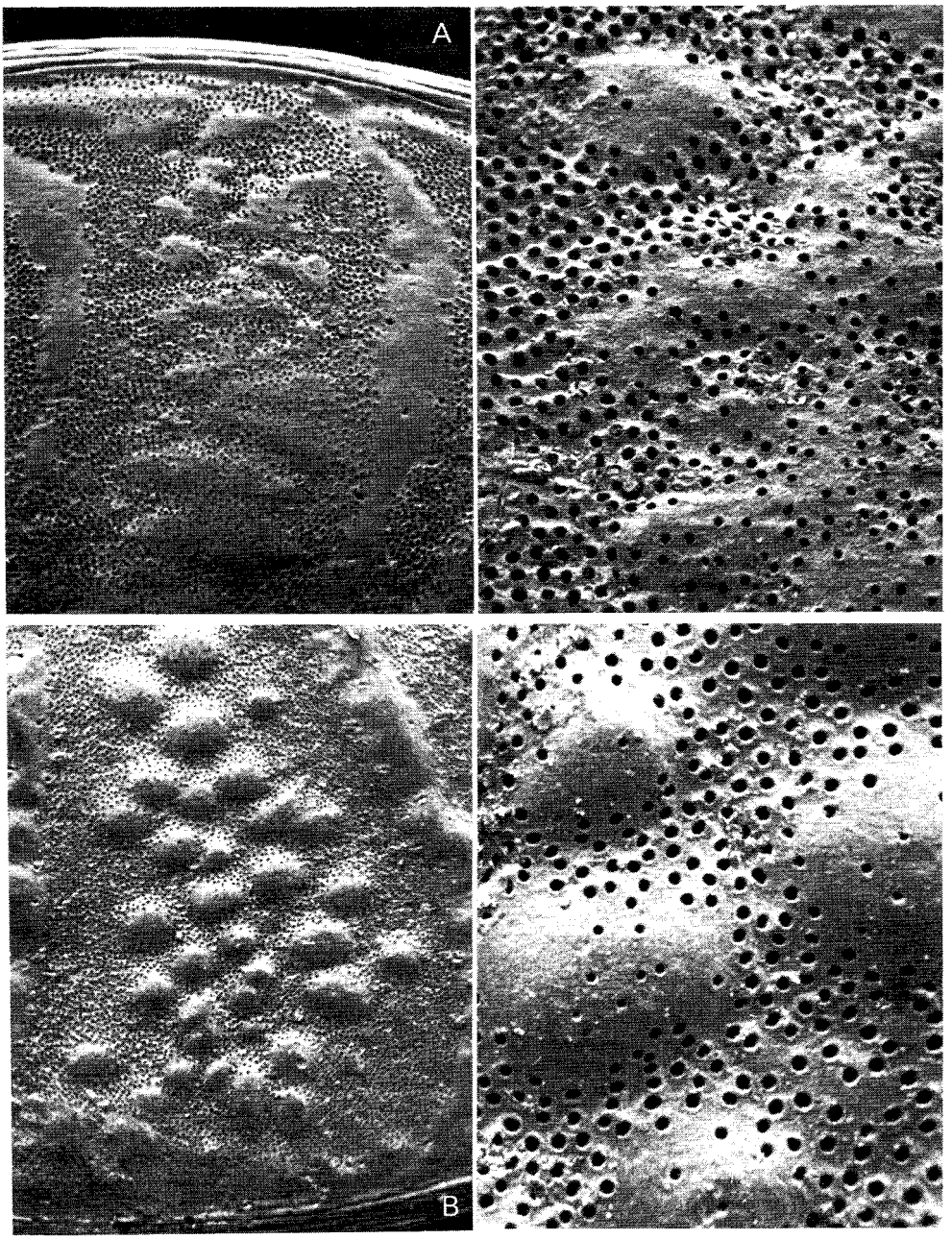
The divergence of pore axes in the median zone of the lateral wall generates imperforate patches on the outer lateral surface of the wall. Where the lateral wall is not perforated, the subsequent outer lamellae are thickened, forming so-called interseptal "pillars". In evolute, flat *O. ammonoides* occurring in the deeper part of the distributional area of nummulitids, below approximately 60 m depth in the Gulf of Elat, the size and particularly the relief of interseptal pillars are more important than in involute and smooth forms from the shallow part of the distributional area (above 60 m). Smooth, involute forms of *O. ammonoides* occur most frequently on coral sand substrates above 60 m depth (fig. 26). Similar intraspecific change of lamellar thickness in interseptal ornaments was observed in *Heterostegina depressa* where the few, large interseptal pillars sitting on the lateral wall of the chamberlets have a high relief on flat, evolute specimens from below 60 m depth whereas involute forms from shallower environments are smooth. The observed intraspecific variation in *O. ammonoides* and *H. depressa* is an estimate based on visual observation of the counted specimens. A suitable biometric method to measure ornaments and in particular the height of interseptal pillars has not yet been found. Biometric research in this direction will be justified when a clear working hypothesis as to the function of ornamental structures will be available.

Scanning electron micrographs of external surfaces of ultimate or penultimate chambers in *O. ammonoides* reflect approximately the primary distribution of pores on the internal surface. In ultimate and penultimate chambers, the amplification of divergent pore axes is very small compared with intraspecific variation of primary perforation. The diameter of the pore mouths opening on the external lateral wall surface depends very much on the conservation of the shell. Fig. 27 shows a lateral surface of a penultimate chamber where the rims of external pore mouths are conserved in the depressions of the relief and eroded on the relief highs. In earlier chambers, all pore rims are eroded. Therefore, the diameter of the pore mouths was not measured, whereas pore density was easily quantified.

Pore density was measured by counting the pores on 2 or 3 circular embrasures with a surface of 10 cm^2 on 100 cm^2 scanning electron micrographs with a uniform enlargement of 1000 (fig. 28). Mean values of pore density in ultimate and penultimate chambers showed no significant differ-

Fig. 26 Ornamentation with "interseptal pillars" on lateral chamber wall in (x-10). chambers of involute *Operculina ammonoides* from shallow water (A: Geziret Faraoûn, site 173, 35 m; x 300 and x 1000) and of evolute specimen from deeper water (B: Geziret Faraoûn, site 014, 79 m; x 200 and x 1000).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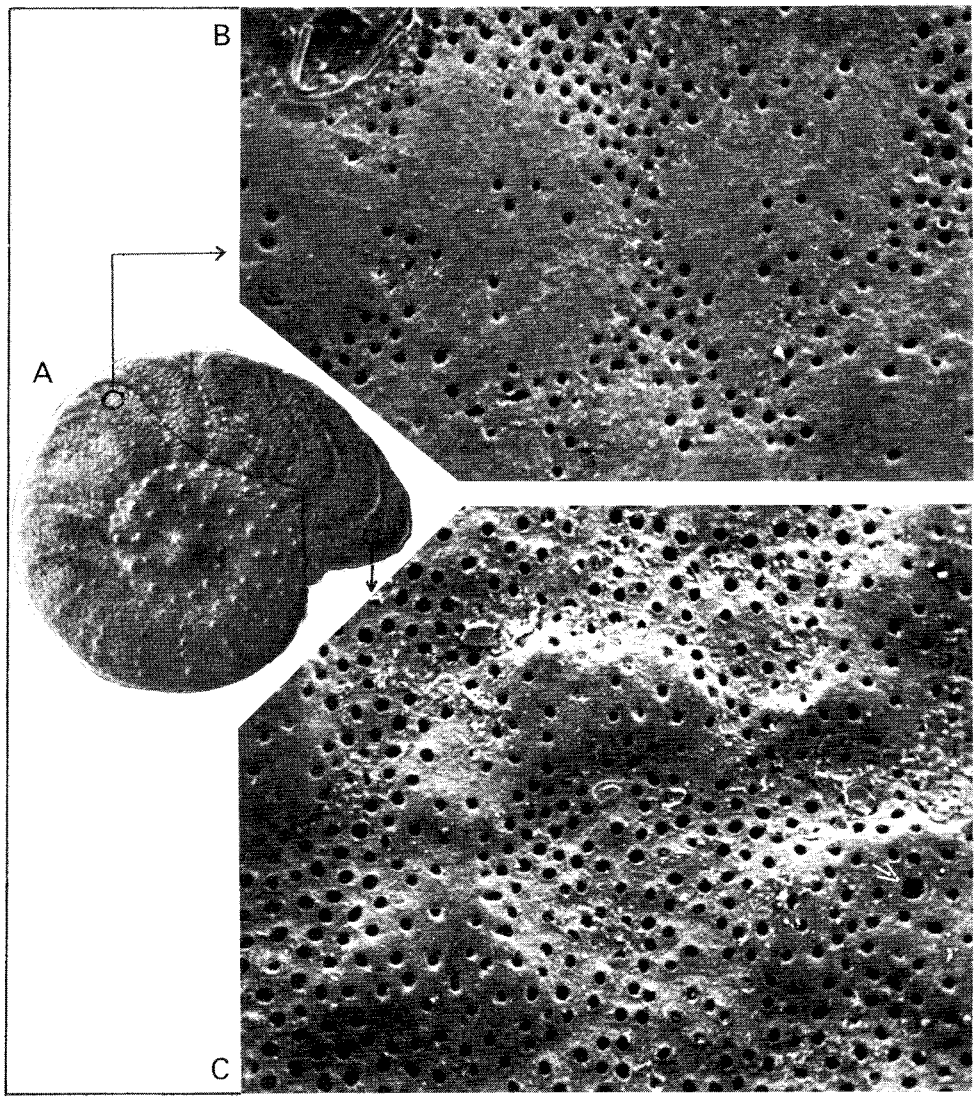


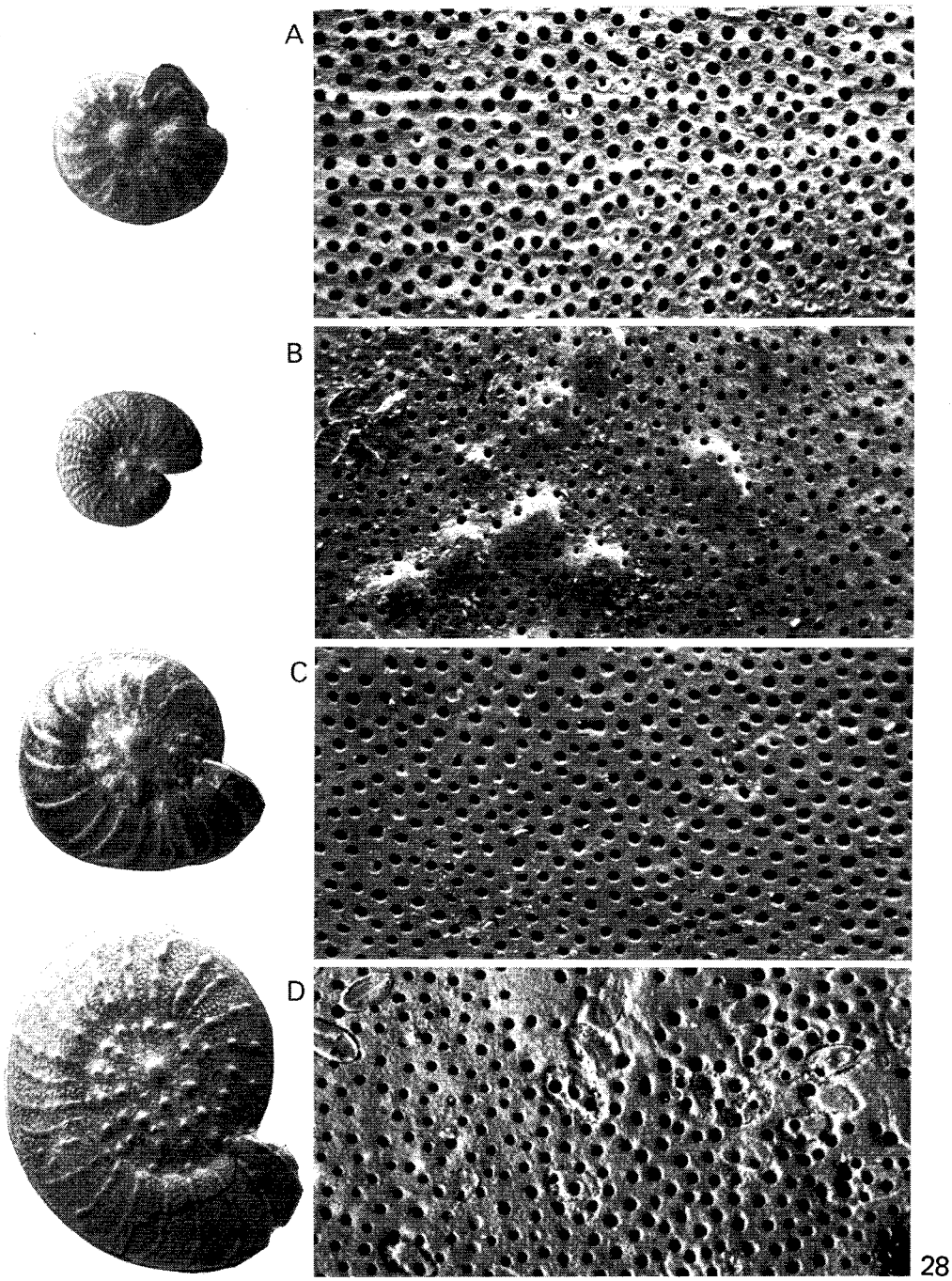
Fig. 27 Pore diameter and superficial erosion of lateral chamber walls in *Operculina ammonoides*, megalospheric specimen (A: Lateral view, x 20). Pore rims eroded on relief highs in (x-2). chamber (C: x 1000) and in all pores of (x-10). chamber (B: x 1000). Arrow indicates site where lateral wall is entirely eroded.

ence in young or adult *O. ammonoides*. No significant difference was found either between pore densities of involute and evolute forms from the same samples, but specimens from shallower environments have a denser perforation than specimens from deeper samples. Density values in specimens collected below 60 m depth vary from 63–84 pores per 0.1 mm² lateral surface (arithmetic mean from 13 specimens: 72). Specimens collected above 60 m depth have pore densities from 69–104 pores per 0.1 mm² lateral surface (mean from 13 specimens: 84). The difference between the two means is 12 and its standard error S_D (for small samples) = 3.7. The least significant difference (LSD) between the two means being 10.98 (the t value at 99% confidence level is 2.97) and the true difference being 12, the difference of pore densities in different depths is significant and justifies further, intensive research.

HYPOTHESES ON SHELL FUNCTION

The distribution patterns of larger foraminifera in the Gulf of Elat give a first hint to functions of the shell which have to be combined of course with all general biological knowledge on foraminifera in general, and on larger foraminifera in particular. Distribution patterns in space and time hint 1. to autecological relationships of foraminifera during vegetative life periods with light, 2. to relationships with substrate and 3. to indirect relationships with nutrients in the medium via the food chain.

Fig. 28 Pore density in ultimate or penultimate chambers of *O. ammonoides* from shallow (A-D) and deeper (E-H) waters.
Pore density in *Operculina ammonoides* on outer surface of lateral walls in ultimate (x). or penultimate (x-1). chambers.
SEM lateral views of specimens x 20; details with pores x 1000.
A-D: Megalospheric specimens from Geziret Faraoûn, site 173, 35 m.
A: (x). chamber, mean density Dp = 94 pores per 0.1 mm² lateral surface.
B: (x). chamber, Dp = 92.
C: (x). chamber, Dp = 100.
D: (x-1). chamber, Dp = 84.
E-G: Megalospheric specimens from Geziret Faraoûn, site 016, 90 m.
E: (x). chamber, Dp = 68.
F: (x). chamber, Dp = 74.
G: (x-2). chamber, Dp = 77.
H: Megalospheric specimen from Geziret Faraoûn, site 014, 79 m. (x-1). chamber, Dp = 76.



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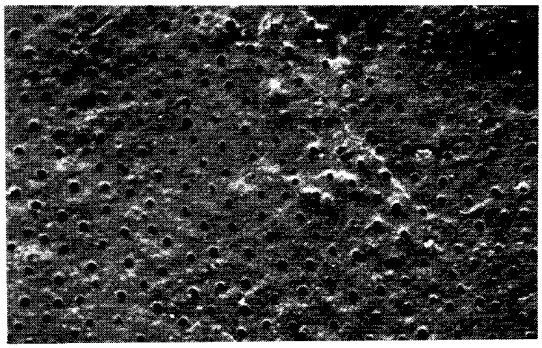

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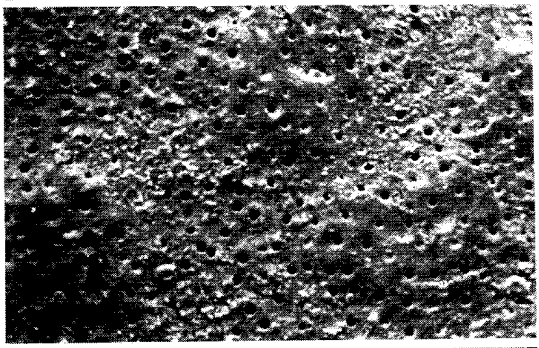

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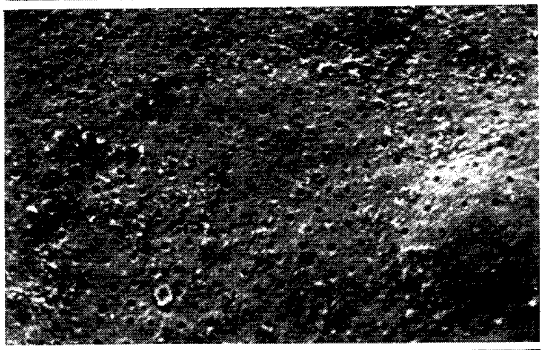

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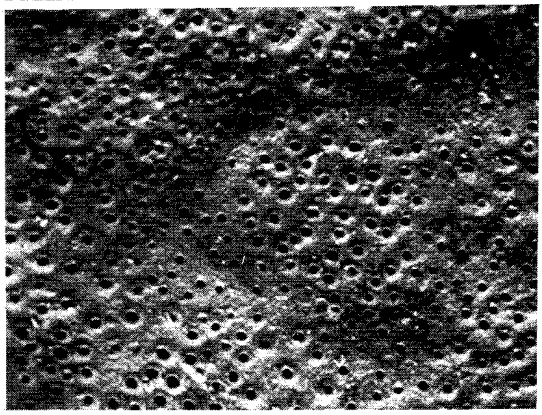

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1. *The foraminiferal shell as a green-house for symbionts*

Combining the arguments from distribution with the positive phototaxis observed in some species of *Amphistegina* (Zmiri et al., 1974), with the presence and location of symbionts (Hottinger and Dreher, 1974; Leutenegger, 1977) and with intraspecific variation depending on water depth, we may formulate as working hypothesis that the shell of larger foraminifera has green-house functions (as discussed already by Marszalek et al., 1969). The most immediate supplementary support for this hypothesis would be given by corresponding optical qualities of the shell and by an understanding of the particular location of the symbionts along the inner surface of the lateral walls. The latter point involves also understanding of pore functions.

2. *Motility and shell geometry*

The selectivity of substrates in particular of foraminiferal species with a free test, their tendency to disperse and (in epiphytic species) to select actively their plant substrate hints to a relative importance of motility during vegetative life. Many features in shell geometry and in particular of canal systems filled with pseudopodial ectoplasm (Hottinger and Dreher, 1974) may be related to motility. Relations between shell geometry and motility are discussed by Hottinger (1977 b) in detail.

3. *Nutrients*

Indirect relationships with nutrients hint to the relative importance of food for larger foraminifera in spite of their symbionts and of their well-being during long periods in raw cultures without particular feeding (Röttger, 1972; personal observations on *O. ammonoides*). The availability of food subjected to seasonal change may be one factor regulating growth rates and reproduction cycles and may indirectly interfere with the intraspecific variability of shell morphology as discussed by Leutenegger (this volume).

Marszalek et al. (1969) discussed the function of the test in foraminiferan shells pointing in particular to shell function as a weight counteracting buoyancy of the protoplasm. Intraspecific variability in larger foraminifera and the morphology of closely related species replacing each other towards depth do not support this attractive idea. Thin-walled, light variants or species predominate in the deepest part of the distributional area where buoyancy of the protoplasm is greatest. *H. tuberculata* having numerous vacuoles filled with fatty substances (Leutenegger, 1977) has particularly thin walled and light shells and occurs as the deepest representative of the nummulitids.

The test function as a barrier to chemical changes in the environment discussed by Marszalek et al. (1969) is in my opinion a very convincing hypothesis. However, all living benthic foraminifera observed so far in Elat are retracting to the inner part of the shell not only after chemical irritation or after sudden change in temperature but also after purely mechanical disturbance. Imperforate and perforate foraminifera all behave in the same manner. Pore function is therefore independent of this phenomenon.

SYSTEMATIC DESCRIPTIONS

Borelis schlumbergeri (Reichel), 1937
Fig. 29

Synonymy: see Reiss and Gvirtzman, 1966.

Diagnosis: Small sized, fusiform alveolinid with the structural characteristics of the genus *Borelis*: irregular coiling in nepionic part of both generations, one row of apertures, no post-septal passage, septula of subsequent chambers in line. Basal layer thickened in polar region. The index of elongation may reach about 5 in microspheric (?) forms, mean values are around 3. Megalosphere about 45 μm in diameter followed by three streptospiral whorls. Main elongation in whorls 5–10; 5 chambers per whorl in adult growth stages.

Scanning electron micrographs (fig. 29D) show external shell sculpture consisting mainly of irregular ridges where the septulum underneath touches the outer chamber wall. Apertural face sculptured by two or three vertical rims per aperture. Aperture surrounded by thickened peristome forming an arch and with one bifid or broadened, lamellar tooth canalising the protoplasm extruding from the apertures in crosswise oblique direction in respect to the equatorial plane of the shell. The teeth are resorbed in intercameral foramina (when a new chamber has covered the apertural face of the previous one).

Remarks: *B. schlumbergeri* must be distinguished from the only other recent species of this genus, *B. pulchra* (d'Orbigny), occurring in the tropical Atlantic. The latter species is spherical and much smaller in size, having less than 0.5 mm in axial diameter. It has a narrower equatorial spiral and a higher number (6–7) of septa per whorl.

B. schlumbergeri from Elat differs from the topotypes of this species from Nosi Bé, Madagascar, by their small size and their high intraspecific variability. They differ from ovoid specimens from the Maledivan Islands by their higher elongation index. In the Gulf of Elat, specimens from deeper water

seem to be more elongated than specimens from shallow water. Systematic research in this direction, on the significance of teeth and on their relation to other alveolinids, in particular to *Alveolinella,* will be published at a later date.

Sorites orbiculus Ehrenberg,
Fig. 9B, 30D, E, 32B.

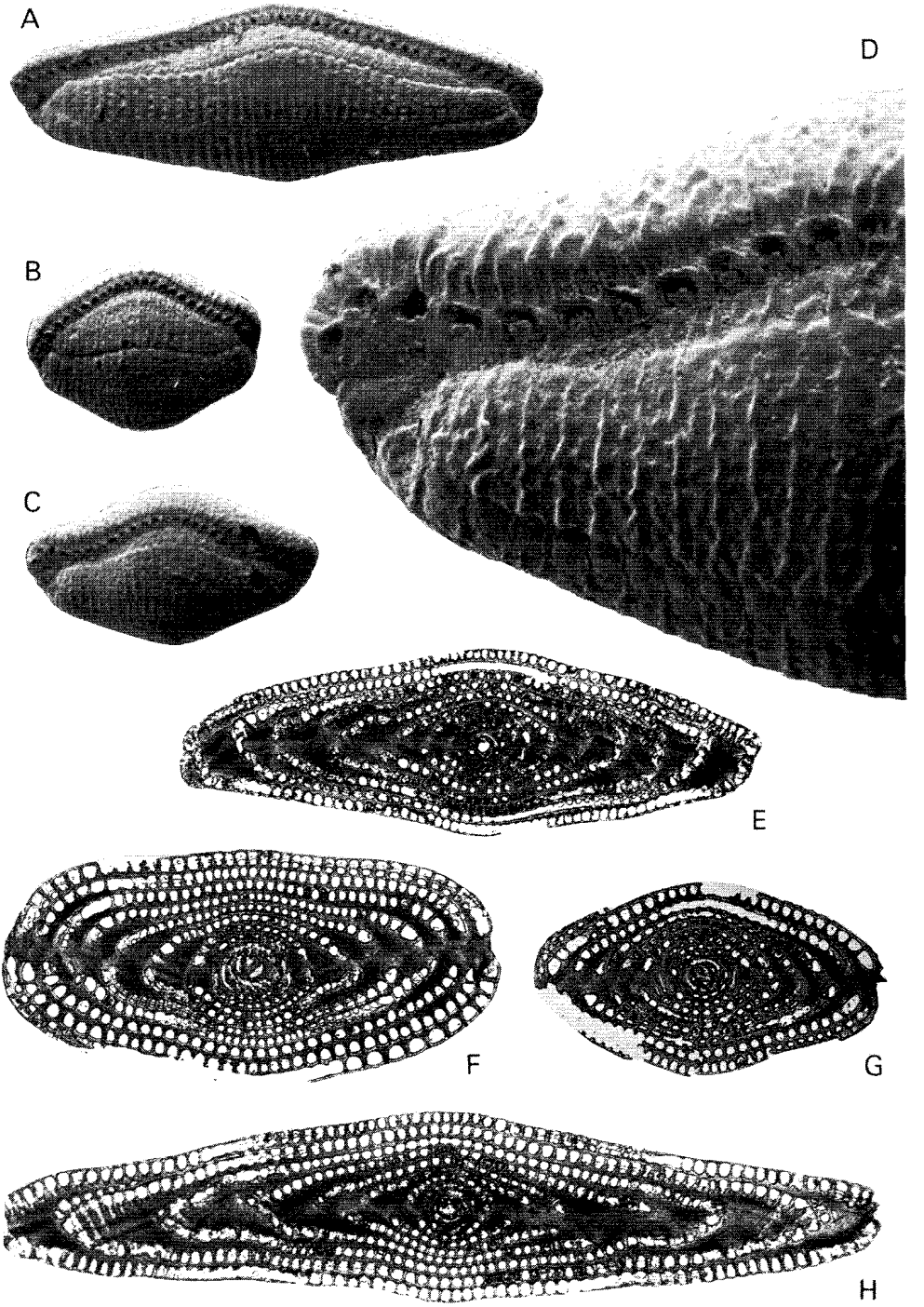
Synonymy: see Lehmann, 1961, p. 641.

Diagnosis: Relatively thick, short spired discoidal peneroplid with the structural characteristics of the genus *Sorites*: stolon system crosswise-oblique, reduced to one stolon layer, median annular passage, lateral chamberlets symmetric in respect to equatorial plane. Largest diameter of megalosphere 50–90 μm. One undivided chamber following the flexostyle canal. 8–12 spiral chambers in megalospheric specimens. Apertures on margin 8-shaped, often divided in two separate apertures by a bridge of shell material, with a peristome forming an irregular, often undulating sharp rim (fig. 30D). Annular passage circular in axial section. Microspheric specimens form breeding chambers.

Remarks: *S. orbiculus* is distinguished from the only other species of *Sorites* present in the Gulf of Elat, *S. orbitolitoides,* by the relative thickness of its discoïdal shell, its larger megalosphere, its larger chamberlets and its smaller number of spiral chambers. It usually does not adapt its shell to irregular surfaces of its substrate.

S. orbiculus differs from *S. marginalis* (Carpenter), living in the central Indian Ocean, by less regular arrangement of its chamberlets, by its rounded annular passage and its shorter secondary septa. *S. marginalis* has a diameter of the megalosphere of 60–90 μm, one undivided chamber following the flexostyle canal and 8–13 spiral chambers. Its annular passage is depressed and narrow; the secondary septa are long, particularly in the thickened rim of the adult growth stage (compare Lehmann, 1961).

Fig. 29 *Borelis schlumbergeri* (Reichel) from Elat, site 037, 60 m.
A-C: Megalospheric specimens, SEM, x 50.
D: Detail of fig. C showing apertural face in the polar region. Note teeth in the primary apertures. SEM, x 240.
E-G: Axial thin-sections of megalospheric specimens, more or less perfectly centered, illustrating variability of shell shape. Optical microscope, transmitted light, x 50.
H: Axial section of microspheric (?) specimen, x 50.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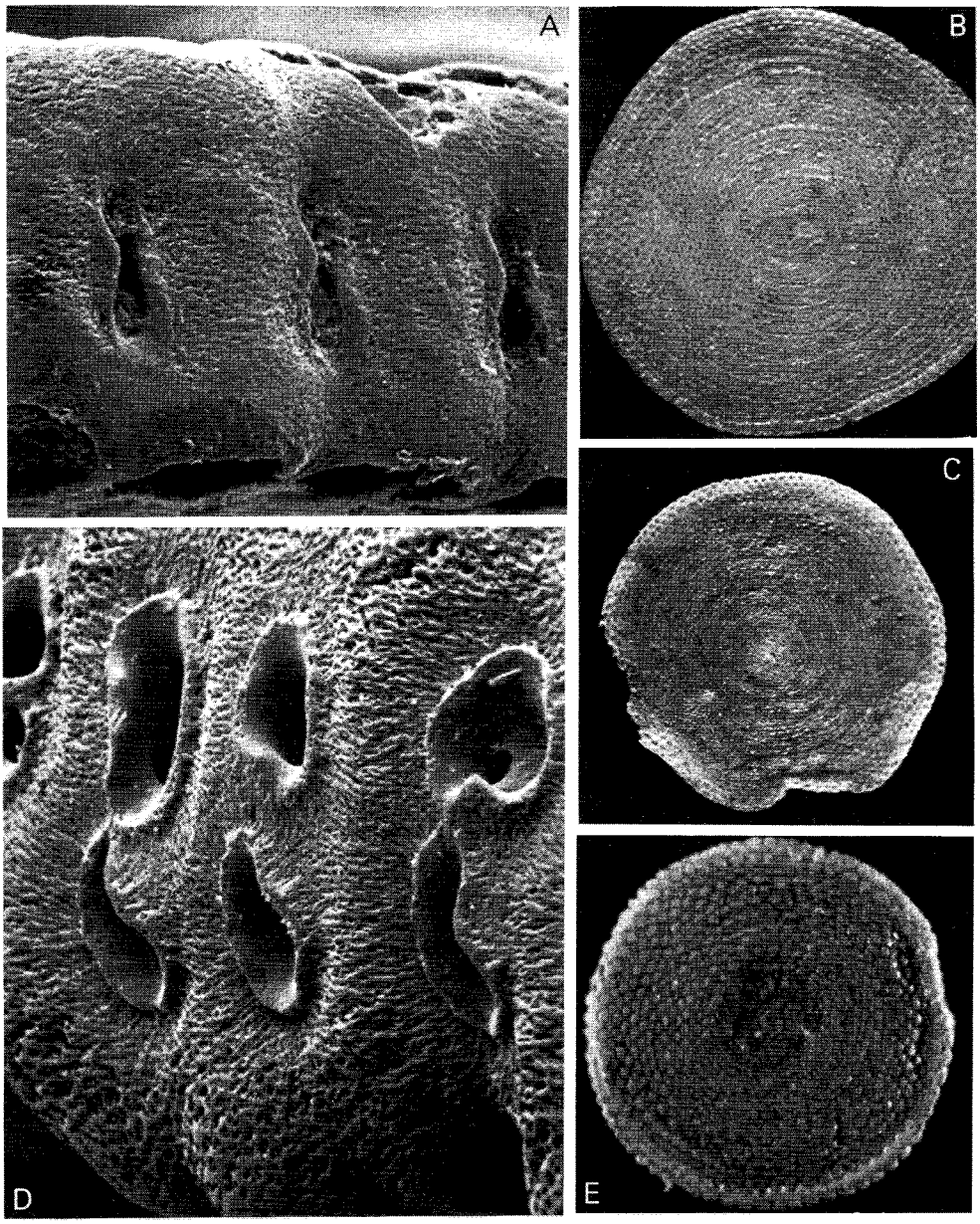


Fig. 30 Megalospheric *Sorites* from the Gulf of Elat. Marginal view showing 8-shaped apertures (SEM, x 600) and lateral view of discoidal shells (Optical microscope, incident light, x 20).
A-C: *Sorites orbitolitoides* from Geziret Faraoûn, site 026, 40 m.
D-E: *Sorites orbiculus* from Geziret Faraoûn, site 047, 1–2 m.

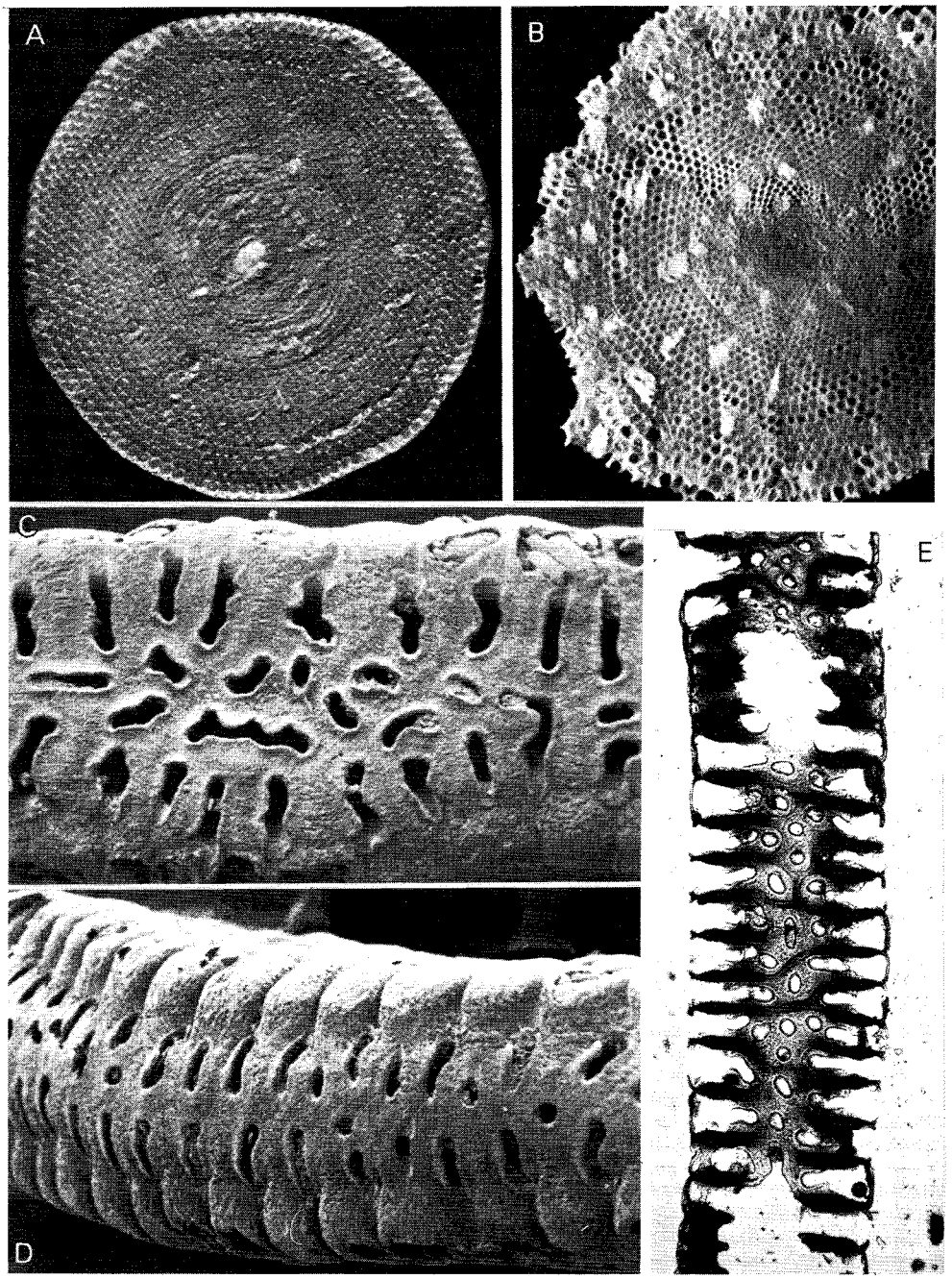
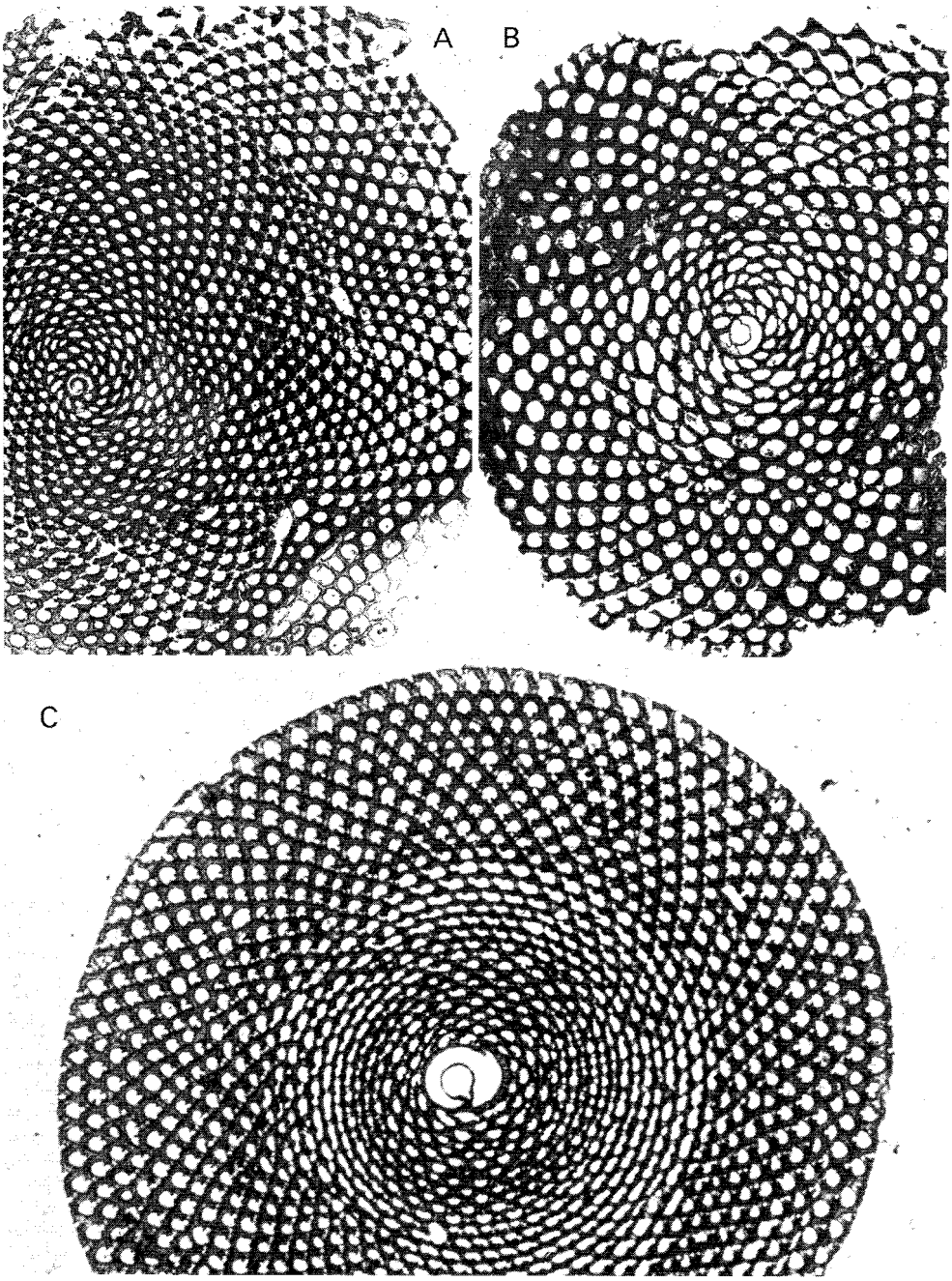


Fig. 31 *Amphisorus hemprichii* from Geziret Faraoûn, site 026, 40 m.
A, B: Lateral views of megalospheric (A) and incomplete microspheric (B) form. Incident light, x 20.
C, D: Marginal views of microspheric (C) and megalospheric form. SEM, x 120.
E: Tangential thin-section of megalospheric form, transmitted light, x 50.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Sorites orbiculus seems to be a cosmopolitan species in tropical and subtropical to temperate shallow waters. It is known to occur in the Mediterranean, the tropical Atlantic and the Pacific. Intensive research is needed to clear up its geologic and phylogenetic history in order to understand its world-wide distribution in contrast to other larger peneroplids that are restricted to faunal provinces.

Sorites orbitolitoides (Hofker), 1930
Fig. 11B, 13, 30A-C, 32A

Synonymy: see Lehmann, 1961, p. 645.

Diagnosis: Thin, biplanar, discoidal peneroplids with the structural characteristics of the genus *Sorites*. Largest diameter of megalosphere 30–40 μm. 3–5 peneroplid, undivided chambers. 12–25 spiral chambers. Apertures on margin 8-shaped, usually not subdivided by bridges, surrounded by regularly thickened peristome (fig. 30A). Annular passage rounded, secondary septa short. Microspheric specimens with breeding chambers have not yet been observed. Specimens growing on irregular surfaces of hard substrate adapt their shell to these irregularities and become definitively sessile. They are easily overgrown by other sessile foraminifera.

Remarks: *S. orbitolitoides* has a longer growth spiral in the megalospheric generation than any other species of this genus. Further research will be necessary to quantify intraspecific variability and to clear up its geographic distribution.

Amphisorus hemprichii Ehrenberg, 1839
Figs. 10, 22B, 31, 32C, 33A

Synonymy: see Lehmann, 1961, p. 649.

Diagnosis: Large, discoidal peneroplids with thickened rims, alternating lateral chamberlets and large annular passages in the median plane of the shell. Stolon system with crosswise oblique stolon axes in two layers. Megalo-

Fig. 32 Equatorial sections of discoidal, megalospheric larger peneroplids. Transmitted light, x 50.
A: *Sorites orbitolitoides* from Elat, site 037, 60 m.
B: *Sorites orbiculus* from Tiran Island, site HU 2054, 1–2 m.
C: *Amphisorus hemprichii* from Geziret Faraoûn, site 049, 35 m.

spheric specimens have a wide, irregular flexostyle canal followed by a particular deuteroconch called "Vorhof" with multiple apertures. First regular chamber subdivided. 3–7 spiral chambers. Microspheric forms with 6 undivided and 6–10 divided, spiral chambers. Apertures on margin alternating, aligned in two rows at the base of the secondary suture and elongated in axial direction. In adult megalospheric forms, supplementary, irregular apertures in the median plane leading from median annular passage radially to the external space. In microspheric adult forms, where the shell margin is often thickened and undulated, the median apertures get more numerous and irregular in form. All apertures have a faint, thickened peristome (fig. 31C-E). Microspheric forms with large breeding chambers.

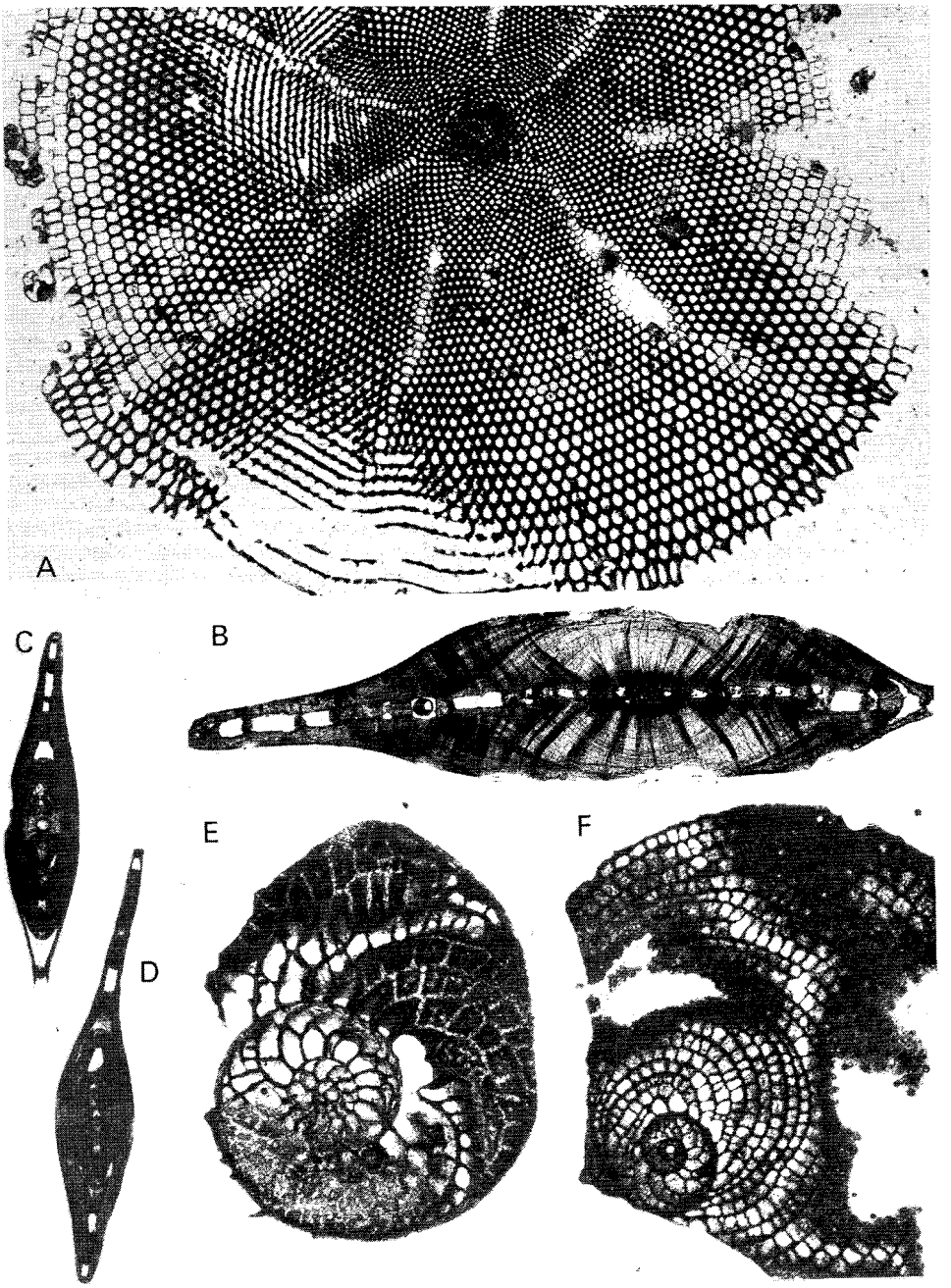
Remarks: *Amphisorus* is a monotypic genus as far as we know today. No systematic research has been carried out to study its specific variability and its phylogenetic history. *A. hemprichii* is distinguished from *Marginopora vertebralis* Quoy and Gaimard, 1830, living in the central Indian Ocean, by its generic structure, in particular by its median annular passage. *M. vertebralis* has two lateral annular passages and an endoskeleton in the median plane of the shell. Its megalospheric apparatus is much larger, its flexostyle canal reduced. The first regular chamber is annular. For details see Lehmann, 1961, p. 654.

Operculina ammonoides (Gronovius), 1781
Figs. 7, 11, 12, 23, 24A, 25–28, 36B.

Synonymy: see Hottinger, 1977.

Diagnosis: Involute or evolute perforate shells with a marginal cord and with the structural characteristics of the genus *Operculina* emended by Hottinger, 1977: simple septa, no folds in the septal flap, irregular secondary stolon system, alternating sutural apertures of intraseptal canal system located in or at margin of the imperforate sutural area, *no trabeculae*. Presence of "interseptal pillars". Diameter of megalospheres 50–125 μm. In megalospheric forms 14–18 chambers per whorl reaching a radius of 1 mm, about

Fig. 33 A: Microspheric *Amphisorus hemprichii*, equatorial section. Geziret Faraoûn, site 049, 35 m, x 20.
B-D: Axial sections of *Heterostegina depressa*, microspheric (B) and megalospheric (C-D) forms from Elat, site 037, 60 m, x 20.
E: Megalospheric *H. depressa*, equatorial section, from Elat, site 021, 77 m, x 20.
F: Megalospheric *Heterocyclina tuberculata*, equatorial section, from Geziret Faraoûn, site 016, 90 m, x 20.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21 chambers per whorl reaching a radius of 2 mm. Characteristics of growth spiral see fig. 23. Variability of ornamentation and perforation see figs. 25, 26, 28.

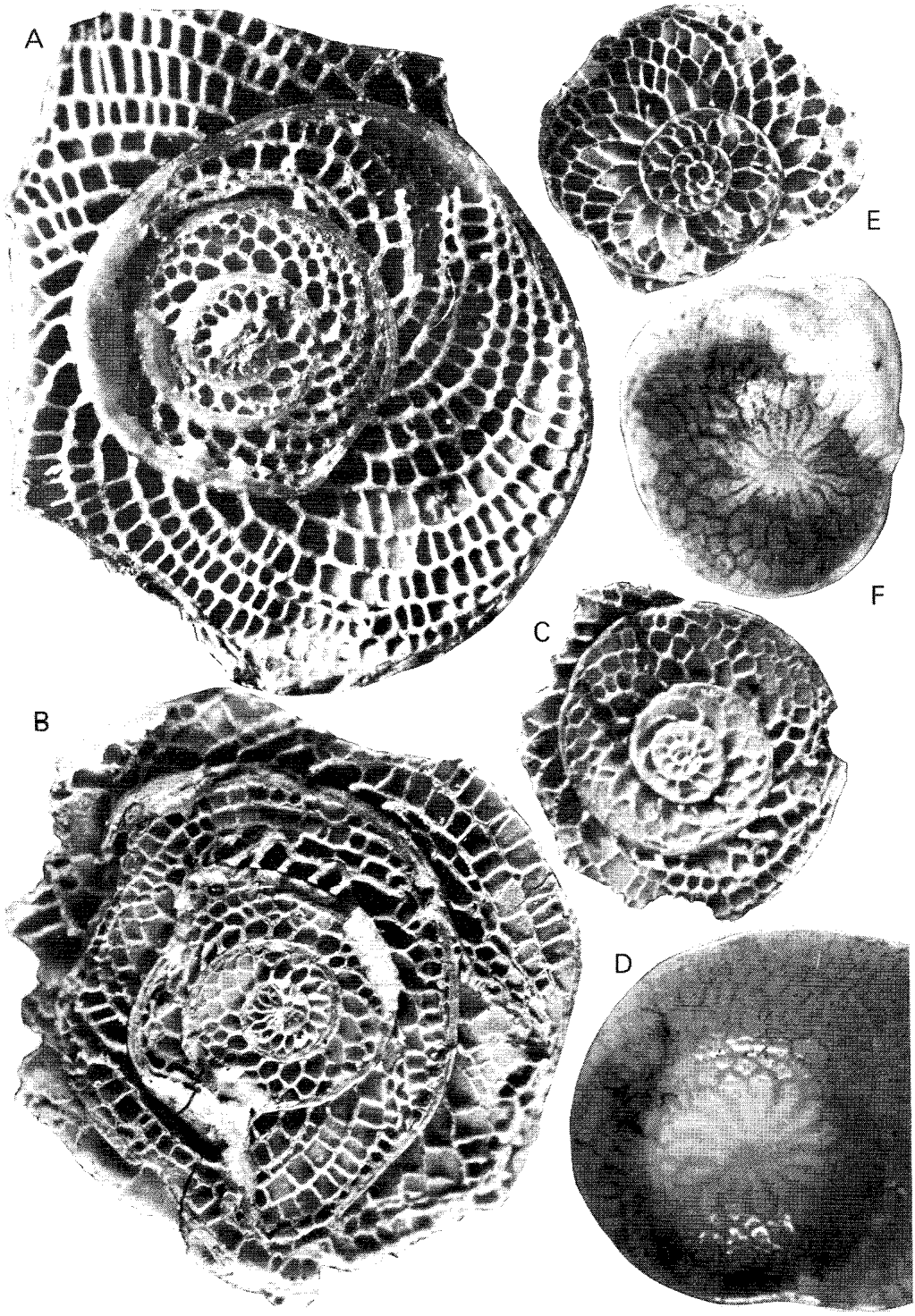
Remarks: Variability in recent operculinids is strikingly complex. I have, however, found only one type of microspheric specimens with high-spired, evolute shells (fig. 23A, 36B). This is the main reason to unite alle recent nummulitids with the generic structure of *Operculina* in *O. ammonoides*. This species is distinguished from other evolute recent nummulitids by its simple, unfolded septa. Involute *O. ammonoides* differ in particular from recent, involute *Nummulites cumingii* (Carpenter), living in the Central Indian Ocean, by their lack of *trabeculae*. *O. ammonoides* is distributed world-wide in tropical and subtropical waters. Its presence has not been observed so far in the Mediterranean.

Heterostegina depressa d'Orbigny, 1826
Figs. 24 B-E, 33 C-E, 34, 35D, 36C

Synonymy: see Hottinger, 1977.

Diagnosis: Involute, more or less thickened nummulitids with complete secondary septa and Y-shaped stolons in the median plane of the shell. There is no direct communication between neighbouring chamberlets of the same chamber. Sutural canals of intraseptal canal system simple, without bifurcations, in both primary and secondary chamber sutures. Ornamentation of "rectangular type" (Hottinger, 1977), consisting of slightly raised, imperforate bands marking the primary and the secondary sutures. 1–6 "interseptal pillars" on lateral chamberlet walls. Polar region swelling up to hemispherical shape in large specimens from shallow water. External lateral surface of ultimate and penultimate chambers with scale-like patterns around each pore (fig. 24B). Megalosphere 60–100 μm in diameter, followed by 12–16 operculinoid, unfolded septa. Microspheric forms with about 30 operculinoid septa.

Fig. 34 *Heterostegina depressa* from Elat, site 020, 40 m (A-D) and from Geziret Faraoûn, site 013, 77 m (E, F). Incident light, x 20.
A: Microspheric form with wide spiral, broken in equatorial direction.
B: Microspheric form with narrow spiral, broken in equatorial direction.
C: Megalospheric form with narrow spiral, broken in equatorial direction.
D: Thick, megalospheric form, lateral view.
E: Megalospheric form with wide spiral, broken in equatorial direction.
F: Thin, megalospheric form, lateral view.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Remarks: *H. depressa* is distinguished from *H. operculinoides* Hofker, the only other heterosteginid species, living today in the Central Indian Ocean, by its involuteness, its higher number of operculinoid septa and its tighter spiral growth.

H. operculinoides emended by Hottinger, 1977, has a megalosphere of 60–100 μm in diameter and only one operculinoid septum following a reniform deuteroconch. Its stolons are almost radial. Annular gaps between the lateral walls and the fold of the septal flap in the front part of the chamber create two lateral annular passages.

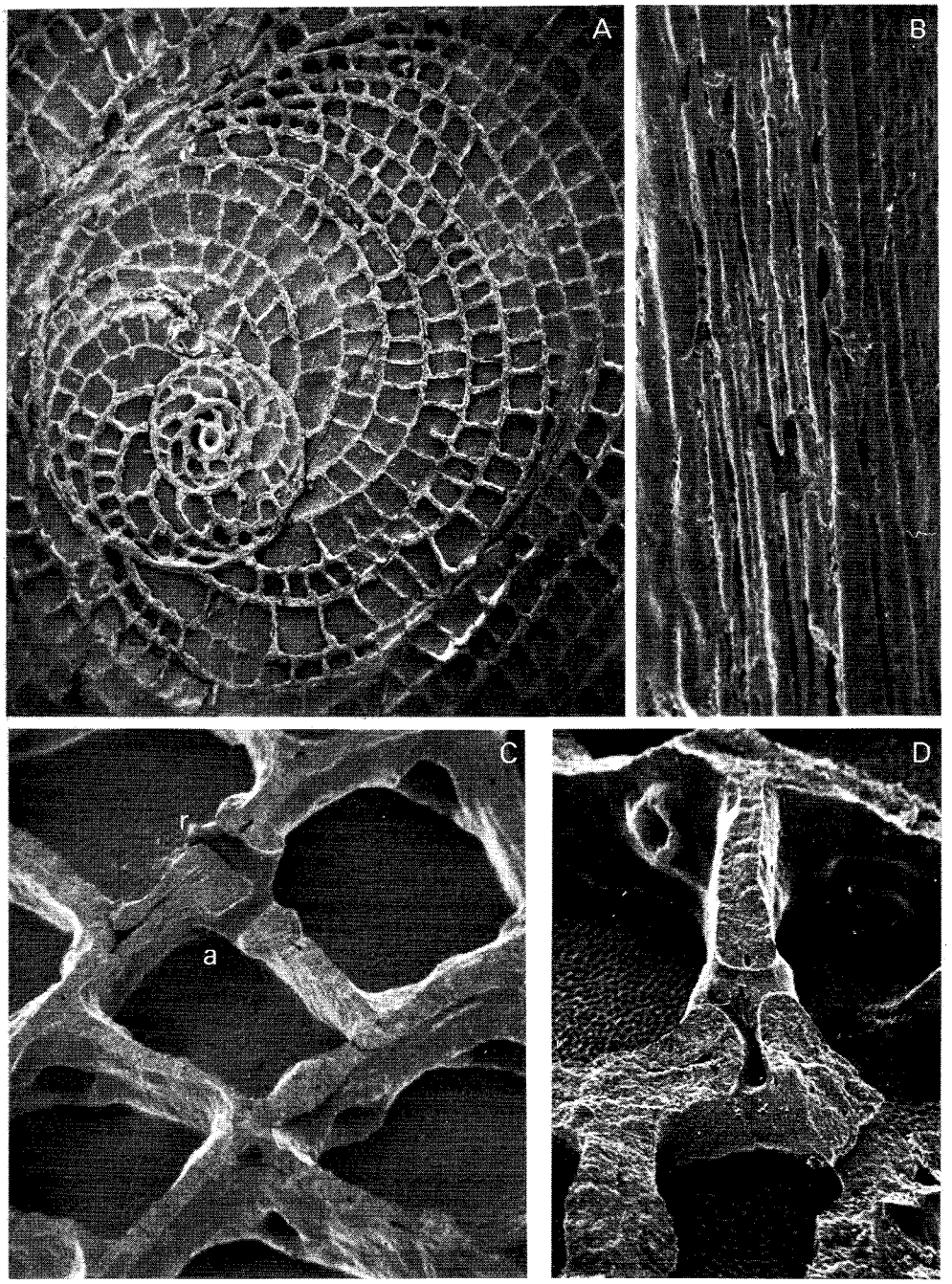
H. depressa is a cosmopolitan species in tropical and subtropical to temperate waters occurring in the central Atlantic and all over the Pacific and the Indian Ocean. In the Mediterranean, this species has been found on the coasts of Israel and Lebanon. Its phylogenetic source, however, seems to be geographically restricted to the central Pacific (*H. duplicamerata* Cole (Miocene) and?*H. aequatoria* Cole (Late Eocene)).

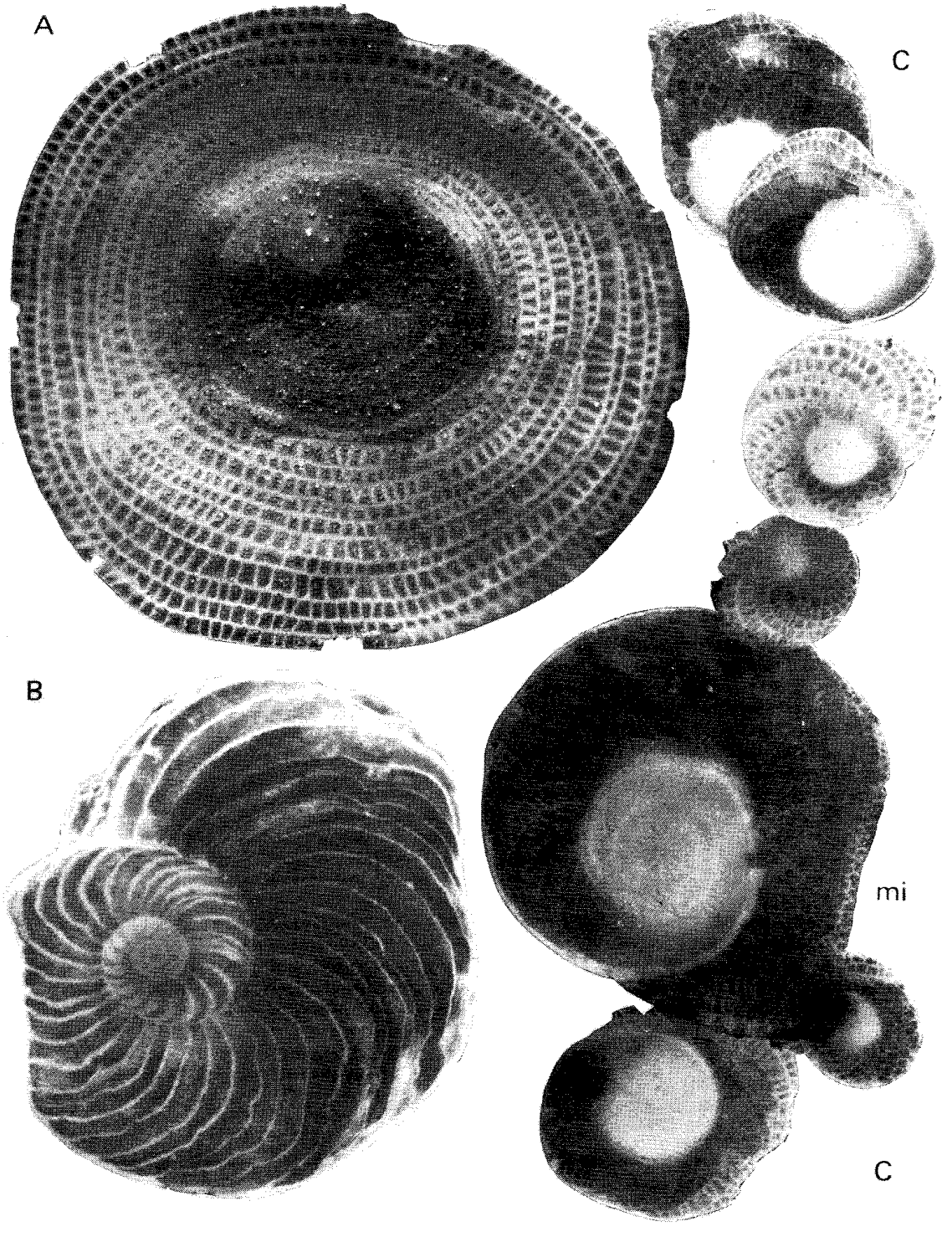
Heterocyclina tuberculata (Moebius), 1880
Figs. 24F, G, 33F, 35 A-C, 36A

Synonymy and definition of the genus *Heterocyclina*: see Hottinger, 1977.

Diagnosis: Discoidal, evolute, extremely thin nummulitids with complete secondary septa, long juvenile growth spirals and late annular growth stages. Stolon system L-shaped, restricted to one layer in the median plan of the shell, with one radial and one annular stolon (fig. 35C). No other passages between neighbouring chambers. Sutural canals without bifurcation in both primary and secondary septa. Ornamentation consisting of single large, almost hemispherical "interseptal pillars" on lateral wall of chamberlets. Sutures usually without ornament. Early spiral part in adult shells obscured and thickened by secondary lamellation. Pores extremely thin. Last chambers with scale patterns as in *Heterostegina depressa*. In earlier chambers, the pores get a raised "peristome" and small pustules appear in between (fig. 24F, G). Apertural face of annular chambers deeply folded, the grooves forming a kind of marginal cord (fig. 35B) having doubtlessly similar functions as a true marginal cord on a spiral periphery.

Fig. 35 *Heterocyclina tuberculata* (A-C) from Geziret Faraoûn, site 156, 90 m.
A: Juvenile, spiral growth stage broken in equatorial direction. SEM, x 50.
B: Marginal view showing apertural face in cyclical growth stage. SEM, x 1000.
C: Detail of A, oblique view showing L-shaped stolons (r = radial stolon, a = annular stolon). SEM, x 500.
D: *Heterostegina depressa,* broken in equatorial direction, showing Y-shaped stolon. SEM, x 500.


A
B
C
r
a
D


A
C
B
mi
C

The megalosphere, circular in equatorial section, has a diameter of 75–100 μm and is followed by one or two operculinid and 23–28 heterosteginid septa forming the spiral growth stage. The last spiral chamber is subdivided into about 50 chamberlets.

Remarks: Identification of the specimens from Elat with the specimens illustrated by Moebius (1880) from Mauritius is easy because this author has figured the L-shaped stolons, a feature known so far only in this species. All other particularities of the shell captured by Moebius' descriptions and illustrations correspond well with the specimens from Elat. Specimens from Mayotte figured by Le Calvez (1965) as *Cycloclypeus carpenteri* belong also to *H. tuberculata* as observed by studying the figured specimens deposited in the Paris Museum.

H. tuberculata is distinguished from *Heterostegina operculinoides* mainly by its cyclical growth stage and by its L-shaped stolons. It differs from *Cycloclypeus carpenteri* by its long spiral juvenile stage, its small embryonic apparatus and by its L-shaped stolons. *Cycloclypeus* has a crosswise-oblique stolon system similar to the one found in *Sorites,* with 8-shaped distal mouths of the intercameral foramina.

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Fig. 36 A: *Heterocyclina tuberculata* from Geziret Faraoûn, site 016, 90 m. Lateral view, incident light, x 20. Dark part in center of shell due to retracted protoplasm.
B: *Operculina ammonoides,* living, microspheric specimen from Elat, site 021, 77 m, in sea water, x 10.
C: *Heterostegina depressa,* living megalospheric and microspheric (mi) specimens from Elat, site 020, 40 m, in sea water, x 10.

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BIOMETRICAL INVESTIGATION OF THE GENUS OPERCULINA IN RECENT SEDIMENTS OF THE GULF OF ELAT

W. J. J. FERMONT

ABSTRACT

In the Gulf of Elat lenticular, involute *Operculina* occur mainly in the uppermost 70 meters. Flat, evolute forms occur throughout the investigated depth range down to 150 meters. The internal parameters do not allow further differentiation of the involute forms. In the evolute forms a subdivision into three types appeared possible. They differ in diameter of the protoconch, probably in test size and total number of chambers, and probably in depth range. In at least one of the groups protoconch values change with depth; the deeper specimens possess a significantly larger protoconch. This increase seems to stop at about 80 m. depth. A similar trend is true for the diameter of the second whorl. No significant relation was found between substrate and the inner morphology of *Operculina*.

INTRODUCTION

The purpose of the present study was twofold. In the first place we wanted to collect data on the relation between the morphology of the genus *Operculina* and its environment. Because the waters of the Gulf of Elat lack significant thermo-, halo- and pycnoclines, substrate, depth and depth-dependent environmental factors may be regarded as the most important parameters influencing the morphology of single species. Hence, special attention was given to possible changes of morphology with depth and substrate.

Secondly, keeping in mind that the present is the key to the past, we tried to get some insight in the consistency of the values found for different parameters, because some of them have been used for biostratigraphical correlations in *Operculina* all over the world (Van der Vlerk and Bannink, 1969) as well as in closely related genera such as *Nummulites* and *Heterostegina* (Drooger, Marks and Papp, 1971; Freudenthal, 1969).

The taxonomic position of the different forms which we were able to distinguish will be dealt with by L. Hottinger (this bulletin). For a general review of the environmental factors in the Gulf of Elat the reader is referred to the paper by Z. Reiss (this bulletin).

P. Tauecchio started this investigation some three years ago by a careful examination of part of the samples. Further research by the present author on many more samples showed the relations between internal and external features to be much more intricate than assumed in the earlier phase. Since

a completely new report had to be written for which only the present author can take the responsibility, the editor decided that the paper should have but one author. I gratefully acknowledge all the work done by my colleague P. Tauecchio (Shell, Borneo), who already had grasped the major lines of today's conclusions.

OUTER MORPHOLOGY

The outer morphology of the *Operculina* specimens in the present material is very variable. There is a large variation in size as well as in the appearance of the test. We were able to distinguish two forms on outer morphology.

The first form – in this paper called type one – is characterized by being evolute and very flat. All the whorls are visible from the exterior. The chamber sutures are radial near the base of the chambers and curve backward near the periphery. These forms are in general strongly ornamented with heavy pustules, which are sometimes concentrated on the chamber sutures forming irregular ridges, and sometimes randomly distributed over the entire surface. The ornamentation is less pronounced or absent in juvenile specimens. The spiral suture is usually more or less depressed.

The second form – referred to as type two – is characterized by being thick, lenticular and strongly involute. In general, only the last whorl is visible. The sutures are sinuous, curved backward and slightly raised. The wall surface is smooth and lacks the strong ornamentation described for type one.

Sometimes, especially in juvenile specimens, discrimination between the two types is difficult, on the one hand because nearly all the juvenile forms lack ornamentation, on the other because the type two-specimens do not start with a completely involute stage. In addition, larger specimens of type two may have last chambers of reduced size, which give the individuals an evolute appearance. Although not used in this paper the (sub)generic names *Operculina* d'Orbigny and *Operculinella* Yabe might be applied to our types 1 and 2 respectively.

SAMPLES

The composition and types of preservation of the *Operculina* assemblages differ considerably from one sample to another. Therefore we will give a brief description of the sample content as far as the *Operculina* are concern-

ed. The samples are described in order of increasing depth. Their location is given in fig. 14 of the paper of Hottinger (this bulletin), the field numbers of this map corresponding to the HU numbers in this paper are listed in table 1 of Thomas (this bulletin). In addition: HU 4766 = 71011, HU 4940 = 71158, and HU 4768 = 71014.

28 and 38 meters (HU 4943 and HU 4942 respectively)

The *Operculina* of these two shallow samples consist of extremely well preserved individuals. Type 2 is strongly predominant. Most of the specimens are full-grown, with more than $2\frac{1}{2}$ whorls completed, but there are juvenile forms with only about $1\frac{1}{2}$ whorls. Also type 1 is represented in both samples, being relatively more frequent in the 38 meter sample.

54 meters (HU 4766)

This sample is not rich in biogenic material. The residue mainly consists of quartz grains. *Operculina* is represented by rather small, but well preserved type 1 individuals although some type 2 specimens were found as well.

66 meters (b and a; HU 4859 and HU 4941)

Both samples are almost entirely composed of biogenic material and very rich in *Operculina*. Both types are represented in about equal numbers. Furthermore, there is a large variation in the way of preservation. Some forms are extremely well preserved, others are discoloured, greenish or brownish-grey, possibly due to the activities of boring algae (Emery, 1963). Many of the larger specimens are damaged, especially in HU 4859. The specimens of type 1 in sample HU 4941 are smaller and in general somewhat better preserved.

77 meters (HU 4940)

This sample contains mainly type 1. The smaller forms are well preserved, the larger ones are in some cases etched or broken. Some type 2 specimens occur as well.

79 meters (HU 4768)

This sample contains a fairly homogeneous assemblage of thin, undamaged type 1 specimens. They are in general small and fragile.

86 and 90 meters (HU 4939 and HU 5250)

These samples contain a mixture of small, relatively well preserved individuals and large, commonly damaged forms, both of type 1. The smaller specimens outnumber the larger ones, especially at 90 meters. Occasionally damaged specimens of type 2 were found as well.

104 and 110 meters (HU 4930 and HU 4931)

These samples contain only type 1. There is a large variation in size and in way of preservation. Many specimens are broken and/or of dark colour.

116 and 124 meters (HU 4876 and HU 4831)

In these samples we found mainly type 1 specimens, and a few type two individuals. The latter are always damaged, sometimes coloured red-brown, sometimes greenish grey, with an etched wall. These forms are supposed to have been exposed for a long time at the sediment surface, and possibly transported. Also some of the type one specimens are damaged or coloured.

130 meters (HU 4803)

The assemblage from this sample is very homogeneous. It consists of fragile undamaged forms, all of type one. Nearly all are very small, with less than 2 whorls.

138 and 140 meters (HU 4950 and HU 4760)

Both samples contain types 1 and 2 in about equal numbers, type one being slightly predominant. Most of the second type specimens have a coloured wall and/or are broken. Also some of the first type individuals are broken or etched.

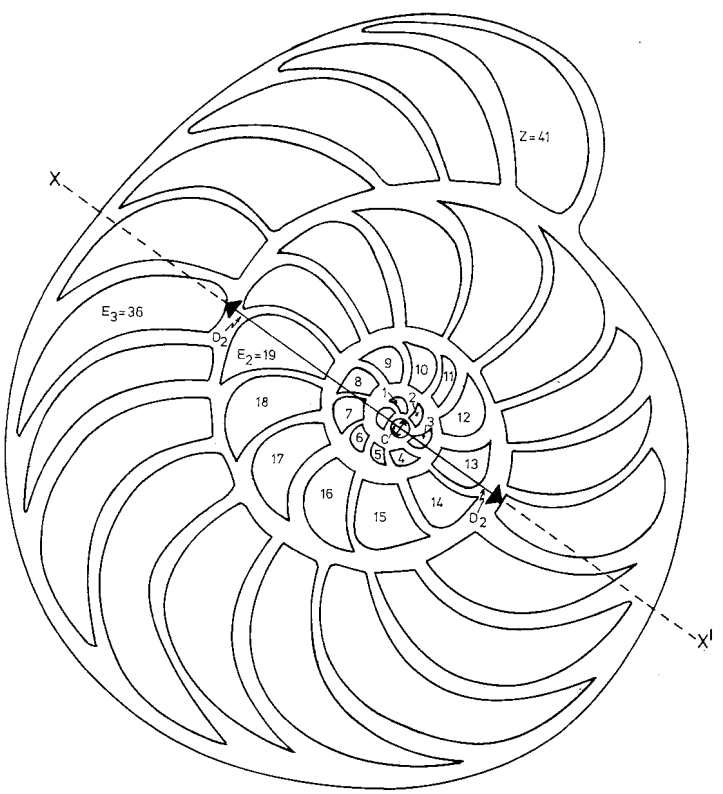


Fig. 1 Median section of *Operculina* with the various parameters indicated.

150 meters (HU 4772)
In this sample we found only type 1 specimens, many of which are broken and some are coloured red.

INNER MORPHOLOGY; OBSERVATION METHODS AND PARAMETERS

Some samples were poor in their *Operculina* content and it was necessary to pick all specimens. Others were very rich and the available residues had to be split. Half-sections were made by sectioning the specimens under a binocular microscope. In general we restricted the number of specimens to 25–30 per sample. Only in highly variable assemblages more specimens were sectioned in order to get reliable information.

The parameters chosen are nearly all the same as those used by Drooger, Marks and Papp (1971) in their study of N.W. European *Nummulites.*

C = The inner diameter of the protoconch. C is the largest diameter measured along a line, perpendicular to the line X-X^1 through the centers of protoconch and deuteroconch (fig. 1).

d_2 = The outer diameter of the first two whorls, measured along the line X-X^1 through the centers of the protoconch and deuteroconch.

E_n = The total number of chambers in the first n whorls, excluding the protoconch and deuteroconch from the counts, but including the last chamber the base of which is cut by the line X-X^1.

z (introduced here) = The total number of chambers. z was counted in part of the assemblages. Only undamaged specimens or slightly damaged ones were counted. The protoconch and deuteroconch were excluded from the counts.

α = This is the E-factor of Van der Vlerk and Bannink (1969). To avoid confusion with other parameters in this paper, we used the symbol α. The parameter α is calculated as follows: $\alpha = \frac{\alpha_1}{\alpha_2} \times 100$ in which α_1 represents the angle of enclosure of the protoconch by the deuteroconch and α_2 the angle

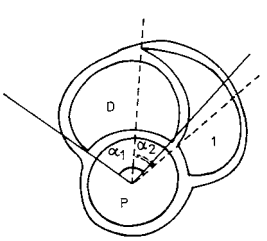


Fig. 2 Median section of the first three chambers of *Operculina* with the angles α_1 and α_2; P = protoconch, D = deuteroconch.

of enclosure of the deuteroconch by the third chamber. These angles are measured from the center of the protoconch (fig. 2).

Measurements were made under a Leitz binocular microscope, equipped with a calibrated scale. The sections were studied with an enlargement of 144 X. The unit of measurement amounts to 12.5 μ. The measurements were rounded off to half a unit for the protoconch diameter and to one unit in measuring the diameter of the whorls. For the measurement of the angles α_1 and α_2 (see below) we prepared drawings with a Leitz projection equipment. The enlargement of these pictures amounts to about 300 X. For the measuring of other angles the microscope was equipped with a cross stage and a rotating object table.

All sectioned specimens are stored in the collections of the Geological Institute of the Utrecht State University.

The observations are compiled in histograms and scatterdiagrams. For all samples the means and standard errors were calculated. The results are given in tables. All calculations were carried out with the aid of a Canon Canola F20P electronic calculator.

RESULTS OF MEASUREMENTS AND COUNTS

When we started to consider the mean values of the different parameters for all specimens per sample, very chaotic pictures arose, which are not reproduced in this paper. In many cases the means were found to differ significantly from each other, but there were no obvious trends. However, there were some clues to filter the available information and clear up the picture. As a first approach we decided to consider types 1 and 2 separately. This could easily be done because the overlap in outer morphology is very small. The numbers of dubious specimens appeared to be restricted to one or two per sample and placing them in the wrong group would have little influence on the mean values of the inner parameters.

Type 1

This type occurs throughout the examined depth range although some residues had to be picked out completely. A large variation occurs between the samples with regard to mean test size and way of preservation.

The pattern of the means of the inner parameters versus depth remains to give a chaotic picture (fig. 3). These means and standard errors are given

in table 1. Several samples were compared with each other to check whether the differences were realistic. In many cases we found them to be significant at a confidence level of 97.5%. The procedure we followed was the Rank Sum test and the results are given in table 2.

Sample	depth	$\bar{C} \pm \sigma_m$	Range	n	$\bar{d}_2 \pm \sigma_m$	Range	n
HU 4943	28	41.5 ± 1.2	30 – 56	25	580 ± 25	165 – 799	25
HU 4942	38	44.2 ± 2.3	23 – 66	25	589 ± 32	353 – 1211	25
* HU 4942	38	47.8 ± 2.8	25 – 81	32	584 ± 38	413 – 912	18
HU 4766	54	67.0 ± 2.8	50 – 119	25	893 ± 39	512 – 1356	25
HU 4941	66a	73.2 ± 3.0	40 – 109	25	1021 ± 49	419 – 1531	25
HU 4859	66b	77.8 ± 2.0	59 – 101	25	1058 ± 38	802 – 1461	25
HU 4940	77	73.4 ± 2.6	31 – 100	34	881 ± 60	325 – 1300	18
HU 4768	79	79.4 ± 3.3	26 – 110	25	1055 ± 38	410 – 1300	25
HU 4939	86	71.0 ± 2.6	36 – 109	40	890 ± 30	500 – 1300	37
HU 5250	90	78.1 ± 2.4	56 – 106	39	929 ± 29	663 – 1262	29
HU 4930	104	69.6 ± 3.9	31 – 106	36	839 ± 38	450 – 1175	32
HU 4931	110	63.5 ± 3.1	25 – 112	36	816 ± 21	475 – 1087	24
HU 4876	116	64.7 ± 4.4	25 – 106	28	853 ± 43	362 – 1200	28
HU 4831	124	51.9 ± 2.6	31 – 75	30	734 ± 40	413 – 1000	24
HU 4803	130	80.9 ± 2.7	56 – 100	34	965 ± 25	850 – 1063	11
HU 4950	138	53.8 ± 4.9	25 – 106	24	717 ± 37	463 – 1088	21
HU 4760	140	56.9 ± 3.9	25 – 93	26	673 ± 41	450 – 938	17
HU 4772	150	53.7 ± 2.5	33 – 86	25	778 ± 29	560 – 1032	25

depth	$\bar{E}_2 \pm \sigma_m$	Range	n	$\bar{\alpha} \pm \sigma_m$	Range	n
28	20.6 ± 0.2	18 – 23	25	276 ± 16	156 – 518	25
38	20.1 ± 0.4	16 – 27	25	338 ± 34	133 – 820	25
38	18.4 ± 0.5	15 – 25	26	—		
54	19.5 ± 0.1	18 – 22	25	326 ± 21	185 – 634	25
66a	21.3 ± 0.2	18 – 24	25	286 ± 22	141 – 709	25
66b	22.4 ± 0.3	18 – 27	25	303 ± 22	160 – 584	25
77	20.2 ± 0.4	18 – 23	23	354 ± 20	214 – 713	31
79	21.4 ± 0.4	17 – 25	25	278 ± 20	123 – 672	25
86	20.2 ± 0.2	18 – 25	40	325 ± 14	205 – 640	38
90	21.0 ± 0.4	16 – 25	34	335 ± 16	203 – 657	39
104	21.0 ± 0.3	19 – 24	32	296 ± 14	144 – 481	35
110	20.6 ± 0.3	16 – 23	24	331 ± 24	172 – 767	35
116	19.8 ± 0.3	16 – 23	27	272 ± 14	154 – 444	26
124	19.9 ± 0.3	16 – 23	28	—		
130	21.6 ± 0.4	17 – 24	21	—		
138	20.2 ± 0.6	18 – 24	23	—		
140	20.9 ± 0.4	18 – 24	21	—		
150	21.1 ± 0.3	19 – 26	25	372 ± 27	202 – 857	25

Table 1. C, d_2, E_2 and α in type 1 *Operculina* of the Gulf of Elat.

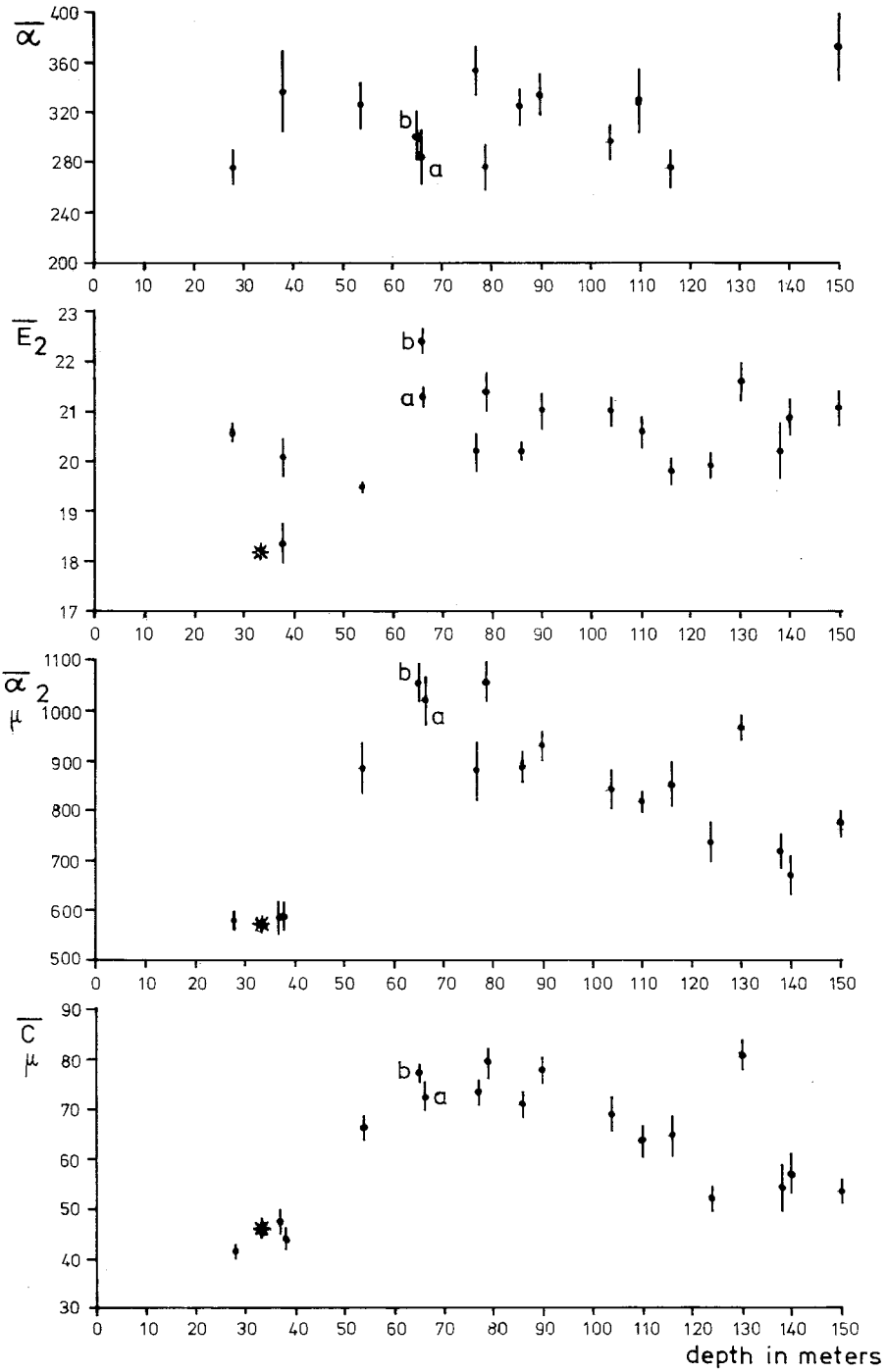
There exists a distinct positive correlation between C and d_2 (table 3). Only in the samples from 28 and 66 (b) meters depth this is less evident but in all the other samples examined the correlation is positive at a confidence level of at least 97.5%.

Also between d_2 and E_2 a general positive correlation is found but here the correlation is significant at the confidence level of 97.5% in only 11 of the 17 samples.

Depth	C		d_2		E_2		a	
28								
	0,63	–	2,40	+	1,78	–	1,15	–
38								
	4,93	+	5,20	+	1,14	–	0,41	–
54								
	9,68	+	3,20	+	4,85	+	0,88	–
66b								
	1,08	–	0,52	–	1,48	+	1,25	–
66a								
	0,05	–	1,28	–	2,70	+	3,23	+
77								
	2,64	+	2,51	+	3,48	+	2,52	+
79								
	4,45	+	2,85	+	2,86	+	2,08	+
86								
	1,69	–	2,90	+	2,66	+	1,13	–
90								
	1,98	+	2,27	+	0,38	–	1,59	–
104								
	1,49	–	0,60	–	0,16	–	1,46	–
110								
	0,20	–	0,33	–	2,02	+	1,83	–
116								
	1,63	–	1,49	–	3,91	+	2,77	+
150								

Table 2. Significance of differences in distributions of parameter values in *Operculina* type 1 between adjoining samples in depth order of the Gulf of Elat, based on rank sum test.
+ difference considered significant, test one-sided, at 2.5%.

Fig. 3 Relation between depth and the parameters $\bar{C}$, $\bar{d}_2$, $\bar{E}_2$ and $\bar{\alpha}$ of type 1. For all parameters the range of $\pm 1\ \sigma_m$ is indicated.
* = 38 meter check sample.


$\overline{\alpha}$
400
360
320
280
240
200
b
a
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
$\overline{E_2}$
23
22
21
20
19
18
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b
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$\overline{\alpha}_{\mu 2}$
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depth in meters

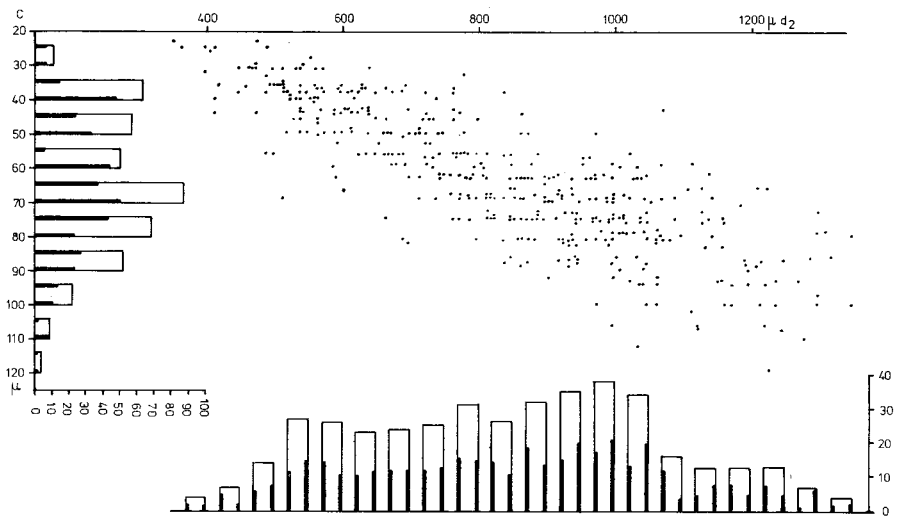


Fig. 4 Scatter diagram and histograms of all the available C and d_2 data of type 1.

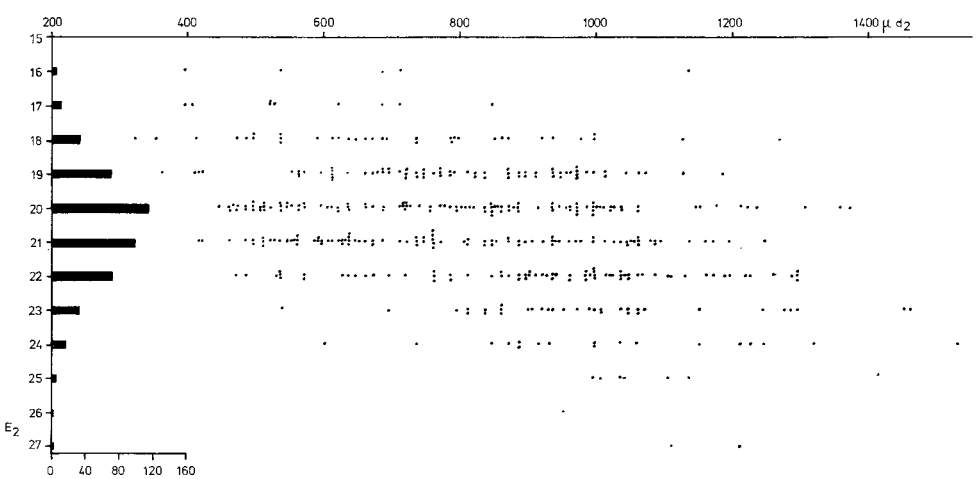


Fig. 5 Scatter diagram of all the available d_2 and E_2 data and bar diagram of all E_2 data of type 1.

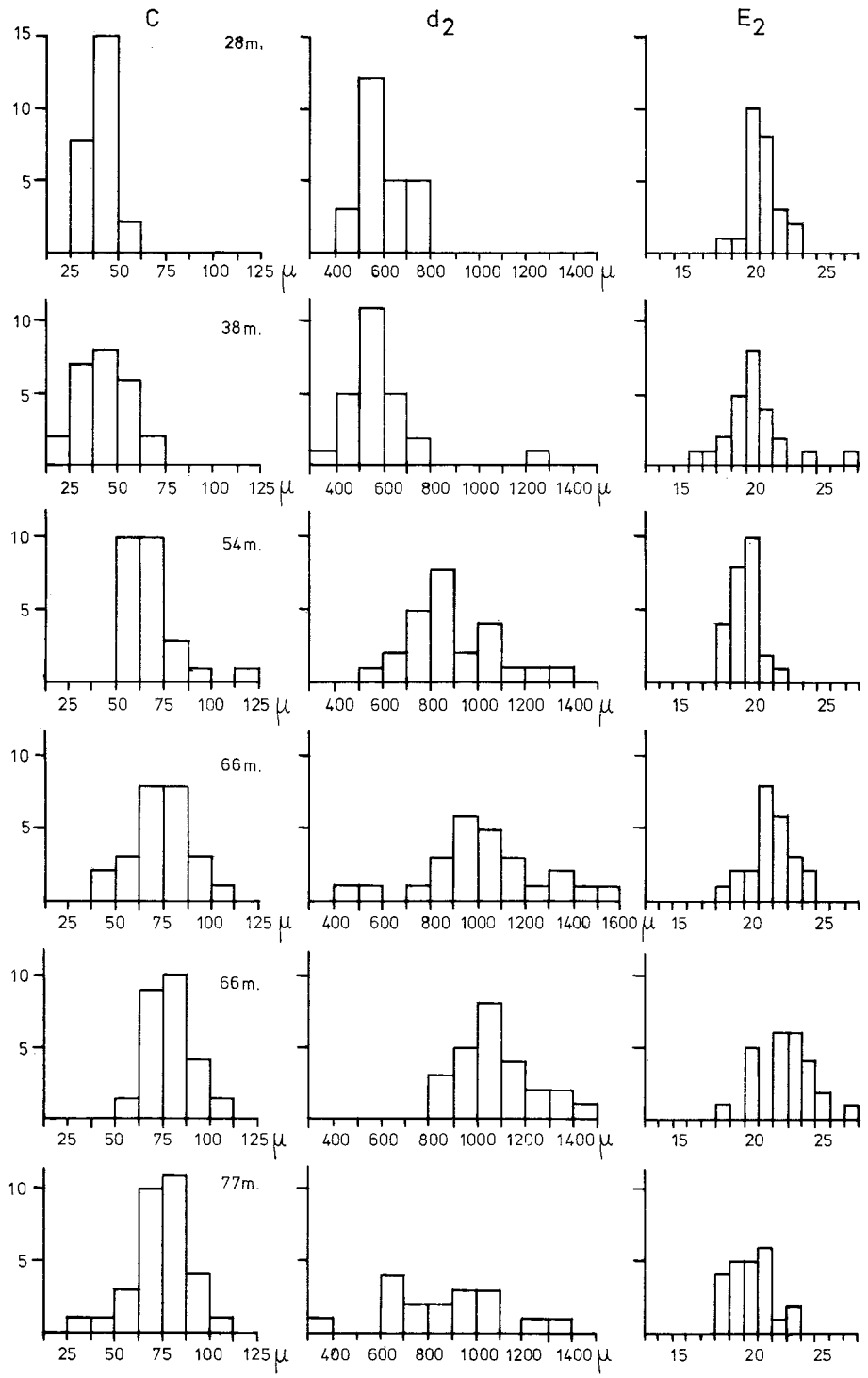
The correlation between C and E_2 is still weaker, being significantly positive at the confidence level of 97.5% in only 7 samples. The positive correlation between C and d_2 and between d_2 and E_2 is also clearly expressed in the scatterdiagrams in which the data from all samples are combined (fig. 4, 5).

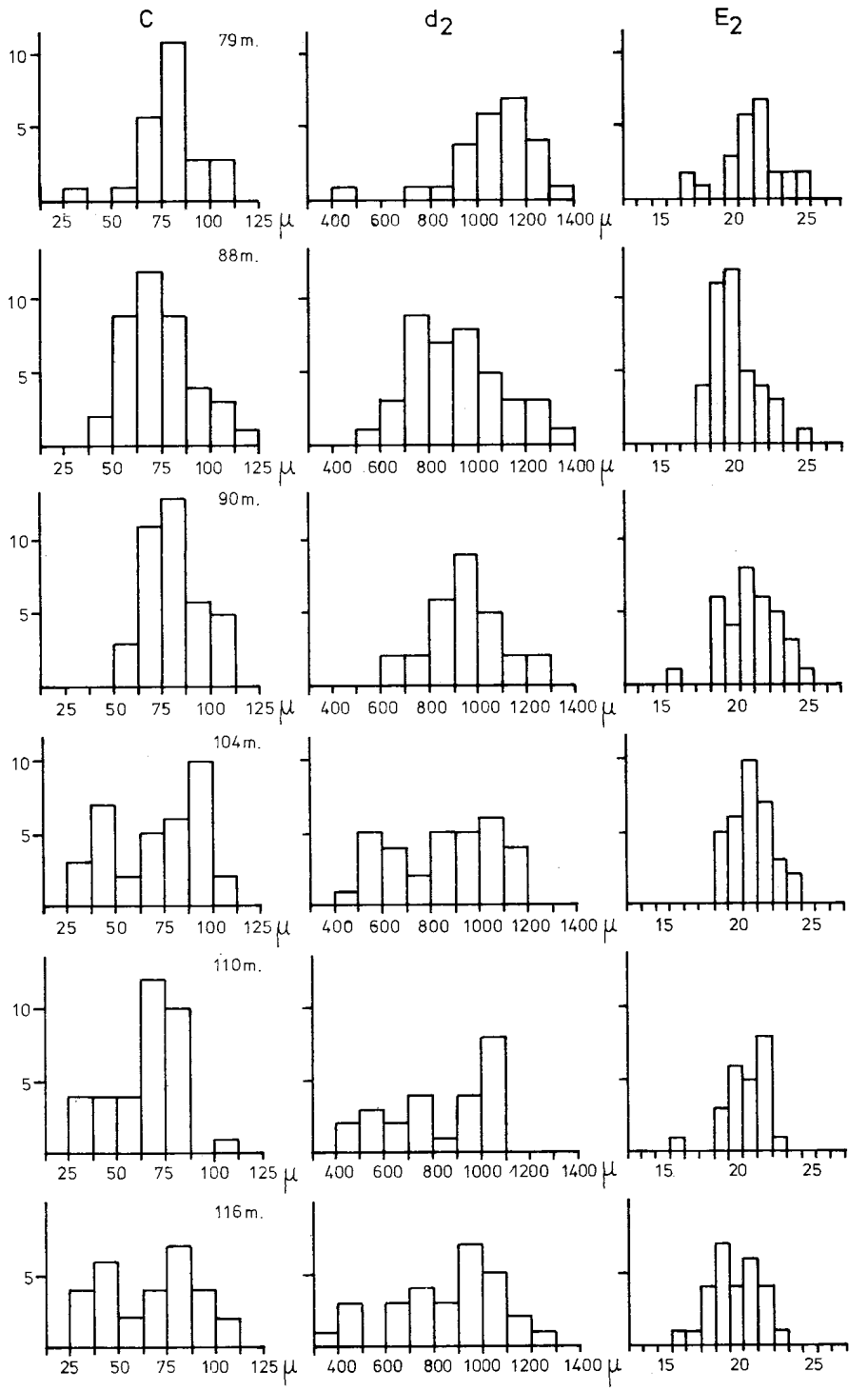
No correlation or a very weak one was found between the factor α and each of the other parameters. Only in four cases a significant negative correlation between α and one of the other parameters was found at a confidence level of 97.5% (see table 3).

If one considers the histograms of C (fig. 6) it appears that some of the samples show a very irregular distribution. We selected three of the samples with such irregularities, i.e. HU 4930, HU 4931 and HU 4876 from 104, 110 and 116 meters depth respectively, and tested them for normality by means of the chi square test for the goodness of fit. First we tested only sample HU 4930. The chi square value amounts to 2.997 (1 d.f.) which value is significant at the 90% confidence level. This means that we may reject the hypothesis that the distribution is normal. The result is more outspoken when the three samples are grouped together. The chi square

Sample	depth	$C - d_2$	$C - E_2$	$d_2 - E_2$	$C - \alpha$	$d_2 - \alpha$	$E_2 - \alpha$
HU 4943	28	+0.34 o	+0.37 o	+0.59 +	+0.24 o	+0.06 o	+0.06 o
HU 4942	38	+0.65 +	+0.19 o	+0.64 +	−0.02 o	−0.12 o	−0.27 o
* HU 4942	38						
71011	54	+0.65 +	+0.69 +	+0.42 +	−0.02 o	−0.12 o	−0.27 o
HU 4941	66a	+0.64 +	+0.40 +	+0.24 o	−0.02 o	−0.43 −	−0.20 o
HU 4859	66b	+0.34 o	+0.79 +	+0.59 +	−0.07 o	−0.37 o	−0.29 o
HU 4940	77	+0.87 +	−0.08 o	+0.47 +	−0.18 o	−0.32 o	−0.19 o
HU 4768	79	+0.90 +	+0.72 +	+0.72 +	−0.41 −	−0.51 −	−0.32 o
HU 4939	86	+0.81 +	+0.49 +	+0.40 +	+0.02 o	+0.15 o	−0.13 o
HU 5250	90	+0.57 +	+0.55 +	−0.18 o	−0.26 o	−0.01 o	−0.07 o
HU 4930	104	+0.90 +	+0.52 +	+0.35 +	+0.30 o	+0.05 o	+0.29 o
HU 4931	110	+0.85 +	+0.32 o	+0.42 +	−0.25 o	−0.31 o	−0.50 −
HU 4876	116	+0.82 +	+0.30 o	+0.50 +	+0.01 o	+0.23 o	+0.07 o
HU 4831	124	+0.89 +	+0.22 o	+0.38 +	—	—	—
HU 4803	130	+0.51 +	−0.02 o	−0.16 o	—	—	—
HU 4950	138	+0.91 +	−0.06 o	+0.09 o	—	—	—
HU 4760	140	+0.89 +	+0.31 o	+0.38 o	—	—	—
HU 4772	150	+0.73 +	−0.02 o	+0.10 o	−0.01 o	−0.11 o	−0.28 o

Table 3. Correlation coefficients between the parameters of *Operculina* type 1. The coefficients are tested at a $2\frac{1}{2}$% significance level. For the check sample HU 4942 (*) no coefficients were calculated.


C
d_2
E_2
28m.
38m.
54m.
66m.
66m.
77m.
15
10
5
25 50 75 100 125 μ
400 600 800 1000 1200 1400 μ
400 600 800 1000 1200 1400 1600 μ
15 20 25


C
d_2
E_2
79 m.
88 m.
90 m.
104 m.
110 m.
116 m.
10
5
25 50 75 100 125 μ
400 600 800 1000 1200 1400 μ
15 20 25

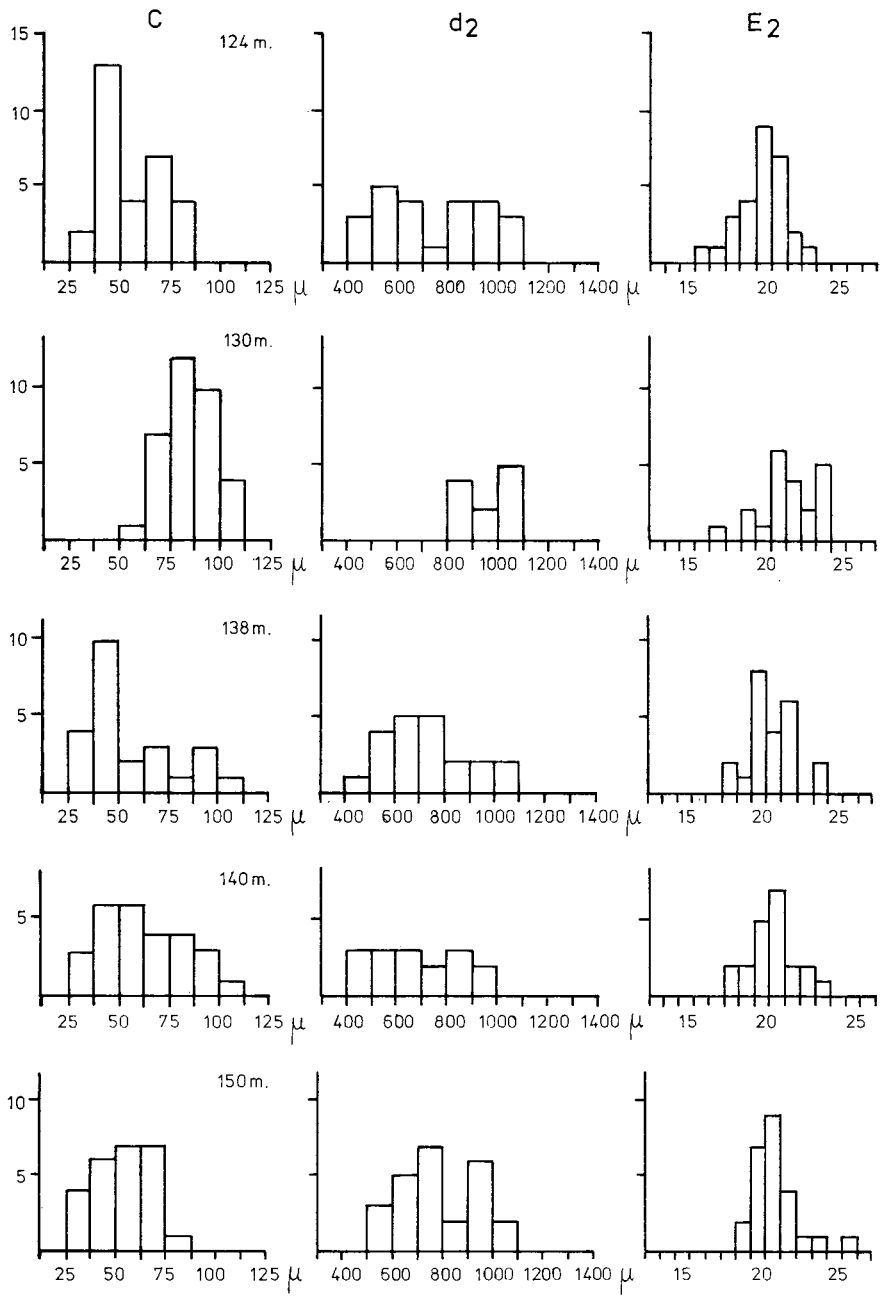


Fig. 6 Histograms of the parameters C, d_2 and E_2 of type 1.

value amounts to 16.418 (1 d.f., P = 0.999); so the hypothesis of normal distribution is rejected. This result suggests heterogeneity within type 1 of the three samples.

We did not check the d_2 and E_2 distributions in this manner. Since d_2 shows strong positive correlation with C nothing new was expected; actually, the d_2 distributions show the same irregular picture as those of C. The E_2 distributions were not checked because the histograms suggest less irregularities (fig. 6).

The suggestion of heterogeneity within type 1 had to be elaborated. The next step chosen was combining all the available data of C, d_2 and E_2 on type 1 specimens (fig. 4, 5) in single histograms. The distribution of E_2 was found to be fairly normal. We made graphically an estimate of the mean and the standard deviation: $E_2 = 20.5$ and $\sigma = 1.4$. The standard error would be in the order of 0.07 (n = 410).

The histograms for C and d_2 (fig. 4) are more irregular. The narrow groupings show irregular frequency distributions. Classes of double width only partly smoothen the curves, because now a bimodality is suggested for both C and d_2. In order to minimize possible effects of the measurement errors we made the class width for C coincide with four times this error. For d_2 we further reduced the number of classes to 13 (fig. 7). However, bimodality remains, although the dents in the distributions are not very impressive. Since there is additional evidence in the distributions within single samples, we assumed that these peaks in fig. 7 were brought forth by mixing of two sets

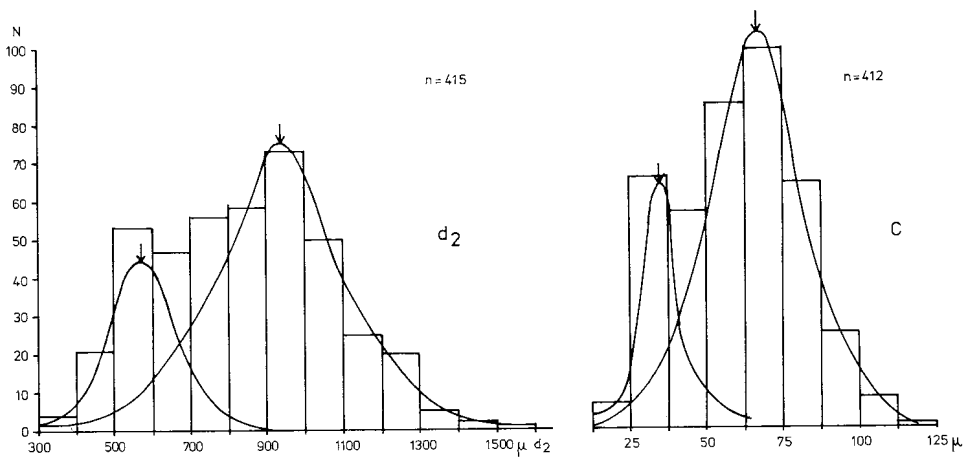


Fig. 7 Histograms of all C and d_2 data with reduced numbers of classes and estimated means of both type 1 groups.

of unimodal distributions. On the basis of this assumption we constructed graphically by trial and error two normal distribution curves that together fit to the observations. Although nonsensical from the statistic point of view, for instance because the number of observations is too small for such a procedure, these hypothetical curves would have means and standard deviations (in μ) as follows:

	M_1	σ		M_2	σ
C =	36	7.5	C =	68	14
d_2 =	570	90	d_2 =	930	190

From the positive C-d_2 correlation in fig. 4 it may be evident that the low C and low d_2 values correspond with each other and the same is true for the high C and high d_2 values. Most of the individual samples fit in with this picture, as may be seen from the scatter diagrams (fig. 6). However, since the assumed normal distributions have a large overlap the existence of two different groups remains questionable and disentangling them is utterly impossible as we have seen in HU 4930 at 104 meters depth.

Yet another approach to prove the heterogeneity in type 1 assemblages appeared possible. While sectioning and measuring our specimens, a further interesting point drew our attention. In many cases the small specimens seemed to have a large protoconch. Therefore one sample with a large variation in size of type 1 specimens was selected. The 38 meter sample HU 4942 fulfils these requirements very well also because it contains very few damaged specimens. We took a new split, because many of the specimens already sectioned were broken, and measured also z, the total number of chambers, as an estimate of test size. The histogram of z in fig. 8 gives a remarkable picture. There are peaks at the extreme left and right sides, and a minimum in between. The abrupt breaks at both ends need some consideration. The left side break in the distribution might be explained in two ways: either smaller specimens are present but we did not recognize them because they are smaller than the about 250 μ limit of the residues, or they are not present at all because the individuals reach anyhow a minimum growth stage of about 10 chambers. The possibility of sorting can be neglected for this sample. The sudden break in the distribution on the other side may at least in part, be explained by larger specimens usually being broken and thus left unconsidered. Although the breaks at the ends of the distribution may be artificial, the minimum in the middle cannot be reasoned away. It is clear that there occur two groups, one with z values larger than about 29, the other with z values smaller than about 29.

If we take both groups together, there exists a remarkable negative cor-

relation between z and C (fig. 8). The correlation coefficient amounts to −0.56 (n = 32), which value is significant at a probability level of 99.9%. For each group separately the r values are of low or no significance, but the numbers of observations per group are few. E_2 and d_2 values were not compared with z, because many of the specimens did not possess a second whorl.

On the basis of recognition of two type 1 groups in the 38 m. sample we calculated the means of z and C with their standard errors for $z > 29$ and $z < 29$. These means are compared with the earlier graphically derived means of C for all samples together (in the right column). The results are given below:

	$\bar{z} \pm \sigma_m$	range	$\bar{C} \pm \sigma_m$	range	n	$\bar{C} \pm \sigma$
$z > 29$	38.4 ± 1.5	30 – 44	33.8 ± 2.3	25 – 56	20	36 ± 7.5
$z < 29$	16.8 ± 2.1	9 – 26	55.3 ± 1.2	31 – 81	12	68 ± 14

The $\bar{C}$ value of the larger specimens from 38 m. fits in very well with the graphically derived "small" $\bar{C}$ value. The difference amounts to less than one σ_m of the former group. For the large $\bar{C}$ value in the small specimens from 38 m. the difference with the corresponding all-group mean is much

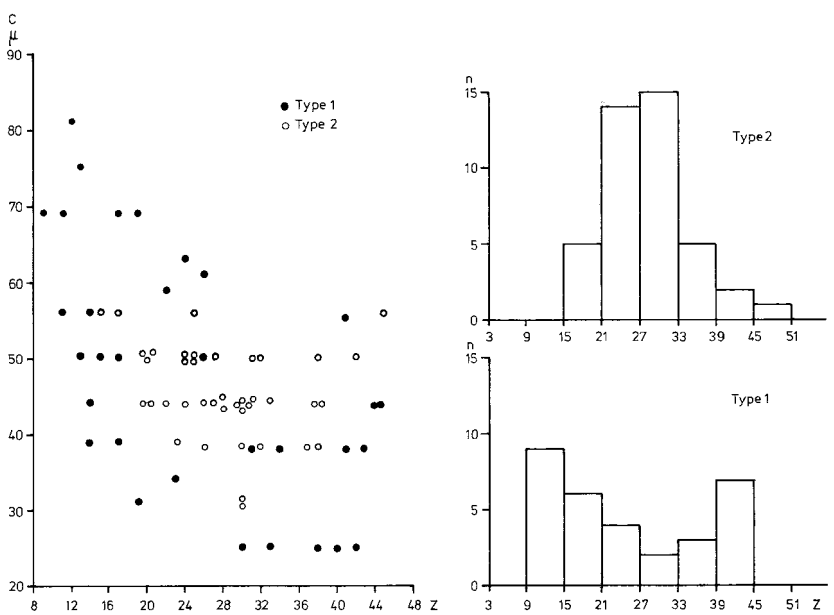


Fig. 8 Histograms of z and scatter diagram of C against z in the 38 meter check sample; types 1 and 2.

greater. The difference is about 10 σ_m of the mean of the 38 m sample and such a difference may be regarded to be highly significant. An attempt to explain this difference will be given in the chapter "Discussion" at the end of the paper.

Recognition of two groups of type 1 *Operculina* seems possible on C, d_2 and z values, but not on the basis of E_2. Probably the E values of both groups are too close. Although it is true that the means of E differ in many cases significantly, $\bar{E}_2$ seems to be the most stable parameter showing least variation. The relative stability (R) of the parameters expressed by the ratio of the highest and the lowest mean × 100 for types 1 combined gives $R_{\bar{C}}$ = 195, $R_{\bar{d}_2}$ = 182, $R_{\bar{E}_2}$ = 121, and $R_{\bar{\alpha}}$ = 132 which shows that $\bar{E}_2$ is least variable.

So far we did not discuss the factor α. The reason is that we did not find any clear relation with the other parameters. Significant negative correlations at the 97.5% confidence level were found only in HU 4931 (110 meters) between α and E_2, in HU 4941 and HU 4768 (66 and 79 meters respectively) between α and d_2, and again in HU 4768 between α and C.

The left-skewed character of the α histograms (fig. 9) is probably explained by the fact that α represents a ratio, in which α_2 is always smaller than α_1. Since α_2 may vary considerably the calculated α values range from slightly more than 100 up to very large. Measurement errors and simple variation on relatively small α_2 values cause the long tails at the right side of all frequency distributions.

We checked the differences in the α means of various samples in depth succession by means of the Rank Sum Test and in many cases the differences are significant. The results are given in table 2. The total range of α is from 123 to 857. The means vary between 272 and 372. We did not find any clue to filter this information. Also the histogram of all data together gives a very regular, left-skewed distribution (fig. 9).

Type 2

Undamaged specimens of the second type in fair quantities are more or less restricted to the uppermost samples. Type two occurs also in the deeper samples, but generally in low frequencies. For reasons of lack of sufficient material and time we investigated only three samples. Amongst the shallow samples the very rich assemblage of undamaged individuals in HU 4942 at 38 meters depth was taken. Farther down only samples HU 4760 and HU 4950

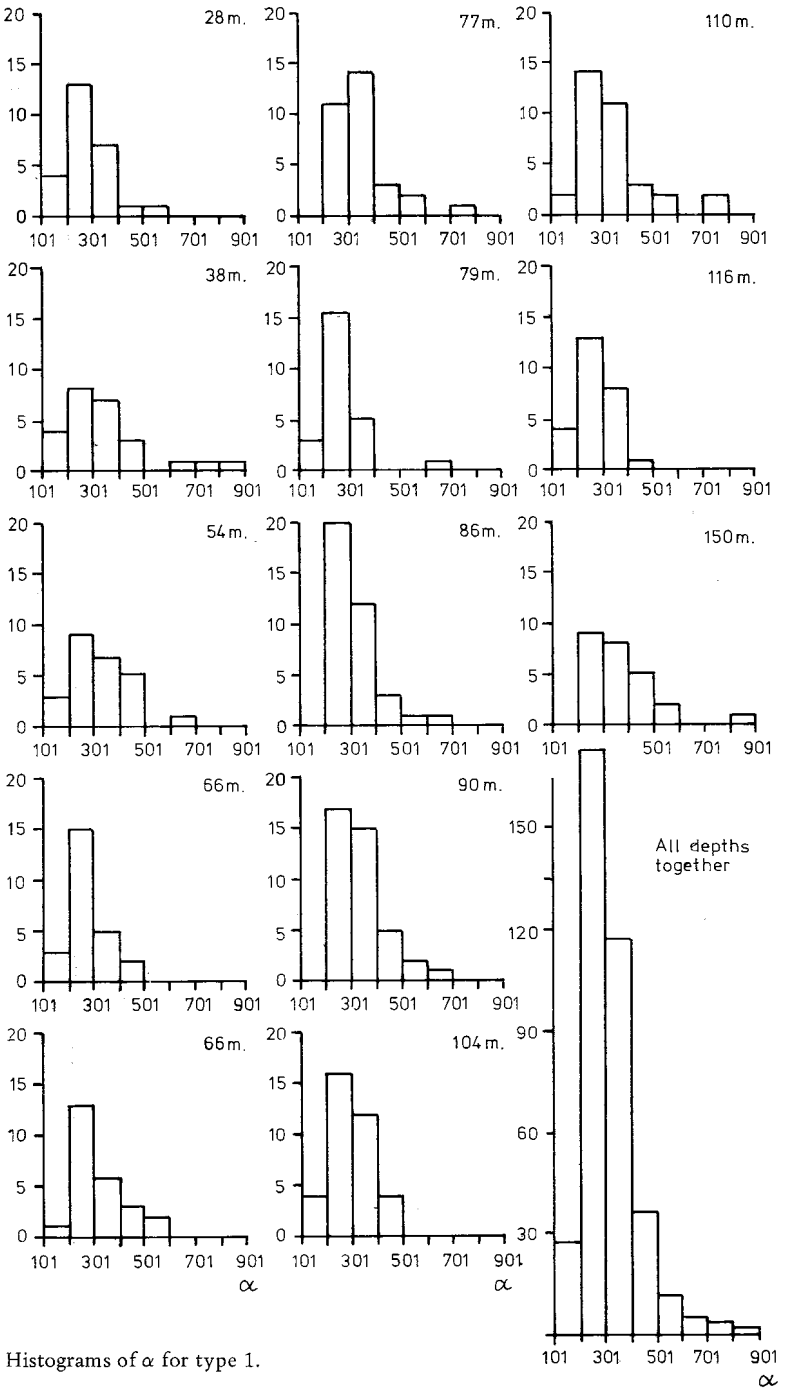


Fig. 9 Histograms of α for type 1.

at 138 and 140 meters respectively contained sufficient specimens. The latter two samples had to be picked completely, and the specimens are much less well preserved than at 38 meters. Many of them are grey or green and part were broken. Not only in the type of preservation there are considerable differences between the shallow and the deeper samples. In the inner parameters we found striking differences as well. The results are given below:

sample	depth	$\bar{C}$	$\pm \sigma_m$	range	n	$\bar{d}_2$	$\pm \sigma_m$	range	n	$\bar{E}_2$	$\pm \sigma_m$	range	n
HU 4942	38	46.02	± 1.07	31 – 63	41	600	± 14.3	488 – 750	39	16.3	± 0.44	14 – 19	42
HU 4950	138	72.57	± 3.17	44 – 94	22	790	± 54	475 – 1375	14	19.4	± 0.4	16 – 21	17
HU 4760	140	67.0	± 3.4	50 – 100	16	754	± 24	588 – 875	11	18.9	± 0.35	17 – 21	14

The means of all parameters in the 138 and 140 meters samples are very close, all differences amounting to less than $2\,\sigma_m$, which differences may be not significant. However, all means of the shallow sample are much lower. The differences between the means of the shallow and both deeper samples always amount to much more than $3\,\sigma_m$ and therefore they are considered to be significant.

The frequency distributions of the parameter values are in general fairly normal as may be seen from the histograms (fig. 10). Only the distribution of d_2 in HU 4950 is irregular, but this histogram is based on 14 specimens only, and it is influenced by one specimen with an exceptionally high d_2 value.

There exists good correlation between C and d_2. In the shallow sample the correlation is significantly positive at the confidence level of 99.5%. In the deeper samples the correlation is positive at the confidence level of 95%.

The correlation between d_2 and E_2 is less pronounced. Only the 38 and the 138 meters samples give significant positive correlations, the former at a confidence level of 97.5% and the latter at 95%.

The correlation between C and E_2 is still worse. Only the 38 meter sample gives a significant positive correlation at a confidence level of 97.5%. The coefficients are given below:

sample	depth	C-d_2	n	conf. level	d_2-E_2	n	conf. level	C-E_2	n	conf. level
HU 4952	38	+ 0.56	38	+ 99.5%	+ 0.36	39	+ 97.5%	+ 0.32	40	+ 97.5%
HU 4950	138	+ 0.45	14	+ 95.0%	+ 0.45	14	+ 95.0%	+ 0.20	17	o --
HU 4760	140	+ 0.55	11	+ 95.0%	– 0.26	11	o --	+ 0.20	14	o --

We also considered the relation between z as an estimate of size and the

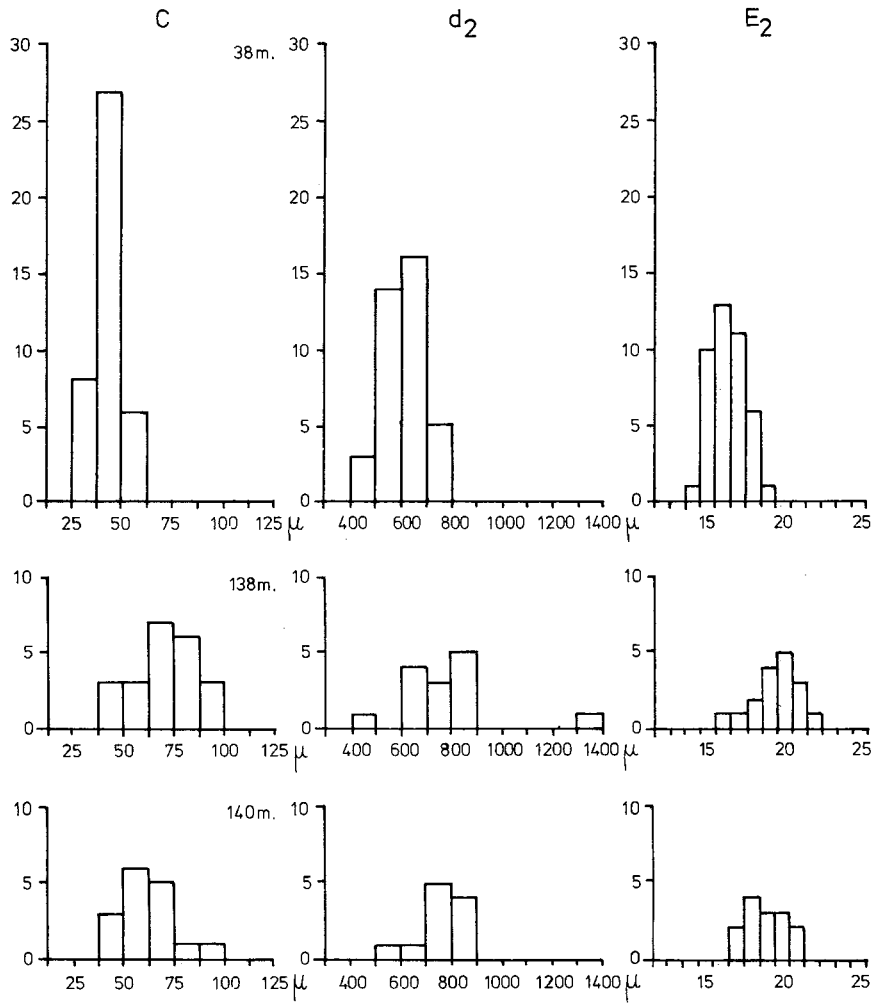


Fig. 10 Histograms of C, d_2 and E_2 of type 2.

diameter of the protoconch. For sample HU 4950 no calculations were made because too many of the specimens were broken or too small. We did not compare either E_2 or d_2 with z, for the same reasons we did not do it in type 1; since many specimens lack a complete second whorl, an unjustified selection would be made. C-z correlation coefficients were calculated for the 38 and 138 meters samples separately and together. There exists a clear negative correlation between the two parameters. The results are given below:

sample	depth	C - z	n	conf. level	$\bar{z}$	$\pm \sigma_m$	range	n
HU 4942	38	– 0.46	41	99.5%	28.07	± 1.02	15 – 45	41
HU 4950	138	– 0.41	21	95.0%	24.19	± 1.85	10 – 41	21
together		– 0.47	62	99.9%				

The distribution of z, as shown in the histograms of fig. 11 are close to normal in both samples. The difference in the means of z is more than 2 σ_m. This may be regarded significant, though not at a very high confidence level. It might mean that the shallower forms had a longer average individual growth.

We did not measure α in the second type because of the utterly poor results in type 1.

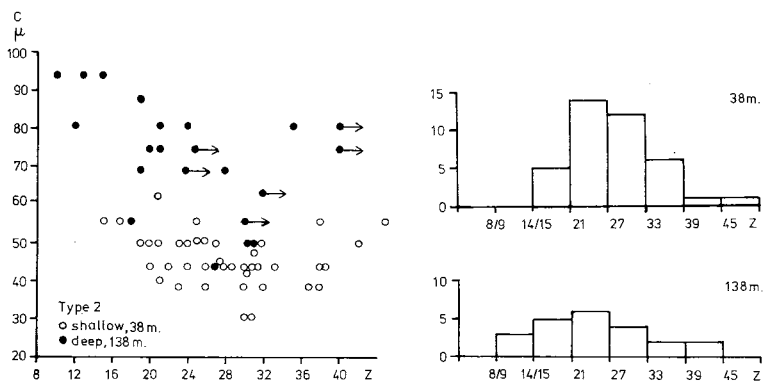


Fig. 11 Scatter diagram of C against z, and z histograms in the 38 and 138 meter samples. Specimens with an arrow are broken and lack the last 2 or 3 chambers.

Differences between type 1 and type 2

It has been remarked already that types 1 (combined) and 2 are well separable on outer morphology, though difficulties arise when very small specimens are regarded. We also wanted to check whether these differences are expressed in the inner parameters. Therefore the means in the HU 4942 sample at 38 meters depth were considered. Only this sample was taken into account because it is rich in both types and it is believed to be the only one investigated in which the type 2 specimens are undoubtedly autochthonous. No differences were found in the $\bar{C}$ and $\bar{d}_2$ values. In the C-d_2 scatterdiagram (fig. 12) the cluster of the type 2 specimens lies almost completely inside the combined type 1 scatter periphery; actually it fills the gap between both type 1 clusters.

The means of both parameters are given below:

	type 1 (combined)			type 2		
	M	± σ_m	range	M	± σ_m	range
C	47.8	± 2.8	25 – 81	46.0	± 1.1	31 – 63
d_2	584	± 38	413 – 912	600	± 14.3	488 – 750

The differences are in the order of one σ_m and therefore considered not significant. If one remembers, however, that the type 1 group is a composite one, this close resemblance becomes of dubious value. Actually, the $\bar{C}$ and $\bar{d}_2$ values of type 2 differ from the corresponding values for the type 1 groups separately.

Only in the E values some difference between the combined type 1 and type 2 was found. We counted the E_1, E_2 and E_3 in the 38 meter sample (fig. 13).

	$\bar{E}_1$	± σ_m	range	n	$\bar{E}_2$	± σ_m	range	n	$\bar{E}_3$	± σ_m	range	n
type 1	7.18	± 0.12	6 – 9	32	18.4	± 0.5	15 – 25	26	34.5	± 1.4	26 – 44	12
type 2	6.74	± 0.08	6 – 8	42	16.3	± 0.4	14 – 19	42	28.0	± 1.0	24 – 33	29

For all three $\bar{E}$-values the differences between types 1 and 2 amount to more than three σ_m values and thus are considered to be significant.

However, if we split the type 1 individuals into the smaller and larger specimens on the basis of $z < 29$ and $z > 29$ the picture becomes different.

type 1	$\bar{E}_1$	± σ_m	range	n	$\bar{E}_2$	± σ_m	range	n	$\bar{E}_3$	± σ_m	range	n
$z > 29$	7.67	± 0.18	7 – 9	12	19.8	± 0.7	16 – 25	12	34.5	± 1.4	26 – 44	12
$z < 29$	6.9	± 0.12	6 – 8	20	17.2	± 0.47	15 – 20	14	- - - - - - - -			

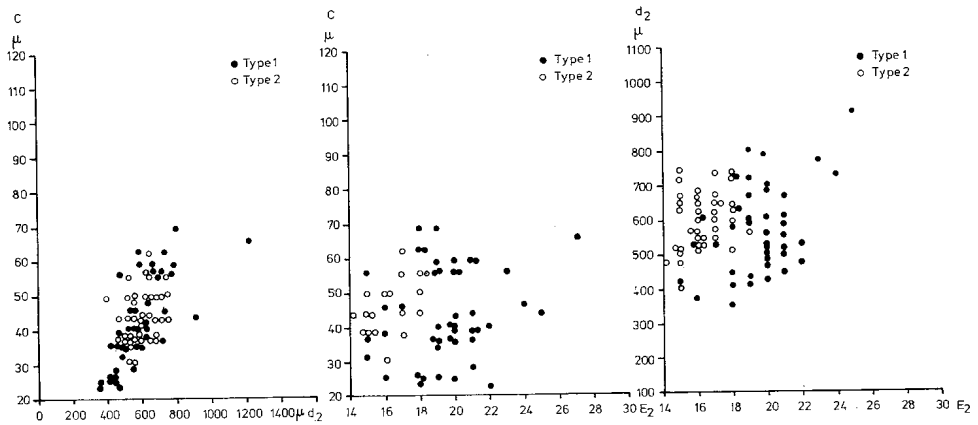


Fig. 12 Scatter diagrams of C/d_2, C/E_2 and d_2/E_2, in the 38 meter check sample; types 1 and 2.

The differences between type 2 and the larger forms of type 1 have become still more striking. In contrast the differences between type 2 and the smaller specimens of type 1 are reduced. They amount to about two σ_m values or less and they cannot be regarded as significant anymore. Thus, as in the outer morphology, the differences between type 2 and type 1 narrow down in the smaller specimens of the latter.

RELATIONS WITH DEPTH AND SUBSTRATE

The actual number of *Operculina* specimens per sample is highly variable and it appears difficult to establish the habitat depth range of types 1 and 2. If one considers the relative frequencies of both types, a serious problem is met with because we ignore whether (part of) the investigated material was

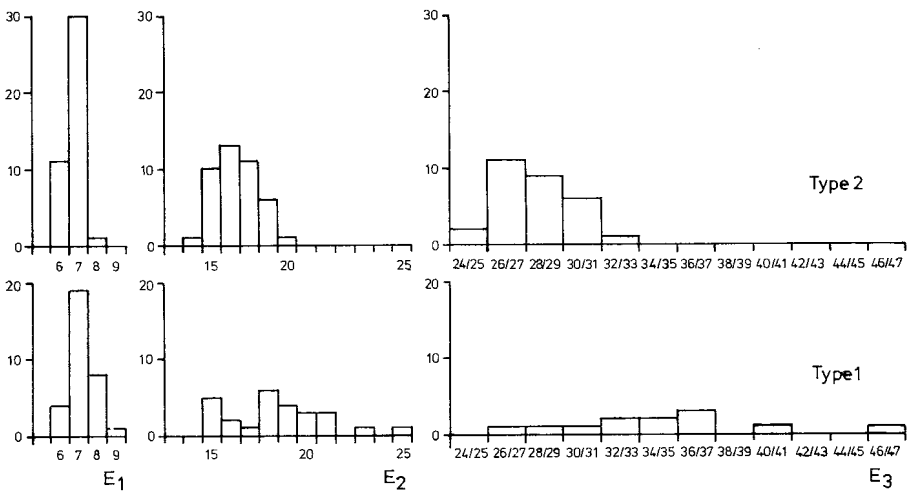


Fig. 13 Histograms of E_1, E_2 and E_3 in the 38 meter check sample.

transported downslope or not. The only way of supposing autochthony was from the type of preservation. Thus, for the best estimate of the depth distribution of types 1 and 2, we took into consideration the samples with well preserved, undamaged specimens.

The distribution of type 2 appears to be mainly restricted to the uppermost samples. In HU 4943 and HU 4942 at 28 and 38 meters depth the type 2 specimens are very well preserved and they are predominant. Also in sample 71011 from 54 meters type 2 occurs, but this sample is poor in

Operculina individuals. HU 4859 and HU 4941, both from 66 meters depth, also contain type 2 specimens but in lower relative frequencies than in the shallower samples. In HU 4940, at 77 meters depth, some well-preserved specimens of type 2 are still present. In the deeper samples type 2 does occur but its specimens are usually damaged or discoloured, especially so in HU 4950 and HU 4760 at 138 and 140 meters depth.

Well preserved specimens of type 1 do occur in the two shallow samples, but they are in the minority. In the poor 54 meters sample there are a few type 1 specimens. In the 66 meter samples type 1 occurs in about equal numbers as type 2. At greater depth most samples consist almost completely of type 1 individuals, though large numbers of them are damaged. Rich and well preserved assemblages are found in HU 4940, HU 4768, HU 5250 and HU 4803 at 77, 79, 90 and 130 meters depth respectively. The three deepest samples from 138 to 150 meters contain very few well preserved specimens.

Summarizing it may be concluded that type 2 occupies the shallower part of the depth range, from at least 28 meters down to about 77 meters, with peak occurrences in the 28 and 38 meters samples. Type 1 occurs throughout the depth range with an optimum between 77 and 130 meters.

One of the major objectives of this investigation was to get an insight in possible changes of the internal parameters with greater depth. Parameter C seemed to be the most appropriate one.

We know from the 38 meter sample that two groups of type 1 may co-occur in the same sample. A small group of small-sized specimens with larger C values seems to be accompanied by a large group of individuals of large size and with smaller C values. Ultimate test diameter seems to be inversely correlated with these C value groups. In many of our samples the C distribution is somewhat irregular, suggesting a similar mixture of both type 1 groups.

Whatever the explanation of both groups may be in a biological sense, it is necessary for a comparison of C with changing depth to use data of both groups separately. The type 1 group with larger C values, i.e. smaller test diameter, appears to be most promising for this purpose. In order to get comparable data, we selected those samples with few or no damaged or discoloured specimens, fairly unimodal distribution of C, and in general smaller, anyhow not too large, specimens. Few samples fulfill these requirements. The shallowest sample that meets the conditions is the one from 38 meters, in which we had been able already to separate a group of small sized individuals of type 1 (fig. 8). Also 71011 at 54 meters, though not very rich, yields an assemblage of well preserved, small type 1 specimens.

HU 4941 from 66 meters is another good sample. It contains only two specimens with exceptionally low C values. $\overline{C}$ values with and without these two specimens were calculated. The corrected $\overline{C}$ – value without them is extremely close to that of the other 66 meters sample, but we discarded the latter sample because its specimens are in general somewhat larger and more of them were broken. The next sample, fulfilling the requirements is HU 4748 at 79 meters, containing a very homogeneous assemblage of small, undamaged specimens. In this sample one specimen occurred with a very small C value and we calculated the mean with and without this specimen. Two more assemblages are well comparable, those from HU 5250 and HU 4803 at 90 and 130 meters respectively, both entirely consisting of small well preserved specimen. In the former sample, however, a few damaged specimens do occur. The means of these selected samples are given below:

		corrected	not corrected
sample	depth	$\overline{C} \pm \sigma_m$	$\overline{C} \pm \sigma_m$
HU 4942	38	55.3 ± 1.2	
71011	54	67.0 ± 2.8	
HU 4941	66	76.0 ± 2.5	73.2 ± 3.0
HU 4748	79	81.6 ± 2.8	79.4 ± 3.3
HU 5250	90	78.1 ± 2.4	
HU 4803	130	80.9 ± 2.7	

It is evident that down to 79 meters depth there is a steady increase in the diameter of the protochonch and from 79 down to at least 130 meters $\overline{C}$ seems to remain constant with minor fluctuations only (fig. 14).

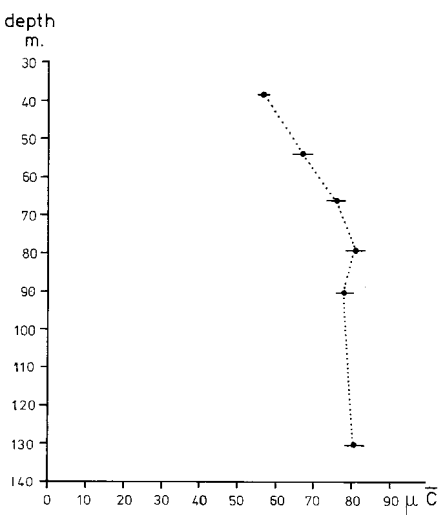


Fig. 14 Relation between depth and the mean diameter of the protoconch in type 1a.

The corresponding $\bar{d}_2$ values seem to follow the trend of $\bar{C}$, as a consequence of the strong positive correlation between C and d_2. However, their fluctuations are larger, and, moreover, the data upon which the d_2 means are based, are not free from selection. For E_2 and α no trends were found.

It appeared impossible to trace changes in $\bar{C}$ in the other type 1 group of specimens (smaller C, larger size) in relation to depth, because in the samples where they occur, they are intricately mixed with individuals of the first group or too many are damaged or otherwise considered displaced.

Although we found a clear difference with increase in $\bar{C}$, $\bar{d}_2$ and $\bar{E}_2$ between one shallow and two deeper samples of type 2, we cannot draw too certain conclusions from these few data. Moreover, the poor preservation suggests that the type 2 specimens in the deeper samples may not be autochthonous. These specimens may have been transported downslope and their original habitat is unknown.

Apart from depth, the distribution of benthonic larger foraminifera in the Gulf is thought to depend on types of substrate (Hottinger, this bulletin).

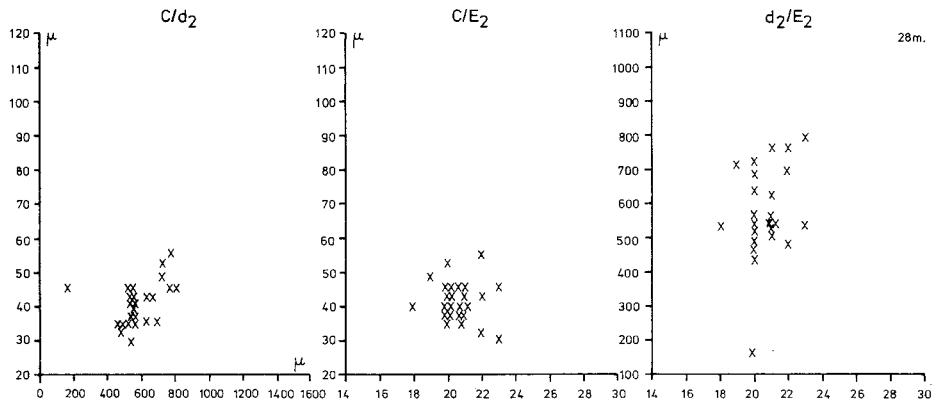
Two *Operculina* samples were available from the same depth but from different substrates, HU 4941 and HU 4859, both from 66 meters. The former (66a) was taken from coral sand, the second (66b) from a substrate with *Halophila* vegetation. The internal data on type 1 are as follows:

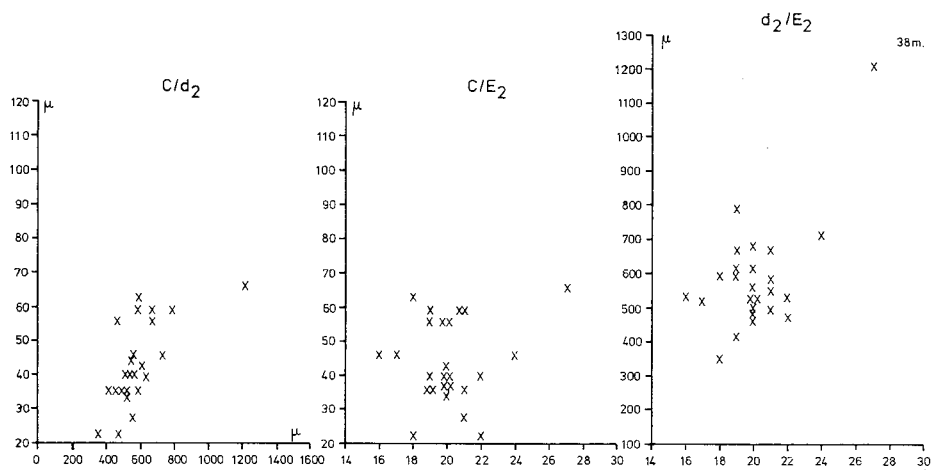
	$\bar{C} \pm \sigma_m$		$\bar{d}_2 \pm \sigma_m$		$\bar{E}_2 \pm \sigma_m$	
Coral sand	73.0 ± 3.0	40 – 109	1021 ± 49	419 – 1531	21.3 ± 0.2	18 – 24
Coral sand (corr.)	76.0 ± 2.5					
Halophila	77.8 ± 2.0	59 – 101	1058 ± 38	802 – 1461	22.4 ± 0.3	18 – 27

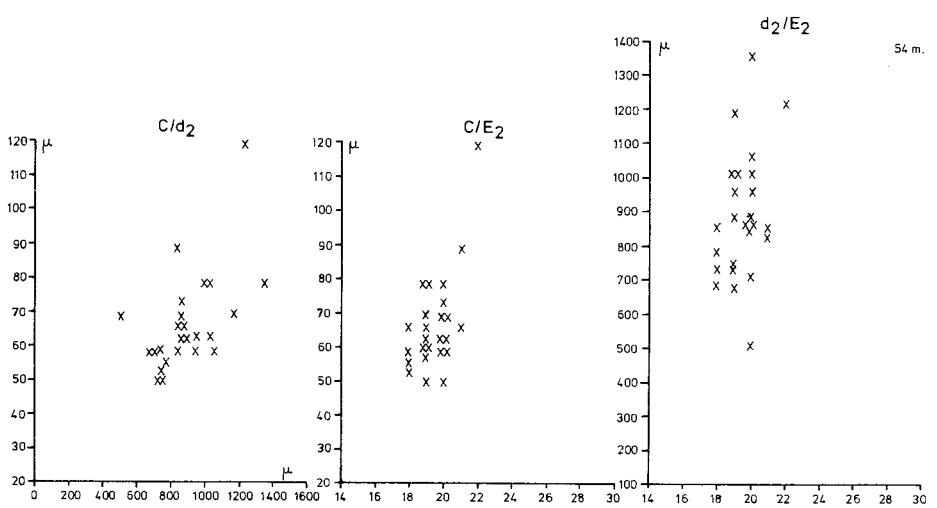
There is no significant difference for $\bar{C}$ at the 97.5% confidence level. Moreover, if one excludes the two very small C-values from the coral sand sample (fig. 15) because they probably belong to the small C group of type one, the $\bar{C}$ difference becomes reduced to less than one σ_m. Evidently, the substrate has no influence on the diameter of the protoconch at least not in the 66 meters samples.

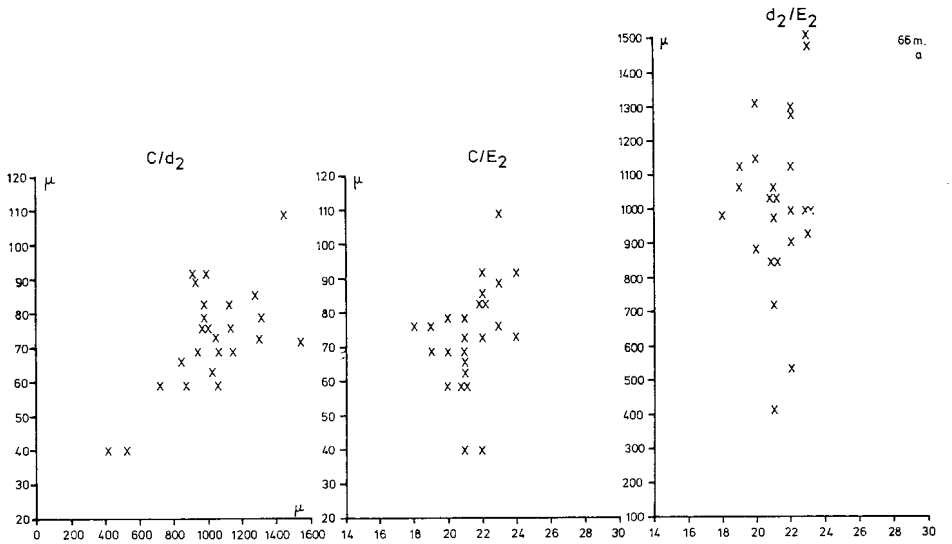
Only the $\bar{E}_2$ values give a significant difference between both samples at a 97.5 confidence level. However, $\bar{E}_2$ values in general give unexplained significant fluctuations, also for samples from the same substrate.

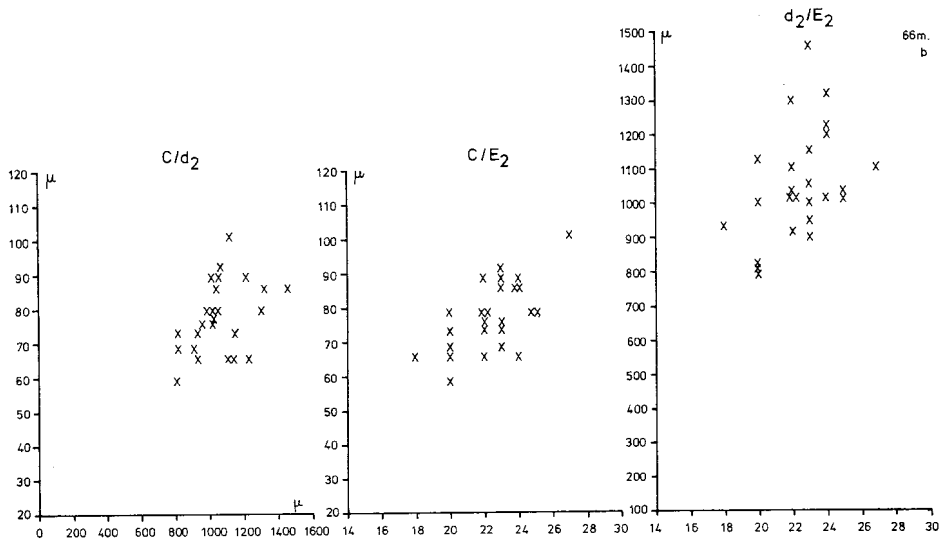
Considering substrates there is another point of interest. Down to 75–80 meters the *Halophila* meadows and coral sands are the major substrates, but in deeper waters red to yellow-brown muds predominate. It is below 75–80 meters that in type 1 the increase in the means of C and d_2 seems to have come to an end to become replaced by a very irregular pattern of the data.

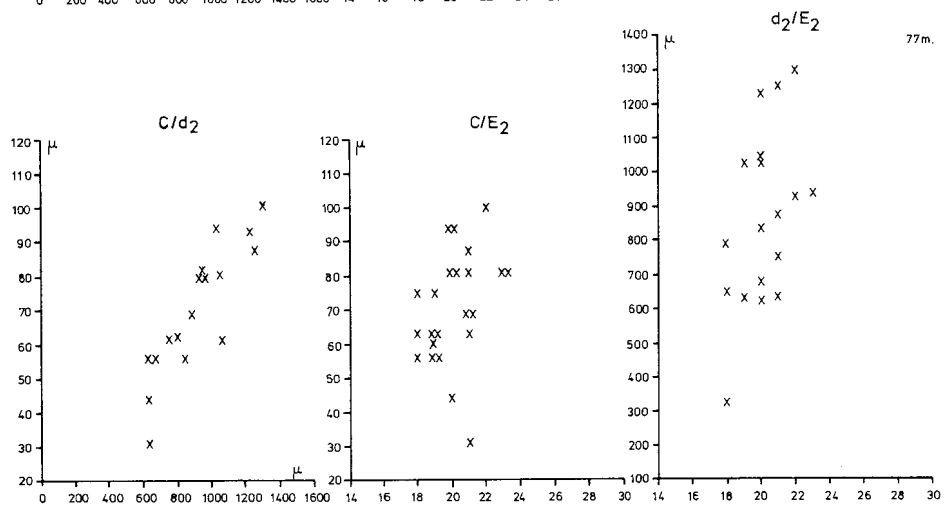

C/d2
C/E2
d2/E2
28m.

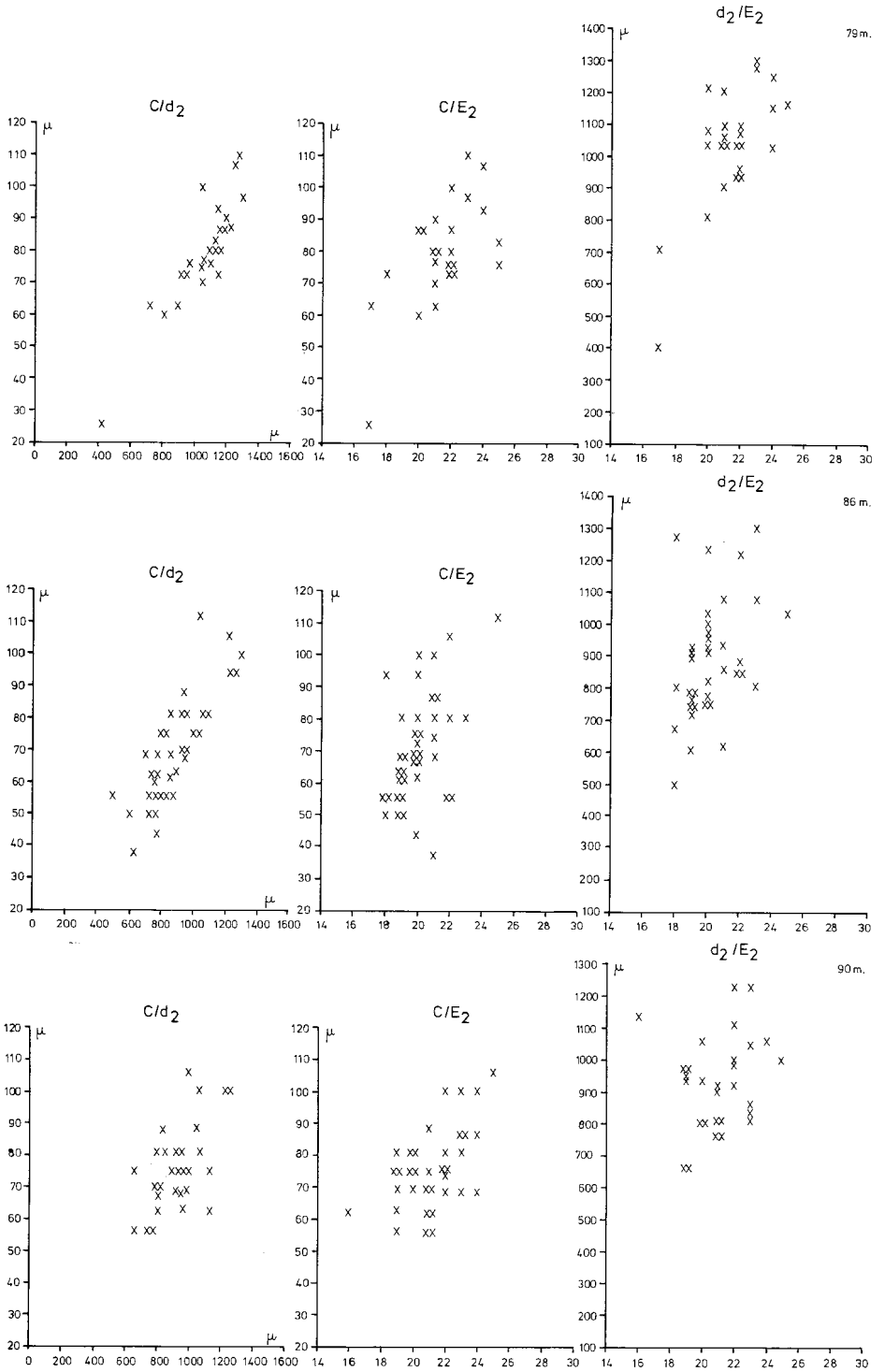

C/d2
C/E2
d2/E2
38m.

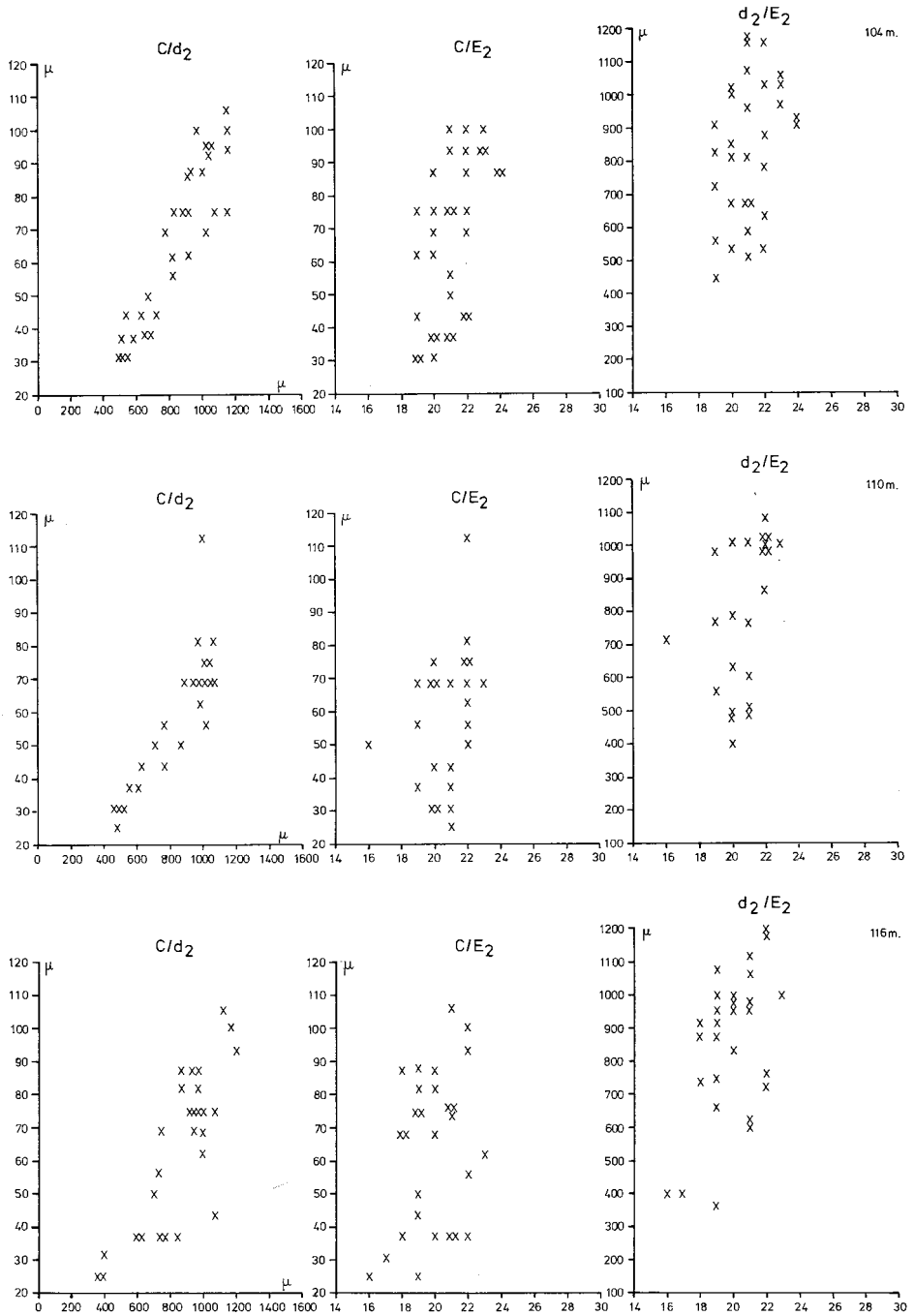

C/d2
C/E2
d2/E2
54 m.

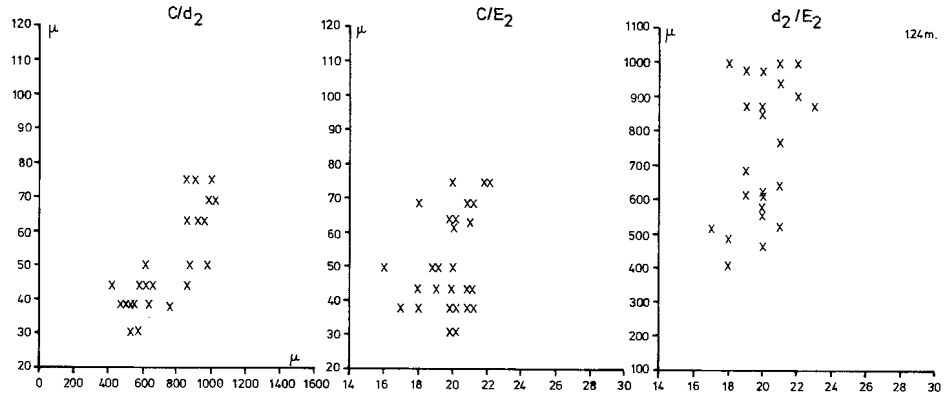

C/d2
C/E2
d2/E2
66m.
a
μ

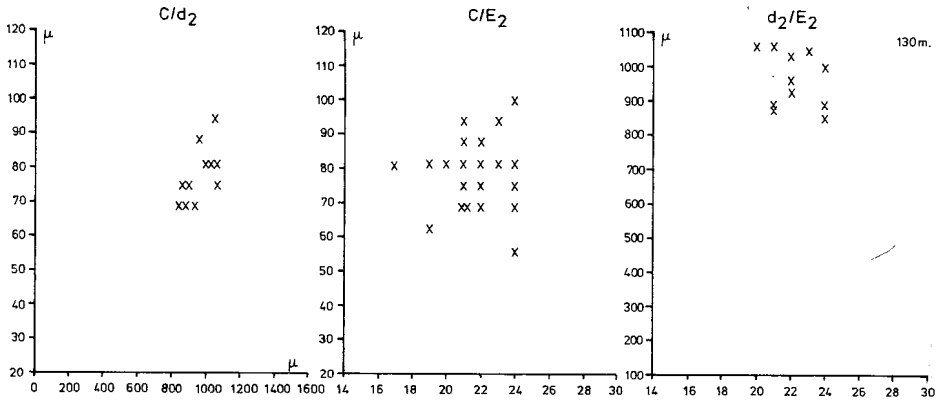

C/d2
C/E2
d2/E2
66m.
b
μ

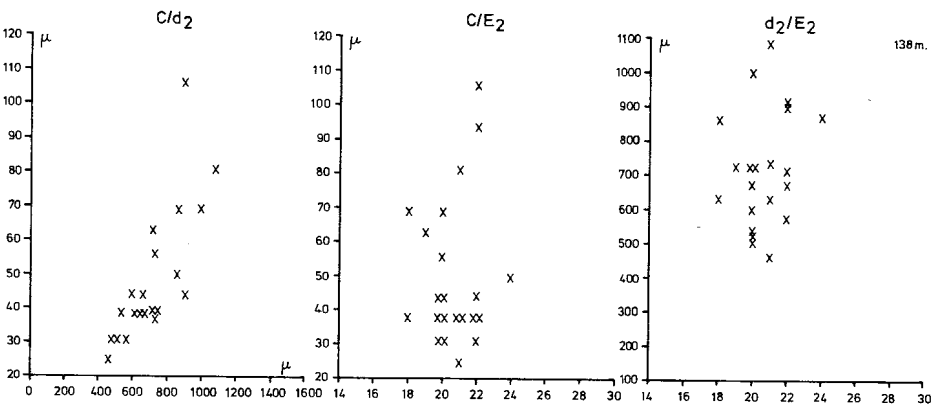

C/d2
C/E2
d2/E2
77m.
μ


C/d2
C/E2
d2/E2
79 m.
86 m.
90 m.
μ


C/d2
C/E2
d2/E2
104 m.
110m.
116m.
μ


C/d2
C/E2
d2/E2
124m.
μ


C/d2
C/E2
d2/E2
130m.
μ


C/d2
C/E2
d2/E2
138m.
μ

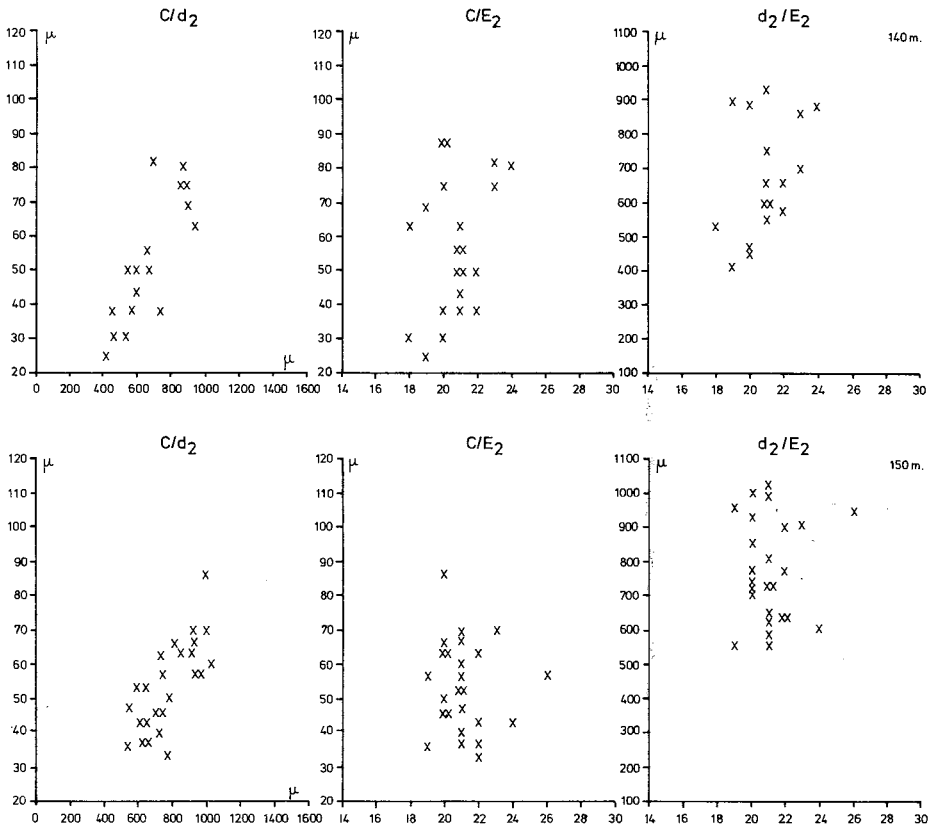


Fig. 15 Scatter diagrams of C/d_2, C/E_2 and d_2/E_2 of type 1 in all samples.

DISCUSSION

In the *Operculina* material of the Gulf of Elat large fluctuations were found in the means of the investigated parameters which at first view all seem to be irregular if considered relative to depth. The obvious separation into types 1 and 2 based on differences in external morphology, did not give much more regularity to the pattern.

Part of the fluctuations in $\overline{C}$ in type 1 may be made to disappear if we accept that we are dealing with a mixture of another two forms. Such a mixture is highly probable, but though a considerable amount of information is available, it remains hard to prove that the C distribution within

each sample is not a normal one, thus indicating the presence of the two type 1 groups. Actually there seems to be still a third flat-evolute *Operculina* type. Hottinger (this bulletin) observed a few evolute specimens in the Gulf of Elat, that normally would be considered to be microspheric. They are characterized by a very small protoconch of about 10 μ and a diameter of approximately 1 cm, thus falling far outside the range of variation in our material. Our specimens range in C values from 21 μ up to about 110 μ and in diameter up to 3 to 4 mm. Probably there exist three groups of type 1, of which one must be considered to represent the microspheric generation of the other(s).

Another factor that strongly diminishes the possiblities of discrimination of both type 1 groups, is the increase in $\overline{C}$ with increasing depth we found in one of them, the larger $\overline{C}$-smaller size group (fig. 14). The theoretically derived mean of 68 μ for the data from all depths together was found to be much higher than the $\overline{C}$ value of 55.3 μ at 38 meters. This great difference may now be understood if we consider our lumping of data along a $\overline{C}$ cline from 55 μ to over 80 μ (fig. 15). Inversely it might be assumed that no real change in $\overline{C}$ with depth takes place in the other type 1 group (smaller $\overline{C}$ – larger size) if we remember that the 33.8 μ value at 38 meters is very close to the theoretical 36 μ for all specimens of the entire depth range.

The $\overline{C}$ increase with greater depth in type 2 is based on too few observations to be free from accidental effects. Anyhow, the direction of change would be the same as it is in the larger-$\overline{C}$ type 1 group, and both changes would fit to the model of size increase of the protoconch with depth, advanced by Drooger and Raju (1973).

If we compile the major data on the various *Operculina* types observed in the Gulf of Elat, the following picture emerges:

	type 1a	type 1b	type 1c	type 2
External morphology	smaller, flat, evolute	larger, flat, evolute	very large, ± 1 cm	relatively small, lenticular, involute
at 38 m	$z < 29$	$z > 29$		
Diameter proloculus ($\bar{C}$)			10 μ	
estimate all data	68 μ	36 μ		
at 38 m	55.3 μ	33.8 μ		46.0 μ
	47.8 μ together			
	cline to about 80 μ at 79 m			cline possible to about 70 μ at 140 m
	seemingly stable to 150 m	no obvious cline to 150 m		
Diameter first two whorls ($\bar{d}_2$)				
estimate all data	930 μ	570 μ		
				600 μ at 38 m 790 μ at 138 m 754 μ at 140 m
Number of chambers in first two whorls ($\bar{E}_2$)				
at 38 m	17.2	19.8		16.3
	18.4 together			
at 138 m				19.4
at 140 m				18.9

If the type 2 specimens represent a homogeneous group they are probably different from type 1a as well as from type 1b. In the sample from 38 meters they are closer to type 1a in their $\bar{E}_2$ value, closer to type 1b in $\bar{d}_2$, but nicely intermediate in $\bar{C}$.

We are clearly restricted in our conclusions by the lack of a sufficient number of more specific observations. For a further disentangling of groups 1a and 1b at all depths one might try the separation with new material on the basis of z values. Possibly the remarkable negative correlation between

the total number of chambers and the diameter of the protoconch may be of general applicability. This strange relation in both types 1 and 2 seems to mean: Once born the dying hour is known.

Finally an attempt was made to see whether types 1a and 1b have different depth ranges that would make sense in some way or another. A closer look at all C-d_2 scatter diagrams (fig. 16) and supposing that there is a smaller $\overline{C}$ group of about 35 μ at all depths enabled to estimate the relative frequencies per sample of each type. In some samples there are vague indications of two clusters, in others variation seems to be continuous.

	type 1b small $\overline{C}$	types 1a + b $\overline{C}$	type 1a large $\overline{C}$
28 m	nearly all	41.5 μ	a few
38 m	half (33.8 μ)	47.8 μ	half (55.3 μ)
54 m	absent	67.0 μ	all (67.0 μ)
66 m	absent	77.8 μ	all (77.8 μ)
66 m	some 2	73.2 μ	nearly all (76.0 μ)
77 m	some 2	73.4 μ	nearly all
79 m	1 specimen	79.4 μ	all others (81.6 μ)
86 m	a few	71.0 μ	most others
90 m	absent	78.1 μ	all (78.1 μ)
104 m	1/3	69.6 μ	2/3
110 m	1/3	63.5 μ	2/3
116 m	2/5	64.7 μ	3/5
124 m	2/3	51.9 μ	1/3
130 m	absent	80.9 μ	all (80.9 μ)
138 m	3/4	53.8 μ	1/4
140 m	3/5	56.9 μ	2/5
150 m	nearly all	53.7 μ	a few

Table 4.

The peculiarly interrupted depth range of type 1b, due to near-absence below 38 m down to 90 meters cannot be explained without further knowledge of downslope transport possibilities and/or details of the reproductive cycle(s) of the *Operculina*. The data point out, however, that the irregularities in the depth sequence of $\overline{C}$ shown in table 1 may be entirely due to the relative proportions of both types 1 per sample.

The results from the α observations are disappointing. When we were sectioning our specimens, we got the impression that the third chamber frequently has a very irregular shape and moreover the angle is strongly influenced by the level of the "median" section. Our results do not fit in well

with the conclusions of van der Vlerk and Bannink (1969). They formulated the hypothesis that the near-identical values of E (is our α) indicate the same relative age. Although the Gulf of Elat is far from Indonesia, where they collected their samples, we compared our results with their relative time scale, based on factor E (our α). This timescale ranges from Late Eocene (E = 250) up to Recent (E = 450). Placed in this timescale our material would range from the Early Oligocene up to the Late Miocene. It is possible, however, that this large variation in α is typical for recent *Operculina* populations. Also van der Vlerk and Bannink give a broad variation in α for recent samples (38 specimens in 13 classes). But there still remains the problem of the procedure which causes, in our opinion plenty of errors. Van der Vlerk and Bannink followed another procedure by means of radiographs, but this method obscures the borders of the first chamber, as clearly demonstrated by their plates.

It may be evident now that our investigation of *Operculina* in the Gulf of Elat raised more problems than we would have thought of before we started. One of the major conclusions seems to be that in contemporaneous populations of one "species" mean protoconch diameter values may vary at least as much as 50% of the smallest calculated mean. $\overline{C}$ values evidently have to be used with great caution in biostratigraphic correlations if protoconch size is considered to show evolution in a nummulitid group.

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DEPTH-GRADIENTS IN INTERNAL PARAMETERS OF HETEROSTEGINA IN THE GULF OF ELAT

W. J. J. FERMONT

ABSTRACT

The *Heterostegina* assemblages of the Gulf show distinct trends of increase of the internal size parameters down to 79 meters. At greater depth there is no clear pattern, with smaller values prevailing. The number of operculinid chambers and the number of secondary septa in the 20th chamber show opposite, though less distinct changes with depth.

INTRODUCTION

The purpose of this investigation was to collect a representative number of data in the Gulf of Elat on the possible relations between the morphology of *Heterostegina* and its environment. Because the Gulf lacks significant thermo-, halo- and pycnoclines our attention was focussed on depth and substrate. Some 200 specimens were investigated from 10 samples between 28 and 104 meters depth and from various types of substrate.

Downslope transport of shells is thought to play a subordinate role in the area; therefore the assemblages are considered to represent more or less autochthonous populations at least in the shallower part of the depth range.

For a review of the environmental factors the reader is referred to the papers of Z. Reiss and L. Hottinger (this bulletin). The work of R. Smit (Utrecht) during the early phase of the investigation is gratefully acknowledged.

OUTER MORPHOLOGY

The variation in outer morphology is primarily size dependent; the external appearance changes during ontogeny.

Juvenile forms are rather flat and involute. The chamber sutures are radial near the base and curve backward near the periphery.

Adult forms are discoid, relatively thick and involute, though a variable part of the last whorl is in general more or less evolute. The chambers are

sample	depth	$\bar{C} \pm \sigma_m$ μ	range	n	$\bar{C}_{1,2} \pm \sigma_m$ μ	range	n	$\bar{h} \pm \sigma_m$ μ	range	n
71161	28	100.8 ± 4.6	80 – 161	20	149.0 ± 4.9	111 – 201	20	392 ± 15	302 – 542	20
71160	38	94.8 ± 2.8	60 – 120	28	141.0 ± 3.9	91 – 171	28	348 ± 8	251 – 453	28
71012	66a	110.2 ± 3.7	91 – 141	26	173.3 ± 6.0	131 – 262	26	404 ± 11	322 – 553	26
71159	66b	105.8 ± 3.8	80 – 131	18	162.1 ± 5.9	131 – 221	18	405 ± 12	332 – 513	18
71206	68	111.3 ± 4.2	80 – 191	28	170.0 ± 5.3	111 – 262	28	408 ± 13	322 – 533	28
71014	79	117.0 ± 3.7	101 – 131	10	179.0 ± 5.1	151 – 211	10	425 ± 13	342 – 473	10
71157	86	100.6 ± 3.3	75 – 137	26	153.6 ± 5.2	112 – 212	26	388 ± 15	268 – 550	26
71148	104	102.1 ± 3.9	75 – 125	16	161.2 ± 7.0	100 – 212	16	390 ± 18	262 – 512	16
71017	116	107.0 ± 5.9	91 – 121	5	167.0 ± 11.5	151 – 181	5	400 ± 17	362 – 463	5
71063	124	90.9 ± 2.4	63 – 113	28	137.8 ± 4.2	100 – 188	28	380 ± 10	294 – 506	27

depth	$\bar{X} \pm \sigma_m$	range	n	$\bar{S}_{10}$	range	$\bar{S}_{15} \pm \sigma_m$	range	n	$\bar{S}_{20} \pm \sigma_m$	range	n
28	12.8 ± 0.6	8 – 18	18	0.15	0 – 1	0.84 ± 0.11	0 – 2	20	1.35 ± 0.12	1 – 2	20
38	12.5 ± 0.4	8 – 17	26	0.08	0 – 1	0.88 ± 0.08	0 – 2	26	1.42 ± 0.11	1 – 3	26
66a	11.6 ± 0.6	7 – 19	26	0.27	0 – 1	0.96 ± 0.14	0 – 3	26	1.83 ± 0.23	1 – 4	24
66b	11.5 ± 0.4	6 – 14	18	0.06	0 – 1	1.04 ± 0.07	1 – 2	16	1.72 ± 0.16	1 – 3	18
68	11.4 ± 0.4	7 – 15	24	0.13	0 – 1	1.04 ± 0.08	0 – 2	26	1.65 ± 0.12	1 – 3	26
79	11.0 ± 0.3	9 – 13	10	0.10	0 – 1	1.10 ± 0.15	1 – 2	10	1.89 ± 0.19	1 – 3	9
86	12.1 ± 0.2	7 – 17	25	0.11	0 – 1	1.00 ± 0.11	0 – 2	26	1.50 ± 0.20	1 – 2	6
104	10.7 ± 0.8	6 – 16	15	0.29	0 – 1	1.00 ± 0.16	0 – 2	15	2.10 ± 0.22	1 – 3	10
116	12.0 ± 1.0	9 – 15	5	0.20	0 – 1	0.80 ± 0.17	0 – 1	5	1.67 ± 0.60	1 – 3	3
124	12.0 ± 0.6	6 – 21	28	0.17	0 – 1	0.86 ± 0.12	0 – 2	27	1.73 ± 0.13	1 – 3	23

Table 1. Means, standard errors and ranges of the various parameters of *Heterostegina* from the Gulf of Elat.

falciform, curving strongly backward near the periphery. This backward curvature is most extreme in the last few chambers. The later chambers are divided in chamberlets by secondary septa. These secondary septa are restricted to the marginal part of the chambers. The surface is highly variable, ranging from smooth without any external expression of the primary and secondary septa to ornamented with small pustules and/or slight ridges on both types of sutures.

Discrimination between flat and discoid forms seemed to make no sense because this difference is clearly related to the successive ontogenic stages.

The microspheric forms in our material were not recognizable as such from the outer morphology. They were recognized only in the halfsections because in the unsectioned specimens the embryonic part is too much obscured by the involute structure of the test.

The *Heterostegina* specimens are easily distinguishable from juvenile *Heterocyclina.* The latter are flatter, with the chambers more strongly bending backward. Their smaller number of operculinid chambers usually amounts to 3 or 4, which values are far outside the range of those of the *Heterostegina* individuals. Also the number of secondary septa in comparable chambers is much higher than in *Heterostegina* (J. E. Meulenkamp, this bulletin).

In the study on *Operculina* much attention was paid to the type of preservation of the specimens (Fermont, this bulletin). In *Heterostegina* differences seemed to be less systematic relative to depth, and the small numbers of specimens in several samples would have been prohibitive for significant results from a further analysis.

INNER MORPHOLOGY

Observation methods

Part of the 10 samples were poor in their *Heterostegina* content and all the specimens had to be picked. For some samples the number of specimens remained low (see table 1). In the richer samples the number of sections was limited to 25–30.

Half sections were made under a binocular microscope. Measurements were made in two investigation periods during which different standard measurement units were used of 10.06 μ and 12.50 μ respectively. The corresponding measurement errors thus amount to about $\pm$ 5 μ and $\pm$ 6 μ. In the second series the measurements of the diameter of the protoconch

were rounded off to half a unit, thus limiting the error to about ± 3 μ. Classes of the histograms were carefully chosen in order to diminish the effects of the different measurement units.

All sections are stored in the micropaleontological collections of the Utrecht State University. The observations are compiled in histograms and scatterdiagrams. For all the samples the means and standard errors were calculated with the aid of a Canon Canola electronic calculator (table 1).

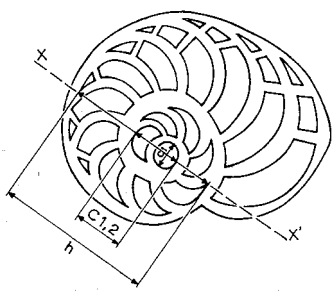


Fig. 1 Median section of *Heterostegina depressa* showing the way of measuring the parameters C, $C_{1,2}$ and h. Furthermore X = 8, S_5 = 0, S_{10} = 1, S_{15} = 2.

The parameters (fig. 1).

Most of the parameters we used are the same as those already chosen by Freudenthal (1969). They all refer to median sections.

C = the inner diameter of the protoconch measured along the line, perpendicular to the line X–X′ through the centers of the protoconch and the deuteroconch.

$C_{1,2}$ = the inner diameter of protoconch and deuteroconch together, measured along the line X–X′.

h = the diameter of the first whorl, measured along the line X–X′, excluding the outer wall.

X = the number of chambers without secondary septa, including the protoconch and deuteroconch in the counts.

z = the total number of chambers, including proto- and deuteroconch.

S_n = the number of secondary septa in the n-th chamber. n = 5, 10, 15 and 20.

Results

Amongst the sectioned specimens only a few appeared to be microspheric. These microspheric individuals are restricted to the deeper samples

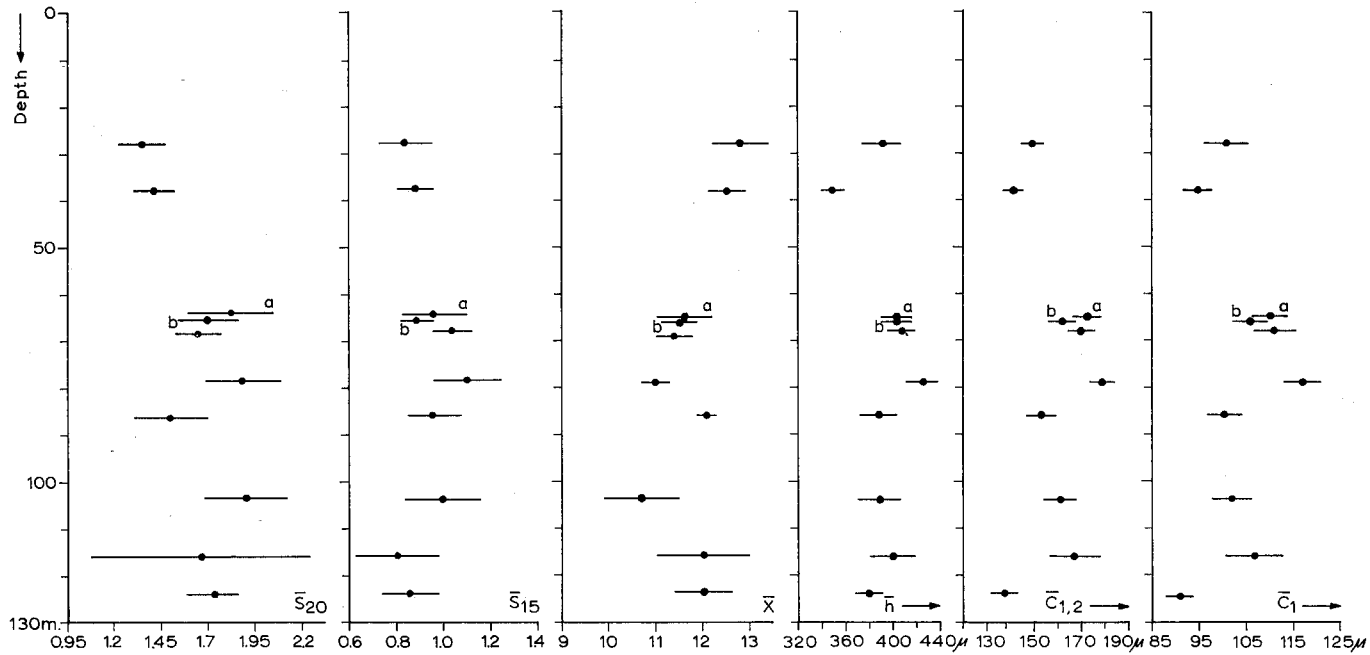


Fig. 2 Mean values ± one σ_m of all investigated *Heterostegina* assemblages in the Gulf of Elat.

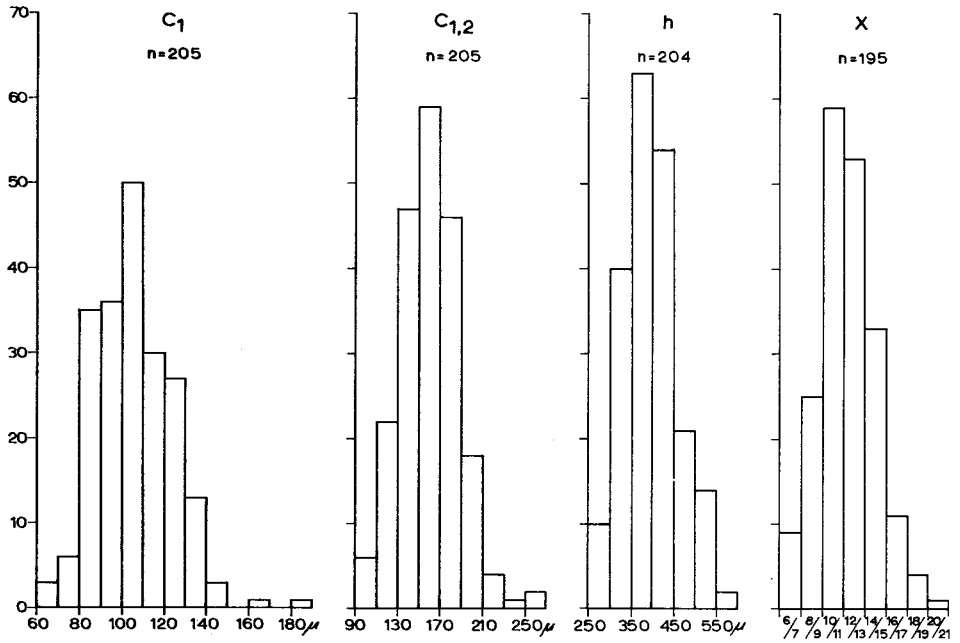


Fig. 3 Histograms of C, $C_{1,2}$, h and X for the *Heterostegina* specimens from all investigated samples.

from 79 meters and deeper. In each of the samples from 79,86,104 and 124 meters one specimen was found. The relative frequency thus would be around 5%. The 79 meter specimen was damaged during the sectioning, for the others the results are:

sample	depth	C	$C_{1,2}$	h	X
HU 4939	86 m	43 μ	75 μ	175 μ	20
HU 4930	104 m	25 μ	50 μ	175 μ	30
HU 4831	124 m	25 μ	38 μ	106 μ	25

For all these parameters the observed values are well outside the range of the accompanying megalospheric individuals.

Megalospheric forms occur throughout the examined depth range. The sample means of the individual parameters show considerable differences. None of the parameters shows a regular pattern of change along the depth profile (fig. 2, table 1). The histograms for all observations on C, $C_{1,2}$, h and X (fig. 3) show distinctly unimodal frequency distributions. The overall means are:

$\overline{C} = 102.7\ \mu$ $\overline{C_{1,2}} = 156.8\ \mu$ $\overline{h} = 390.4\ \mu$ $\overline{X} = 11.8$

Sample	depth	$r_{C-C_{1,2}}$	n	r_{C-h}	n	r_{C-X}	n	$r_{C_{1,2}-h}$	n
71161	28	+0.80	20 +	+0.36	20 o	− 0.21	19 o	+0.53	20 +
71160	38	+0.80	28 +	+0.32	28 *	− 0.49	26 −	+0.86	26 +
71012	66a	+0.64	26 +	+0.83	26 +	− 0.65	26 −	+0.49	26 +
71159	66b	+0.89	18 +	+0.90	18 +	− 0.51	18 −	+0.81	18 +
71206	68	+0.92	28 +	+0.69	28 +	− 0.63	24 −	+0.76	28 +
71014	79	+0.01	10 o	+0.40	10 o	− 0.53	10 o	+0.77	10 +
71157	86	+0.88	26 +	+0.87	26 +	− 0.61	25 −	+0.92	26 +
71148	104	+0.90	17 +	+0.90	17 +	− 0.86	16 −	+0.93	17 +
71017	116	+0.91	5 +	+0.73	5 +	− 0.52	5 −	+0.88	5 +
71063	124	+0.80	28 +	+0.62	27 +	− 0.50	28 −	+0.63	27 +

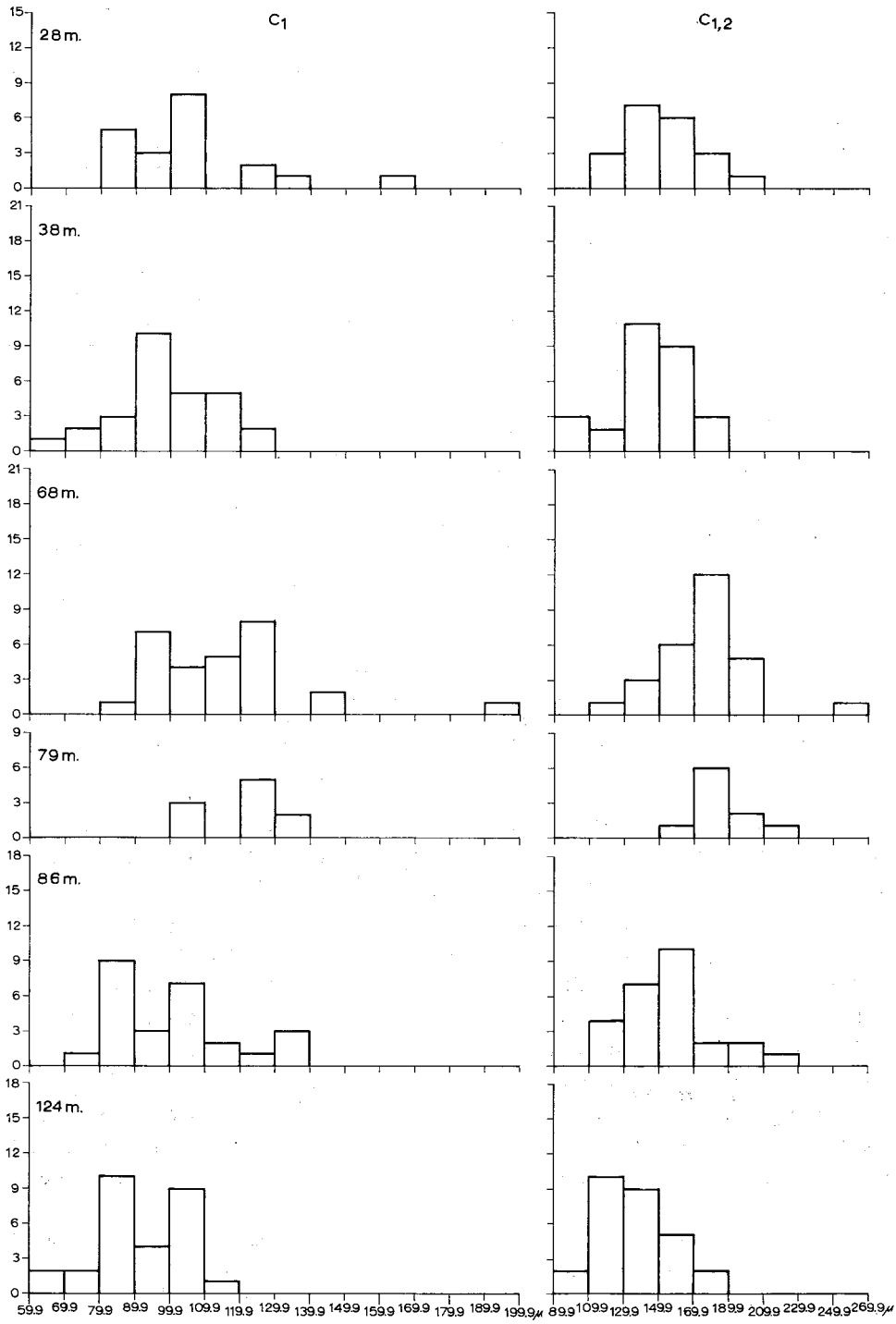
depth	$r_{C_{1,2}-X}$	n	r_{h-X}	n	$r_{S_{20}-X}$	n	$r_{S_{20}-C}$	n
28	− 0.07	19 o	− 0.19	19 o	− 0.26	19 o	+0.38	19 o
38	− 0.49	26 −	− 0.48	26 −	− 0.31	26 o	+0.43	26 +
66a	− 0.21	26 o	− 0.70	26 −	− 0.41	24 −	+0.23	24 o
66b	− 0.60	18 −	− 0.61	18 −	− 0.73	18 −	+0.72	18 +
68	− 0.62	24 −	− 0.70	24 −	− 0.36	23 *	+0.34	26 *
79	− 0.27	10 o	− 0.64	10 −	− 0.41	9 o	+0.07	9 o
86	− 0.36	25 *	− 0.56	25 −	− 0.78	6 *	+0.80	6 *
104	− 0.80	16 −	− 0.77	16 −	− 0.71	10 −	+0.45	10 o
116	− 0.37	5 o	− 0.58	5 o	------		------	
124	− 0.67	28 −	− 0.49	27 −	− 0.57	22 −	+0.53	22 +

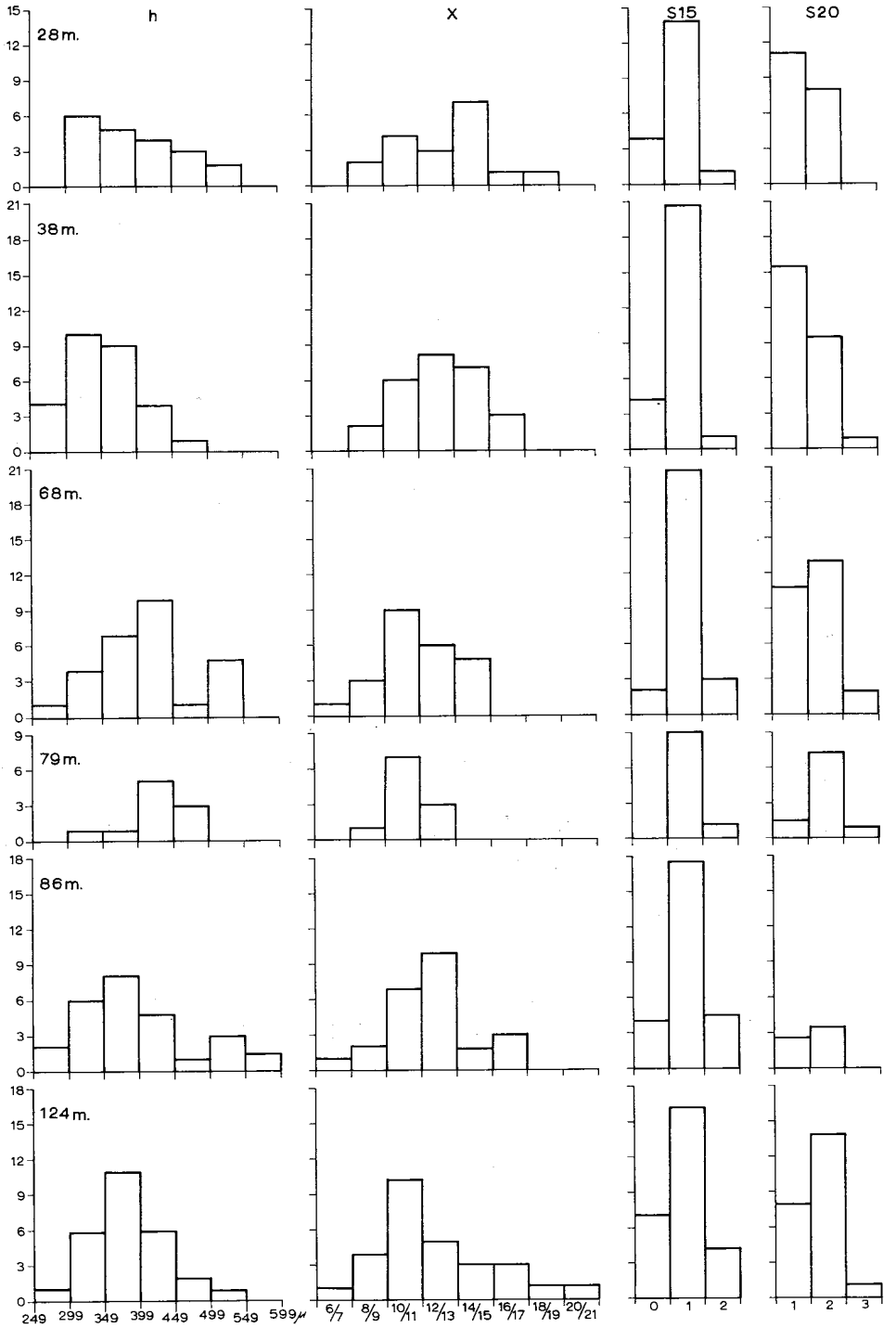
Table 2. Correlation coefficients between the various parameters of *Heterostegina* from the Gulf of Elat. 97.5 and 95% confidence levels are used, one sided. + and − = significant positive and negative respectively, at 97.5% c.l., * = significant positive or negative at 95% c.l., o = no correlation at 95% c.l.

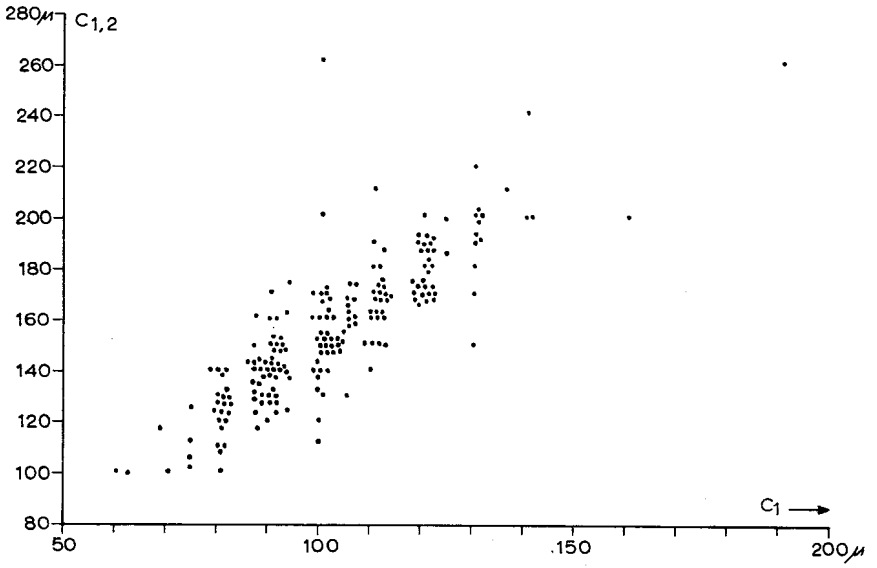
The relatively low numbers of observations per sample and especially the two sets of measurement data cause many of the sample histograms to have a ragged appearance if one choses a class width of 10 μ. For some samples these histograms are given in fig. 4. With double class intervals for C, $C_{1,2}$ and h all histograms appear to become unimodal, except one in which there is a slight dent in the C distribution (104 m). These modified histograms contain so little information with only three or four, or even two classes left, that none of them is figured. The histograms give no indication that any of the *Heterostegina* assemblages would be heterogeneous.

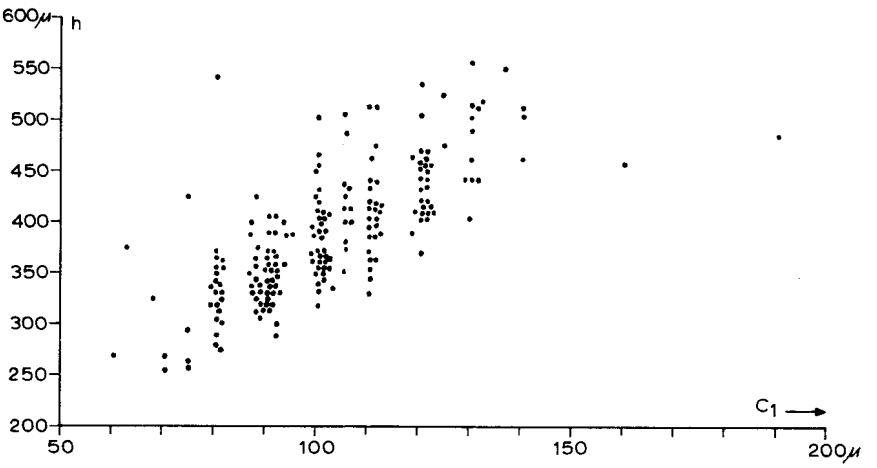
The S_5 values are always zero. S_{10} values (table 1) show considerable fluctuations in the means because there are relatively few individuals with one secondary septum. The S_{15} and S_{20} means have a less wide range of

Fig. 4 Histograms of C, $C_{1,2}$, h, X, S_{15} and S_{20} for the *Heterostegina* samples from 28, 38, 68, 79, 86 and 124 meters depth.


C1
C1,2
28 m.
38 m.
68 m.
79 m.
86 m.
124 m.
59.9 69.9 79.9 89.9 99.9 109.9 119.9 129.9 139.9 149.9 159.9 169.9 179.9 189.9 199.9μ
89.9 109.9 129.9 149.9 169.9 189.9 209.9 229.9 249.9 269.9μ


h
X
S15
S20
28m.
38m.
68m.
79m.
86m.
124m.
249 299 349 399 449 499 549 599μ
6/7 8/9 10/11 12/13 14/15 16/17 18/19 20/21
0 1 2
1 2 3


280µ
C1,2
260
240
220
200
180
160
140
120
100
80
50
100
150
200µ
C1


600µ
h
550
500
450
400
350
300
250
200
50
100
150
200µ
C1

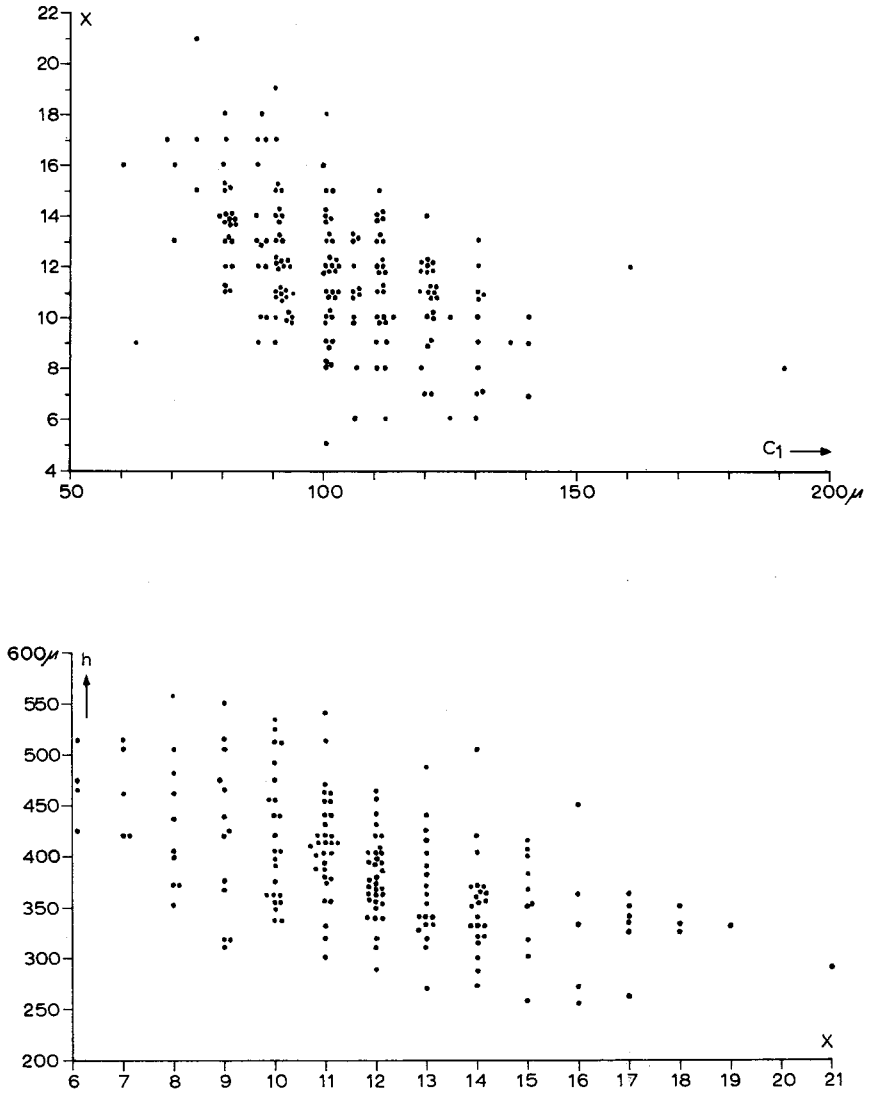


Fig. 5 Scatter diagrams of C, $C_{1,2}$, h and X combinations for the *Heterostegina* specimens from all investigated samples.

variatons. The small numbers of S_{20} data in the 86 and 104 meters samples are due to the fact that the specimens of these samples are very small and generally do not posses a twentieth chamber.

All the parameters considered hitherto are related to each other in one way or another. For each sample correlation coefficients were calculated for combinations of various parameters (table 2). Scatter diagrams of all the available data were prepared for combinations of C, $C_{1,2}$, h and X (fig. 5).

Distinct positive correlations exist between the three size parameters C, $C_{1,2}$ and h. In nearly all cases the correlations are positive and significant at the confidence level of at least 97.5%.

In general, specimens with a large proloculus start earlier with the production of heterosteginid chambers. All the correlations between X and each of the parameters C, $C_{1,2}$ or h are negative, being significant at the confidence level of 97.5% in 20 of the 30 examined cases. The less pronounced correlation values occur generally in samples with only few specimens. During the ontogenic development the number of secondary septa per chamber increases. This is easily demonstrated by comparing the S_n values (table 1). When specimens have a large number of operculinid chambers, the number of secondary septa in the n-th chamber is relatively low. The correlation coefficients between S_{20} and X show negative values that are significant at the 97.5% confidence level in four of the ten samples. In two others they are significant at the 95% confidence level. We also calculated the correlation coefficients between S_{20} and C. In three of the nine samples the positive correlation is significant at 97.5%, in two others at the 95% confidence level.

Relations with substrate

Three samples from about the same depth but from different substrates were compared:

sample	depth in m.	substrate
HU 4941	66b	coral sand
HU 4859	66a	*Halophila*
71206	68	intermediate between coral sand and red mud

None of the differences in mean values is of statistical significance (see table 1). The means fit fairly well together, thus indicating that there is no evidence for a relation between inner morphology and substrate.

Relations with depth

If the means of all parameters are placed along the depth profile there appear to be no sustained changes (fig. 2). In at least one group of *Operculina* we found an increase in $\overline{C}$ from 28 down to 79 meters. A similar change seems to be true for *Heterostegina.*

The $\overline{C}$ values show a fluctuating increase from 100.8 μ to 117.0 μ, the significance between these 28 and 79 m samples (t test) being in the order of the 96% confidence level. However, the drop in $\overline{C}$ from 79 to 86 meters is still more significant and the lowest $\overline{C}$ value of all occurs in the deepest sample at 124 meters. As might be expected the patterns in $\overline{C_{1,2}}$ and $\overline{h}$ are parallel to that in $\overline{C}$.

Evidently the pattern of fluctuations is less similar in $\overline{X}$. There is a distinct decrease in $\overline{X}$ from 28 to 79 meters but in the deeper part of the depth range the fluctuations are not clearly correlated with those in $\overline{C}$ anymore.

The $\overline{S}_{15}$ value sequence remotely resembles the changes in $\overline{C}$, but differences are nowhere really significant. For $\overline{S}_{20}$ they are, but here extremely high values are found at 79 and 104 meters if compared with that from 28 meters.

Summarizing it may be stated that the data suggest an increase of protoconch diameters and correlated size parameters down to about 80 meters, whereas at greater depth an erratic picture of again lower values is found. The number of operculinid chambers shows a fair negative correlation with the size parameters and thus a reduction trend in $\overline{X}$ down to 79 meters. For the higher $\overline{S}_n$ values the data give a more confused picture, but at least for $\overline{S}_{20}$ an extra trend of increase with increasing depth seems to be superimposed.

The numbers of observations should be expanded for more reliable conclusions. Since the number of operculinid chambers and the number of secondary septa in the n-th chambers might be used for the reconstruction of evolutionary lineages, our data include the warning that mean values of these parameters may show deviations of ± 10% and ± 20% respectively at any time level.

Heterogeneity within the samples

In the study on *Operculina* from the Gulf of Elat evidence was found for the presence of different morphological groups. One of the parameters which enabled to demonstrate this heterogeneity, is the total number of

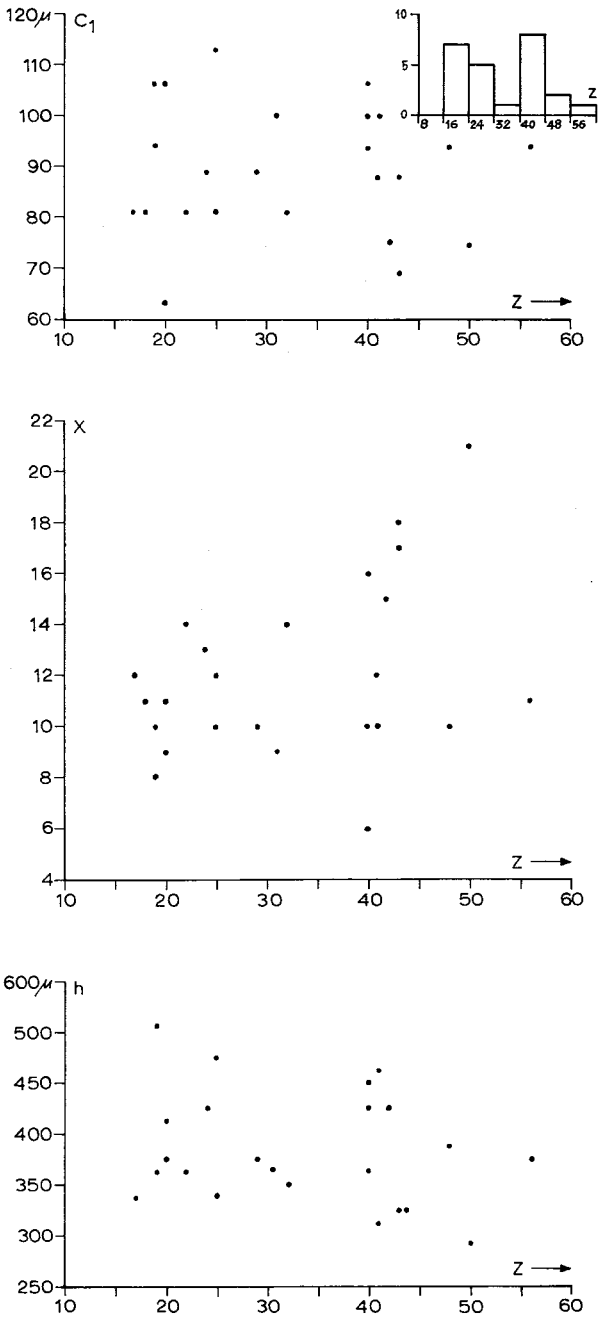


Fig. 6 Scatter diagrams of the total number of chambers z versus C, X and h and histogram of the z values for the *Heterostegina* specimens from 124 meters depth.

chambers (z). In the case of *Heterostegina* the sample from 124 meters was taken to count z, because it shows a broad range in size of the specimens and only few of them are broken.

The histogram of z gives a rather irregular picture (fig. 6), but the Kolmogorov Smirnov test for the goodness of fit shows that the hypothesis of normal distribution cannot be rejected ($D_n = 21; n = 24$).

The scatter diagrams of z with each of the parameters C, X and h give no clear indications of either correlation or separable clusters (fig. 6), thus leaving no evidence for heterogeneity within the sample.

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BIOMETRICAL DATA ON HETEROCYCLINA

J. E. MEULENKAMP

ABSTRACT

Counts and measurements on the number of spiral chambers and the size of the protoconch in five assemblages of Recent *Heterocyclina tuberculata* from the Gulf of Elat-Aqaba show that these *Cycloclypeus*-like forms cannot be separated from Oligocene, primitive assemblages of the *Cycloclypeus* lineage(s) on the basis of biometrical criteria.

It is suggested that *Cycloclypeus*-like forms evolved more than once from different *Heterostegina* stocks.

INTRODUCTION

Cycloclypeus-like forms are fairly common in the bottom sediments of the Gulf of Elat between 86 and 116 meters. The specimens show a striking similarity to Recent representatives of *Cycloclypeus,* but they have a different stolon system. For this reason Hottinger (1977, and this volume) places them in the new genus *Heterocyclina.*

This investigation presents the relation between the internal features of *Heterocyclina* and depth, and a comparison of the biometrical data with those of the representatives of the *Cycloclypeus* lineage(s).

The author wishes to express his thanks to L. Hottinger, Basel, for putting the material at his disposal. The critical reading of the manuscript by C. W. Drooger, Utrecht, is gratefully acknowledged. The drawings and the photograph were made by J. P. van der Linden and A. van Doorn.

MATERIAL

Although the depth-range of *Heterocyclina tuberculata* in the Gulf is reported to be from 70 to 150 meters (Hottinger, this volume), grab samples containing a sufficiently high number of specimens for a biometrical analysis were available only from the interval between 86 and 116 meters. The five samples studied are 71157 (86 m), 71156 and 73310 (both at 90 m), 71148 (104 m) and 71017 (116 m). In all samples the number of specimens is low; altogether 65 thin sections were made, all but one of megalospheric speci-

mens. The single microspheric form (fig. 3) can easily be distinguished by the extremely small size of its protoconch (about 20 μ) and the very high number of pre-cyclic chambers, which exceeds forty.

The preservation is fairly good to excellent. Most specimens have a distinct ornamentation, but there is complete gradation to nearly smooth individuals.

INTERNAL FEATURES

The number of pre-cyclic chamber (X) is high, varying between 27 and 39 (the first two chambers included). The diameter of the protoconch (C) ranges from 65 to 105 μ. All measurements were rounded off to values of 5 μ. In addition, counts and measurements were performed on the number of operculinid chambers and on the diameter of the first two chambers (D, along the line connecting the centres of protoconch and deuteroconch; i.e. at right angles to the line along which C is measured). The number of operculinid chambers is either 3 or 4 (I and II included), in a few specimens it is five.

From the biometrical data, summarized in table 1, it appears that for none of the parameters real differences exist between the ranges or the means of the values. Therefore, it seems justified that all specimens are taken together and treated as being derived from one population, in order to have a sufficiently high number of observations for the calculation of correlation coefficients and the construction of histograms.

The X frequency distribution for 64 specimens (fig. 1a) shows a wide, but fairly normal distribution. The same is true for the histograms of C and D. The relations between the number of spiral chambers and both the diameter of the protoconch, and the diameter of the first two chambers (graphically

		X			C_μ			D_μ		
Sample	depth	N	Range	M ± σ_M	N	Range	M ± σ_M	N	Range	M ± σ_M
71157	86 m	18	27–39	33.06 ± 0.74	16	70–100	88 ± 2	16	100–170	134 ± 5
71156	90 m	7	31–38	34.00 ± 0.87	7	70–100	87 ± 4	7	110–150	129 ± 5
73310	90 m	17	27–37	32.65 ± 0.67	18	65–105	86 ± 2	18	110–160	128 ± 4
71148	104 m	9	29–36	32.56 ± 0.80	7	75–100	83 ± 3	7	105–150	124 ± 6
71017	116 m	13	29–37	33.38 ± 0.69	13	70–105	85 ± 3	13	105–150	128 ± 4
All samples:		64	27–39	33.04 ± 0.34	61	65–105	86 ± 1	61	100–170	129 ± 2

Table 1. Results of counts and measurements on *Heterocyclina tuberculata* from the Gulf of Elat.

represented in figs. 1b and 1c, respectively) suggest negative correlations of low intensity. However, r values for the relation X versus C and X versus D are – 0.475 and – 0.428 respectively (number of pairs of observations is 56), indicating negative correlations at a confidence level of at least 99%.

CONCLUSIONS

If we compare the average number of spiral chambers and the average diameter of the protoconch of the Elat *Heterocyclina* with the means of C and X of Recent *Cycloclypeus* assemblages from the Indo-Pacific a striking difference can be seen. The Recent *Cycloclypeus* species have very low $\overline{X}$ and much higher $\overline{C}$ values (see fig. 2). These Recent species are considered to be the most advanced representatives of one or more *Cycloclypeus*

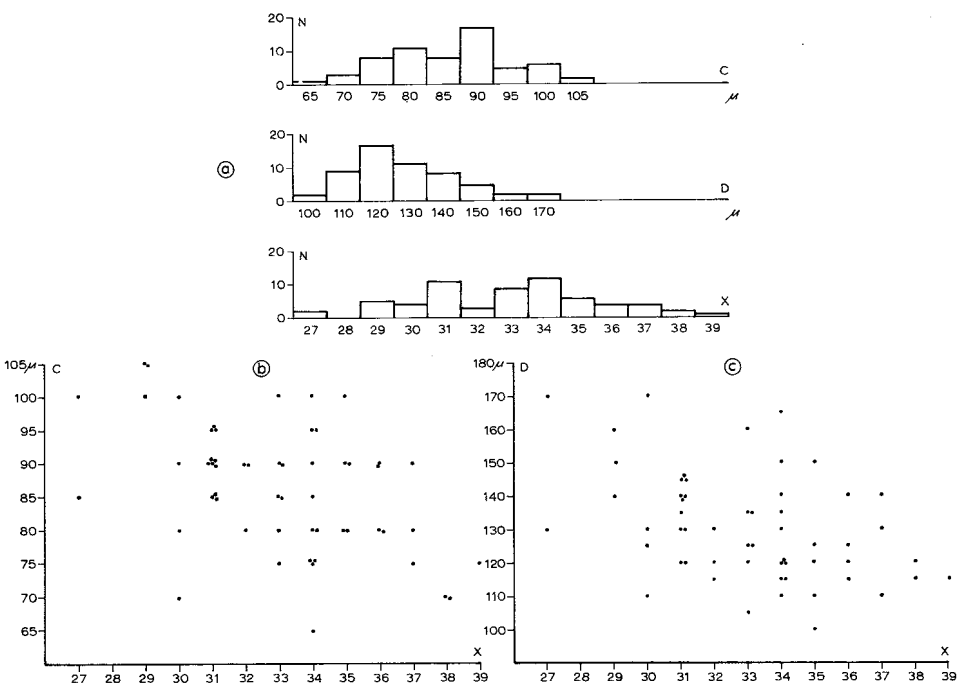

Fig. 1 a. Frequency distributions of the number of pre-cyclic chambers (X), the diameter of the protoconch (C), and the diameter of the first two chambers (D) in *Heterocyclina* from Elat. b, c. Scatter diagrams showing the relation between the number of pre-cyclic chambers (X) and the diameter of the protoconch (C), and between X and the diameter of the first two chambers (D) in *Heterocyclina* from Elat.

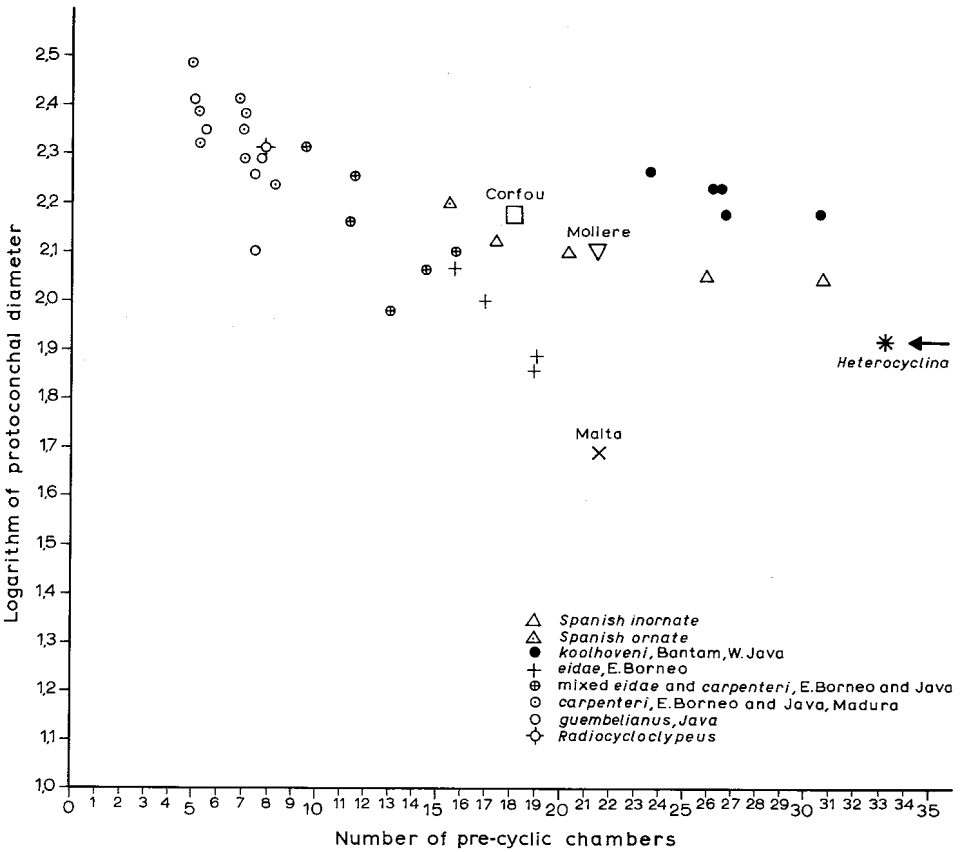

Fig. 2 Relation between the average number of pre-cyclic chambers ($\bar{X}$) and the average diameter of the protoconch ($\bar{C}$) in *Cycloclypeus* assemblages from Indonesia and Europe and in *Heterocyclina* from Elat. Mainly after Meulenkamp and Amato (1972).

lineages that evolved from *Heterostegina* since the Oligocene. These phylogenetic trends are well-known from Indonesia and the Mediterranean (Tan Sin Hok, 1932; Cosijn, 1938; MacGillavry, 1956, 1962; Drooger, 1958; Meulenkamp and Amato, 1971).

In fact, the Elat *Heterocyclina* closely resemble the most primitive Oligocene *Cycloclypeus* from Indonesia belonging to the *C. koolhoveni* group, and from Spain ("Spanish inornate forms" of Cosijn, 1938) in means of C and X. The $\bar{C}$–$\bar{X}$ diagram of fig. 2 clearly illustrates that the Recent *Heterocyclina* and Oligocene *Cycloclypeus* cannot be separated on the basis of the biometrical criteria, that have been widely used to define the stage of phylogenetic development in the evolution of *Cycloclypeus*.

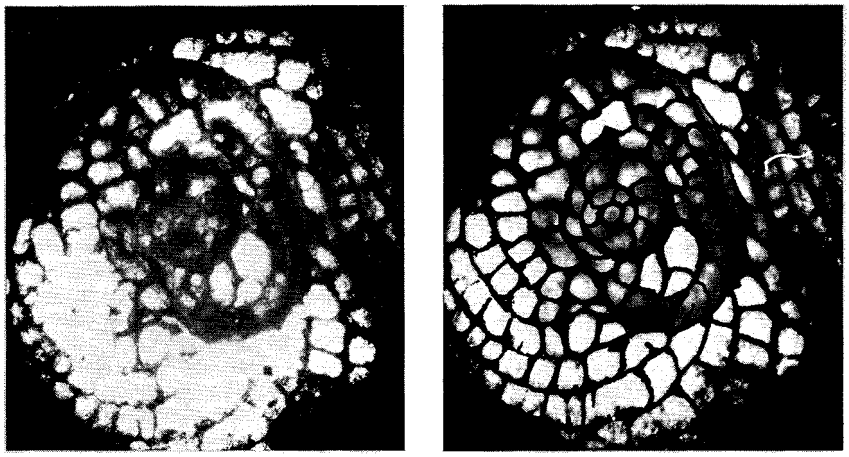

Fig. 3 Half-section of the only microspheric *Heterocyclina* individual in our collection. Left photograph, right the same with interpretation of the draughtsman. x 100.

The Elat results point to a new offspring of *Cycloclypeus*-like forms from another *Heterostegina*-stock, probably during the Late Neogene or even Quaternary. There seems to be no reason to doubt a future evolutionary development of *Heterocyclina* along lines similar to those known to have occurred in *Cycloclypeus.*

Our data would justify a reconsideration of the existing, opposed views on the presence of one or more *Cycloclypeus* lineages (Drooger, 1958; and MacGillavry, 1962, respectively) evolving independently of one another from different *Heterostegina* stocks. The *Heterocyclina* example shows that we cannot reject the hypothesis that the older *Cycloclypeus*-like forms originated more than once. If the stolon-system difference between Recent *Cycloclypeus* and *Heterocyclina* is consistent in the fossil forms of the former genus and not simply a functional adaptation to greater or smaller flatness of the test, one might be able to understand the origin of the *C. eidae* and *C. carpenteri* groups. The earlier discussions showed that the biometrical data alone were insufficient to solve this problem.

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BIOMETRIC STUDY OF RECENT PLANORBULINELLA FROM THE GULF OF AQABA (ELAT)

E. THOMAS

ABSTRACT

Two species of *Planorbulinella, P. larvata* (Parker & Jones) and *P. elatensis* nov. spec. are recognized in the Gulf of Elat on the basis of biometric analysis of the internal features. Both species are easily separable on size and configuration parameters of the early chambers. *P. larvata* ranges from shallow water down to a depth of about 120 meters, *P. elatensis* is found in deeper waters between 100 and 240 meters.

INTRODUCTION

The primary objective of the investigation was to check whether Recent larger foraminifera show an increase of protoconch-diameter with greater depth. Such a relation was recently suggested to exist for the fossil foraminifera of the family Miogypsinidae (Drooger & Raju, 1973).

Another purpose of the present study on recent *Planorbulinella* was to investigate whether these larger foraminifera show any change with increasing depth in the internal parameters that are commonly considered to give information on the stage of evolution in the group. As the evolutionary lineages of most extinct orbitoidal larger foraminifera have been based on differences in such internal parameters, better information on possible environment dependence of such "evolutionary" features in one of the few still living groups is urgently needed.

An evolutionary lineage of Miocene *Planorbulinella* in the Mediterranean has been outlined by Freudenthal (1969), who recognized sustained changes in the configuration of the nepionic spiral(s).

For the purpose of the investigation the foraminifera from the Gulf of Elat have certain advantages because changes with depth of such factors as temperature and salinity are extremely insignificant. For differences found in the morphology we thus have a more limited choice of factors that are depth-dependent, such as light-penetration.

Since the main purpose is to facilitate extrapolation to fossil thanatocoenoses, we were satisfied to use Recent death-assemblages instead of groups of living individuals. The consequence of this choice of material is, of course,

that the results are difficult to correlate with living populations, considering the insufficient information on the amount of downward sediment transport.

MATERIAL AND METHODS OF INVESTIGATION

The investigated *Planorbulinella* specimens were obtained from 25 of the samples available. The depth of provenance of these samples ranges from 15 to 240 meters. The samples were kindly made available by Z. Reiss, L. Hottinger and H. J. Hansen. The localities of the samples are listed in table 1, together with general information on bottom conditions and sampling methods. The greater part of the localities is situated in the region around Coral Island, in the northwestern corner of the Gulf of Elat, some six kilometers south of the town of Elat. Some samples have been taken at localities much farther to the south, along the southwestern coast of the Gulf, and one sample is from the Red Sea proper, outside the Straits of Tiran.

The number of *Planorbulinella* specimens per sample varies considerably. It was tried to obtain about 25 macrospheric specimens from each sample, which was, however, not possible for all of the samples. From 25 samples enough specimens could be obtained. The number of microspheric individuals per sample also varies widely, from zero to about 30% of the total number of specimens.

For the *Planorbulinella*-rich samples the residues were first scanned to make a rough guess on how much material would be needed for an aselect collection of sufficient individuals. Next, splits were made in all cases where less than the whole sample was estimated to be sufficient, and all the specimens from such splits were picked. From some samples previously picked material was available only.

Almost all specimens obtained were very well preserved. In a rather large number of individuals the chambers are filled with yellowish, calcareous material which, however, did not seriously impair the accuracy of counts and measurements. In all but the smallest specimens the earlier chambers are covered with an opaque mass of calcareous pustules and are thus not visible from the outside. For this reason it was decided to prepare thin sections, or occasionally half-sections, of all the specimens, in order to exclude mixtures of data through different observation techniques.

Counts and measurements were carried out on several internal characteristics (fig. 1), chosen and described earlier by Freudenthal (1969). Linear measurements, such as the dimensions of the first three chambers, were made

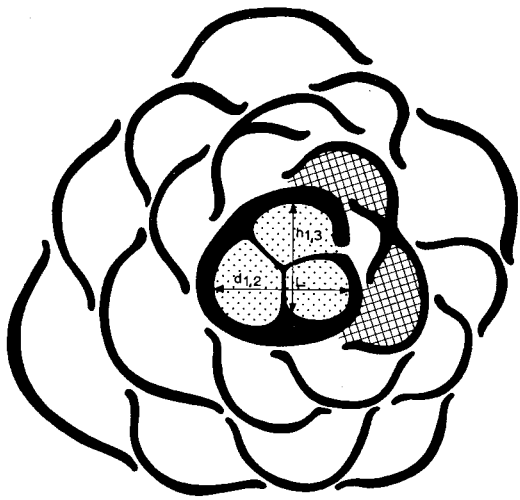


Fig. 1 Schematic drawing of early chambers of *Planorbulinella* showing $d_{1,2}$, $h_{1,3}$, Y (= 3) and R (= 2).

by means of an ocular micrometer. The symbols and the definitions of the parameters used are those employed by Freudenthal (1969). They are given below:

$d_{1,2}$ = the diameter of protoconch and deuteroconch together, measured along a line through their imaginary centres, the wall thickness being excluded, except for that of the wall separating the protoconch and deuteroconch. Values are expressed in μ.

$h_{1,3}$ = the diameter of the first three chambers, measured along a line perpendicular to that of $d_{1,2}$ through the imaginary centre of the third chamber.

All measurements were made with a Leitz binocular microscope, ocular 16 and objective 10, with a precision of half a micrometer unit, corresponding to 5.2 μ. It must be realized that measured values are given in μ, though the inaccuracy range of individual measurements actually is as much as approximately 5 μ.

Y = the number of chambers in the initial spiral with only one proximal stolon, protoconch and deuteroconch included in the counts.

R = the number of chambers in the spirals, originating from the first chamber with two stolons, that again lack the second stolon (relapse to the one-stolon configuration).

(Y + R) = the sum of Y and R; hence, the total number of chambers with only one stolon in the nepionic part of the test.

For each sample the mean values of $d_{1,2}$, $h_{1,3}$, Y, R and (Y + R) have been calculated on the basis of all observations, regardless of the suspected heterogeneity of the assemblages in some of the samples. These mean values are given in table 2, together with the range, and standard error of the mean. For each sample the $\overline{d}_{1,2}/\overline{h}_{1,3}$-value is given in the same table.

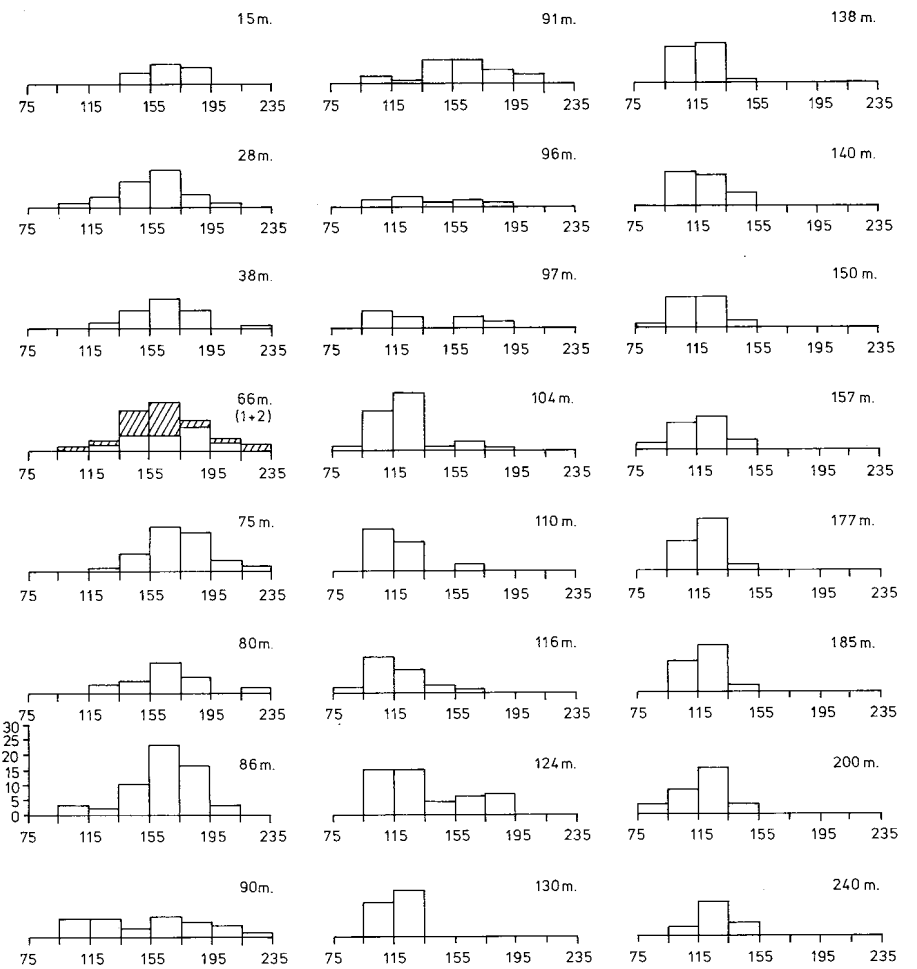


Fig. 2 Histograms of $d_{1,2}$ (in μ) for all *Planorbulinella* samples.

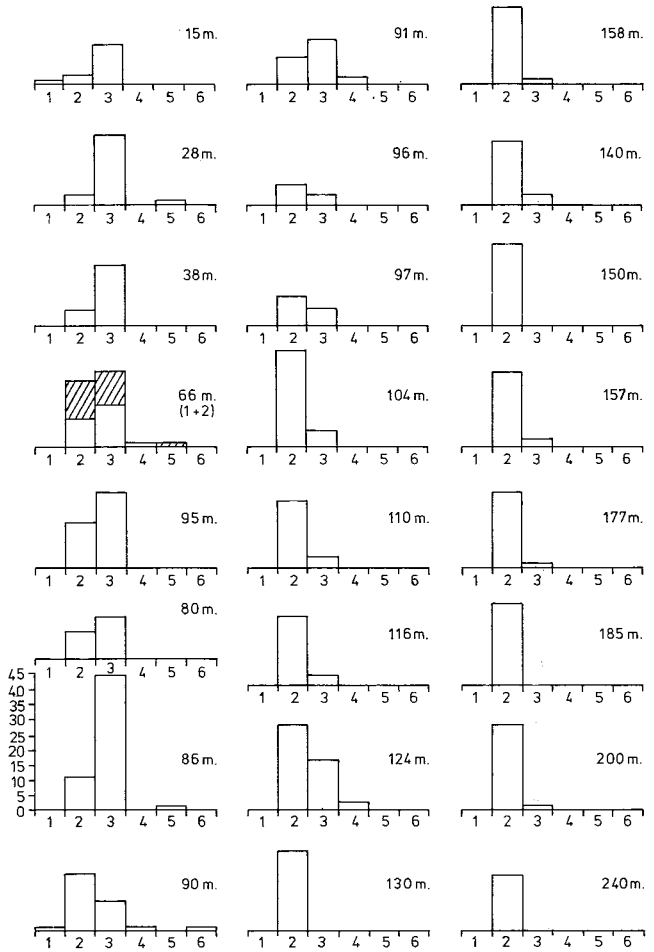


Fig. 3 Histograms of Y for all *Planorbulinella* samples.

For all samples the correlation coefficients were computed for the combinations $d_{1,2}$ and $h_{1,3}$; $d_{1,2}$ and Y; and $d_{1,2}$ and (Y + R). In addition the values for slope and intercept of one of both regression lines have been entered in this table. In all three cases $d_{1,2}$ is taken as the independent variable, which does not imply that we consider the other three variables really dependent on the combined size of protoconch and deuteroconch.

For all individual samples the frequency distribution of the values of $d_{1,2}$, Y and (Y + R) are shown in the histograms in figures 2, 3 and 4. All paired observation of $d_{1,2}$ and (Y + R) are shown in the scatter-diagrams

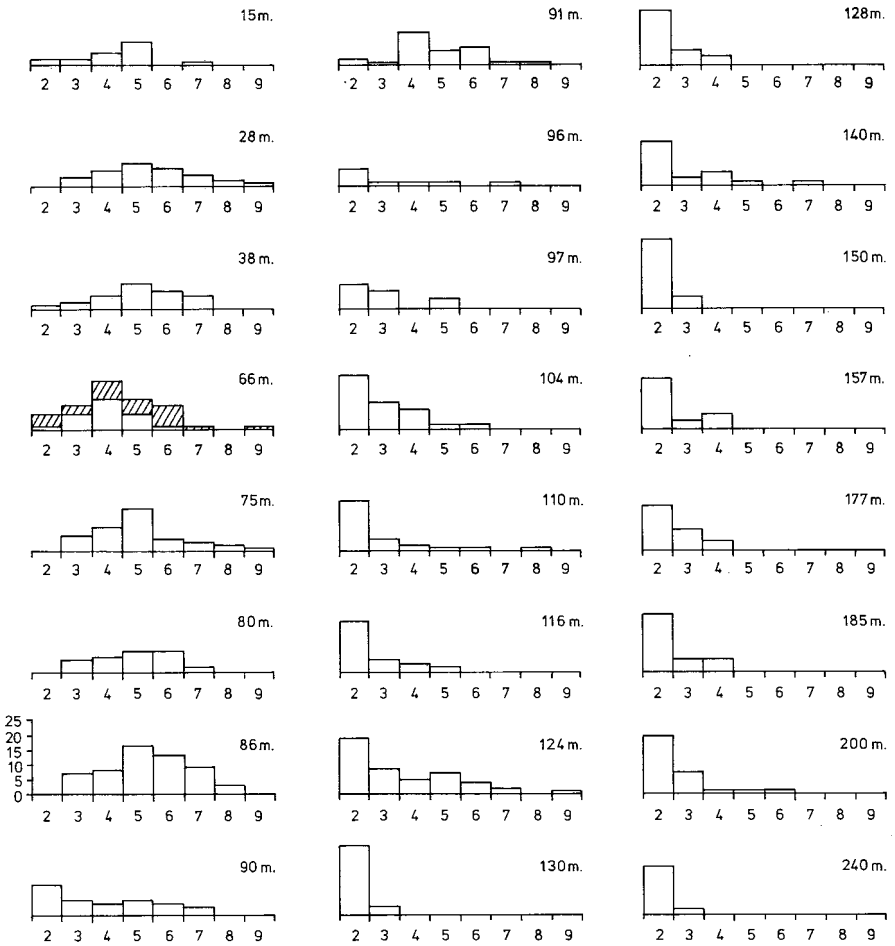


Fig. 4 Histograms of (Y + R) for all *Planorbulinella* samples.

of figure 5, each scatter representing the data of one of the samples. The $d_{1,2}$-(Y + R) combinations for all specimens from all samples together are given in figure 6. Paired observations of $d_{1,2}$ and $h_{1,3}$ for some samples are shown in the scatter-diagrams of figure 7.

In figure 8 the calculated mean values per parameter are shown with the corresponding range of (±) one standard error for all samples, arranged in depth-sequence with correct spacing.

The $d_{1,2}/(Y + R)$ frequency diagram for all studied specimens (fig. 6) shows two distinct, adjoining clouds of greater density, one with relatively large values for both $d_{1,2}$ and $(Y + R)$, the other with much smaller values for both these parameters. If we consider the corresponding scatter-diagrams for the separate samples (fig. 5), the following observations can be made:

In each of the samples from 15 to 80 meters depth only one of the smaller fields is occupied, corresponding in position with the righthand cluster of figure 6.

In the samples from 86 and 91 meters the majority of the individuals cluster in the same upper right field, but some three individuals in each sample are more remote, corresponding in position with the larger lefthand group of figure 6.

In the samples from 104, 110, 116, 140 and 157 meters the relative numbers show completely reversed proportions: most specimens are found inside the lefthand field, a few occur in the upper right.

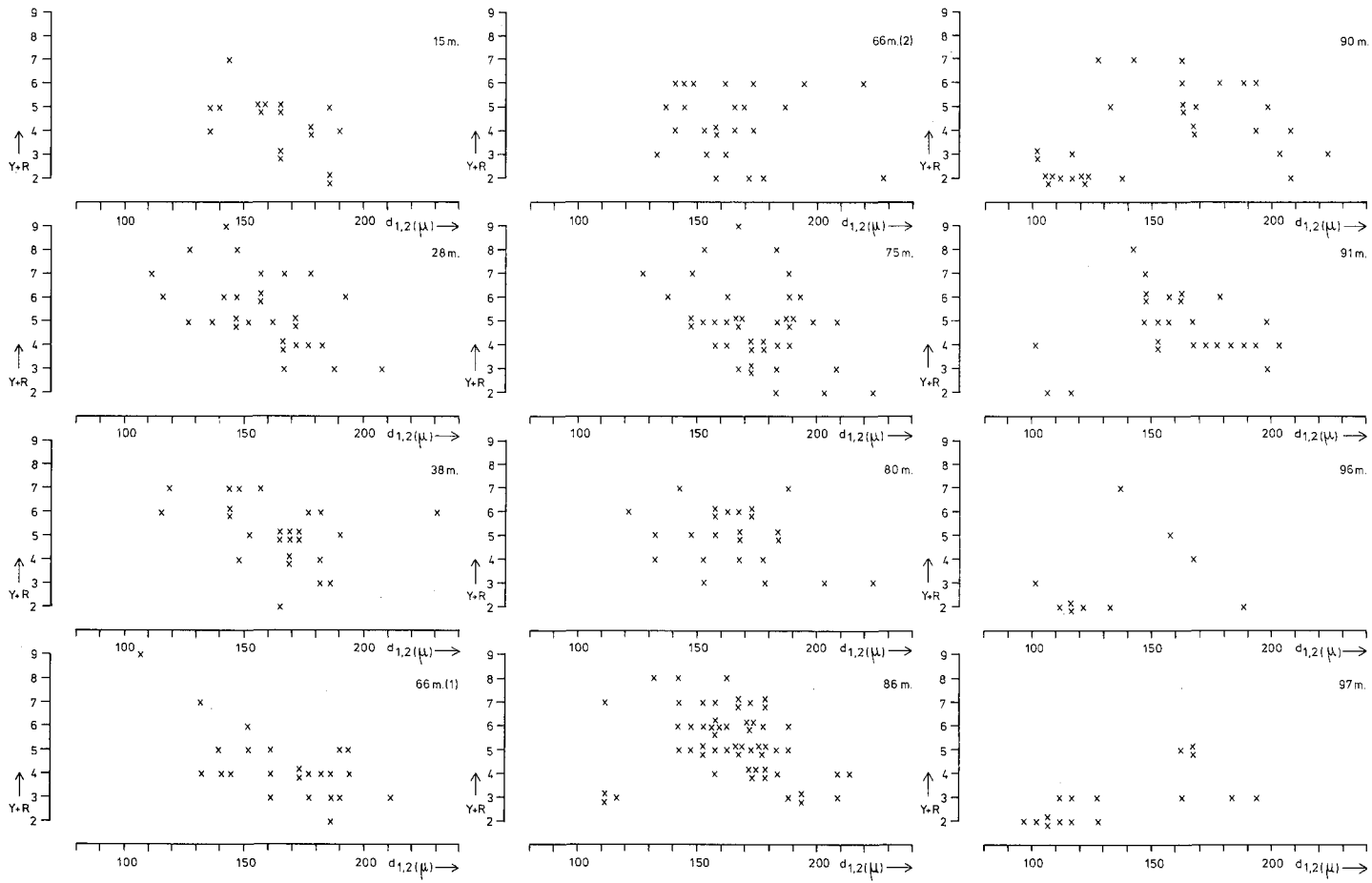
In the figures for the samples from 90, 96, 97 and 124 meters depth two distinct clusters are present, both filled by about the same number of individuals and each cluster corresponding in position with on of the fields of figure 6.

In the figures for the samples from 130, 138 and 150 meters and in the samples from 177 to 240 meters the only cluster present corresponds with the lower left cloud of greater density of figure 6.

The mean values for different parameters, arranged in depth-sequence in fig. 8 all show roughly the same pattern: high values for the samples from 86 meters depth and less, low values below 86 meters depth, with the exception of the samples from 90, 96, 97 and 124 meters, which show intermediate values. It is very conspicuous that the same picture emerges for all parameters, i.e., samples with high, intermediate or low mean values for one parameter have also high, intermediate or low values for the others. This pattern is true even for the $\overline{d}_{1,2}/\overline{h}_{1,3}$ values.

As might be expected, the histograms of figs. 2, 3 and 4 give another representation of the same pattern. Both larger groups of samples, one down to 86 meters and the other below 124 meters, are clearly different in modal values as well as in the ranges of the observations. From 90 to 124 meters especially the $d_{1,2}$ and $(Y + R)$ histograms lack the clear modal values in most of the samples and the ranges tend to cover the entire width of both groups together.

Fig. 5 Scatterdiagrams of $d_{1,2}$ versus (Y + R) of the separate *Planorbulinella* samples.



104 m.
110 m.
116 m.
124 m.
130 m.
138 m.
140 m.
150 m.
157 m.
177 m.
185 m.
200 m.
240 m.
Y+R
d1,2(μ)

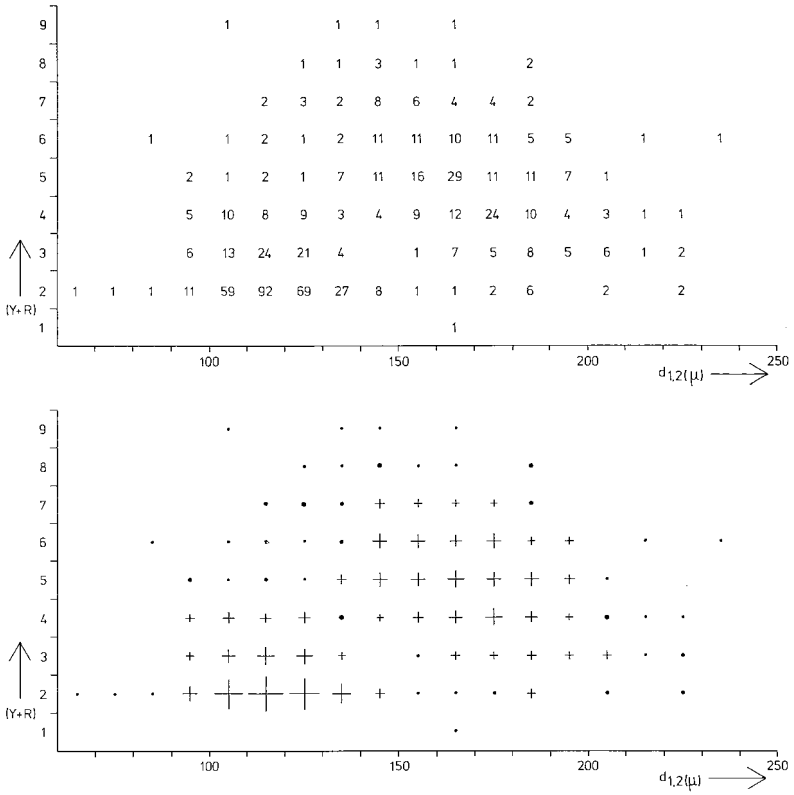


Fig. 6 Scatterdiagrams of $d_{1,2}$ versus (Y + R) for all *Planorbulinella* specimens from the entire depth range together.

All data given in the histograms, means-sequence and scatter-diagrams suggest a heterogeneity of the investigated *Planorbulinella* "populations" in the Gulf of Elat if one considers the entire depth range. A further attempt to clarify the heterogeneity from the raw data is shown in table 3, in which the correlation coefficients of three combinations of parameters have been entered.

As to the correlation between the embryon size parameters $d_{1,2}$ and $h_{1,3}$ the r-values indicate a positive correlation for all samples, significant at a 0.975 confidence level. If one considers the fairly regular shape of the embryon in horizontal section the result is not surprising. No uniform results are found for the correlation between $d_{1,2}$ and Y, and $d_{1,2}$ and (Y + R). A very confused picture appears if one considers the columns in table 3. In the samples down to 80 meters depth all correlation coefficients are negative, significant at a confidence level of 0.975 in most cases. In some cases the

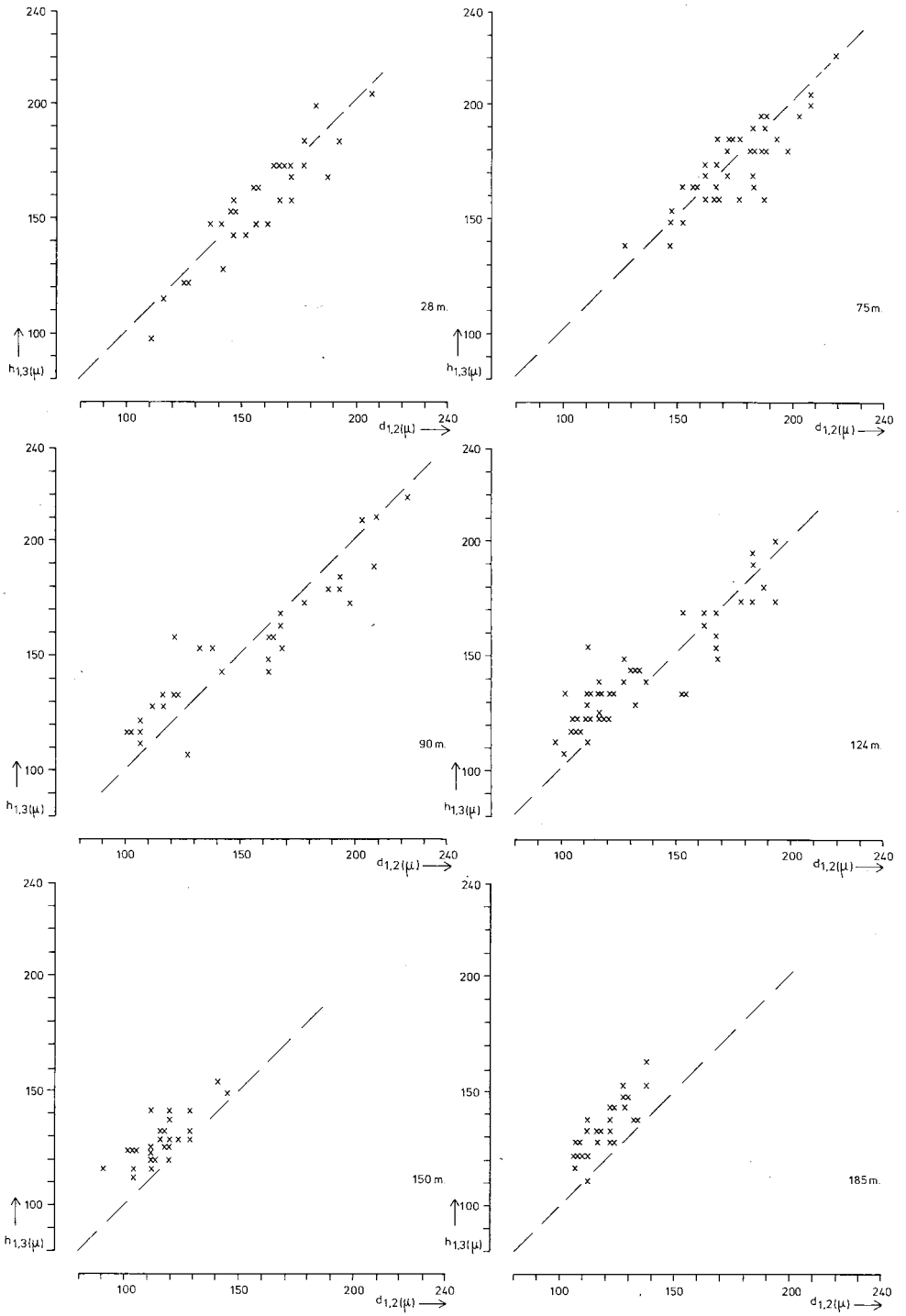


Fig. 7 Scatterdiagrams of $d_{1,2}$ versus $h_{1,3}$ for some of the *Planorbulinella* samples.

correlation is significant at a confidence level of only 0.95, and in one sample the correlation coefficient between (Y + R) and $d_{1,2}$ is of no real significance.

In the deeper samples, below 80 meters, the pattern seems to become very irregular.

In the $Y/d_{1,2}$ correlation the irregularity and low values of the coefficients may be explained by the predominance of a single (Y = 2)-class in most deeper samples. Although such prevailing weight of the lowermost class in the (Y + R) distributions may be less pronounced, the skewed frequency distribution for this parameter in the group of deeper samples may be considered responsible for the low r-values. Nevertheless the negative $d_{1,2}$/(Y + R) correlation recurs as a regular feature below 124 meters, although the actual values are but rarely significant at 0.975 or 0.95 confidence level. In contrast to the negative correlation pattern of shallow and deepest groups of samples, the intermediate group from 86 to 124 meters shows occasionally high positive r-values, even of unmistakable significance.

EXPLANATION OF THE RESULTS

Combining the evidence from the histograms, the scatter-diagrams, the mean-sequence against depth, and the correlation coefficients, there seems to be little reason to assume a depth-related cline in *Planorbulinella* in the Gulf of Elat. On the other hand, the variation certainly has no checker-board pattern, but there seem to be two distinct, fairly homogeneous groups of assemblages at smaller and greater depths, with peculiar, mixed assemblages in between. The most plausible explanation seems to be that in Elat two biometrically different populations of *Planorbulinella* do exist, one found in relatively shallow water, down to about 90 meters depth, the other in deeper water, from 90 meters depth downwards. There would be a zone of "mixture" in the overlap interval between roughly 80 and 125 meter.

These populations will be referred to below as group 1 (shallow) and group 2 (deep) respectively. Group 1 differs from group 2 by higher $\overline{Y}$,$\overline{R}$ and $(\overline{Y+R})$ values and on the average larger first chambers, as well as by a larger $\overline{d}_{1,2}/\overline{h}_{1,3}$ ratio.

For the explanation of the data from the samples from intermediate depths two theories may be considered: either group 1 changes gradually, but quickly into group 2, with but a few intermediate populations, or group 1 and group 2 are entirely separate, occupying different depth habitats and occurring in some samples together, because of the existence a zone of

overlap between their habitats and/or as a consequence of mixing due to sediment-transport. If the first theory is correct, the intermediate populations will be homogeneous, if the second theory would be applicable, the intermediate populations will appear to be heterogeneous. Both theories will be tested statistically below.

It was decided to test differences in the values of the parameter $d_{1,2}$, as this is a continuous variable. Regarding the histograms, we may assume that this variable might very well have a normal distribution, at least in the samples from 86 meters and shallower and in the samples from 104 meters and deeper with the exclusion of the sample from 124 meters depth. To test this assumption a goodness-of-fit test was used, which compares the observed frequency distribution with an ideal normal distribution with the same mean and standard deviation for two of the samples, those from 75 and 200 meters. The results of this test are shown in table 4. It is evident that the parameter $d_{1,2}$ may be considered to be normally distributed in both there samples, neither of which was suspected to be heterogeneous.

Next the hypothesis was tested, that no distinct, biometrically separable groups of populations do exist in the Gulf of Elat, i.e. whether selected pairs of assemblages might belong to two populations with the same mean value. We have to concentrate on those samples that can without doubt be assigned to one of the groups or the other, and have to leave out the samples of intermediate depth, because of suspected heterogeneity.

The results of the comparison of some pairs of samples are given in table 5. From this table it follows quite clearly that in all cases very large and highly significant deviations from the hypothesis exist between the selected assemblages from the group of samples from 15 to 80 meters depth and those from the group of samples from 130 to 240 meters depth, a result which could already be expected from the figures 8. The probability that these two groups of samples contain two clearly different groups of populations and not one and the same is much larger than 99%, which is rather conclusive.

Significant, though much smaller differences turn out to exist between some samples in either group, for instance between the samples from 28 and 75 meters, and between the samples from 130 and 240 meters. In all cases of (near)-significant values it is remarkable that they point in the same direction, i.e. towards greater embryon size with increasing depth. In each group, however, there are several samples with values intermediate between the two significantly differing samples, for instance the samples from 80 meters and from 200 meters, which samples do not differ significantly from either of the two samples mentioned from their respective intervals, that between

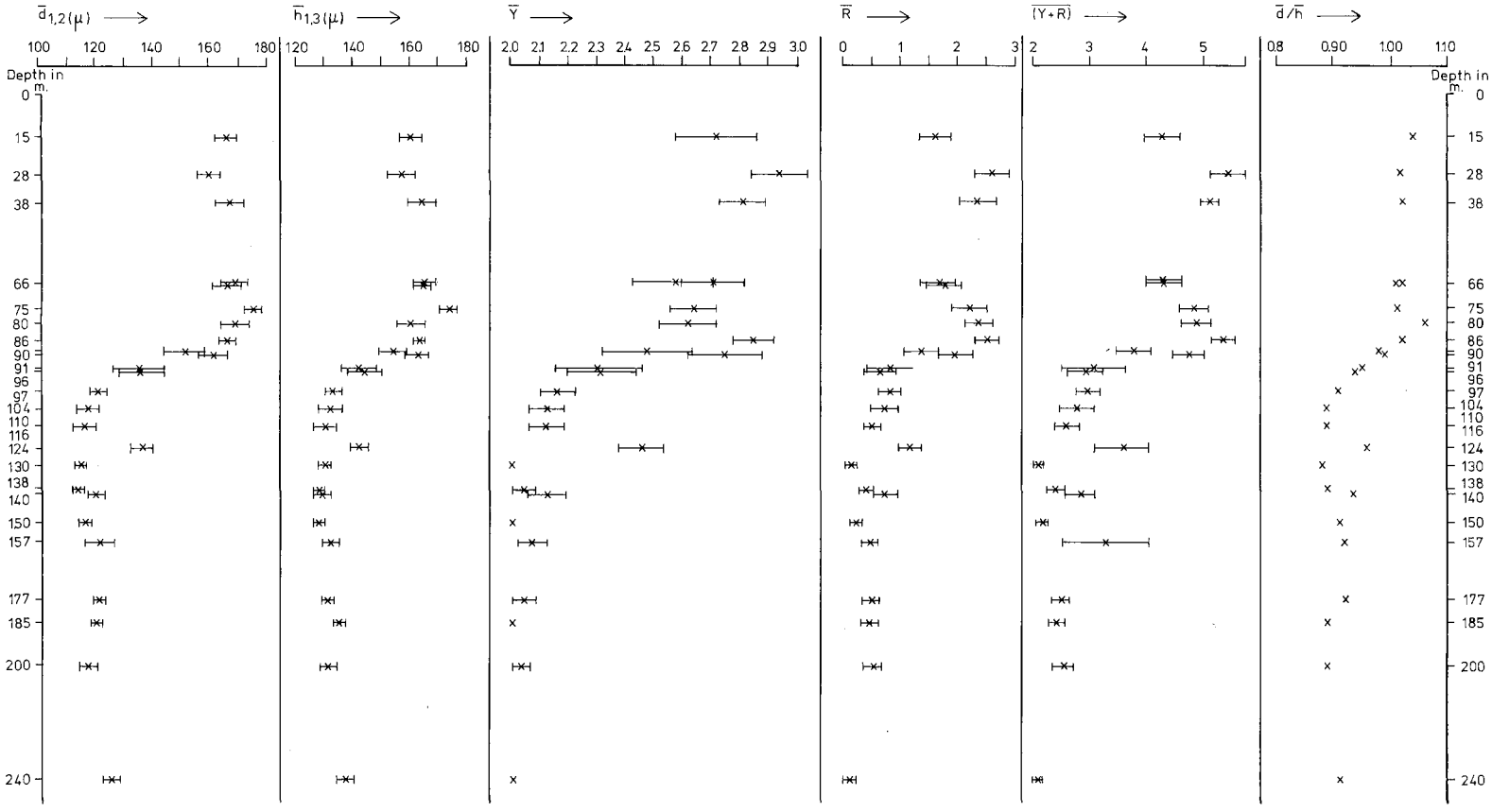


Fig. 8 Depth distribution of the mean values ($\pm$ 1 σ_m) of $d_{1,2}$, $h_{1,3}$, Y, R, (Y + R) and of $\bar{d}/\bar{h}$ for all *Planorbulinella* specimens per sample.

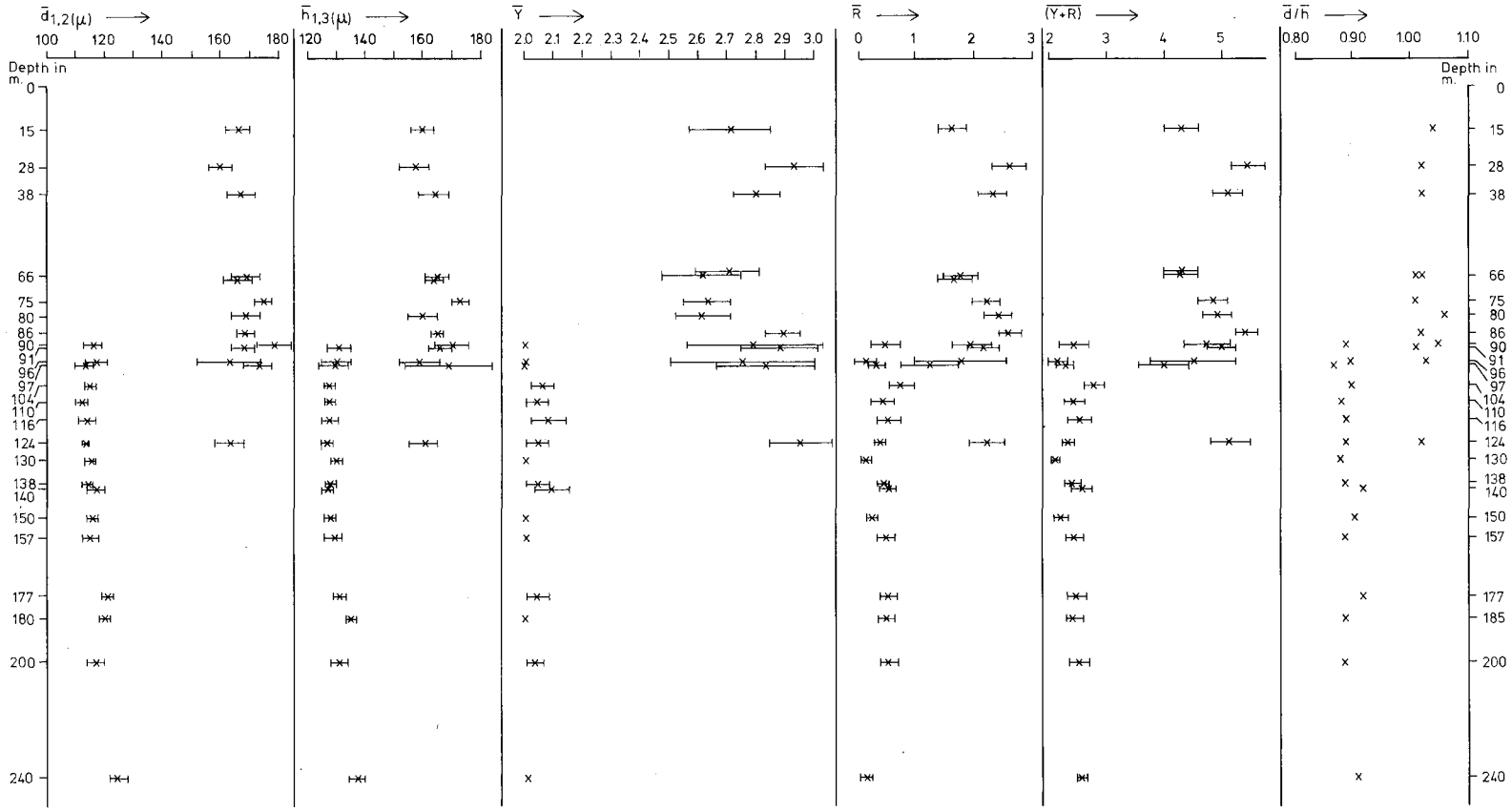


Fig. 9 Depth distribution of the mean values ($\pm$ 1 σ_m) of $d_{1,2}$, $h_{1,3}$, Y, R, (Y + R) and of $\bar{d}/\bar{h}$ for *Planorbulinella larvata* and *P. elatensis* separately.

themselves are significantly different.

It is remarkable, that in the deeper living group 2, the deepest sample, from 240 meters, is the most extreme, with the largest $\bar{d}_{1,2}$ and $\bar{h}_{1,3}$ values within the entire group. There is however no trend of sustained change with depth. Evidently, the suggestion of trends in embryon size in each of the groups is so weak that the mean values per group give a pattern of random variation.

So it seems, that each group of samples comes from a population, within which considerable variation does exist. This variation gives a fairly continuous range of mean values; there are no "gaps" in the values within either of the populations, whereas a very large "gap" is present between both.

Having established now beyond reasonable doubt that two different biometric groups do exist, we can turn our attention to the problem of the somewhat confused data from the intermediate depth range. The samples from 96 and 97 meters depth, which have nicely intermediate mean values, consist of too few specimens. Therefore only the samples from 90 and 124 meters could be used. The same goodness-of-fit test used before was applied again to test the possibility that the populations represented in these samples are normally distributed. A very different picture appears if one compares table 6 with table 4. The probability that the $d_{1,2}$ values of the specimens of these samples fit to a normal distribution is less than one percent. A closer look at table 6 shows that in both samples the largest contribution to the Chi-square values has been furnished by the same class of $d_{1,2}$ values, the class from about 120 to 160 μ. In both cases the observed frequencies are too low. This evidence, combined with the evidence of all the samples (fig. 5), strongly suggests bimodality in the $d_{1,2}$ distributions of the intermediate samples. These intermediate samples thus contain a mixture of both groups of *Planorbulinella*; they are heterogeneous.

From the scatter-diagrams it becomes apparent, that while only four samples contain about equal numbers of individuals of the two groups, there are some other samples that consist predominantly of specimens of one group, but which are "contaminated" with a few specimens of the other (table 7). New mean values and standard errors have been computed for these samples, after elimination of the few "misplaced" individuals. These new values thus are based on the specimens belonging only to the dominant group in the sample. The samples from 90, 96, 97 and 124 meters were split into two parts, for each of which mean values were calculated (table 8). With these values a new figure with mean parameter values versus depth was prepared (figure 9). In table 9 the corrected correlation coeffic-

ients are shown for the cleaned or split assemblages of formerly mixed associations. In all samples containing *Planorbulinella* specimens from group 1 a significant negative correlation of $d_{1,2}$ and Y, and of $d_{1,2}$ and (Y + R) at a confidence level of 5% is now apparent. In the samples with *Planorbulinella* belonging to group 2 these corrected correlation-coefficients have much lower values and are but rarely significant. The majority of the r-values are negative, however, especially so for the correlation between $d_{1,2}$ and (Y + R) in which only one insignificant positive value remains. The high positive values in the intermediate depth range (table 3) all have disappeared. They were evidently due to mixing of both groups.

Considering the relative proportions of both groups in the continuous sequence of samples from 86 meters down to 104 meters, one may assume a gradual change from associations with predominance of individuals belonging to group 1 to others in which specimens of group 2 outnumber those of group 1. At greater depths no further trend is detectable from decreasing numbers of individuals of group 1 with increasing depth. In samples below 160 meters not a single specimen of group 1 has been found anymore. Probably the depth range from about 85 to 105 meters corresponds to the zone of overlap between the habitats of both groups of *Planorbulinella,* whereas the occurrences of specimens of group 1 at greater depth may be considered the result of down-slope displacement. The last-mentioned explanation certainly is the most likely one for the unexpected high number of group 1 individuals in the sample from 124 meters.

TAXONOMY

The presence of two biometrically different and separable groups of *Planorbulinella* in the Gulf of Elat raises a taxonomic problem. In the literature about the foraminiferal fauna of the Gulf of Elat, as well as in the literature on recent *Planorbulinella* from other places in today's oceans only one species is mentioned, viz. *Planorbulinella larvata* (Parker & Jones). In the type description by Parker and Jones and in the description by Cushman (1927), in which he created the genus *Planorbulinella,* no details on the internal features are presented. Freudenthal (1969), in his review of the genus *Planorbulinella,* investigated the internal characteristics of rather few specimens of *P. larvata* from a number of localities in the Western Pacific and from the Gulf of Elat. If we compare Freudenthal's results of counts and measurements with ours, it appears that the group-1 *Planorbulinella* is very close to or near-identical with Freudenthal's *P. larvata* (Parker & Jones).

His mixed sample value for $\bar{Y}$ is somewhat lower (2.35 ± 0.13), for $\bar{d}_{1,2}$ slightly higher (178.3 μ ± 6.0). There is no reason for hesitation to give the specific name *P. larvata* to the shallower group-1 *Planorbulinella* of the Gulf of Elat.

Nowhere in the literature there are reports of Recent *Planorbulinella* that resembles our group 2. Therefore it was decided to create the new species *P. elatensis,* which thus far is no more than a group of populations, based on morphology only and separable from *P. larvata* on biometrical grounds. It cannot be decided with certainty whether *P. elatensis* is a separable biological species, but as *P. larvata* and the new species occupy different habitats (different depths) in the Gulf of Elat, this type of separation is probable.

One might imagine that both Elat species still belong together in one biological species, different for some dubious reason in, for instance, one step in primordial protoplasma fission, if such a thing would be plausible. Considering the near-globular shape of the embryon, the mean $d_{1,2}$ values of both groups lead to a volume proportion of about three to one, which does not make sense. Some other factors, such as the admittedly small, but consistent difference in $\bar{d}_{1,2}/\bar{h}_{1,3}$ values, and the distinct difference in $\bar{Y}$ and $\bar{R}$ values against the general negative correlation with embryonic size parameters, also favour the assumption of the presence of two distinct species in the biological sense.

The possibility that the differences in internal characters of the embryon, number of chambers, etc. is due to the presence of different sexual and asexual generations of one species (trimorphism?) has been considered, but rejected, because in that case we would deal with four forms, 2 megalospheric and 2 microspheric.

Planorbulinella elatensis nov. spec.

Textfig. 10, 11a, plate 1, fig. 3, 4, plate 2, fig. 1, 2, plate 3, fig. 3

Derivatio nominis: named after the Gulf of Elat, Aqaba.
Holotype: fig. 10a, b, coll. no. T 300.
Paratypoids: coll. no. T 301–303.
Type locality: sample HU 4948, waterdepth 177 meters, situated in the Gulf of Elat, in the Coral Island area.
Type level: Recent.
Occurrence: as yet only known in the Gulf of Elat, at depths from about 90 to 240 meters.

Depository: Micropaleontological collections Geological Institute, State University of Utrecht.

Diagnosis: a *Planorbulinella* species resembling *P. larvata* (Parker & Jones) in external features, but with smaller $\overline{Y}$-values and smaller first three chambers.

Description: *External features.* The test is discoidal, neatly rounded in outline, with maximum diameter about 1.60 mm., flattened at both sides, slightly planoconvex or concavoconvex. Both sides are provided with pustules. The flat to slightly concave side frequently bears only few and small pustules, especially small or even absent in the central part of the test. In the centre of the more convex side the pustules often coalesce to a rather irregular pattern. On this convex side the pustules are in most cases largest in the center, on the opposite side their maximum size is attained about halfway between centre and periphery. Chambers near the periphery lack pustules, commonly one row on the convex side, often two or three rows from the periphery inwards on the other side. On both sides these smooth chambers show numerous large pores. The peripheral chambers have arched, interiomarginal apertures, two to a chamber, each opening being provided with an imperforate lip.

Internal features: Only slight variation exists in the configuration of the early three chambers. The majority of the specimens possess a Y-value of two, Y = 3 occurs but rarely. Other values than Y = 2 and Y = 3 have not been observed. The mean values of Y range from 2 to 2.12. Relapse to the one-stolon system in the later chambers of the nepionic part of the test does occur, but only in relatively few specimens. R-values range from 0 to 4, $\overline{R}$-values from 0.11 to 0.75. The (Y + R)-values range from 2 to 6, mean values for this parameter from 2.11 to 2.84.

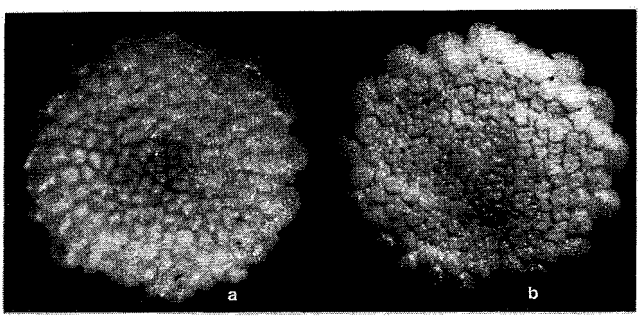


Fig. 10. Holotype of *Planorbulinella elatensis* from 177 m, Gulf of Elat. x 25. Coll. no. T 300. a. ventral side, b. dorsal side.

Plate 1

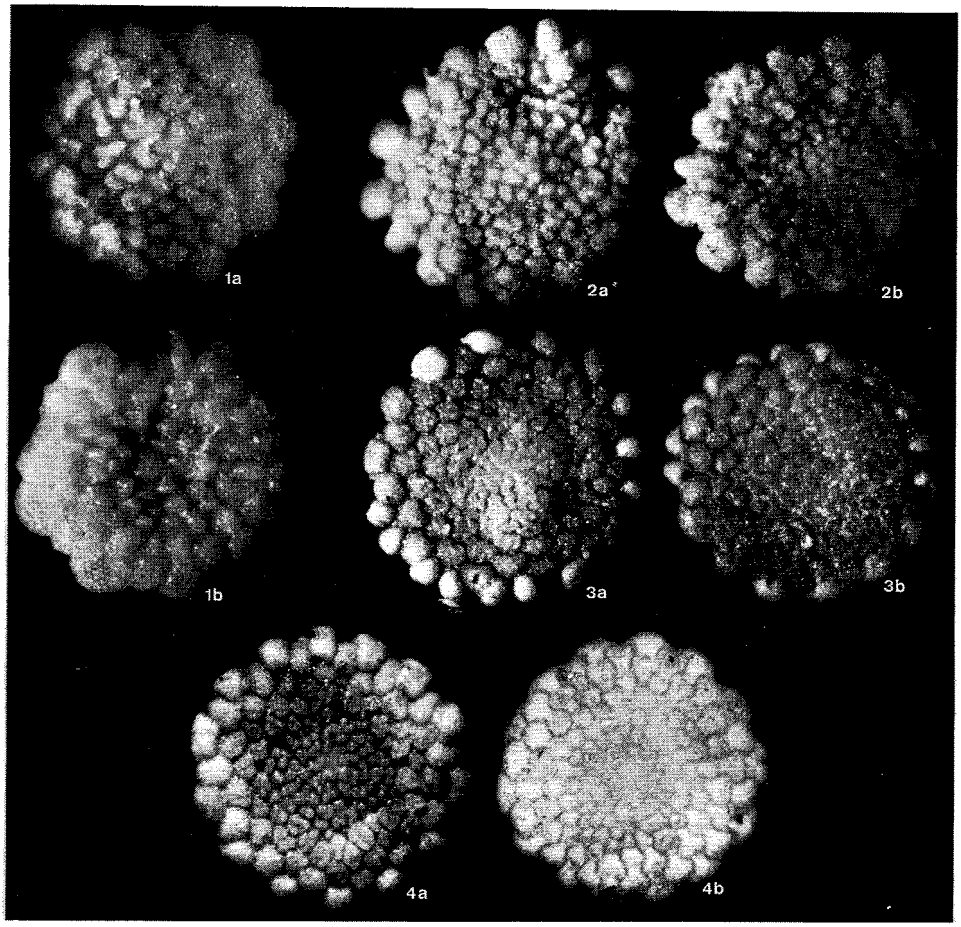


Plate 1. External views.

Fig. 1, 2 *Planorbulinella larvata* (Parker en Jones), Gulf of Elat, 28 m. fig. 1, x 35; fig. 2, x 18.

Fig. 3, 4 *Planorbulinella elatensis* n.sp., Gulf of Elat, 177 m., x 25.
a. dorsal views; b. ventral views.

The first three chambers are relatively small. The $d_{1,2}$ values range from 70 to 155 μ, the mean values for $d_{1,2}$ from 112 to 125 μ. For the parameter $h_{1,3}$ ranges are between 90 and 165 μ, and the means of this parameter range between 125 and 137 μ. The protoconch and deuteroconch are rounded, the third chamber is semicircular in section. For all examined samples the mean

$d_{1,2}$ value is smaller than the mean $h_{1,3}$ value. In all samples there is a clear positive correlation between $d_{1,2}$ and $h_{1,3}$. A negative or positive correlation between $d_{1,2}$ and Y cannot be demonstrated for the majority of the samples. In a few cases there is a negative correlation of low significance. In the $d_{1,2}$ versus (Y + R) relation negative correlation occurs more regularly but again it is of no statistical significance in the majority of the samples.

In many individuals the first three chambers, or these first chambers and the nepionic part of the test and sometimes even including some chambers outside the nepionic part of the test, are provided with a brown, chitinous inner lining, visible from the outside as a vague, brown spot in the centre of the test. Sometimes the first three chambers together have a slightly thickened wall. The first chambers are always situated in the centre of the test, towards the convex side.

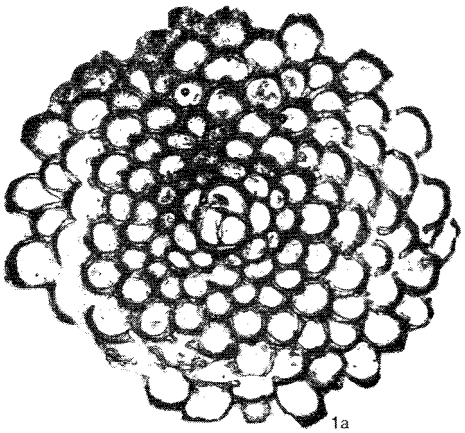
The chambers outside the nepionic part of the test increase regularly in size towards the periphery and they have a very regular arrangement.

Twin specimens are rare but do occur. Also microspheric specimens are scarce; some three percent of all studied specimens are microspheres. In the different samples these percentages range from zero to about 10 percent.

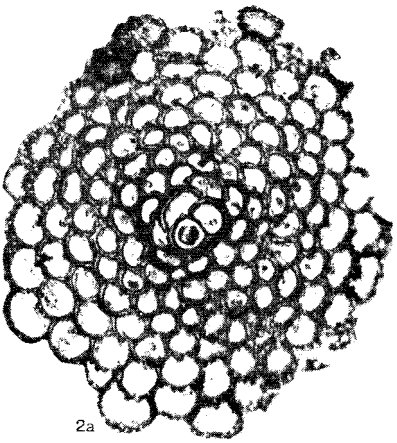
Remarks: On external features the distinction between *P. larvata* and *P. elatensis* is but rarely feasible. The *P. larvata* individuals from Elat and from the Pacific (according to Freudenthal's data) may be larger (up to 2.5 mm) than the *P. elatensis* specimens. In our material the *P. larvata* individuals are often not flattened but queerly twisted, oval rather than rounded in outline. The peripheral chambers in *P. larvata* are often of irregular shape and/or arrangement (plate 1).

On internal characteristics the distinction is easier (fig. 11). Y and R values are more variable in *P. larvata* than in *P. elatensis*. Y ranges from 1 (observed only once) to 6; values 3 and 2 are most frequent (plate 2, fig. 3, 4). $\bar{Y}$ ranges from 2.50 to 2.95. R-values of *P. larvata* range from 0 to 6, and the mean values from 1.17 to 2.58. The value R is equal to zero is exceptional. For the parameter (Y + R) the ranges are between 2 and 9, the mean values range from 4.00 to 5.50. The $d_{1,2}$ and $h_{1,3}$ ranges of *P. larvata* and *P. elatensis* show a certain amount of overlap, but specimens of *P. larvata* with Y = 2 have much larger $d_{1,2}$ values than comparable individuals of *P. elatensis*; confusion should be impossible. $d_{1,2}$-values for *P. larvata* range from 108 to 224 μ, means from 160 to 179 μ. For $h_{1,3}$ the ranges are from 97 to 232 μ, with means between 157 and 178 μ. In *P. larvata* mean $d_{1,2}$-values are larger than mean $h_{1,3}$ values for all samples. In *P. larvata* the shape of the third chamber is often much less clearly semicircu-

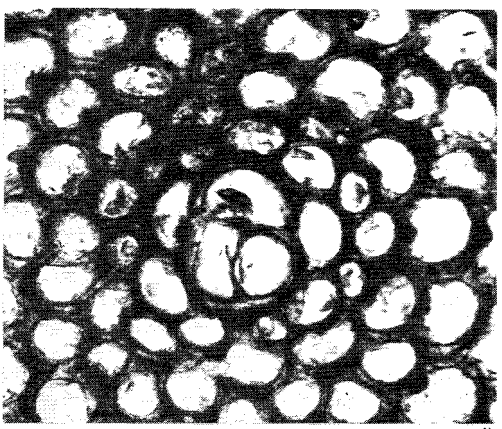
Plate 2



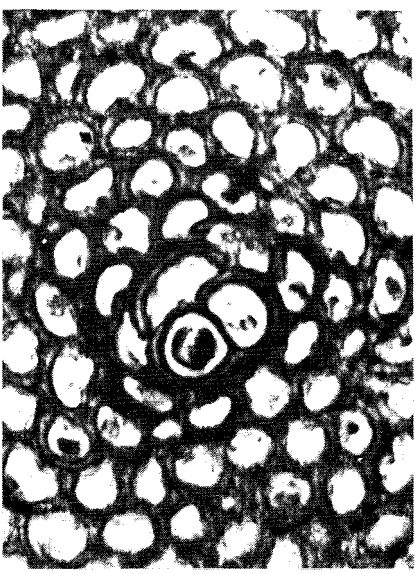
1a



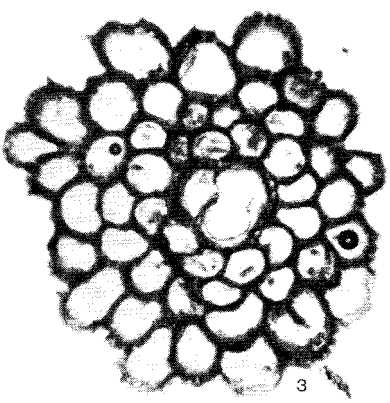
2a



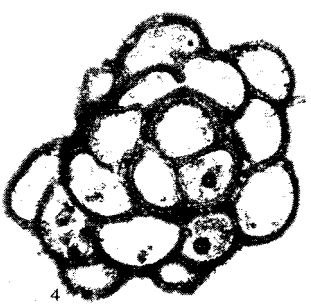
1b



2b



3



4

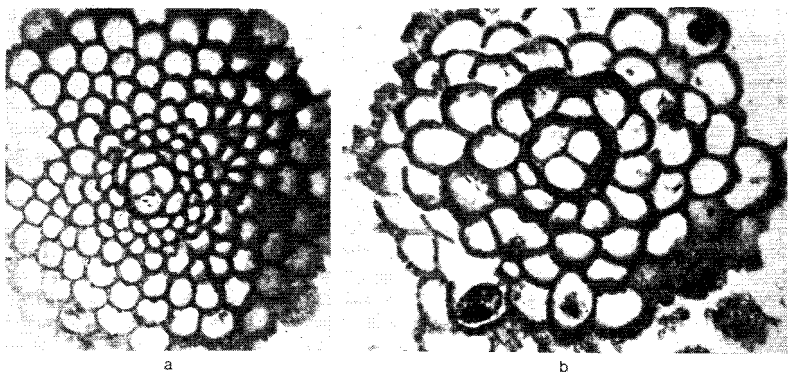


Fig. 11 Median sections of megalospheric *Planorbulinella elatensis* (138 m, a) and *P. larvata* (66 m, b) at the same enlargement of x 50.

lar in section. In *P. larvata* the first chambers often do not occupy the centre of the test but are situated somewhat eccentrically. In our material twin specimens of *P. larvata* were not observed.

Also outside the nepionic part of the test differences exist. The equatorial chambers in *P. larvata* are more irregularly arranged and relapse to the one-stolon system outside the nepionic part of the test is rather frequent. Outside the nepionic part of the test such relapses are very rare in *P. elatensis*. In *P. larvata* the chambers are larger than in *P. elatensis*, and they increase only slightly and rather irregularly in size from the centre towards the periphery.

On the basis of differences in chamber size and regularity in chamber arrangement it appears to be possible to differentiate microspheric specimens of both species. Microspheric individuals belonging to *P. larvata* (plate 3, fig. 1, 2) are more frequent than those belonging to *P. elatensis* (plate 3, fig. 3). From all *P. larvata* specimens studied about 27% are microspheres. This percentage ranges from three to thirty in the different samples.

Plate 2. Median sections megalospheric specimens.

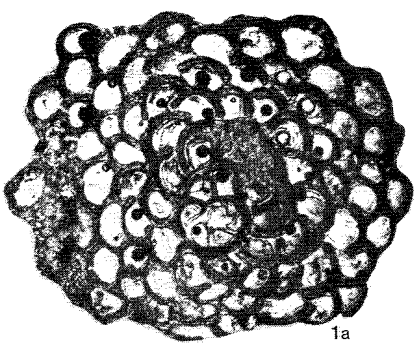
Fig. 1 *Planorbulinella elatensis* n.sp., Gulf of Elat, 177 m., a. x 50; b. x 115.

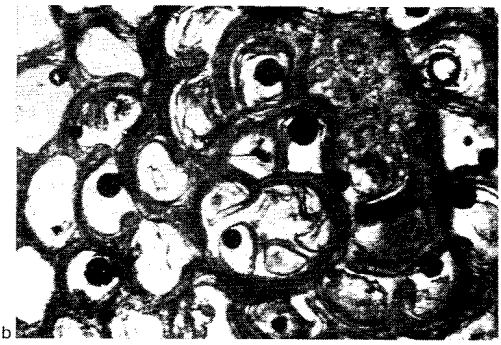
Fig. 2 *Planorbulinella elatensis* n.sp., Gulf of Elat, 177 m., a. x 50; b. x 115.

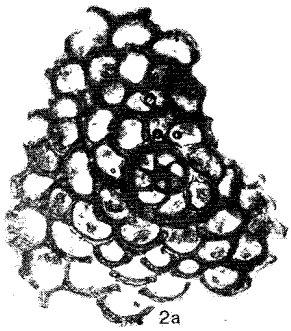
Fig. 3 *Planorbulinella larvata* (Parker and Jones), Gulf of Elat, 124 m., x 56.

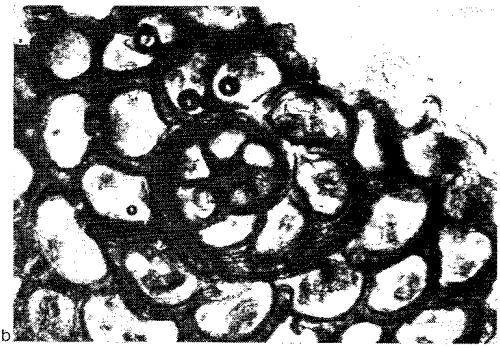
Fig. 4 *Planorbulinella larvata* (Parker and Jones), Gulf of Elat, 66 m., x 76.

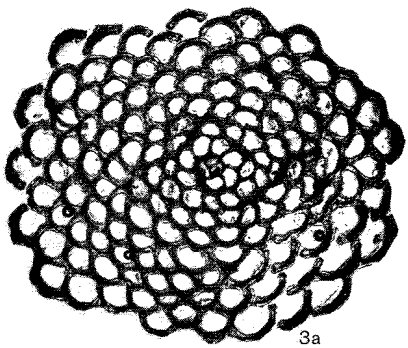
Plate 3


1a


1b


2a


2b


3a

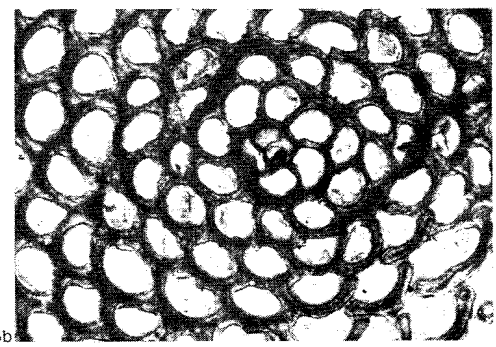

3b

Plate 3. Median sections microspheric specimens.

Fig. 1 *Planorbulinella larvata* (Parker and Jones), Gulf of Elat, 66 m. a. x 46; b. x 100.

Fig. 2 *Planorbulinella larvata* (Parker and Jones), Gulf of Elat, 86 m. a. x 46; b. x 100.

Fig. 3 *Planorbulinella elatensis* n.sp., Gulf of Elat, 200 m. a. x 46; b. x 100.

Since two distinct species are recognized in the Gulf of Elat, the sudden drop in size of the embryonic chambers at about 90 meters depth has no contradictory value for the hypothesis of size increase with greater depth. Within each species there are indications of size increase of $\bar{d}_{1,2}$ towards deeper water, but these indications are of dubious nature considering the

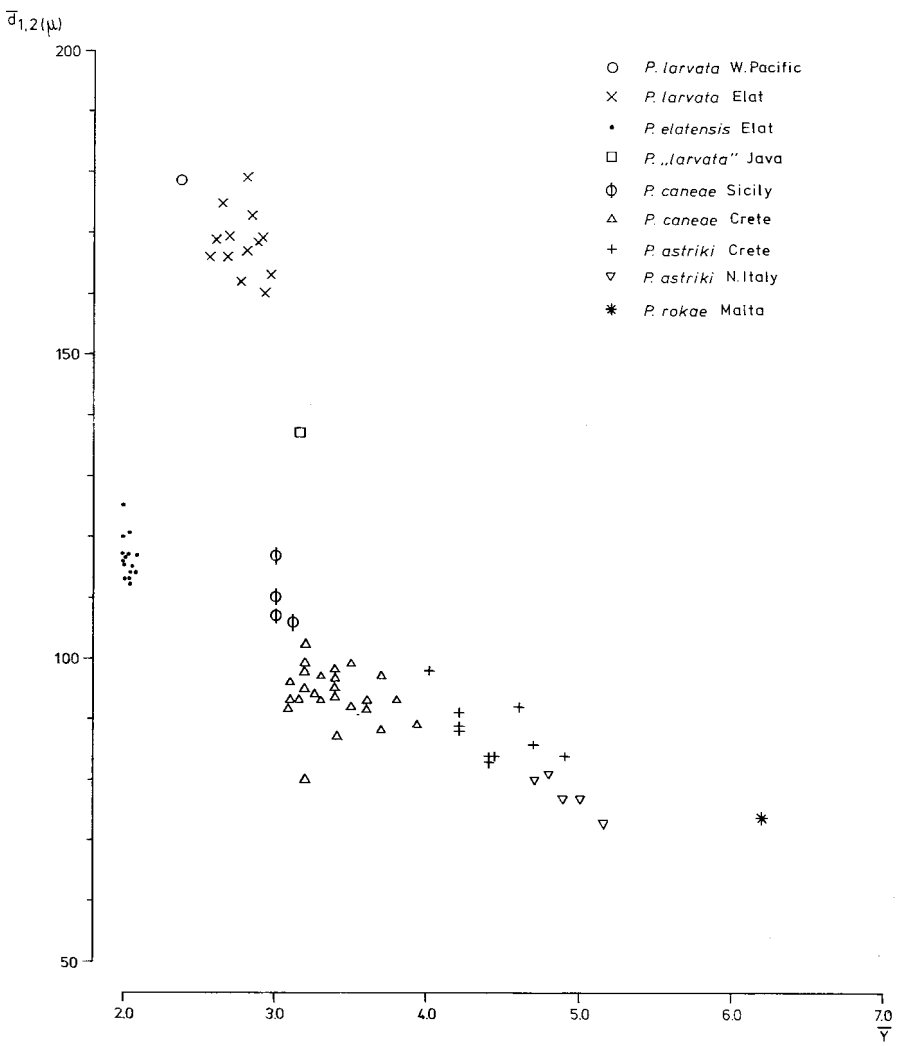


Fig. 12 $\bar{d}/\bar{Y}$ scatter diagram of all described *Planorbulinella* assemblages.

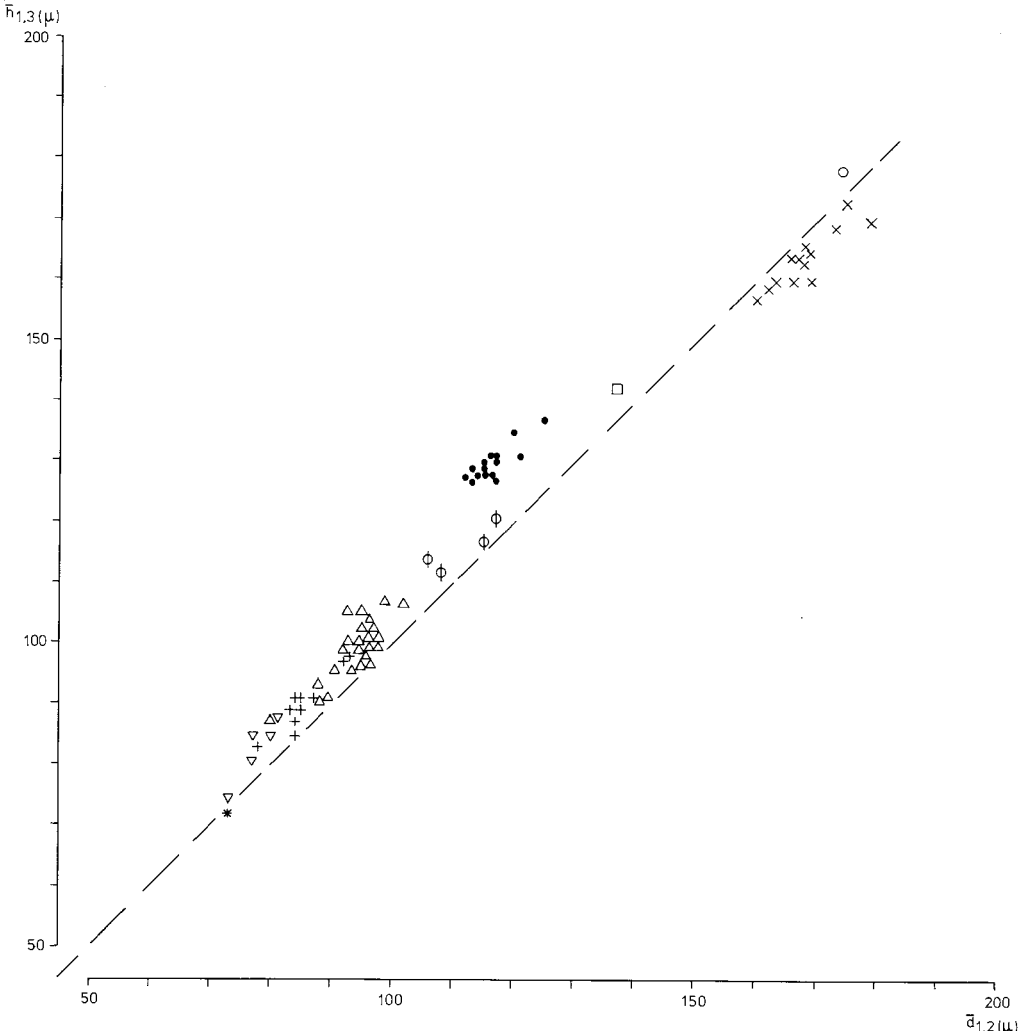


Fig. 13 $\bar{d}_{1,2}/\bar{h}_{1,3}$ scatter diagram of all described *Planorbulinella* assemblages. For explanation of the symbols see fig. 12.

fluctuating pattern. Since $d_{1,2}$ and Y, and $d_{1,2}$ and (Y + R) show variable negative correlation one might expect $\bar{Y}$ and $(\overline{Y+R})$ to decrease with depth in each of the species, which would invalidate to a certain extent the major yardstick of measuring the evolutionary level of populations. Especially for the shallower *P. larvata* group of assemblages such a decreasing tendency may be present (fig. 9), but the wide fluctuations again render such a change with depth doubtful. If one considers the actual values calculated, we had better allow for some 15 percent inaccuracy range on the calculated mean

of any sample if we wish to conclude on its relative position in the lineage.

The data Freudenthal gathered in 1969 led him to the acceptance of one *P. larvata* lineage, from his Middle Miocene *P. rokae* to the Recent species. In this lineage Drooger (1974) thought to see another example of hyperbolic trends in the $\bar{d}/\bar{Y}$ changes in the course of the evolution of orbitoidal larger foraminifera. Plotting again Freudenthal's data together with the new ones (figs. 12, 13) serious doubt may be expressed about the validity of the theories of both these earlier authors. The fairly straight "development" line which may be drawn through the clusters of means of Maltese, North Italian, Sicilian and Cretan assemblages seems to lead directly to the recent *P. elatensis*. A possible connection between the Miocene group of species and the Recent *P. larvata* from the Gulf of Elat and the Western Pacific is indicated by Freudenthal's data from Java only; this if one wishes to assume that both Recent species had a common Miocene ancestor. The assumption that *P. elatensis* is a relic of the Miocene Mediterranean *Planorbulinella* group and *P. larvata* a recent Indo-Pacific species of unknown origin, is no more than an attractive speculation. It is certainly worthwhile to consider this speculation in the reinvestigation of Miocene Cretan *Planorbulinella* (D.S.N. Raju, in preparation). In this context it is worth mentioning that *P. larvata* from the Gulf of Elat is also different in $\bar{d}/\bar{h}$ relation from the Mediterranean Miocene forms and *P. elatensis* (fig. 13).

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depth (meters)	*field nr.*	*HU nr.*	*way of sampling*	*environment*	*locality*
15	HR 37	HU 5139	by hand	reefflat & slope	Ras Muhammed
28	71161	HU 4943	dive	coral	Coral Island
38	71160	HU 4942	dive	coral	Coral Island
66 (1)	71012	HU 4859	grab	Halophila	Coral Island
66 (2)	71159	HU 4941	grab	coral	Coral Island
75	–	HU 5210	Willemoes'	not known	Ras Atantur (Wadi Kid)
80	–	HU 5211	Willemoes'	not known	Ras Atantur (Wadi Kid)
86	71157	HU 4939	grab	mud	Coral Island
90	73310	HU 5250	grab	not known	off Biol. Stat. Elat
91	71051	HU 4867	grab	mud	Coral Island
96	HR 8	HU 4804	grab	beige Operculina clay	Coral Island to Wadi Taba
97	–	HU 5213	Willemoes'	not known	Ras Atantur (Wadi Kid)
104	71148	HU 4930	grab	mud	off Biol. Stat. Elat
110	71149	HU 4931	grab	mud	off Biol. Stat. Elat
116	71017	HU 4876	grab	rocky bottom	Coral Island
124	71063	HU 4831	grab	sandy mud	South of Coral Island
130	71168	HU 4803	grab	sandy mud	Coral Island to Wadi Taba
138	71168	HU 4950	grab	sandy mud	Coral Island
140	71053	HU 4760	grab	sandy mud	Coral Island
150	71019	HU 4772	grab	rocky bottom	Coral Island
157	71165	HU 4947	grab	sandy mud	Coral Island
177	71166	HU 4948	grab	sandy mud	Coral Island
185	71198	HU 4977	grab	sandy mud	Coral Island
200	71018	HU 4854	grab	sandy mud	Coral Island
240	HR 4	HU 4800	grab	sandy mud	Coral Island to Wadi Taba

Table 1. List of samples

depth	n	$\bar{d}_{1,2}$ (μ)	se_m	range $d_{1,2}$	$\bar{h}_{1,3}$ (μ)	se_m	range $h_{1,3}$	$\bar{Y}$	se_m	range Y	$\bar{R}$	se_m	range R	$(\overline{Y+R})$	se_m	range (Y+R)	$\bar{d}_{1,2}/\bar{h}_{1,3}$
15	17	166	4	138–191	160	4	133–195	2.71	0.14	1–3	1.59	0.26	0–4	4.29	0.31	2–7	1.04
28	29	160	4	112–209	157	5	97–204	2.93	0.10	2–5	2.58	0.29	0–6	5.45	0.29	3–9	1.02
38	25	167	5	116–232	164	5	112–232	2.80	0.08	2–3	2.32	0.26	0–4	5.12	0.27	2–7	1.02
66 (1)	24	169	5	108–212	165	4	116–212	2.70	0.11	2–4	1.67	0.29	0–6	4.33	0.30	2–9	1.02
66 (2)	25	166	5	133–229	164	3	133–203	2.56	0.14	2–5	1.76	0.29	0–4	4.32	0.29	2–6	1.01
75	40	175	3	128–224	173	3	138–224	2.63	0.08	2–3	2.20	0.27	0–7	4.83	0.26	2–9	1.01
80	24	169	5	122–224	160	5	117–219	2.61	0.10	2–3	2.36	0.25	0–5	4.92	0.24	3–7	1.06
86	57	166	3	112–214	163	2	128–194	2.84	0.07	2–5	2.48	0.19	0–5	5.34	0.19	3–8	1.02
90	31	151	7	102–224	154	5	107–219	2.47	0.16	2–6	1.34	0.26	0–4	3.81	0.32	2–7	0.98
91	26	161	5	102–204	162	4	122–209	2.74	0.13	2–4	1.96	0.26	0–6	4.73	0.27	2–8	0.99
96	10	135	9	102–189	142	6	112–179	2.30	0.15	2–3	0.80	0.42	0–4	3.10	0.55	2–7	0.95
97	16	136	8	97–194	144	6	112–194	2.31	0.12	2–3	0.63	0.24	0–3	2.94	0.28	2–5	0.94
104	38	121	3	92–179	133	3	107–194	2.16	0.06	2–3	0.82	0.17	0–4	2.97	0.19	2–6	0.91
110	26	117	4	97–173	132	4	102–173	2.12	0.06	2–3	0.69	0.25	0–5	2.81	0.29	2–8	0.89
116	26	116	4	79–162	130	4	91–179	2.12	0.06	2–3	0.50	0.17	0–3	2.62	0.19	2–5	0.89
124	47	136	4	97–194	142	3	107–199	2.45	0.08	2–4	1.15	0.21	0–6	3.57	0.43	2–9	0.96
130	26	115	2	97–128	130	2	112–148	2	–	2	0.12	0.06	0–1	2.12	0.06	2–3	0.88
138	26	114	2	97–138	128	2	112–153	2.04	0.04	2–3	0.38	0.12	0–2	2.42	0.14	2–4	0.89
140	25	120	3	97–153	129	3	107–158	2.12	0.07	2–3	0.72	0.23	0–4	2.84	0.26	2–7	0.93
150	27	116	2	91–145	128	2	112–154	2	–	2	0.22	0.08	0–1	2.19	0.08	2–3	0.91
157	27	121	5	92–204	132	3	107–179	2.07	0.05	2–3	0.46	0.15	0–2	3.31	0.76	2–4	0.92
177	26	121	2	107–138	131	2	112–153	2.04	0.04	2–3	0.48	0.14	0–2	2.52	0.14	2–4	0.92
185	27	120	2	107–138	135	2	112–163	2	–	2	0.44	0.14	0–2	2.44	0.14	2–4	0.89
200	29	117	3	82–148	131	3	97–163	2.03	0.03	2–3	0.52	0.15	0–4	2.55	0.18	2–6	0.89
240	18	125	3	102–143	137	3	107–153	2	–	2	0.11	0.08	0–1	2.11	0.06	2–3	0.91

Table 2. Mean values, standard errors of the mean and ranges of $d_{1,2}$, $h_{1,3}$, Y, R, (Y+R), and a separate column for $\bar{d}_{1,2}/\bar{h}_{1,3}$ values.

depth	n	$d_{1,2}/h_{1,3}$			$d_{1,2}/Y$			$d_{1,2}/(Y+R)$		
		r	a	b	r	a	b	r	a	b
15	17	**0.76**	45.08	0.70	*– 0.42*	4.99	– 0.01	**– 0.55**	10.65	– 0.04
28	29	**0.92**	0.04	0.98	**– 0.46**	4.66	– 0.11	**– 0.53**	11.25	– 0.37
38	25	**0.92**	10.26	0.93	**– 0.44**	4.05	– 0.01	*– 0.35*	8.38	– 0.02
66 (1)	24	**0.94**	38.02	0.76	**– 0.41**	4.23	– 0.01	**– 0.66**	10.75	– 0.04
66 (2)	25	**0.81**	68.42	0.58	**– 0.49**	5.05	– 0.01	– 0.13	5.66	– 0.01
75	40	**0.86**	3.37	0.79	**– 0.34**	4.07	– 0.08	**– 0.41**	10.58	– 0.34
80	24	**0.86**	2.19	0.82	**– 0.55**	5.38	– 0.17	*– 0.35*	7.79	– 0.17
86	57	**0.87**	4.64	0.70	– 0.00	2.85	– 0.00	– 0.22	7.63	– 0.14
90	31	**0.95**	3.87	0.75	– 0.02	2.53	– 0.00	0.16	2.75	0.07
91	26	**0.86**	3.81	0.76	0.05	2.52	0.01	0.05	4.33	0.03
96	10	**0.96**	4.95	0.68	0.47	1.18	0.08	0.25	0.96	0.16
97	16	**0.91**	4.68	0.71	**0.84**	0.61	0.13	**0.67**	–0.25	0.24
104	38	**0.87**	3.79	0.77	**0.64**	0.67	0.12	0.25	1.14	0.15
110	26	**0.79**	5.77	0.63	**0.60**	0.91	0.11	**0.72**	–3.79	0.58
116	26	**0.86**	23.25	0.92	0.13	1.86	0.00	– 0.11	3.28	– 0.01
124	47	**0.90**	4.43	0.71	**0.50**	1.09	0.13	**0.55**	–0.89	0.34
130	26	**0.63**	5.55	0.64				– 0.20	2.96	– 0.07
138	26	**0.62**	5.91	0.60	*– 0.34*	2.80	– 0.07	– 0.22	4.21	– 0.16
140	25	**0.79**	4.77	0.67	0.24	1.52	0.05	*0.37*	–0.86	0.32
150	27	**0.77**	50.51	0.67				– 0.03	4.21	– 0.16
157	27	**0.71**	7.21	0.48	**0.84**	0.99	0.09	– 0.20	7.08	– 0.32
177	26	**0.39**	7.22	0.47	0.14	1.68	0.03	– 0.25	4.84	– 0.20
185	27	**0.82**	1.35	1.01				– 0.09	6.64	– 0.36
200	29	**0.90**	2.90	0.87	0.00	2.03	0.00	**– 0.53**	6.64	– 0.36
240	18	**0.76**	4.03	0.76				– 0.17	2.74	– 0.04

Table 3. Correlation coefficients and regression line parameters in the formulae:
$h_{1,3} = a + b.d_{1,2}$
$Y = a + b.d_{1,2}$
$(Y+R) = a + b.d_{1,2}$
r values bold type significant at 2.5% level
r values in italics significant at 5% level

depth	class (μ)	f_i	F_i	$(f_i-F_i)^2/F_i$
75 m	$d_{1,2} \leqslant 148$	5	3.6480	0.5011
	$148 < d_{1,2} \leqslant 176$	16	17.0560	0.0650
	$176 < d_{1,2} \leqslant 194$	14	12.2480	0.2560
	$d_{1,2} > 194$	5	7.0480	0.5951
				+
				$\chi^2 = 1.4122$
200 m	$d_{1,2} \leqslant 95$	3	2.0039	0.4951
	$95 < d_{1,2} \leqslant 115$	9	10.7271	0.2781
	$115 < d_{1,2} \leqslant 135$	14	12.7919	0.0944
	$d_{1,2} > 135$	3	3.4797	0.0661
				+
				$\chi^2 = 0.9337$

Table 4. Chi square values in a goodness-of-fit test on normal distributions of $d_{1,2}$ values in the samples from 75 and 200 meters depth.
f_i = observed frequency
F_i = expected frequency
Percentiles of χ^2 distributions.
Number of degrees of freedom = 1, being the number of classes − 3.

χ^2_1:	$P_{97.5}$	P_{99}
	5.02	6.64

depth	class (μ)	f_i	F_i	$(f_i-F_i)^2/F_i$
90 m	$d_{1,2} \leqslant 125$	11	7.1328	2.0967
	$125 < d_{1,2} \leqslant 160$	4	10.7136	4.2070
	$160 < d_{1,2} \leqslant 194$	11	9.0830	0.4046
	$d_{1,2} > 194$	5	4.0675	0.2138
				+
				$\chi^2 = 6.9921$
124 m	$d_{1,2} \leqslant 123$	24	15.7036	4.3831
	$123 < d_{1,2} \leqslant 151$	7	17.1597	6.0152
	$151 < d_{1,2} \leqslant 179$	10	10.8288	0.0634
	$d_{1,2} > 179$	6	3.3041	2.1997
				+
				$\chi^2 = 12.6652$

Table 6. Chi square values in a goodness of fit test on normal distributions of $d_{1,2}$ values in the samples from 90 and 124 meters, to test the suspected heterogeneity of these samples.
f_i = observed frequency
F_i = expected frequency
Percentiles of the χ^2 distributions.
Number of degrees of freedom = 1, being the number of classes − 3.

χ^2_1:	$P_{97.5}$	P_{99}
	5.02	6.64

pairs of samples	t-values	degrees of freedom
28 – 75	– **2.82**	29
28 – 80	– 1.35	24
28 – 130	**9.74**	26
28 – 177	**8.44**	26
28 – 200	**8.45**	29
28 – 240	**7.01**	18
75 – 80	0.99	24
75 – 130	**16.56**	26
75 – 177	**14.91**	26
75 – 200	**13.76**	29
75 – 240	**12.22**	18
80 – 130	**10.00**	24
80 – 177	**8.88**	24
80 – 200	**8.94**	24
80 – 240	**7.69**	18
130 – 177	– *2.40*	26
130 – 200	0.61	26
130 – 240	– **3.18**	18
177 – 200	1.21	26
177 – 240	– 1.27	18
200 – 240	– *2.10*	18

Table 5. Difference between $\bar{d}_{1,2}$ values.
t-values in bold type are significent at a 1% level.
t-values in italics are significant at a 2.5% level.
(both tested one sided).

$$t = \frac{(\bar{X}_1 - \bar{X}_2)}{\sqrt{(s_1^2/N_1) + (s_2^2/N_2)}}$$

$\bar{X}_1$ and $\bar{X}_2$ are the mean values of the first and the second sample respectively, s_1 and s_2 are the standard deviations and N_1 and N_2 are the numbers of specimens in the samples.

depth	n (macro)	n_1 (n group 1)	n_2 (n group 2)	n (micro)	n_1 (n group 1)	n_2 (n group 2)
15	17	17 (100 %)	0 (0%)	1	1 (100 %)	0 (0%)
28	29	29 (100 %)	0 (0%)	13	13 (100 %)	0 (0%)
38	25	25 (100 %)	0 (0%)	5	5 (100 %)	0 (0%)
66 (1)	24	24 (100 %)	0 (0%)	5	5 (100 %)	0 (0%)
66 (2)	25	25 (100 %)	0 (0%)	4	4 (100 %)	0 (0%)
75	40	40 (100 %)	0 (0%)	11	11 (100 %)	0 (0%)
80	24	24 (100 %)	0 (0%)	4	4 (100 %)	0 (0%)
86	57	54 (94.7%)	3 (5.3%)	17	17 (100 %)	0 (0%)
90	31	18 (59.4%)	13 (40.6%)	7	7 (100 %)	0 (0%)
91	26	23 (88.5%)	3 (11.5%)	4	4 (100 %)	0 (0%)
96	10	4 (40.0%)	6 (60.0%)	3	3 (100 %)	0 (0%)
97	16	6 (37.5%)	10 (62.5%)	0		
104	38	4 (10.5%)	34 (89.5%)	1	1 (100 %)	0 (0%)
110	26	2 (7.7%)	24 (92.3%)	3	1 (33.3%)	2 (66.7%)
116	26	1 (3.9%)	25 (96.1%)	4	3 (75.0%)	1 (25.0%)
124	47	21 (44.7%)	26 (55.3%)	6	5 (83.3%)	1 (16.7%)
130	26	0 (0%)	26 (100 %)	1	0 (0%)	1 (100 %)
138	26	0 (0%)	26 (100 %)	4	1 (25.0%)	3 (75.0%)
140	25	2 (8.0%)	25 (92.0%)	0		
150	27	0 (0%)	27 (100 %)	3	1 (33.3%)	2 (66.7%)
157	27	2 (7.4%)	25 (92.6%)	0		
177	26	0 (0%)	26 (100 %)	0		
185	27	0 (0%)	27 (100 %)	0		
200	29	0 (0%)	29 (100 %)	1	0 (0%)	1 (100 %)
240	18	0 (0%)	18 (100 %)	0		

all samples	group 1 *P. larvata*	group 2 *P. elatensis*	sum
macrospheres	321	374	692
microspheres	86	11	97
sum	407	392	789

Table 7. Numbers of specimens belonging to group 1 and group 2.

depth	n	$\bar{d}_{1,2}$ (μ)	se_m	$\bar{h}_{1,3}$ (μ)	se_m	$\bar{Y}$	se_m	$\bar{R}$	se_m	$\overline{(Y+R)}$	se_m	$\bar{d}_{1,2}/\bar{h}_{1,3}$
86	54	169	3	165	2	2.89	0.06	2.57	0.20	5.45	0.18	1.02
90 (1)	18	179	6	170	6	2.79	0.24	1.95	0.35	4.74	0.39	1.05
(2)	13	116	3	131	4	2	—	0.46	0.24	2.46	0.24	0.89
91	24	168	4	166	4	2.88	0.13	2.13	0.26	5.00	0.25	1.01
96 (1)	4	163	11	159	7	2.75	0.25	1.75	0.85	4.50	1.04	1.03
(2)	6	117	4	130	5	2	—	0.17	0.17	2.17	0.17	0.90
97 (1)	6	173	5	169	6	2.83	0.17	1.17	0.54	4.00	0.45	1.02
(2)	10	117	3	129	5	2	—	0.30	0.15	2.30	0.15	0.87
104	34	115	2	128	2	2.06	0.04	0.74	0.18	2.79	0.18	0.90
110	24	112	2	128	2	2.04	0.04	0.42	0.17	2.46	0.17	0.88
116	25	114	3	128	3	2.08	0.06	0.48	0.17	2.56	0.19	0.89
124 (1)	21	163	5	160	5	2.95	0.11	2.20	0.33	5.15	0.34	1.02
(2)	26	113	1	127	2	2.04	0.04	0.35	0.11	2.35	0.11	0.89
140	23	117	3	127	2	2.09	0.06	0.48	0.18	2.57	0.18	0.92
157	25	115	3	129	3	2	—	0.46	0.16	2.46	0.16	0.89

Table 8. Mean values, standard errors of the mean of $d_{1,2}$, $h_{1,3}$, Y, R, (Y+R) and a separate column for $\bar{d}_{1,2}/\bar{h}_{1,3}$ values for the mixed samples after correction for the heterogeneity.

depth	n	$d_{1,2}/h_{1,3}$			$d_{1,2}/Y$			$d_{1,2}/(Y+R)$		
		r	a	b	r	a	b	r	a	b
86	54	**0.84**	4.25	0.72	**− 0.30**	4.12	− 0.07	**− 0.59**	12.20	− 0.41
90 (1)	18	**0.95**	− 1.53	1.03	**− 0.63**	7.21	− 0.24	**− 0.72**	12.52	− 0.43
(2)	13	**0.88**	− 0.64	1.84				0.19	0.75	0.15
91	24	**0.82**	1.55	0.89	**− 0.41**	5.14	0.14	**− 0.62**	11.58	− 0.40
96 (1)	4	**0.98**	4.86	0.67	*− 0.80*	5.83	− 0.19	**− 1.00**	20.50	− 1.00
(2)	6	**0.90**	0.68	1.05				*− 0.73*	5.62	− 0.30
97 (1)	6	**0.95**	− 2.63	1.13	0.20	1.70	0.07	− 0.60	13.07	− 0.53
(2)	10	**0.68**	0.40	1.11				− 0.21	2.37	− 0.00
104	34	**0.66**	4.23	0.74	− 0.05	2.13	− 0.00	*− 0.31*	6.12	− 0.00
110	24	**0.46**	6.95	0.51	*− 0.34*	2.86	− 0.08	− 0.03	2.73	− 0.03
116	25	**0.81**	28.27	0.88	− 0.22	2.51	− 0.00	− 0.30	4.52	− 0.02
124 (1)	21	**0.84**	2.31	0.84	**− 0.68**	5.59	− 0.16	**− 0.50**	10.96	− 0.36
(2)	26	**0.59**	3.02	0.85	0.11	1.71	0.03	− 0.07	−2.97	− 0.06
140	23	**0.68**	5.15	0.64	0.02	2.04	0.00	− 0.23	4.43	− 0.16
157	25	**0.43**	7.94	0.42				− 0.08	4.33	− 0.11

Table 9. Correlation coefficients and regression line parameters for the mixed samples after correction for heterogeneity.
r values in bold type significant at 2.5% level
r values in italics significant at 5% level.
Line parameters in formulae:
$h_{1,3} = a + b.d_{1,2}$
$Y = a + b.d_{1,2}$
$(Y+R) = a + b.d_{1,2}$

DEPTH DISTRIBUTION OF AMPHISTEGINA IN THE GULF OF ELAT, ISRAEL

HANS JØRGEN HANSEN AND BJØRN BUCHARDT

ABSTRACT

Four species of *Amphistegina* are shown to be distinctly depth-distributed. Some of the species are shown to contain ultrastructurally different symbiontic algae at different times of the year. It is suggested that primary light sensitivity is the main factor determining the depth distribution.

INTRODUCTION

The amphisteginids are a very abundant foraminiferal group in shallow waters of tropical and subtropical seas. Their geographic distributional limit appears to coincide with the 14° winter isotherm (Larsen, 1976).

The *Amphistegina* group has attracted considerable attention since it is locally a major contributor to carbonate sediment production (Muller, 1974) but also due to the potential value it may have for ecological and paleoecological interpretations.

The present study is in some respects complementary to that of Larsen (1976) in which the taxonomy and ecophenotypical variation was described.

This work is part of the joint "Micropaleontology, Ecology and Paleoecology Program" in the Gulf of Elat coordinated by Prof. Z. Reiss, the Hebrew University, Jerusalem.

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The Marine Biology Station of The Hebrew University, Elat aided in sampling.

Figures 2 and 3 were drawn by Mr. H. Egelund.

Materials and methods

Samples were collected by aid of the Willemoes three-point sampler while plants (mainly *Halophila*) were collected from shallow waters with the assistance of divers from the Marine Biology Station in Elat. In the laboratory naturally coloured specimens were picked and fixed according to standard procedures. Earlier samplings (i.e. prior to September 1976) were fixed in 1–2% glutaraldehyde aboard the ship and the specimens were picked later in the laboratory. The latter method was necessary but yielded, in general, unsatisfactory preservation of the ultrastructures of the soft body.

Ultrasections were cut with either glass knives or diamond knives on LKB ultramicrotome III.

OBSERVATIONS

During the senior author's stay in Israel in 1972–73 profiles were sampled in the northern and southern parts of the Gulf of Elat (fig. 1). The individual

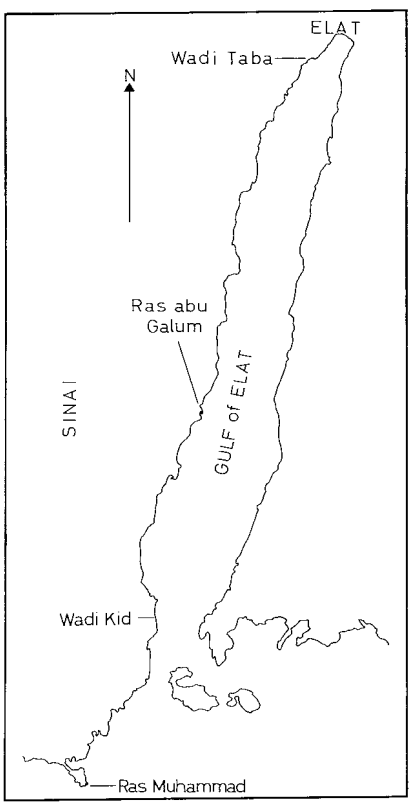

Fig. 1 Location map of sampled area.

samples of the profiles were taken at about 10 meters' depth intervals. The profile at Wadi Taba (fig. 2) covers the depth interval from 4 to 122 meters while the profile north of Wadi Kid (fig. 3) covers the interval from 35 to 150 meters. The sediments at Wadi Taba were described by Perelis (1974).

At Wadi Taba the sedimentation rate in shallow water (i.e. 10 m) appears to be rather high (estimated to be about 3.5 mm/year, Larsen, pers. comm.)

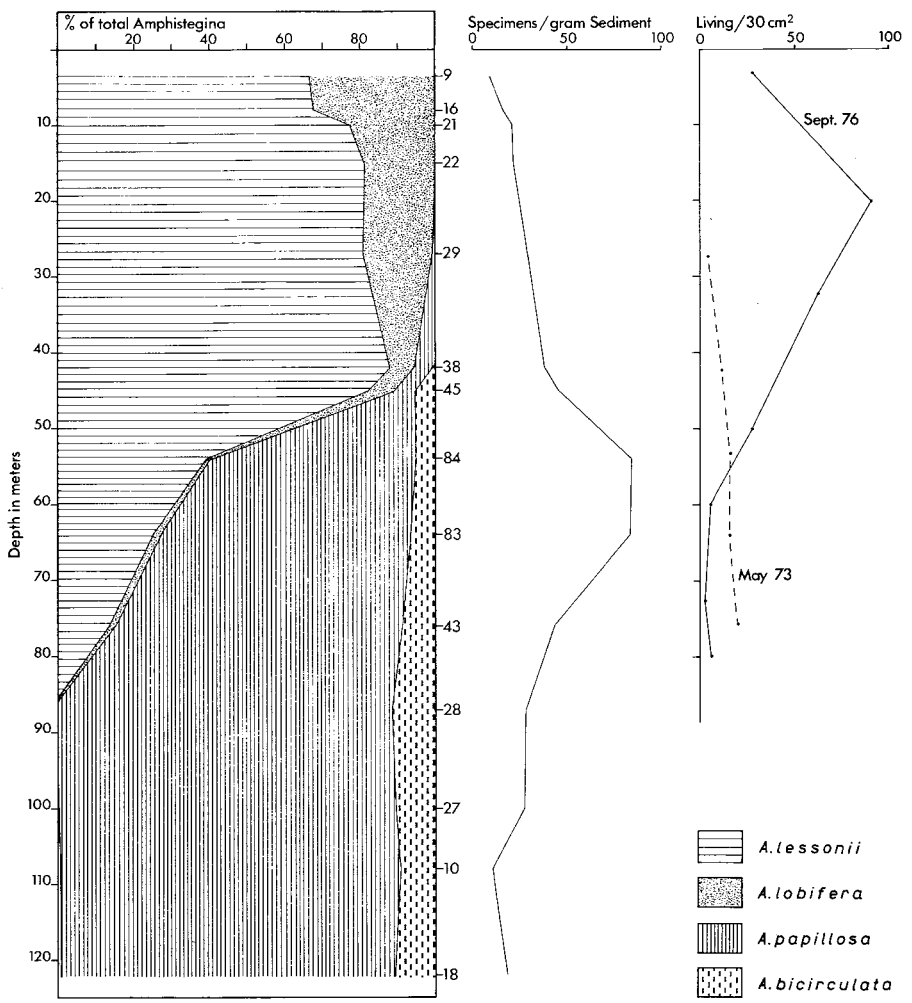

Fig. 2 Depth distribution of *Amphistegina* off Wadi Taba showing standing crop as well as number of dead shells per gram sediment.

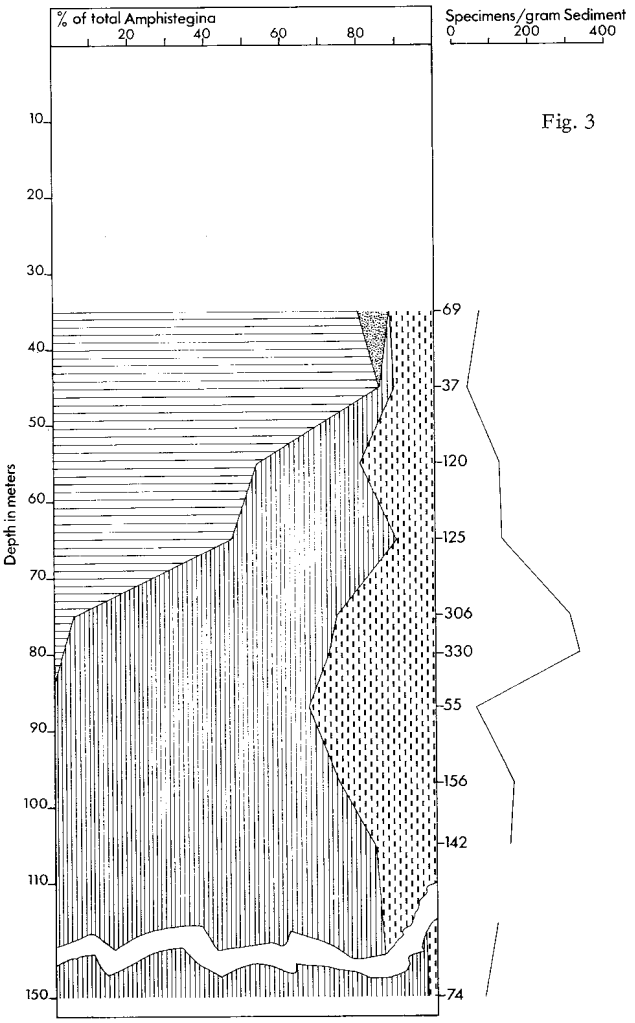

Fig. 3 Depth distribution of *Amphistegina* from north of Wadi Kid.

and the area has a high influx of terrigenous material brought into the sea following the 25 mm/year rainfall, precipitated in a very limited period of time during the winter.

The depth distribution in the sediments of the four species of *Amphistegina* present in the Gulf of Elat namely *A. lessonii, A. lobifera, A. papillosa* and *A. bicirculata* (Larsen, 1976; Larsen and Drooger, this volume), is presented in fig. 2 (off Wadi Taba) and fig. 3 (off Wadi Kid). The counts are shown in percentages of the total number of *Amphistegina* (living and dead).

Each count represents at least 245 specimens and in a few cases as many as 11,000 individuals. There is great similarity between the two profiles although they are separated by a distance of about 150 km.

A. lobifera is rather well represented in the shallowest samples and apparently does not live at depths greater than about 40 meters. *A. lessonii* is the dominant species down to about 40 meters after which its importance decreases down to about 80 meters which appears to be its maximum living depth.

Already at about 30 meters *A. papillosa* makes its appearence being dominant from about 60 meters to more than 120 meters. 122 meters is the greatest depth at which living *A. papillosa* were found.

A. bicirculata is less well represented in the Wadi Taba profile than in the southern profile at Wadi Kid. At Wadi Taba it does not occur shallower than 40 meters, whereas it appears at even shallower depths in the southern profile. Samples from depths of less than 10 meters from Ras Muhammad (fig. 1) in the Red Sea proper contained specimens of *A. bicirculata* with a frequency of 2–5%, thereby indicating that the ecological conditions in the Gulf of Elat are not favourable for this species. Observations on dead specimens show that this species in the Gulf of Elat never attains the larger size reached by those in the samples from Ras Muhammad.

The shallowest sample from off Wadi Kid is less dominated by terrigenous material than the sample from the corresponding depth from off Wadi Taba. The profile was sampled on the northern flank of the Wadi Kid submarine fan which apparently in this area receives less terrigenous material than does the central part of the Wadi Taba fan. Depths shallower than 35 meters off Wadi Kid were not sampled due to the danger of wrecking the research vessel on the nearby fringing reef front.

With respect to displacement and downslope transportation of sediment both figs. 2 and 3 show surprisingly small "tails". Thus at Wadi Kid (fig. 3) the number of shells of *A. lessonii* found below 84 meters is too small to be depicted. At Wadi Taba the corresponding value does not exceed 2%. The same phenomenon applies to *A. lobifera.* Thus it may be concluded, that in spite of slope inclinations in the order of 20–30° no down-slope sediment transport occurs and the depth distribution as shown by the dead shells in the sediment most likely represents the true distribution of the living species.

The number of *Amphistegina* shells per gram sediment is shown in figs. 2–3. At Wadi Taba a distinct maximum occurs around 60 meters while the corresponding maximum in the southern profile is somewhat deeper,

around 78 meters.

If we assume a uniform shell production from 4 to 60 meters in the Wadi Taba area the curve showing numbers of specimens/gram sediment can be assumed to represent a decreasing overall sedimentation rate with increasing depth. However, the decrease below 60 meters in the Wadi Taba profile must be explained as a consequence of lower foraminiferal shell production. In the most shallow part of the profile where wave action is effective the foraminiferal shell production may be low. Larsen (1976) showed that *Amphistegina* density is rather high at a depth of around 10 meters. This is, however, below the depth at which wave action is effective (6 meters according to Hottinger, 1972).

The figures for standing crop (fig. 2) would indicate that the decreasing number of *Amphistegina* shells in the sediments below 60 meters is in fact due to low shell production.

The data for standing crop of *Amphistegina* clearly indicate that the assumption made above, that shell production is uniform from 4 to 60 meters, is incorrect. The true situation is rather that the apparent maximum of shell production as expressed in number of *Amphistegina* shells per gram sediment at arond 60 meters depth in the Wadi Taba profile is a sum of two factors, namely: 1) a general decrease in *Amphistegina* shell production from shallow to deeper water and 2) a more rapid decrease in non-biogenic sediment influx which in this case would have to be envisaged as a "dilution factor". That the latter explanation is probable is supported by the investigation of Perelis (1974), who found an increasing carbonate percentage from shallower towards greater depth in this area being 2% at 2 meters, 10% at 50 meters and reaching about 80% in 100 meters, as well as by the figures for standing crops (fig. 2).

Thus the maximum values for *Amphistegina* shells per gram sediment at Wadi Taba are around 60 meters and around 78 meters at Wadi Kid. The relative abundance of the four species in the two profiles is almost identical and the difference in shell number maxima can only be explained as due to a shallower effect of the "dilution factor" at Wadi Taba. However, none of the maxima represents the depth at which maximum shell production takes place.

Seasonal Variation

It must be emphasized that the two curves showing standing crop are based on data collected at different times of the year, namely May and Sep-

tember. The main *Amphistegina* reproduction in shallow water takes place in June-July (Larsen, 1976) and the May densities are therefore low while the September curve probably shows the population density close to its maximum. Another factor should be mentioned since the recognition of living specimens is based on the staining process involving rose bengal (Walton, 1954 *ad modum* Hansen, 1965). Thus, individuals here recorded as living may in fact have been dead for some time (one week – one month?). The extremely low values in the May sampling compared to the values given by Larsen (op. cit.) may well be due to the fact that all plant debris were removed from the raw samples before they were processed, while this was not done during the September sampling.

Further discrepancies in *Amphistegina* density between the collection by Larsen and by the present authors are caused by the different methods applied. Larsen's samples were collected by diver while the material discussed here was sampled by the Willemoes three-point sampler. The chances of getting plant material (e.g. *Halophila*) are rather poor with the latter sampling gear.

ECOLOGICAL CONSIDERATIONS

The depth distribution shows some remarkable features. Thus the depth at which *A. lessonii* disappears, i.e. 80 meters, in both profiles coincides with the disappearence level of *Halophila* which is at about 80 meters according to Hottinger (1972). It is well established that *Halophila* plays an important role as a substrate for both *A. lessonii* and *A. lobifera* (compare Larsen op. cit.). However, these species are not restricted to this substrate but may utilize almost any bottom feature that will allow them to climb up.

The disappearence of *A. lessonii* and *Halophila* at the same depth may be purely coincidental. It may also signify, however, that the light intensity has become too low for the plants inside the shell of *A. lessonii* to receive sufficient light for photosynthesis at this depth. The test of *A. lessonii* is not equipped with supposedly light concentrating devices (papillae) like in *A. papillosa* and it has a thicker shell than *A. bicirculata.*

The disappearence of *A. lobifera* at about 40 meters depth may well relate to the fact that the shell of this species is much thicker than that of *A. lessonii.* It is believed that the thick shell of *A. lobifera* is the limiting factor since it most likely absorbs or reflects more light than does the shell of

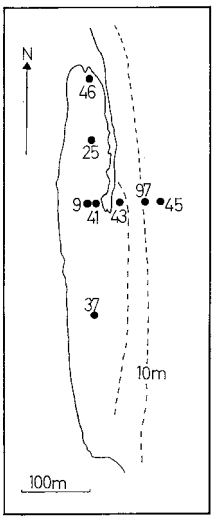

Fig. 4 Map showing location of stations sampled at Ras abu Galum. Stations shown as circles. The numbers adjacent to the circles indicate percentage of *A. lobifera* per total of *Amphistegina* specimens. (map after Dr. Y. Erez, unpublished).

A. lessonii.

Larsen (1976) pointed out that the shell construction of *A. lobifera* probably makes this species better suited to live in a more mechanically disturbed environment than would be tolerated by the more delicate *A. lessonii*. This causal relationship of *A. lobifera* and turbulence was investigated through the study of a series of samples, collected in a lagoonal area at Ras abu Galum (fig. 1) by Dr. Y. Erez, which he kindly placed at our disposal. The positions of the samples are shown in fig. 4. Only the species *A. lessonii* and *A. lobifera* occurred in the samples. The very strong dominance of *A. lobifera* at the reef edge in front of the the lagoon might indicate that a correlation between higher energy environment and *A. lobifera* does exist. In the relatively more quiet waters of the lagoon *A. lessonii* is the dominant form.

All four species of *Amphistegina* from Elat contain supposedly symbiontic algae inside their cytoplasma. Their shells all show a peculiar, corresponding structure of the inner surface (figs. 5–8). They have a polygonal pattern made of cups, in which each cup corresponds to one pore (compare also Hansen, 1972). The pattern resembles a honeycomb except for the protuberances or spine-like projections present where three cups meet. Generally one algal cell is found in each of the cups (sometimes only on the "sunny side"; fig. 10). The system strongly resembles an egg-holder in its construction (figs. 9–10).

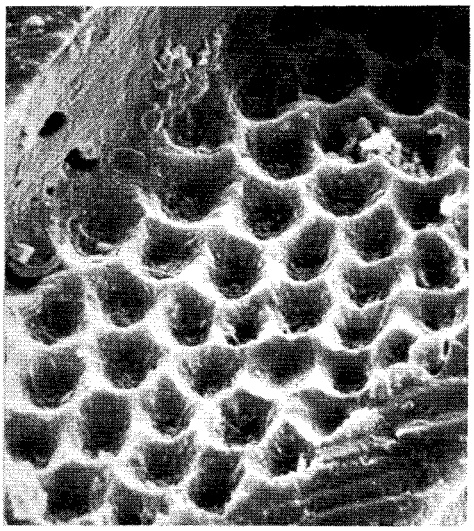

Fig.5

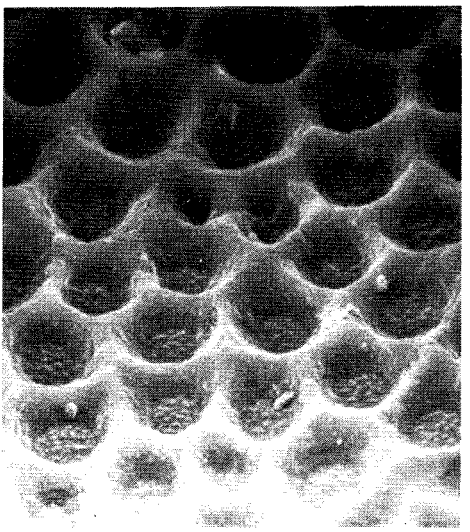

Fig.6

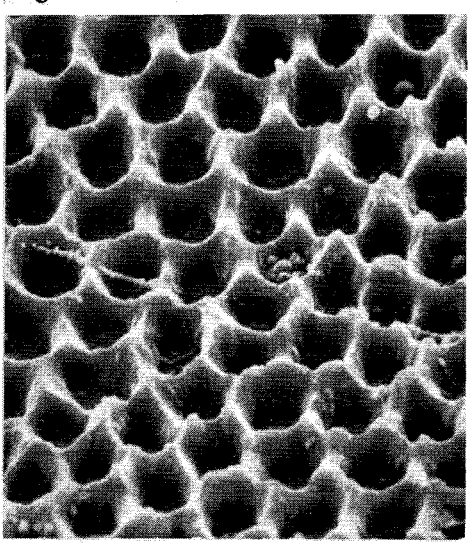

Fig.7

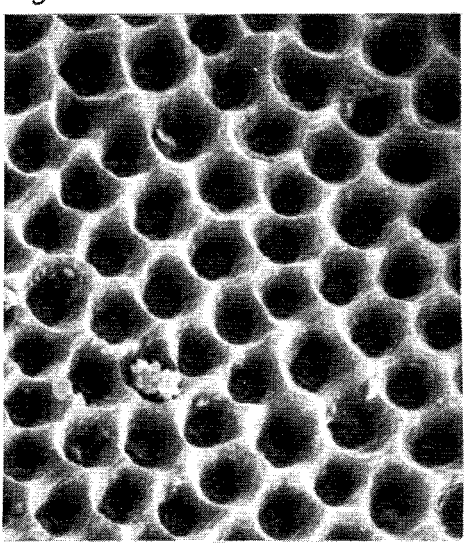

Fig.8

Figs. 5–8 Inner surface showing polygonal cup-shaped depressions with projections at meeting points in the inner calcareous lining, each cup corresponding to a pore. Fig. 5. *A. papillosa.* 2,100 x. Fig. 6. *A. lobifera.* 2,350 x. Fig. 7. *A. lessonii.* 2,425 x. Fig. 8. *A. bicirculata.* 2,400 x.

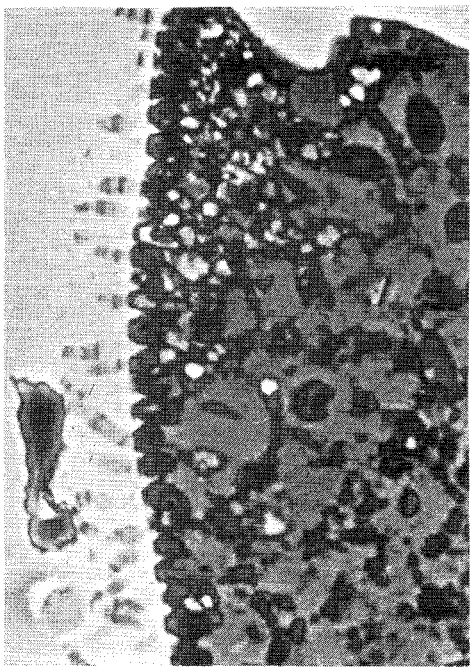

Fig. 9

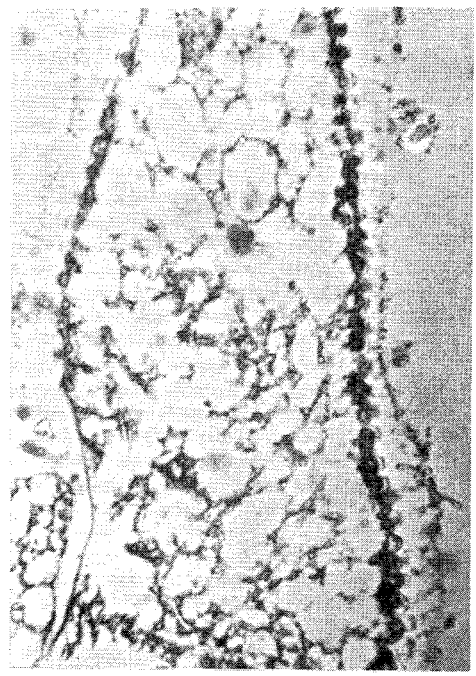

Fig. 10

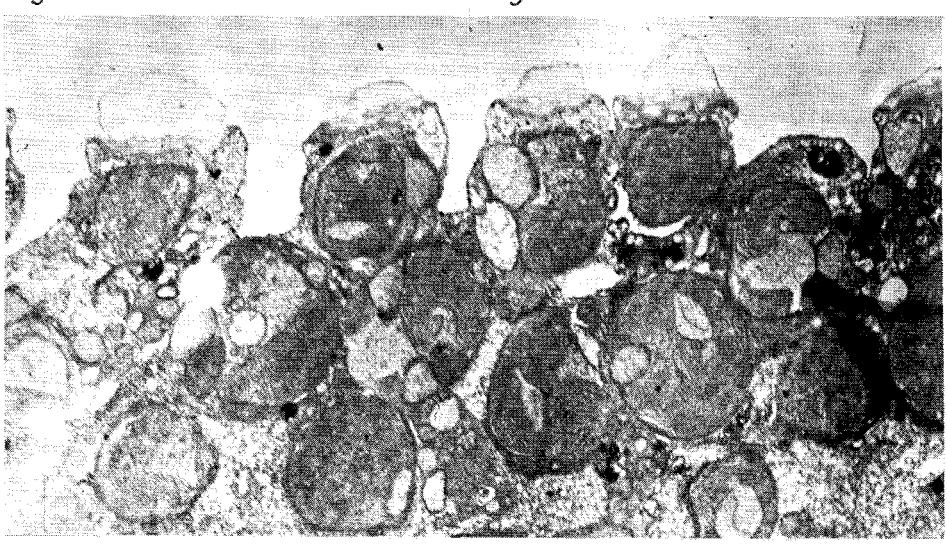

Fig. 11

Fig. 9 Light micrograph (phase contrast) of 2 μm thick section of laterally placed symbiontic algae in decalcified specimen of *A. lessonii.* Wadi Taba, depth 10 m. ca. 800 x.

Fig. 10 Light micrograph (phase contrast) of 2 μm thick section of symbiontic algae concentrated on spiral side in decalcified specimen of *A. papillosa.* Wadi Taba, depth 122 m. ca. 310 x.

Fig. 11 Symbiontic algae (no. 1) Lying in cup-like "depressions" on the inner lateral wall of *A. lessonii* from Wadi Taba, depth 10 m, June 1971. 6,350 x.

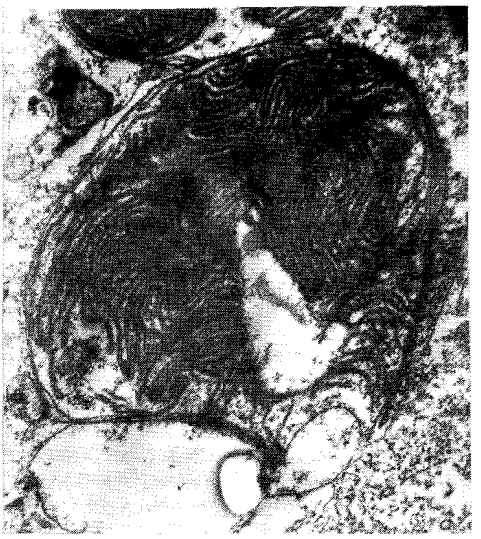

Fig. 12

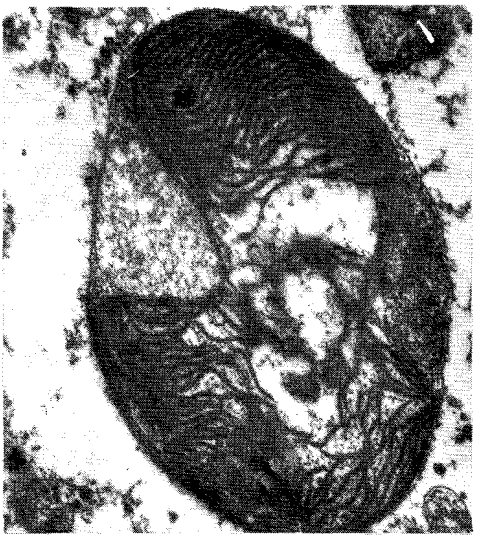

Fig. 13

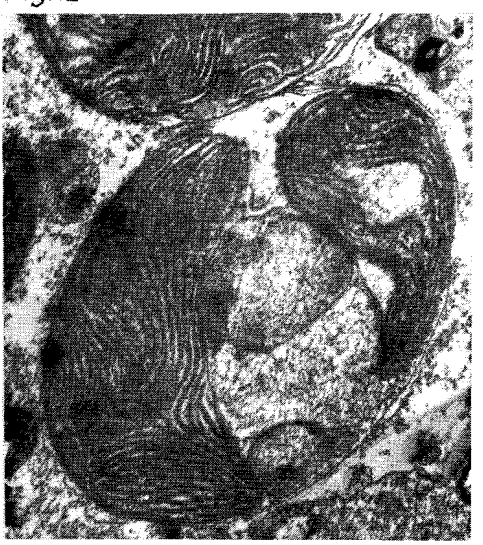

Fig. 14

Figs. 12–14 Algae (no. 1) from *A. lessonii*. Wadi Taba, depth 10 m, June 1971. Fig. 12. 15,400 x. Fig. 13. 16,140 x. Fig. 14. 16,000 x.

Identical structures were demonstrated in *Operculina* by Hansen and Reiss (1971) and by Hottinger and Dreher (1974). Hansen and Reiss (1971) further demonstrated that the cups are formed in the inner calcareous lining exclusively. It is worth mentioning that Hansen and Reiss (1973) in their work on asterigerinids found this cup-pattern in some forms (*Asterigerina carinata, A. planorbis* and *Amphistegina* spp.), while other forms possibly

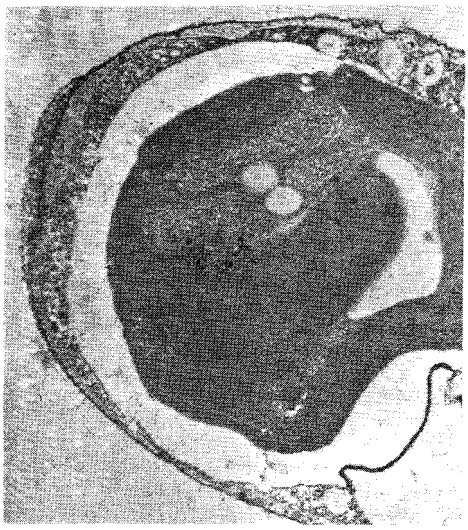

Fig. 15

Fig. 16

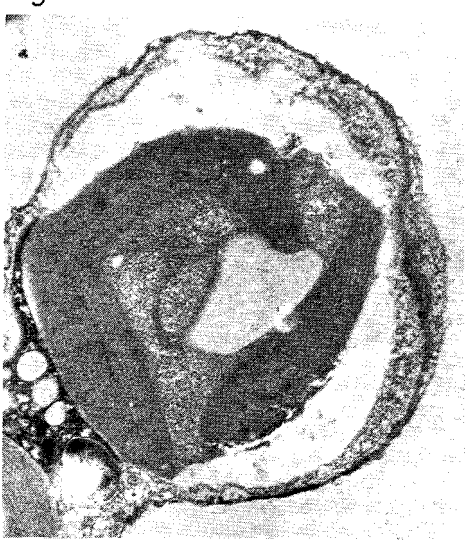

Fig. 17

Figs. 15–17 Algae (no. 2) from *A. lessonii*. Wadi Taba, depth 10 m, Sept. 1976. Fig. 15. 13,700 x. Fig. 16. 13,200 x. Fig. 17. 13,700 x.

not associated with algal symbionts like *Asterigerinata guerichi* and *A. mamilla,* lacked such structural features. Hansen and Reiss (1971) also found such a polygonal pattern on the inner shell surface of *Rotalia trochidiformis.*

It would not be unreasonable to see this inner cup pattern as a structural/morphological adaptation to algal symbiosis so that forms having such a structure belong to the group of foraminiferida having obligate symbiosis

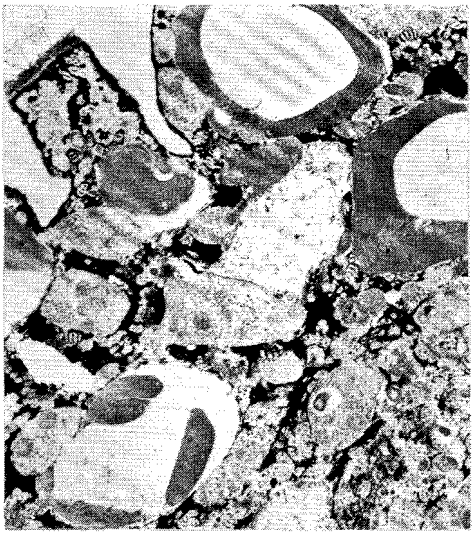

Fig.18

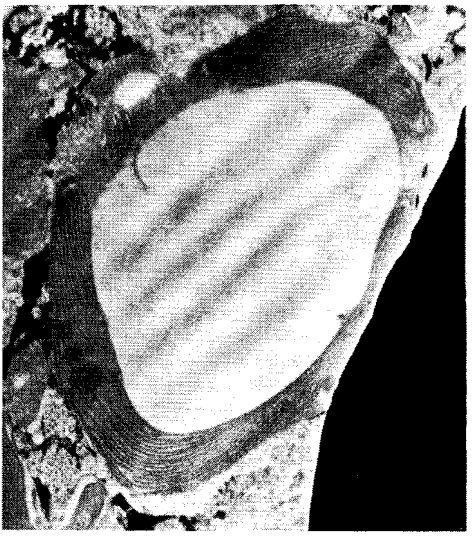

Fig.19

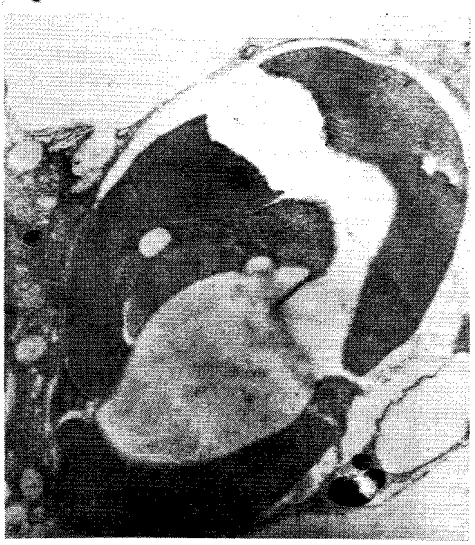

Fig.20

Figs. 18–20 Algae (no. 2) from *A. lobifera.* Wadi Taba, depth 10 m, Sept. 1976. Fig. 18. 4,600 x. Fig. 18. 11,100 x. Fig. 20. 12,200 x.

while perforate forms without this structure of the inner surface have no obligate symbiosis. Imperforate forms like *Archaias* and *Amphisorus* known to have symbiosis do not show cups on their inner surfaces.

If the above mentioned hypothesis holds true we would have a very useful tool for paleoecological interpretations since fossil perforate forms with cup

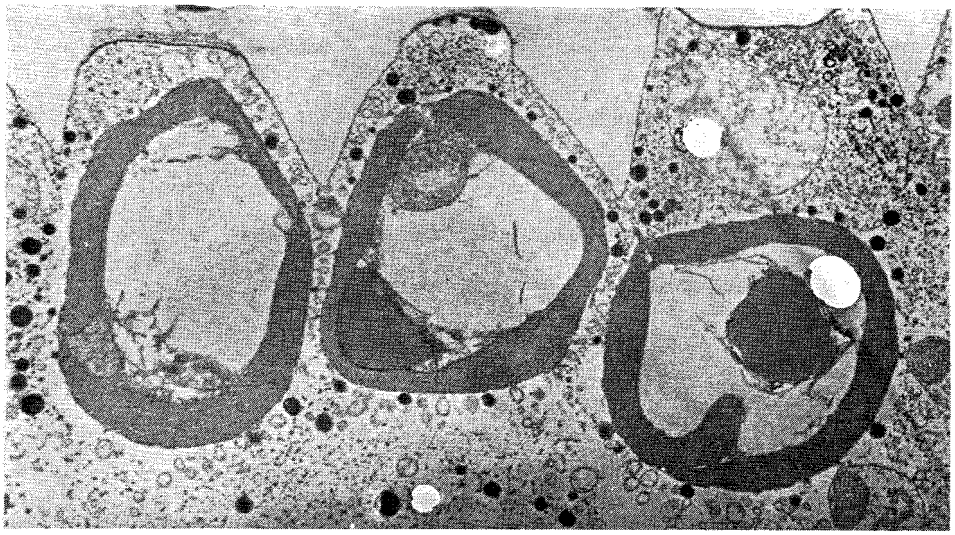

Fig. 21

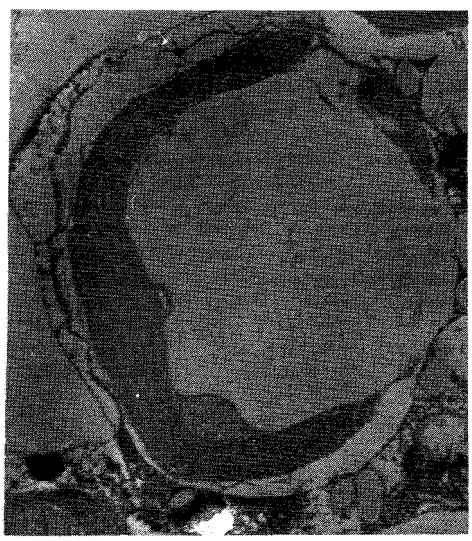

Fig. 22

Figs. 21–22 Algae (no. 2) from *A. bicirculata*. Wadi Taba, depth 60 m, Sept. 1976. Fig. 21. 9,200 x. Fig. 22. 14,800 x.

pits on the inner surfaces would indicate a depth of deposition within the euphotic zone if we are dealing with a non-transported thanatocoenosis.

Light microscopy as well as transmission electron microscopy (TEM) shows that algae are particularly concentrated in the areas corresponding to the inner cups (figs. 9–11).

The term "symbiontic algae" is used below following common practice,

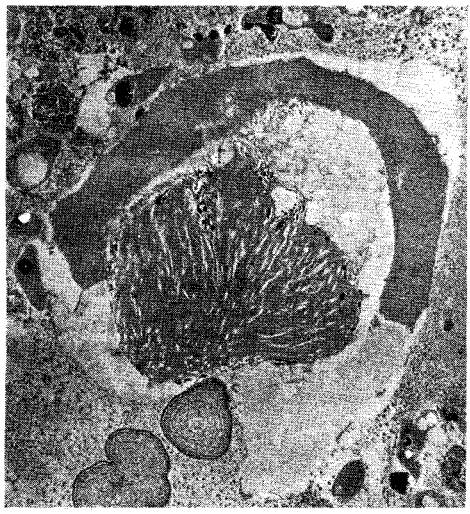

Fig.23

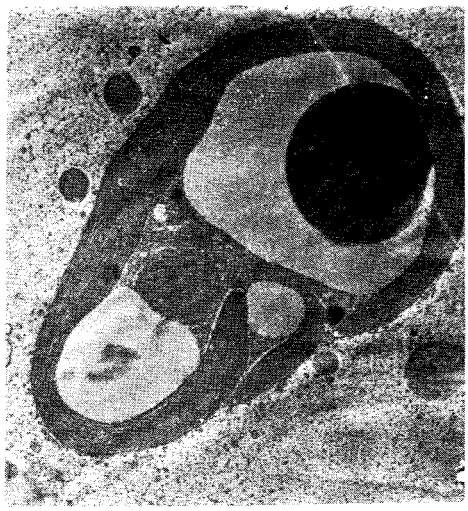

Fig.24

Figs. 23–24 Algae (no. 3) from *A. papillosa.* Wadi Taba, depth 60 m, Sept. 1976. Fig. 23. 4,900 x. Fig. 24. 6,100 x.

although the purely symbiontic relationship in the present case appears to be only temporary. However, the problems of drawing boundaries between symbiosis, parasitism and commensalism are well known.

In TE micrographs the algal symbionts in *A. lessonii* collected in June, 1971 (figs. 12–14) appear to be different typologically from those found in specimens collected in September, 1976 (figs. 15–17).

Specimens of *A. lobifera* from Elat collected in September, 1976 (figs. 18–20) show symbionts that appear to be different from those seen in specimens from Rhodes, Greece, collected by the senior author in October 1973. The latter algae seem to be identical to those found in *A. lessonii* from Elat in March, 1971 (see figs. 12–14).

A. bicirculata from collections prior to 1976 showed such poor preservation (dead specimens only) that only specimens from September 1976 are at hand (figs. 21–22). The algae resemble the ones from *A. lessonii* and *A. lobifera* from September, 1976.

A. papillosa collected in September, 1976 has an algal crop which seems to be different from that of *A. lessonii, A. lobifera* and *A. bicirculata* collected at the same time (figs. 23–24). However, earlier collected specimens (October, 1972 same place and depth) showed algae (fig. 25) which resemble those described by Hottinger and Dreher (1974) from *Heterostegina depressa.*

The species with their associated algae are listed in Table I in which the various algae have been termed alga no. 1, no. 2 etc.

	Algae			
	no. 1	no. 2	no. 3	no. 4
A. lessonii coll. 1971, June	x			
A. lessonii coll. 1976, Sept.		x		
A. lobifera coll. 1976, Sept.		x		
A. lobifera coll. 1973, Oct.	x			
A. bicirculata coll. 1976, Sept.		x		
A. papillosa coll. 1976, Sept.			x	
A. papillosa coll. 1972, Oct.				x

Table 1. Observed combinations of *Amphistegina* species and algal types.

In addition to the supposed symbiontic algae a great variety of other vacuolated material was seen. Much of this material is in the state of decomposition and attemps to identify it have been futile. However, vacuolated skeletons of pennate diatoms are generally recognizable (figs. 26–27). They illustrate that the foraminifer has a veried diet in addition to the products offered by the algal symbionts. Freeze-dried so-called "feeding cysts" also show a high number of diatom skeletons (fig. 28).

Generally speaking, the colours of the symbiont-carrying *Amphistegina* are shades of green to olive-green ranging into brownish shades. However,

Fig.25

Fig. 25 Algae (no. 4) from *A. papillosa*. Wadi Taba, depth 60 m, Oct. 1972. 26,000 x.

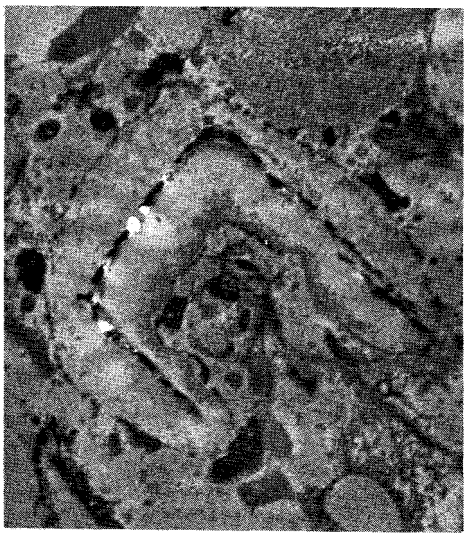

Fig. 26

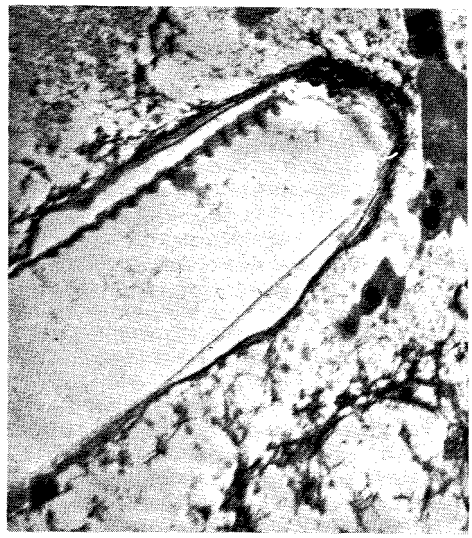

Fig. 27

Fig. 26 Vacuolated diatom from *A. lobifera.* Wadi Taba, depth 10 m, Sept. 1976. 10,000 x.
Fig. 27 Vacuolated diatom from *A. lessonii.* Wadi Taba, depth 10 m, Sept. 1976. 13,600 x.

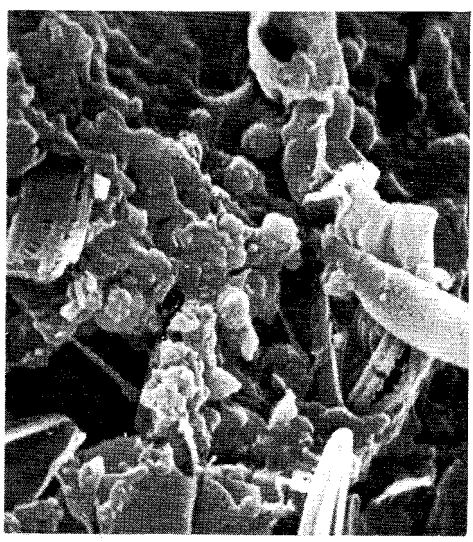

Fig. 28

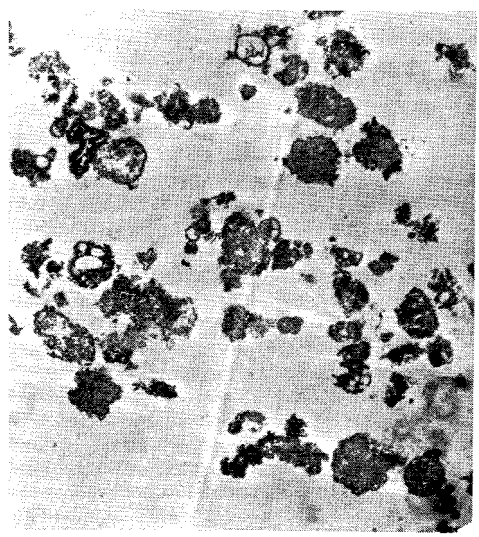

Fig. 29

Fig. 28 Detail of freeze-dried so-called feeding cyst from *A. lessonii.* Note diatoms. 4,270 x.
Fig. 29 Detail of section of "red" specimen of *A. lessonii.* Wadi Taba, depth 10 m, showing decomposing cytoplasmatic remains. 4,600 x.

specimens that are brown with a reddish tint were met with as well. Prof. Lukas Hottinger who collected specimens one month later than the present author described the colour of *Operculina* as brownish while the specimens collected earlier by the senior author were bright green. A parallel phenomenon was observed in other forms as well, and the authors therefore studied specimens of the same species with different colouring. It is evident from the observed ultrastructure of the cytoplasma that the forms having a reddish tint are dead specimens in the process of decomposition (fig. 29). It is believed that the reddish brown colour is due to the breakdown of chlorophyll.

From the above it is evident that the material not forming part of the cytoplasma is vacuolated. This is true of both the pennate diatoms and the supposed algal symbionts. The different symbiontic algae found at different times of the year in the same species of foraminifer would indicate that there is only a limited, if any, specific relationship between foraminifer and symbiont. This would emphasize that the observed depth distribution is governed by factors other than the light requirements of the symbiontic algae. As stressed by Z. Reiss in the first paper of this bulletin the only factors changing with depth are the light-intensity and light composition. From the results of the work of Zmiri et al. (1974) it appears possible that the depth determining factor is a primary light dependency of the foraminifer.

In general the symbionts that are looking "healthy" are placed close to the outer walls. By contrast, examples apparently in the state of being digested are met with in the chamber interior. This again leads to the tentative conclusion that all material of the potential food categories is ingested and vacuolated and that organisms not being immediately digested may temporarily function as symbionts. After being exhausted they are finally digested by the foraminifer and the waste products expelled.

This hypothesis would readily explain why at different times of the year the same species of foraminifera contains different algal symbionts. This may be related directly to the different fluxes in algal productivity in the area (see Klinker et al., in press and ms). It should be noted that no algal reproduction (cell devision) has been observed in any of the specimens studied.

Dr. P. Muller (pers. comm., 1976) showed by ^{14}C experiments that *Amphistegina* from Hawaii during continuous exposure to light had a recycling of carbon of the order of 50%. This points to the distinct role of the symbionts in the metabolic system of the foraminifer. The effect of the photo-

synthesising system in the algae has a further effect, since the composition of the shell with respect to oxygen isotopes is out of equilibrium with the surrounding watermass. Duplessy et al. (1970) showed that some benthonic foraminifera from below the euphotic zone have shells that are depleted in ^{18}O relative to the equilibrium values with the surrounding sea water. In a later paper Vinot-Bertouille and Duplessy (1973) found ^{18}O depletion in shells of larger and smaller foraminifera of shallow water. They did not, however, ascribe the ^{18}O depletion to algal symbiosis.

In order to determine the magnitude of the vital effect not caused by symbiosis (the one mentioned by Duplessy et al. 1970) a series of populations of *Bolivina* spp. were analysed from different depths from off Wadi Taba (fig. 30). Living specimens were not found to contain algal symbionts. In order to determine the non-vital equilibrium value for $^{18}O/^{16}O$ in biogenic carbonates, bulk samples of aragonitic molluscan shells were analysed. This demonstrated that the vital non-symbiontic ^{18}O depletion for *Bolivina* spp. is in the range of 1 ‰. In addition a series of species which through TEM studies of their soft body appear to have algal symbiosis, were analysed. These forms are: *Amphistegina lessonii, A. lobifera, A. papillosa, A. bicir-*

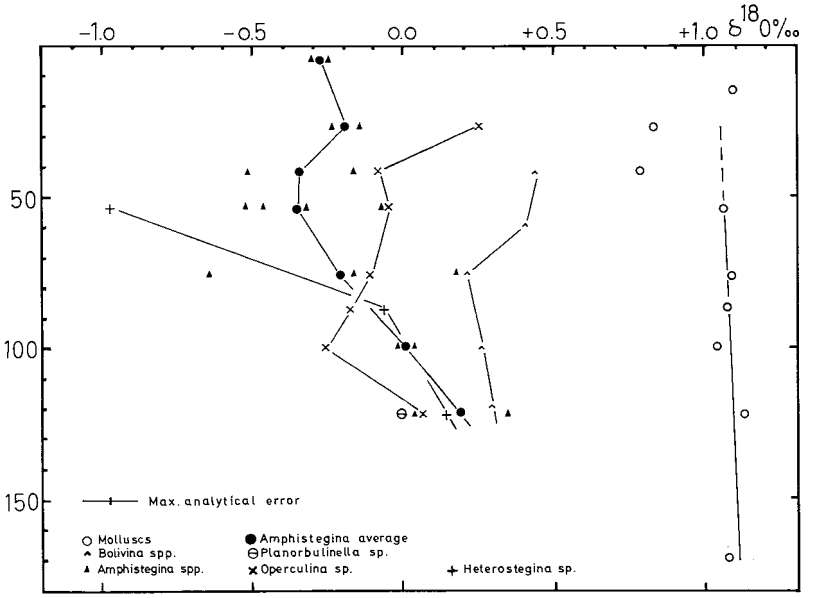

Fig. 30 Oxygen isotope composition of selected shell carbonates from molluscs and foraminifera. $^{18}O/^{16}O$-ratios are expressed in delta units as permill deviation from the PDB-standard. Analytical error less than ± 0.1 ‰. All are bulk samples based on more than 25 specimens.

culata, Operculina sp. *Heterostegina* sp. and *Planorbulinella* sp. and the values obtained are shown in fig. 30.

It is evident from the presented values, than an additional ^{18}O depletion of up to 1.0 ‰ is present. Thus a total depletion up to 2.0 ‰ relative to that of biogenic carbonate (formed in equilibrium with the surrounding water as shown by the molluscs) is possible. It seems plausible from the data presented in fig. 30 that the vital effect supposedly caused by algal symbionts is more pronouced in shallow waters while the effect becomes almost insignificant close to their deeper distributional limit. A more detailed report on the oxygen and carbon isotopes of the forms mentioned here is in preparation and will appear elsewhere.

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RELATIVE THICKNESS OF THE TEST IN THE AMPHISTEGINA SPECIES OF THE GULF OF ELAT

A. R. LARSEN AND C. W. DROOGER

ABSTRACT

Allometric growth of test size parameters seems to be valid for all four *Amphistegina* species in the Gulf of Elat; larger specimens tend to have relatively flatter tests. In *A. lessonii, A. lobifera* and *A. papillosa* there is a general trend of test flattening towards greater depth. The few data on *A. bicirculata* suggest an opposite trend, or none at all. The frequent irregularities in the trend pattern are not yet understood.

INTRODUCTION

Four different species of *Amphistegina* were recognized in the Gulf of Elat in the recent paper by Larsen (1976). The species appeared to be easily distinguishable from one another by differences in features readily visible from the outside, such as arrangement of the supplementary chambers, shape of the sutures, shape and position of the aperture, and relative thickness and ornamentation of the test (plate 1).

Amphistegina lobifera Larsen is characterized by strongly lobate sutures due to the shallow overlap of each chamber over a set of parallel apertural ridges near the primary opening of the previous chamber. These lobations tend to obliterate the configuration of the supplementary chambers. The aperture is interiomarginal and slitlike on the umbilical side. The test is relatively thick.

Amphistegina lessonii d'Orbigny has a simple star-shaped pattern of the supplemenary chambers, linear sutures, an interiomarginal, slitlike aperture on the umbilical side, and a more moderate relative test thickness.

Amphistegina bicirculata Larsen shows an inner circle at the umbilical side about half way between center and periphery. This is caused by simple loops in the toothplate sutures of successive chambers, which at the umbilical surface seem to near-separate the supplementary chambers into a full-width umbilical part and a narrow peripheral prolongation. The interiomarginal, slitlike aperture is close to the periphery on the umbilical side, and the test is relatively thin.

Amphistegina papillosa Said with indistinct pattern of the supplementary

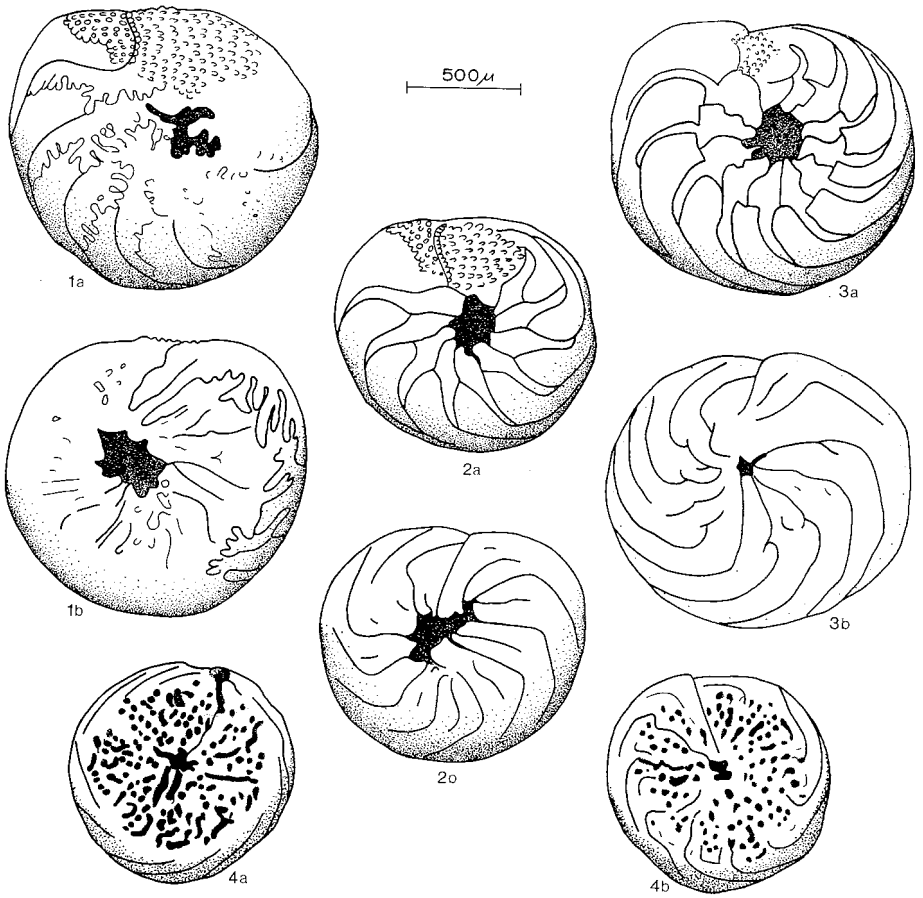

Fig. 1 The four *Amphistegina* species of the Gulf of Elat.
1a, b. *Amphistegina lobifera* Larsen.
2a, b. *Amphistegina lessonii* d'Orbigny.
3a, b. *Amphistegina bicirculata* Larsen.
4a, b. *Amphistegina papillosa* Said.
a. umbilical views, b. dorsal views.

chambers is characterized by a rounded aperture in nearly peripheral position, and a relatively thin test that is commonly profusely papillate.

The size ranges of the four species are very similar (0.3–2.2 mm in our measurements), which seems to rule out the possibility that one might be the adult stage of another. In the Gulf of Elat the species appear to have different, though overlapping depth ranges (Larsen, 1976; Hansen and Buchardt, this volume).

The interspecific variation in relative test thickness shows an overall decrease at greater depth. In order to prove these changes measurements were performed on some 2,300 individuals from 17 samples (12 published in 1976), collected between 5 and 90 meters. Most of the samples had been taken off Coral Island and off Wadi Taba in the northernmost part of the Gulf. The measurements carried out on (largest plus smallest diameter/ 2 =) diameter (D) and maximum thickness (T) of the test were presented in D frequency diagrams and by reduced major axes of D versus T values for one of the samples per species only (Larsen, 1976). It was considered acceptable that the computed single D-T regression line of all individuals per species per sample coincides with the average growth line of the separate individuals. Isometric growth (*A. lessonii, A. lobifera*) and anisometric growth (*A. bicirculata, A. papillosa*) were recognized, but it was beyond the scope of Larsen's paper to make a more detailed analysis of the growth lines.

The biometric data as expressed in the published regression lines suggest but little difference between *A. lessonii* and *A. lobifera* on one side, and between *A. bicirculata* and *A. papillosa* on the other. The closeness of these lines may raise doubt as to the biometric species distinctness in each of both cases. Since biometric data often enable the separation of very similar species or species groups it was considered worthwhile to make a careful re-evaluation of the original data. A number of additional observations are incorporated in order to cover a more representative part of the depth range of *A. lessonii* (cf. Hansen and Buchardt, this volume).

THE GROWTH PATTERNS

First of all it had to be checked whether the suggested rectilinear D-T relations are fully justified simplifications, or not. In spiral larger foraminifera the diameter of the test commonly tends to increase more strongly during ontogeny than its thickness. If such a relation would be true in *Amphistegina* as well, the suggestion of curvilinear regression would necessitate us to consider comparable diameter groups per species for all samples in order to investigate the changes of D/T with increasing depth.

We started with a quick review of the D/T values of three samples of the Wadi Taba traverse, which samples had been reported to contain but a single *Amphistegina* species each. The samples from 25 m., 35 m., and 90 m. contain *A. lessonii, A. lobifera* and *A. papillosa* respectively, other species having been disregarded. In each of these samples the specimens were subdivided into three subequal groups on decreasing D values, and for each D

group the $\overline{D}/\overline{T}$ relation was calculated. As may be guessed already from the D-T scatter diagram for *A. papillosa* at 90 meters (fig. 2), the calculated subgroup $\overline{D}/\overline{T}$ values of 2.81, 3.54 and 4.02 with increasing D give fair evidence that in the *Amphistegina* population at 90 meters depth the test diameter does grow more rapidly during ontogeny than the thickness. Similar, though less convincing $\overline{D}/\overline{T}$ suites were found for *A. lessonii* at 25 m. (2.04, 2.11, 2.25) and for *A. lobifera* at 35 m. (1.86, 1.95, 2.01).

It was accepted therefore as a working hypothesis that the *Amphistegina* species in the Gulf of Elat do show allometric growth. It was not tried to calculate any curvilinear regression line, which after all might have been of little practical value if one considers the wide variation in the final results. A rough estimate of the change in D-T relation with increasing size is given per sample and for all individuals per species (table 1).

For this purpose all measurements were grouped per sample and per species according to progressive D classes with limits at 500 μ, 900 μ, 1300 μ and 1700 μ, the boundary values being included in the next higher class. For each group $\overline{D}/\overline{T}$ was calculated as a parameter that could be plotted in the scatter diagrams (fig. 2), whereas $\overline{D/T}$ values and the standard errors of these means were computed for the sake of comparison between samples. The $\overline{D/T}$ values with their standard errors and the numbers of specimens per group are given in table 1. Since the $\overline{D}/\overline{T}$ values appear to deviate less than 0.03 from the corresponding $\overline{D/T}$ (for *A. papillosa* up to 0.06) no separate table is given.

It is apparent from table 1 that the hypothesis of allometric growth with D increasing more strongly than T, must be considered correct for all four *Amphistegina* species, though some minor deviations on the general rule seem to be present. Altogether 62 comparison pairs are available, only eight of which suggest an opposite growth trend. In nearly all of these eight cases small numbers of observations are involved in one of both adjoining classes. Most deviations occur in the thickest species, *A. lobifera.*

Notwithstanding the blurring effect of suspected depth trends in $\overline{D/T}$, the "all" data show the validity of the general rule for all four species. One deviating value in the lowermost size class of *A. lobifera* is not understandable in this respect, whereas the deviation in the largest size class of *A. papillosa* is clearly caused by the data from the shallowest sample.

It now becomes equally clear that the $\overline{D/T}$ values distinctly separate *A. lobifera* and *A. lessonii.* Actually, the scatter diagrams for the shallower samples down to 20 meters, in which both species are reported to occur together (fig. 2), suggest a rectilinear regression for both species combined. In table 2 it is shown that the $\overline{D/T}$ values, and especially those for "all" data,

depth	→500 μ			→900 μ			→1300 μ			→1700 μ			> 1700 μ		
	M	σ_m	n	M	σ_m	n	M	σ_m	n	M	σ_m	n	M	σ_m	n
	Amphistegina lobifera														
5 m				1.80	0.04	9	1.79	0.02	56	1.87	0.02	33	1.80	0.10	2
9 m				1.80	0.03	15	1.84	0.02	62	1.97	0.03	20	2.15	0.10	3
10 m				1.83	0.03	12	1.82	0.02	37	1.92	0.02	45	2.11	0.05	6
14 m	1.92	0.06	12	1.85	0.03	26	1.88	0.02	59	1.91	0.02	28			
20 m				1.80	0.05	12	1.82	0.02	55	1.82	0.02	32	1.92		1
35 m				1.89	0.03	19	1.95	0.02	73	2.06	0.05	8			
45 m				1.78		1	1.89	0.02	46	2.01	0.02	42	2.11	0.04	11
all	1.92		12	1.836		94	1.861		388	1.924		208	2.080		23
	Amphistegina lessonii														
5 m				1.98	0.02	51	2.09	0.02	44	2.38	0.16	5			
9 m				2.04	0.02	34	2.10	0.02	64	2.26		2			
10 m	2.09		2	2.01	0.04	19	2.14	0.02	65	2.22	0.05	12	2.38		2
14 m	1.93	0.03	37	2.01	0.02	46	2.08	0.03	29						
20 m				2.10	0.02	75	2.12	0.03	24	2.13		1			
25 m				2.06	0.02	45	2.13	0.02	48	2.28	0.06	7			
28 m				2.28	0.04	31	2.37	0.03	62	2.39	0.05	7			
38 m				2.20	0.03	60	2.34	0.03	35	2.65	0.14	5			
45 m				2.12	0.06	7	2.15	0.02	64	2.22	0.04	24	2.38	0.09	5
54 m	1.84		2	2.07	0.02	54	2.19	0.06	13						
64 m	2.17		3	2.14	0.02	82	2.21	0.09	5						
76 m	2.16		2	2.13	0.08	6	2.46		3						
87 m				2.16	0.06	5	2.44	0.08	5						
all	1.959		46	2.096		515	2.179		461	2.292		63	2.38		7
	Amphistegina bicirculata														
28 m							3.42	0.09	13	3.51	0.07	4			
38 m				3.23		3	3.28	0.06	25	3.68	0.10	12			
45 m							3.13	0.11	4	3.28	0.12	8	3.98		3
all				3.23		3	3.309		42	3.518		24	3.98		3
	Amphistegina papillosa														
45 m				2.66	0.09	14	2.87	0.04	46	3.09	0.11	12			
50 m	2.62	0.07	16	3.04	0.07	50	3.57	0.08	32						
70 m	2.59	0.13	7	2.79	0.04	56	3.16	0.10	19	3.00		1			
90 m	2.65	0.05	34	3.45	0.06	62	4.09	0.06	44						
all	2.634		57	3.074		182	3.449		141	3.083		13			

Table 1. Partial $\overline{D/T}$ values of the *Amphistegina* species along the depth profile from 5 to 90 meters in the Gulf of Elat.

	→500 μ		→900 μ		→1300 μ		→1700 μ		> 1700 μ	
	M	n	M	n	M	n	M	n	M	n
	Amphistegina lobifera and *A. lessonii* together									
5 m			1.953	60	1.922	100	1.937	38	1.80	2
9 m			1.967	49	1.954	126	1.996	22	2.15	3
10 m	2.09	2	1.940	31	2.023	102	1.983	57	2.178	8
14 m	1.928	49	1.952	72	1.946	88	1.91	28		
20 m			2.059	87	1.911	79	1.829	33	1.92	1
45 m			2.078	8	2.041	110	2.086	66	2.194	16
all	1.934	51	1.987	307	1.969	605	1.976	244	2.150	30
	A. lobifera in the same samples:									
	1.92	12	1.822	75	1.840	315	1.918	200	2.08	23
	A lessonii in the same samples:									
	1.938	39	2.040	232	2.118	290	2.238	44	2.38	7

Table 2. Partial $\overline{D/T}$ values for *Amphistegina lobifera* and *A. lessonii* combined in the samples from the Gulf of Elat in which they occur together.

confirm the near-rectilinear pattern. Curvilinear growth lines cannot be defended for the combination since out of 19 comparison pairs 10 suggest $\overline{D/T}$ decrease with growth, 9 the opposite. The hypothesis of isometric growth in *Amphistegina* we rejected already above, amongst others on the separate assemblages of *A. lessonii* and *A. lobifera* at 25 and 35 meters respectively. The biometric analysis gives further support for the separation of both species co-occurring in the shallower part of the depth range. The pseudo-linear regression of both together is brought about by the addition of two curvilinear scatter fields which have slightly different positions in the diagrams. It should be noted, however, that in the 20 meters sample the $\overline{D/T}$ values suggest a rectilinear regression for each of both species (table 1).

The numbers of samples with *A. bicirculata* and *A. papillosa* are too few for a similar separation on biometrical grounds, but at 45 meters where they do occur together their corresponding $\overline{D/T}$ values are well apart.

CHANGES WITH DEPTH

As to the changes in $\overline{D/T}$ with increasing depth one has to be very careful in the interpretation of the observations. Especially the standard errors are

of dubious value. Although the D frequency distributions as a whole per sample are no doubt unimodal, the class subdivision may cause observation clusters and means to have different positions in a class from one sample to another. The plotting of the $\overline{D/T}$ values in the scatter diagrams (fig. 2) shows differences of position within the class interval as a consequence of different concentrations of the observations towards one of the class limits. This was expected to be especially true for the data in the lowermost and uppermost D classes. As a consequence the 900–1300 μ D class probably gives the most reliable results for comparisons, but the means in both adjoining classes appear to show the same patterns.

In *A. lobifera,* the species with the thickest test, comparison of the 5 meters sample with both deepest ones from 35 and 45 meters shows a decrease of relative test thickness that is statistically distinctly significant at a confidence level of more than 99%. In between these extreme samples $\overline{D/T}$ values fluctuate up and down, differences frequently being on the verge of significance. Actually, the drop from 35 m to 45 m is such a near-significant deviation.

In *A. lessonii* the results are more complex, also if one considers the 500–900 μ fractions, which in this species are of greater importance because of the overall smaller size of the tests. From 5 meters down to 25 meters nothing much is changing; there seems to be a fluctuating pattern of $\overline{D/T}$ increase, but the actual differences to substantiate such a trend are but rarely significant. At 28 and 38 meters the tests are suddenly much flatter, but the 45 meters sample shows a significant (99%) set-back to $\overline{D/T}$ values comparable to those of the upper group of samples. The samples from 54 to 87 meters suggest a renewed, or even resumed, trend of test flattening, but except for the 500–900 μ groups at 54 and 64 meters, $\overline{D/T}$ values are too close and/or observation numbers too small to verify this suggestion.

The data on the three samples of *A. bicirculata* seem to suggest a $\overline{D/T}$ decrease with depth, i.e. opposite to the trend in the other species, but the major change from 28 to 38 meters has to be considered statistically non-significant.

In *A. papillosa* the highly significant trend of test flattening from 45 to 90 meters depth is disturbed by the set-back in the 70 meters sample, which recurrences of lower $\overline{D/T}$ values are on the verge of statistical significance relative to the $\overline{D/T}$ of the next higher sample at 50 meters.

Summarizing it may be stated that an overall trend of test flattening towards greater depth occurs in all three *Amphistegina* species on which a sufficient number of data is available. There are no smooth trends, how-

ever, and statistically significant recurrences of "too low" $\overline{D/T}$ values were observed in *A. lessonii* and *A. papillosa* at 45 m and 70 m respectively. The aberrant *A. lessonii* assemblage at 45 meters is accompanied by *A. lobifera,* showing a similar, but less significant drop in $\overline{D/T}$ values. Thicker *A. lessonii* predominate below 45 m, thus suggesting on exaggerated $\overline{D/T}$ increase wave at 28–38 meters, superimposed on an otherwise slow thinning trend in the same direction.

For a good explanation of the general trend as well as its irregularities we lack significient data on internal features and on environmental details. For instance, the $\overline{D/T}$ values in both samples taken from dense *Halophila* vegetation (9 and 10 meters) show no peculiarities that might be related to the special type of substrate.

The flattening trend may be dependent on the amount of light to be captured, either as a response to unknown needs of the animals' own physiology, or via its symbionts. Anyway, the trend extends so far below wave base (Hottinger, this volume) that a simple explanation of intraspecific test thickening as a response to the influences of higher water energy, brought about by mechanical strengthening of the tests in shallower water (e.g. Larsen, 1976), may be safely discarded as the sole causal factor.

Explaining the distinct irregularities in the trends is impossible. It might be considered feasible that the populations consist of highly variable relative numbers of individuals of both major reproductive generations. There is little doubt that growth starting from a megalospheric proloculus will lead to a test that is relatively thicker than those of the microspheric generation of comparable diameter. It is possible, for instance, that the low $\overline{D/T}$ of *A. lessonii* at 28 and 38 meters is caused by relatively high numbers of microspheric individuals. If sexual reproduction of a species is favoured at a certain depth level this might cause a pattern like the one we found. Our ignorance of proloculus size in the assemblages leaves us for the moment at the speculation level.

For the 45 meters sample it might be considered possible that longshore and downslope transport of material from 10 to 20 meters depth caused the low $\overline{D/T}$ values, since the aberrant results were found for both *A. lessonii* and *A. lobifera,* though for *A. lessonii* more distinctly so. For the latter species it has to be kept in mind, however, that the smaller $\overline{D/T}$ values prevail in the lower part of the species' depth range as well. It may be doubted that downslope contamination was of such great importance.

Although growth-related and depth-related trends in Recent *Amphistegina* species seem to become outlined sufficiently well, we evidently need knowledge of more details on the inner morphology, and on biology as well as

environments, to be able to use these trends for paleoecological analyses of fossil assemblages.

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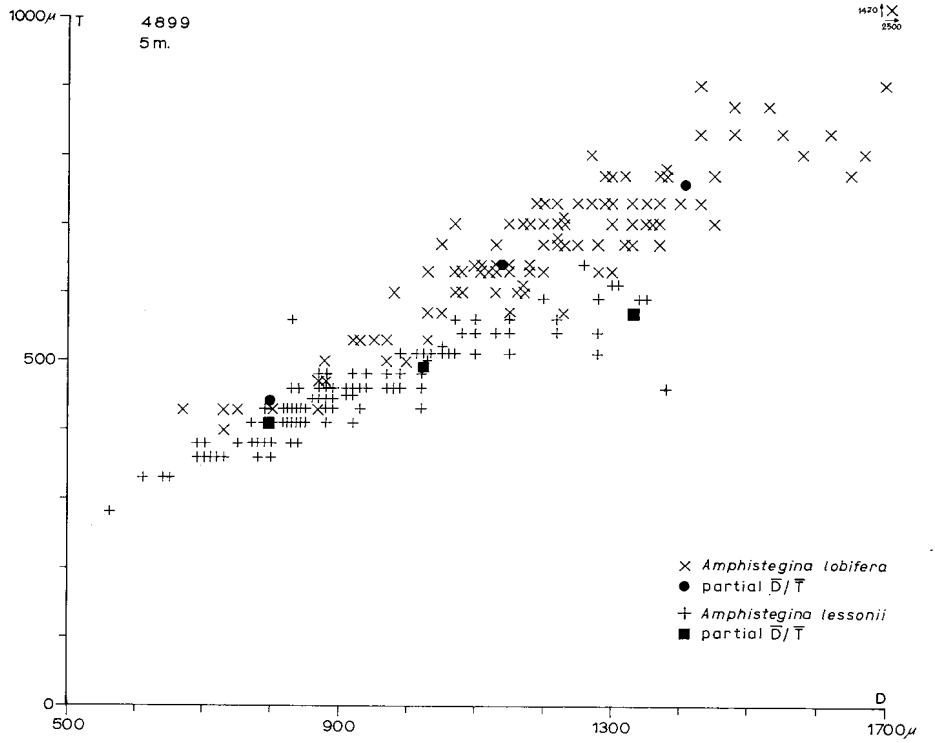
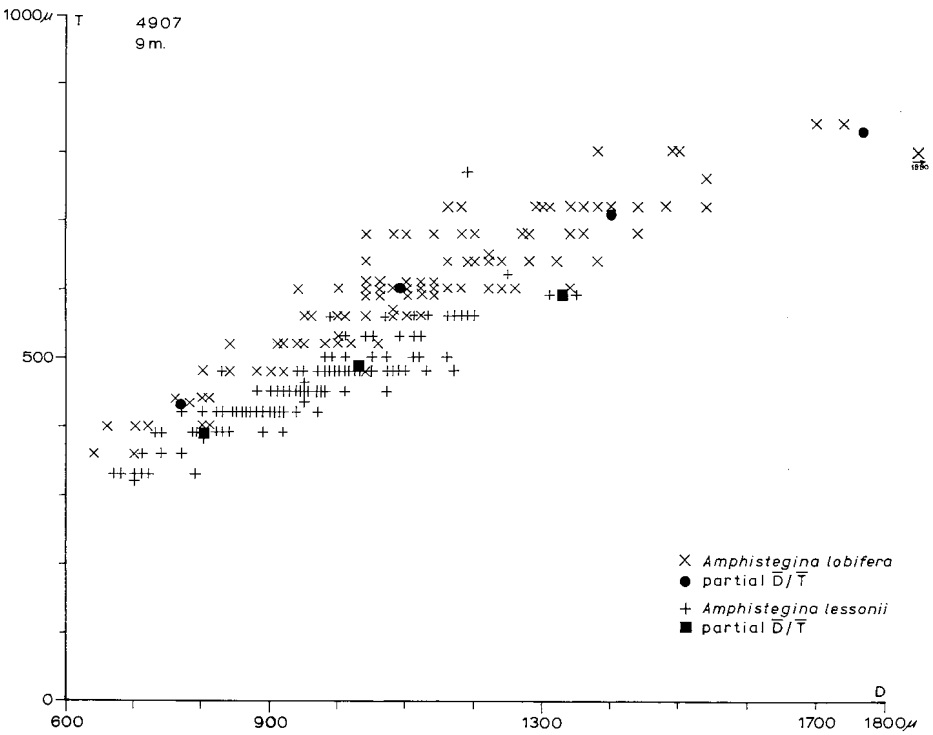
Fig. 2 Scatter diagrams of test diameter versus thickness in the *Amphistegina* specimens of 13 samples from the Gulf of Elat. Class means are given with a heavier symbol.


1000μ
T
4899
5 m.
1420
2500
500
0
500
900
1300
1700μ
D
× Amphistegina lobifera
● partial D/T
+ Amphistegina lessonii
■ partial D/T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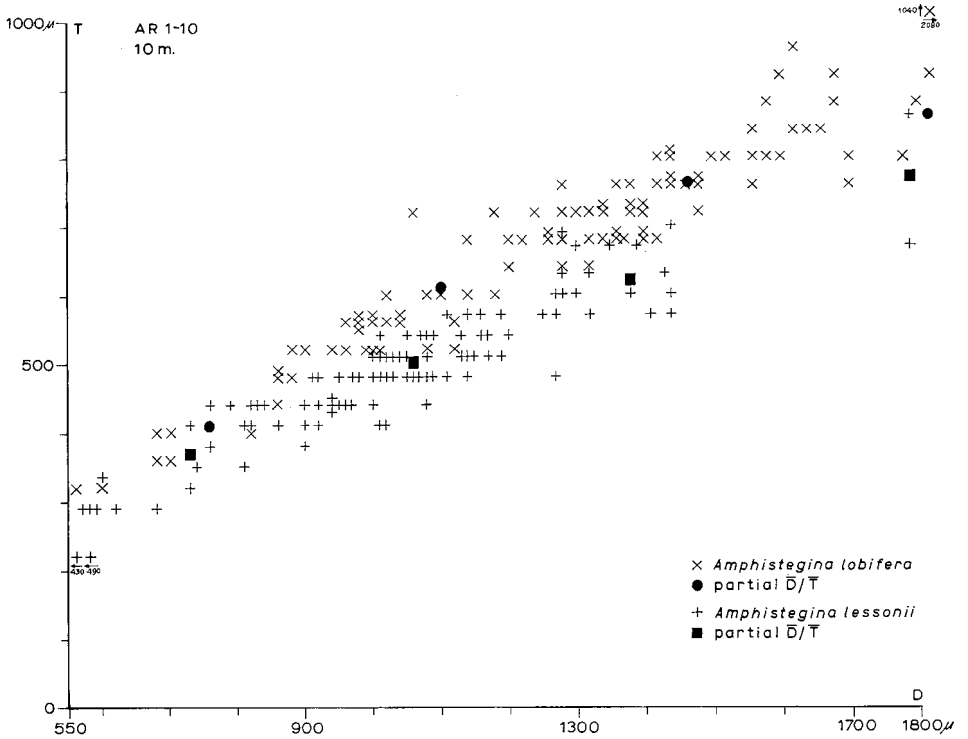
D
× Amphistegina lobifera
● partial D/T
+ Amphistegina lessonii
■ partial D/T


1000μ
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AR 1-10
10 m.
500
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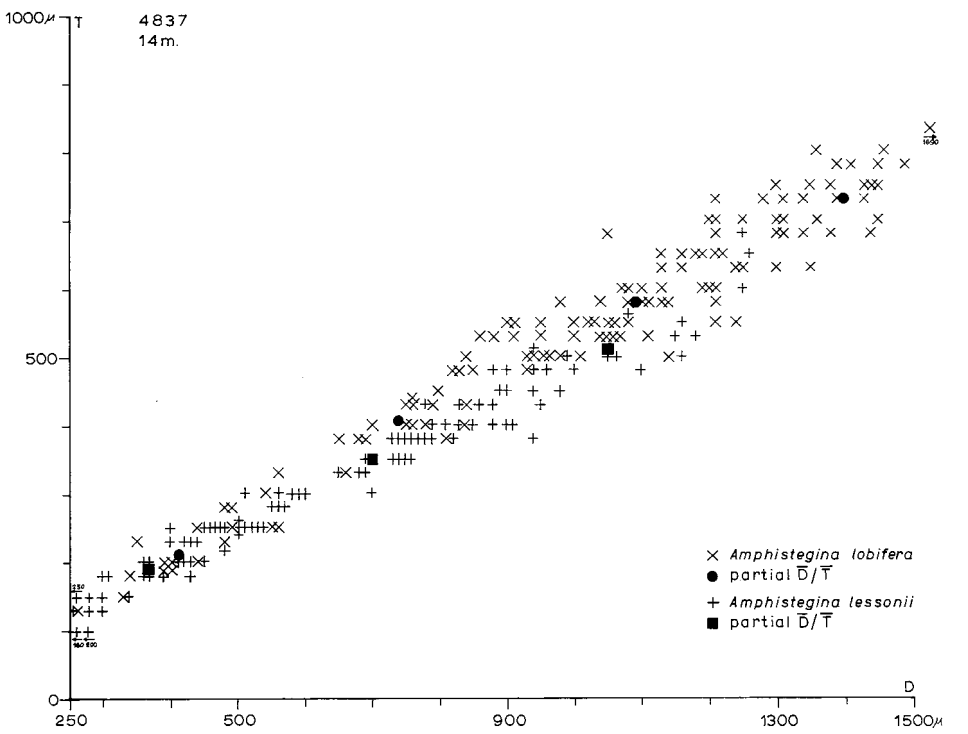
550
900
1300
1700
1800μ
D
× Amphistegina lobifera
● partial D/T
+ Amphistegina lessonii
■ partial D/T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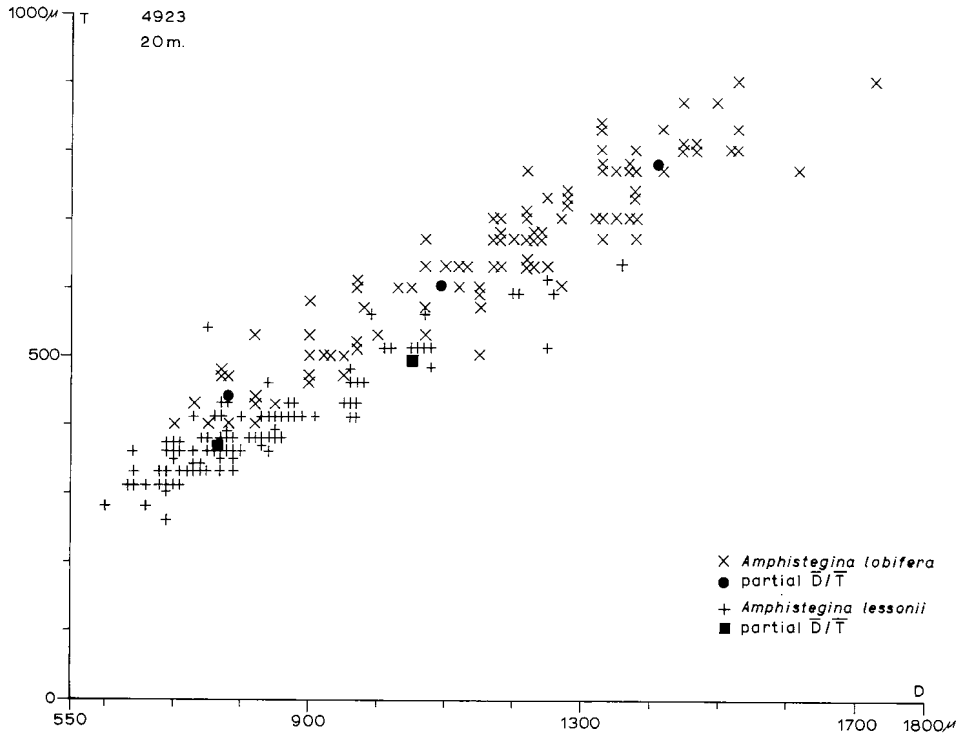
+ Amphistegina lessonii
■ partial D/T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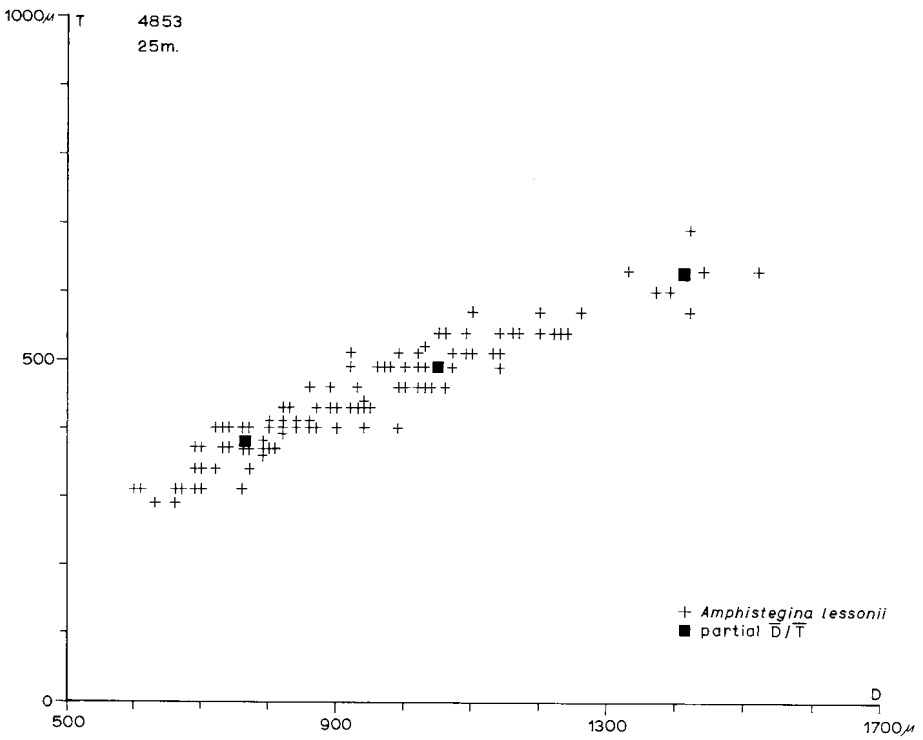
× Amphistegina lobifera
● partial D/T
+ Amphistegina lessonii
■ partial D/T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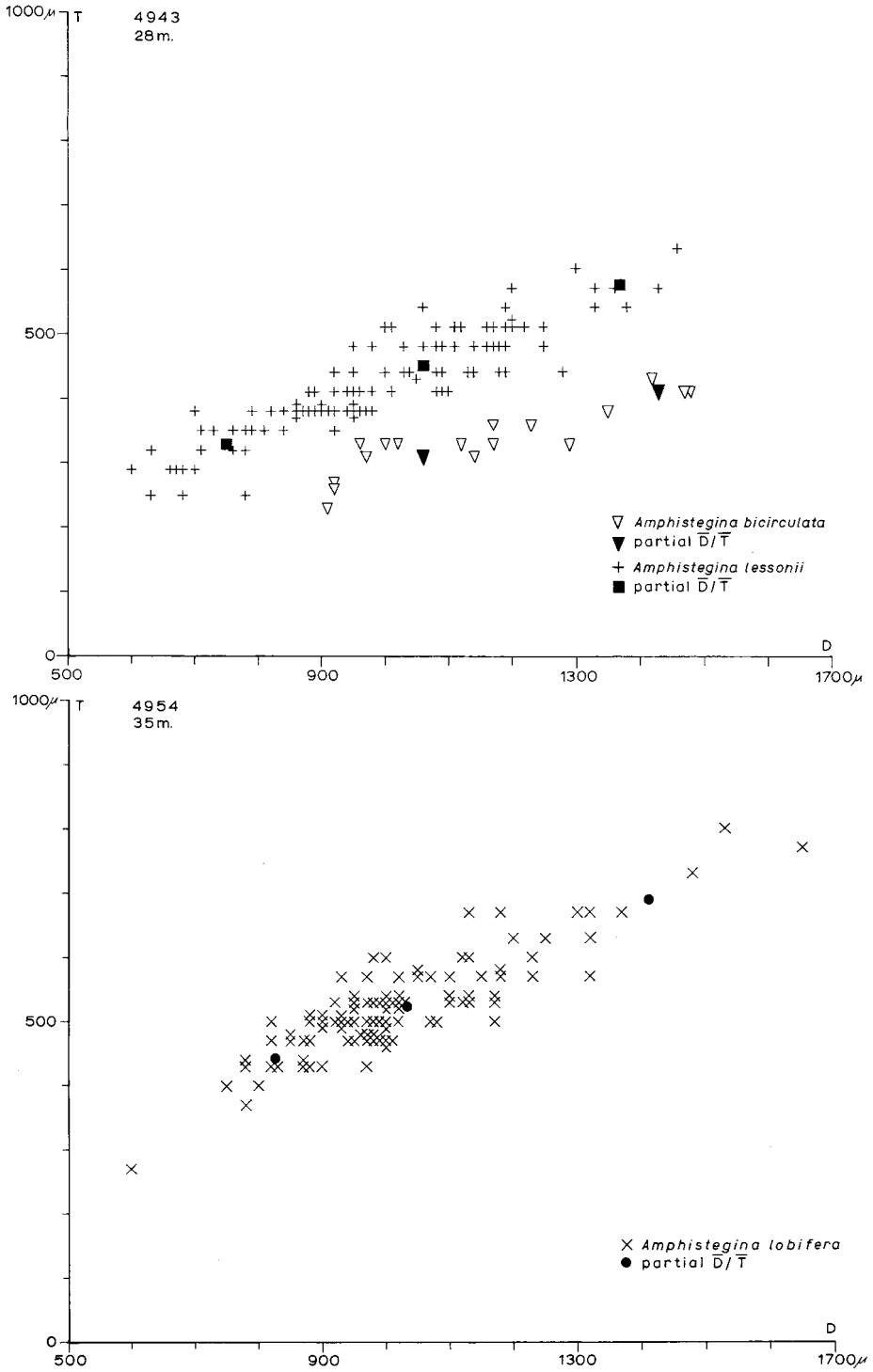
D
+ Amphistegina lessonii
■ partial D/T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28m.
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Amphistegina bicirculata
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Amphistegina lessonii
partial D/T
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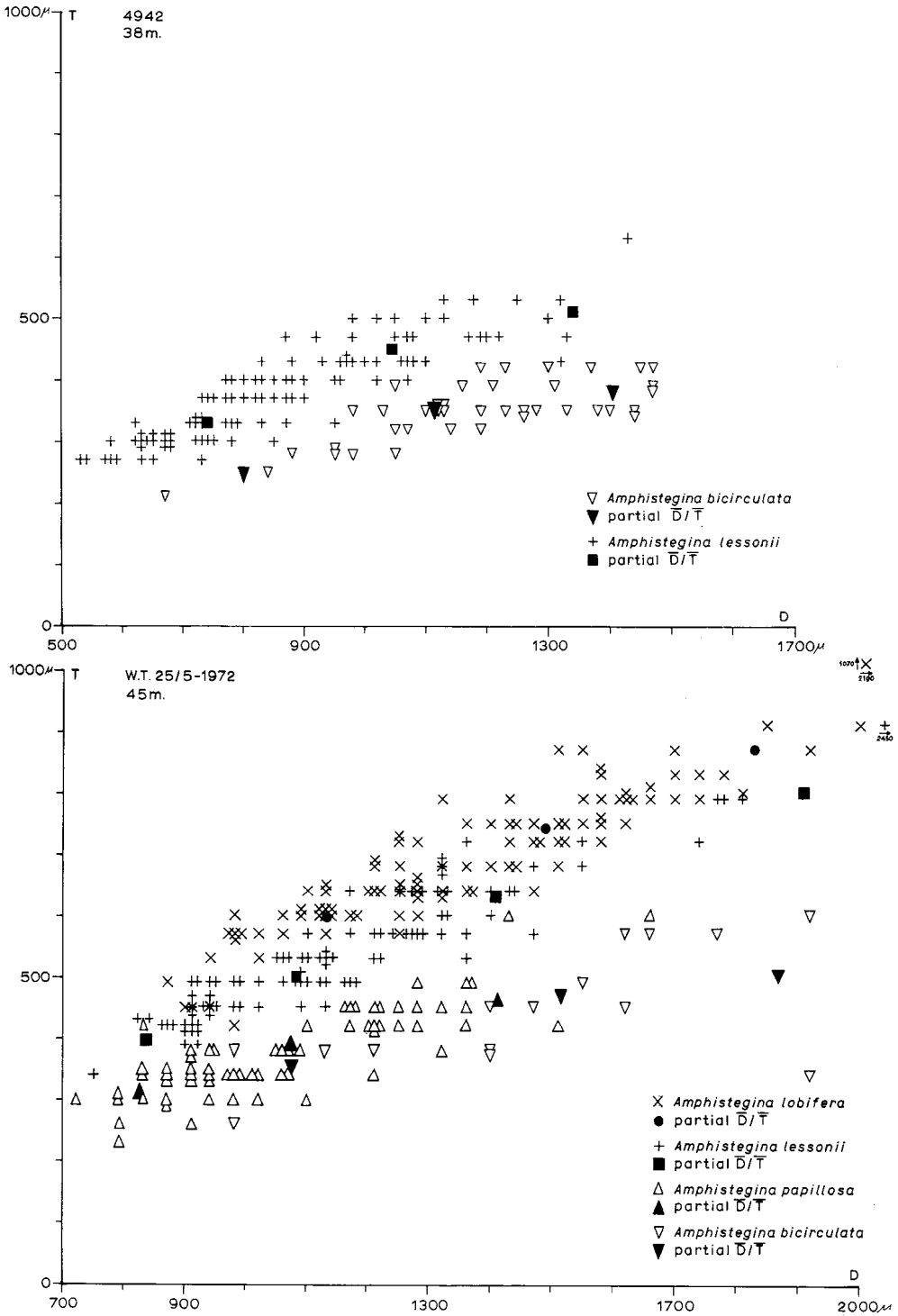
Amphistegina lobifera
partial D/T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Amphistegina bicirculata
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Amphistegina lessonii
partial D/T
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45m.
500
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700
900
1300
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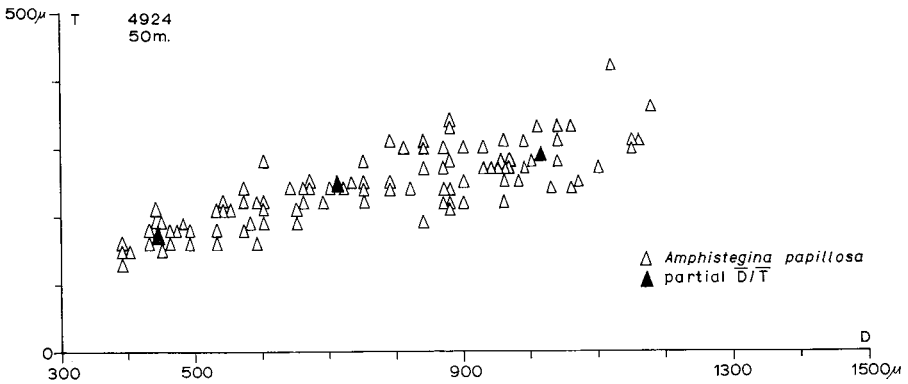
2000μ
D
Amphistegina lobifera
partial D/T
Amphistegina lessonii
partial D/T
Amphistegina papillosa
partial D/T
Amphistegina bicirculata
partial D/T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Amphistegina papillosa
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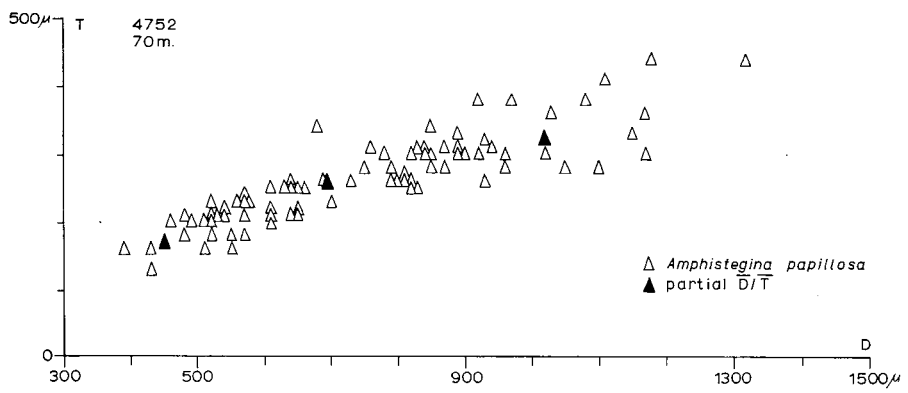
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Amphistegina papillosa
partial D/T
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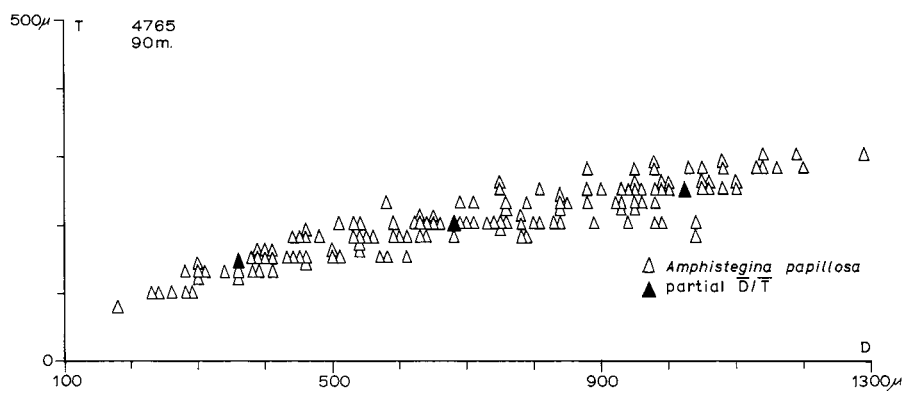
500μ
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4765
90m.
Amphistegina papillosa
partial D/T
0
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100
500
900
1300μ

SYMBIOSIS BETWEEN LARGER FORAMINIFERA AND UNICELLULAR ALGAE IN THE GULF OF ELAT, RED SEA

S. LEUTENEGGER

The symbionts of *Operculina ammonoides, Heterostegina depressa, Heterocyclina tuberculata, Amphistegina lobifera, Peneroplis planatus, Amphisorus hemprichii, Sorites orbiculus* and *Sorites orbitolitoides* have been investigated in situ (Leutenegger, 1977), within the host cytoplasm, by means of the electron microscope and classified after ultrastructural features of the cells (see Dodge, 1974).

A. lobifera is associated with spherical diatoms (fig. 1). The symbionts are abundant in all chambers. They preferentially line the perforate, lateral walls. I suggest that the immobile symbionts, while being transported by the currents of the host cytoplasm, become lodged in the pits beneath the pores on the test interior.

H. depressa, H. tuberculata and *O. ammonoides* harbor amoeboid diatoms (fig. 2). The symbionts of *H. depressa* and *O. ammonoides* can be clearly separated by means of the different ultrastructures of their chloroplasts. The symbionts of *H. tuberculata* resemble those of *H. depressa.* In all three species, most symbionts are concentrated directly below the perforate walls. It is not known, whether they have reached this particular position by means of an amoeboid movement or passively, by a mechanism as described above. The inner surface of the perforate walls is less sculptured in these nummulitids as compared with *A. lobifera.*

Peneroplis planatus is symbiotic with rhodophyceans of the order Bangiales, probably of the genus *Porphyridium* (fig. 3). The spherical, immobile

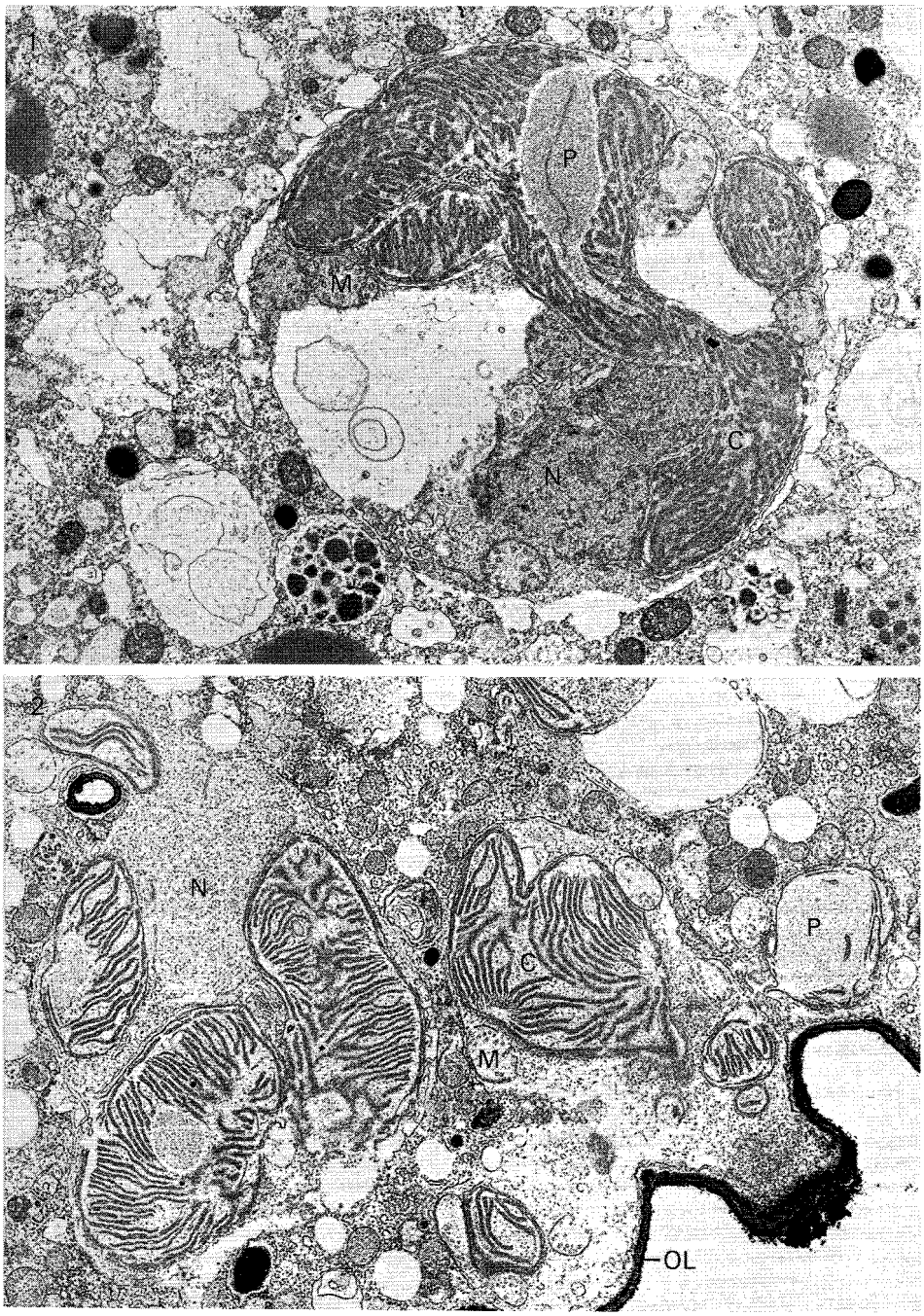
Figs. 1–4: Electron micrographs of symbiotic algae showing chloroplasts (C), pyrenoids (P), nuclei (N) and mitochondria (M).

Fig. 1 Diatom symbiotic with *Amphistegina lobifera.* x 10,200.

Fig. 2 Diatom symbiotic with *Operculina ammonoides.* Note symbionts closely adjoining the sculptured, inner test surface covered by the organic lining (OL). x 7,400.

Fig. 3 Red algae symbiotic with *Peneroplis planatus,* containing numerous starch grains (S). x 11,300.

Fig. 4 Dinoflagellate symbiotic with *Amphisorus hemprichii.* Note flagellum (F) and spongy-like host cytoplasm containing a lacunary system (LS). x 11,400.


1
P
M
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2
N
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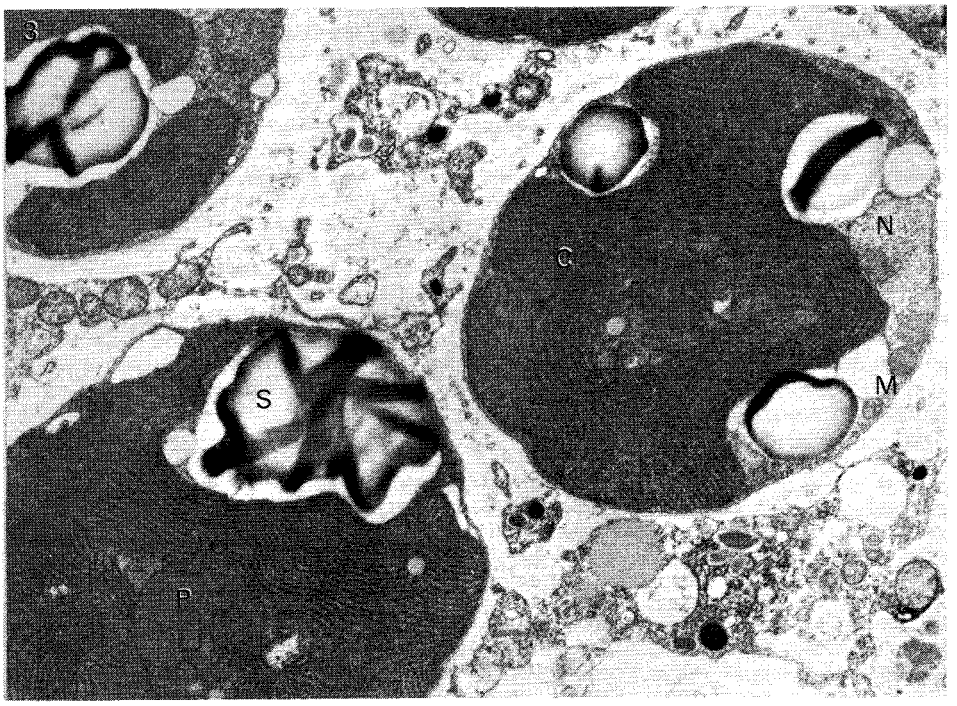
OL


3
N
G
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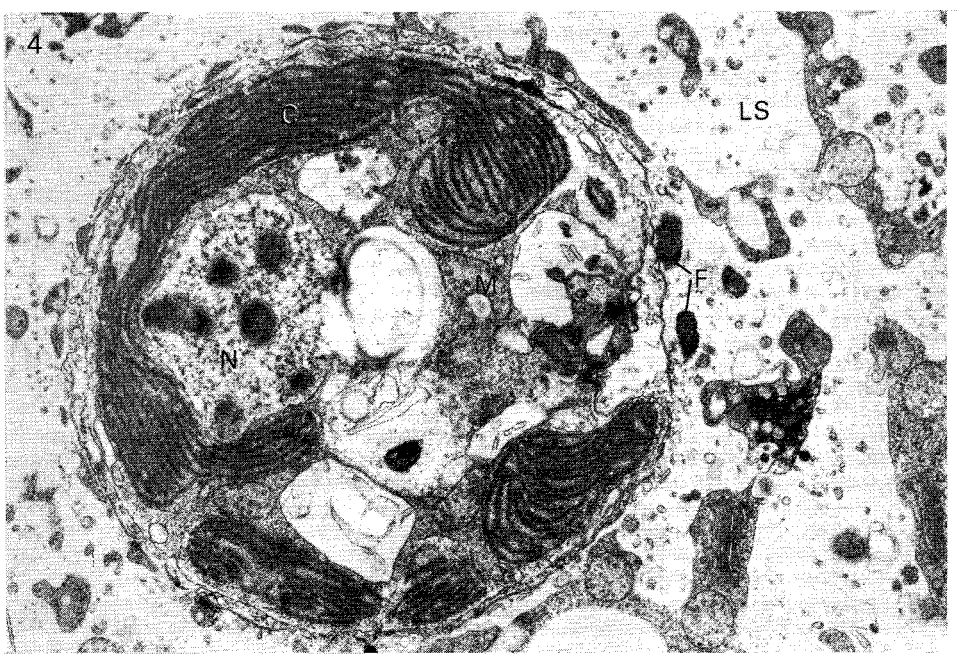
4
G
LS
M
F
N

symbionts are abundant in all chambers. They are distributed randomly throughout the cytoplasm.

Amphisorus hemprichii, Sorites orbiculus and *S. orbitolitoides* have a symbiotic relationship with dinoflagellates resembling, but not identical with *Symbiodinium microadriaticum* (fig. 4). The symbionts are concentrated in the chamberlets, directly below the lateral walls of the side oriented toward the light. If a living animal is turned over, the symbionts will move to the new upper side within approximately two hours. I suggest that the symbionts can actively move by means of their flagella within the lacunary system of the host cytoplasm (fig. 4).

For several reasons, a true symbiotic relationship is indicated: *Peneroplis planatus, Sorites orbiculus* and *Amphistegina lobifera* which have been collected in the Mediterranean Sea (Crete) harbor the same symbionts as the foraminifera collected in the Gulf of Elat. Symbiotic algae of *S. orbiculus* have been observed to reproduce asexually within the host cell. Further, in all species investigated except *P. planatus,* symbionts are rarely seen to be digested by the foraminiferal cells. In *P. planatus,* numerous starch grains have been observed within the host cytoplasm. They must be interpreted as residual bodies of decomposed algae. However, no transitional stages have been found between healthy and decomposed symbionts; the former are extremely abundant. Perhaps a constant relation exists between the number of symbionts and the volume of the host cytoplasm.

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