FORAMINIFERA AND PARALLEL EVOLUTION – HOW OR WHY?[1,2]

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ABSTRACT

Mac Gillavry, H. J. (1978). Foraminifera and parallel evolution – how or why? (Staring Memorial Lecture, 1977). Geol. Mijnbouw, 57, p. 385-394.

Directional changes are distinguished from yes-or-no changes. The latter lack the quality of direction; in the evolution of larger foraminifera they manifest themselves at first at a late ontogenetic stage as individual monstrosities, but lead, by the deuterogenetic mode, to new genera or families. Further evolution within a lineage is characterized by the directional gradualism of nepionic reduction. Various hypotheses why this complex evolution could have been of selective advantage are reviewed; complicating factors are discussed; there is still a large unexplained residue. Gradualism is considered to be rare and to be associated with faunas of low diversity, consisting of related but genetically isolated subunits which react to extra-group factors as one population, but which may evolve through intra-group competition; hence the frequent coexistence of related lineages. Still unexplained is the following of the same evolutionary pathway by forms of no near relationship. This may be due to severe structural limitation of possibilities; one pathway is followed by forms derived from planispiral ancestors, another by forms derived from trochoid ancestors.

Three appendices give details on the phylomorphogenesis of *Cycloclypeus*, notes on Indonesian larger foraminifera, and notes on the stratigraphy of South Sumatra.

The Chandogya Upanisad (VIII, 7-12) tells how Indra stayed with the Lord of Creation, Prajāpati, for thirty-two years, living the life of a religious student, in order to learn the truth about thruth. Then, having received a first instruction which he heard but dit not understand, he went away with peace in his heart. But before he reached the abode of the Gods, he saw the danger of this teaching and thought: I cannot find any joy in this doctrine. And so he went back to Prajapati with the offerings of a student in his hands and stayed another thirty-two years. So the story goes on for a total of a hundred-and-one years.

My experience has been somewhat similar. Each time I think I have found a satisfactory answer I feel like Indra, but then I see a danger in this answer; so back I go to the study of nature. Then, perhaps, a new answer will come up which at second thought is seen to be equally unsatisfactory. But I keep trying; after all I have only been at it for less than half the time of Indra.

[1] Staring Memorial Lecture, 1977-10-20.

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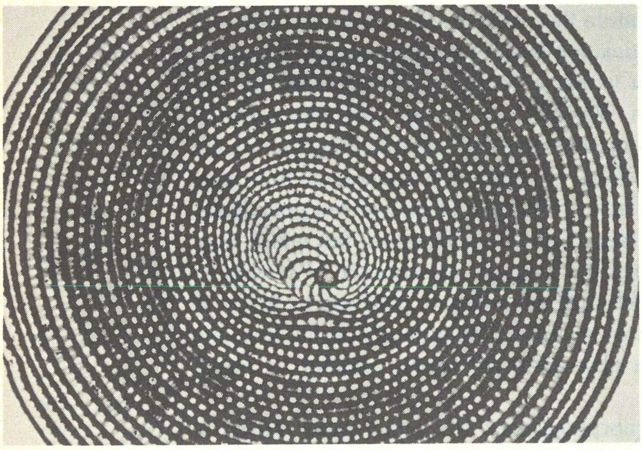
Fourty years ago I went to Sumatra as a junior palaeontologist to work with what was later called the Standard Vacuum Petroleum Company (oil companies change their names even more frequently than some genera of foraminifera). At the time I was already familiar with parallel evolution among rudists, but I knew next to nothing about foraminifera. So for several months I did nothing but study and learn, doing what I enjoyed doing and, to my surprise, getting paid for it. Hans Thalmann was the chief palaeontologist; on his advice the management sent me in 1938 to Tan Sin Hok in Bandung to learn Tan's method of phylomorphogenetic analysis of larger foraminifera. Since that time I have been a friend of Hok and his family.

Since that time also I have been fascinated by these foraminifera, awed by the complexity of structure they have been able to achieve, and intrigued by the remarkable similarity of structure achieved by forms with no closer relationship than that they are foraminifera: a similarity of structure, moreover, which these different forms acquired by the same succession of evolutionary events and pathways.

But let us first look at one of these structure-patterns which I will discuss in some detail. Figures 1 to 5 show the structure-pattern of what I have termed the Type-I or *Cycloclypeus*-type of phylomorphogenesis (MAC GILLAVRY, 1963). This structure is characterized in the adult by cyclic growth (Fig. 1): at each growth step or budding a new annular chamber is added to the entire circumference of the test. However, this annular growth is not attained until a certain age (a certain growth stage) has been reached; it is preceded in the centre of the test by spirally arranged juvenile chambers, the primary chambers. The young animal, accordingly, has a different construction, a different manner of chamber addition.

Actually the ontogeny of the animal, as expressed and preserved in its skeleton, is characterized by three successive ontogenetic innovations (Fig. 5). The earliest chambers have only one single aperture near the base of the frontal wall. The first ontogenetic innovation is the introduction of additional apertures in the frontal wall of the primary chambers; in *Cycloclypeus* this leads to the partitioning of succeeding chambers into chamberlets (Figs. 4 and 5). The second ontogenetic innovation is the introduction of a retrovert aperture, *i.e.* an additional aperture in the retrovert corner of a chamber; in *Cycloclypeus* this at the same time terminates the external spiral wall of the juvenile spiral; this new aperture is therefore also a marginal aperture. The introduction of this retrovert aperture permits subsequent retrovert overlap of later chambers and, because of its marginal position, retrovert overlap outside the spiral wall of the earlier whorl. The third ontogenetic innovation is the achievement of cyclic growth: as the retrovert end of a chamber meets the other end, the two ends coalesce to form the first cyclic or annular chamber (for a more detailed analysis see explanation of figure 5 and Appendix A).

This successive ontogenetic expression of new features



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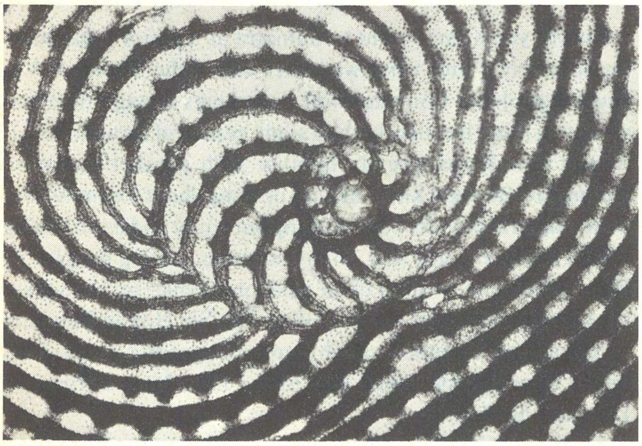

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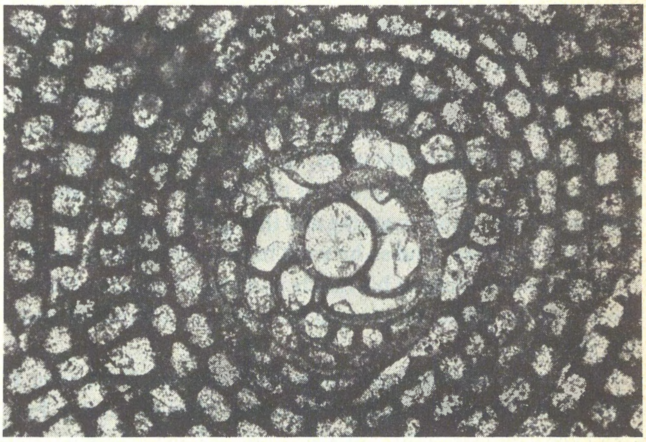

Figs. 1-4
1. *Sorites orbitolitoides* Hofker. Saba Bank, Caribbean. Sample Van Harten 45A; 25m. depth. Magnification 33.5x.
2. Same specimen of figure 1, centre. Magnification 134x.
3. *Cycloloculina annulata* Heron-Allen & Earland. Tertiary of northern Puerto Rico. San Sebastian quadrangle. Sample Mac Gillavry M64-226. Magnification 250x.
4. *Katacycloclypeus annulatus* (Martin). Sample G. L. Smit Sibinga, Luisa concession, East Kalimantan, Indonesia. Magnification 110 x.

The primary spiral is clockwise in all four figures; retrovert overlap anti-clockwise. Primary spiral terminated at or near to the base in figures 2 to 4. Number of primary chambers: 9 in *Cycloloculina* and *Katacycloclypeus*, 25 in *Sorites* (the 22d primary chamber is incomplete, just visible at the top of the photograph; it is normally developed on the retrovert side).
Additional apertures in frontal wall faintly visible in *Cycloloculina* (Fig. 3); in this form the chambers are not partitioned into chamberlets. For a more detailed analysis of figure 4 (*Katacycloclypeus*) see explanation of figure 5.

repeats the successive acquisition of new features during its phylogeny: *Heterostegina* originated out of *Operculina* through the acquisition of additional apertures in the frontal wall, *Cycloclypeus* out of *Heterostegina* through the acquisition of a retrovert marginal aperture and the attainment of cyclic growth. A prime example, accordingly, of evolution in the Haeckelian deuterogenetic mode. Thus there were at least two genetic changes (or sets of genetic changes), one leading from *Operculina* to *Heterostegina* and another leading from *Heterostegina* to *Cycloclypeus*. It will be clear that these genetic innovations, incorporated as they are in the genome of *Cycloclypeus*, are also present in the juvenile *Cycloclypeus*, but that they are not expressed morphogenetically until after a certain ontogenetic lag.

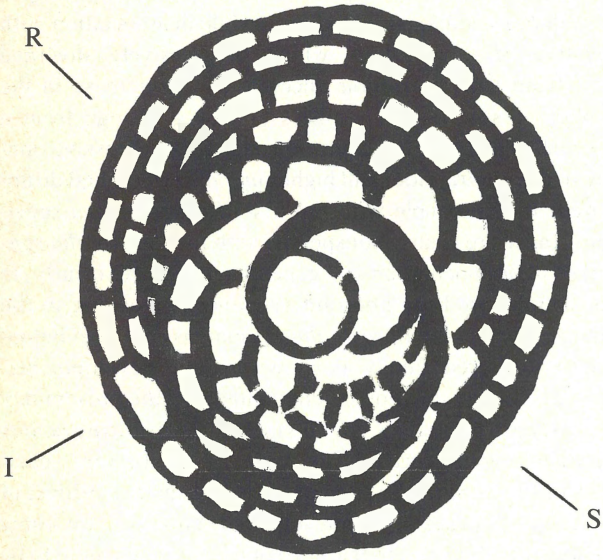

Fig. 5
Centre of *Katacycloclypeus* specimen of the photograph of figure 4, first 11 chambers.
Interpretation based upon Tan's description of the apertures (stolon system), as indicated in the frontal walls of the third and fourth primary chambers.
The clockwise spiral of primary chambers consists of nine chambers. The tenth chamber is the first annular (cyclic) chamber. Ninth and tenth chambers interrupted at the left side of the figure (i). True coalescence point of the retrovert and normal ends of the tenth chamber situated slightly to the right of the base of the figure (s: 'symmetrical chamber').
Only two primary chambers (protoconch and deuteroconch) with but one aperture, the primary aperture. Third primary chamber with additional apertures in frontal wall. Fourth primary chamber partitioned into chamberlets. Note absence of annular connection. Apertures not indicated in subsequent chambers.
First retrovert overlap (r) realised by ninth primary chamber. The arrow points to a chamberlet of the ninth primary chamber which must have been formed through a marginal aperture of the eigth primary chamber. However, the ninth primary chamber continues much further beyond the interruption, with four more chamberlets. These four chamberlets must have been formed through apertures in the frontal wall of the fifth primary chamber and through a marginal aperture of the sixth primary chamber. The ontogenetic introduction of the marginal aperture feature does not immediately lead to retrovert overlap.
The significant ontogenetic lags are therefore: I:2 chambers without additional frontal apertures; II:5 (possibly 4) chambers without marginal apertures; III:9 pre-cyclic chambers.

By a similar pathway, but in an entirely different family and with some differences in detail, *Peneroplis* originated out of some simple ancestor by the appearance of additional frontal apertures, and out of *Peneroplis* originated several complex forms, such as the *Sorites* of figures 1 and 2, by the attainment of annular growth.

In primitive forms of *Cycloclypeus* annular growth is only attained at a late ontogenetic stage. Its subsequent evolution is characterized by nepionic reduction, *i.e.* by the progressive reduction of the number of precyclic chambers: cyclic growth is attained progressively at earlier and earlier ontogenetic stages. Primitive forms are still very similar in appearance to *Heterostegina;* more advanced forms are quite different and characterized during the greater part of their life by the new feature of cyclic growth. This nepionic reduction has been exhaustively analysed by TAN (1932) and has since been confirmed by later investigators (see MAC GILLAVRY, 1962; and MEULENKAMP, 1977, for further references).

The evolution of *Cycloclypeus* is thus composed of two different kinds of changes: (1) the successive phylogenetic introduction of new features which are expressed in the same succession in the ontogeny of the animal; and (2) nepionic reduction of the ontogenetic lag in the expression of these new features. The first kind led to the emergence of the genus, the other kind characterizes evolution within the genus.

The new features are of the either-or, the yes-or-no, the presence-absence type; nepionic reduction on the other hand is gradual or gradational and, as a consequence, has the quality of direction: it is a directional change.

There has been much loose talk about the causes of direction in evolution. The usual statement, which one finds repeated over and again, is that it is natural selection which gives direction to evolution. But what is meant with the word direction is usually not made clear. Sometimes the word direction is used for something vague like increase in size; sometimes it only means a change in the frequency of an allele from one generation to the next (Ayala in AYALA & DOBZHANSKY, p. 366). There is an additional complication of a purely linguistic nature: one may say that natural selection directs a certain type of change, which then suggests that this change has the quality of direction. My thesis is that yes-or-no changes do not have this quality of direction; nepionic reduction, on the other hand, does.

SIMPSON (1955, chapter VIII) makes a distinction between direction, orientation and trend, but at the end of his chapter it is still not quite clear to me what is meant by each of these terms. I myself have tried to give more precise definitions for the terms dimensional change along an axis of reference in diversification, trend and directional change, but the results are still not quite satisfactory. Ayala (in AYALA & DOBZHANSKY, p. 339-354) gives a more rigorous definition of the term direction, but in such a way that it is equally applicable to the different types of change distinguished by me. There has, for example, been a stepwise increase in complexity of form by the successive introduction of the new features which led to the emergence of *Cycloclypeus*, and in this sense its phylogeny would be contained in Ayala's definition of directional change. In my view this would be a trend, effected by changes which themselves are dimensionless and thus not directional. Nepionic reduction on the other hand does not lead to more complexity and would thus not be directional in this sense; in the sense of a progressive (or if you wish regressive) reduction of the number of primary chambers, it is directional both from Ayala's viewpoint and mine.

Then there has also been much discussion as to whether there are macro- and micro-mutations. As SIMPSON (1955, p. 93) states, judgement as to the size of a mutation is actually in the evident degree of its phenotypic effect. The yes-or-no changes discussed above are clearly phenotypic effects having little effect at their first introduction but great consequences in the end. In my opinion, however, one cannot speak about their size or magnitude: since they do not have the quality of direction, there is no dimension nor any unit of measurement against which their magnitude can be measured.

These yes-or-no changes can be negative or positive; negative as in the case of a deficiency, positive if, as in our case, they lead to new form. The judgement is *a posteriori* to a certain extent. The introduction of a retrovert aperture can be regarded as positive or negative from a purely morphologic point of view: positive as the introduction of a new type of aperture, negative in the sense of the termination of the spiral wall. The decision to call it positive is based on what comes out of it, on the fact that it leads to an entirely new type of morphology. In an advanced species of *Cycloclypeus* one can no longer recognize the ancestral *Operculina*.

The case of *Miogypsinoides* is an even better illustration. This genus follows a different type of phylomorphogenesis: the Type-IIC or *Miogypsinoides*-type (MAC GILLAVRY, 1963). The different variants of the Type-II of phylomorphogenesis are again characterized by the introduction of a retrovert aperture, but they lack the prior introduction of the additional frontal apertures. The consequences are entirely different: in these forms the appearance of a retrovert aperture does not lead to retrovert growth by means of retrovert lengthening and overlap of primary chambers, but by the addition of retrovert secondary chambers.

At its first phylogenetic appearance the new feature occurs rather as an aberration than as something which will eventually lead to what is considered to be a new family (or subfamily): a typical example of the hopeful monster which played some role in the discussions on evolution but which is usually discredited (see, however, VAN VALEN, 1974). Nevertheless here it is: a monstrosity and a hopeful one. The situation is well illustrated by the photographs published by SALMERON (1972) and has been observed in various parts of the world: BARKER & GRIMSDALE (1937) and SALMERON (1972) in Mexico; RAJU (1974) in India; MAC GILLAVRY (1968, p. 71) in Kalimantan; DROOGER (1963) in southern France (showing a somewhat later stage of development). My observations were based on samples from the Stanvac Kahajan wells of southern Kalimantan. A lower sample contained typical specimens of *Pararotalia*; a somewhat higher sample contained a population of the same *Pararotalia* which now, however, comprised a few aberrant specimens with a few secondary chambers, similar to those pictured by Salmeron; higher up in the well *Pararotalia* persisted for a while in association with primitive *Miogypsinoides* which progressively diverged away from the *Pararotalia* ancestor by an increase in the number of secondary chambers and by a change from a trochoid to a planispiral centre through the progressive opening of the ventral side; still higher up *Pararotalia* had disappeared. In the sample with the first *Miogypsinoides* specimens, these are clearly conspecific with the *Pararotalia* specimens in ornamentation and general appearance; clearly, in this sample, we have aberrant specimens belonging to the same species as the *Pararotalia* specimens, but also belonging to a different family as shown by later developments. Should a similar situation be encountered at the present day (as in some species of *Cibicides*), then the *Miogypsinoides* specimens would certainly be regarded as aberrant specimens of the *Pararotalia* species, as simple monstrosities, of no account; because of what followed, however, we know that they heralded the appearance of what is considered to be a new family (or subfamily).

I have insisted on this example at some length because of the problem of the origin of higher taxa. One of the suggestions offered in the past has been that perhaps a new genetic feature could be expressed at an early ontogenetic stage, causing a switch into a new and different ontogenetic pathway. It has been objected that this would necessitate a number of additional changes in order to make the switch selectively acceptable. All this has usually been mere speculation, but here we have a well documented case; with this exception that the new feature, at its first phylogenetic appearance, is only expressed at a *late* ontogenetic stage, causing a switch into a new ontogenetic pathway late in life and of little morphologic consequence at its first phyletic appearance. The new and aberrant form was immediately acceptable and accepted by selection, if any. The consequences are elaborated by the supporting changes which effect the nepionic reduction, the reduction in the number of primary chambers, which also characterizes further evolution in this group, with the result that the new morphology gets expressed earlier and earlier in ontogeny and hence becomes more and more characteristic of the animal's morphology, in combination with an increase in the number of secondary chambers and some further complications.

When the ultimate stage of nepionic reduction has been attained (see MAC GILLAVRY, 1963, for the morphologic consequences), the new form may persist and flourish for a while. In many cases, ironically, it then becomes extinct.

I think that I have shown to some extent how the evolution of larger foraminifera operates. Much of what we are doing starts from the work of Tan and is based upon his penetrating analysis of their phylomorphogenesis. Naturally, later authors who applied his method have added to it; foremost among these are, I think, the schools of Utrecht and of Amsterdam. Naturally much more could be said and would have to be said in order to give a full account of what has been done and what is going on in this kind of investigation. However, what I have said above will have to suffice to clarify the following discussion.

It will have become clear that one of the great advantages of larger foraminifera is that they preserve evidence of their ontogeny in their skeleton and that this ontogeny preserves a meaningful record of their phylogeny. This is equally true for other groups of fossils but foraminifera have the additional advantage that you can study them in large numbers and preserve them in a limited space, a great boon if you were accustomed to work with rudists.

Many foraminifera, like other organisms, have a life-cycle of alternating diploid and haploid generations; accordingly, like all sexual organisms, they can profit from the evolutionary advantages of genetic recombination. The great difference with all other organisms, however, is that the diploid and haploid generations have the same gross morphology. The diploid generation is usually very rare and thus can contribute to evolution in an exploratory manner by genetic drift. The haploid megalospheric generation produces gametes which may be released into the sea in enormous numbers, but few of which, like human sperm, have a chance to copulate.

The fact that, as a rule, the megalospheric haploids are far more numerous than the microspheric diploids is important, for it means that such communities consist for the greater part of haploids which thus would be highly vulnerable to whatever selective forces can act upon them. Add to this that most forms reproduce only once, at the end of their life-span after they have attained full adult size (compare this with Kurtén's cave-bears which can produce a cub once a year); add to this that the life-span of some species can be considerable and you have a real problem. Any hypothesis suggesting that the pictured situation is selectively advantageous will also have to explain why it does not occur more frequently.

In several genera of larger foraminifera there is yet a further reduction of the sexual phase in that the megalospheric adults instead of producing gametes, reproduce by multiple fission (schizogony). This is for instance the case in *Heterostegina* (RÖTTGER, 1974), *Sorites* (HOFKER, 1964, 1976) and *Marginopora* (ROSS, 1972). In the case of *Heterostegina* (LEUTENEGGER, 1977) and *Sorites* (LACROIX, 1941) a microspheric form is known to exist; their life-cycle is therefore not exclusively apogamic. We do not know whether these megalospherics which reproduce by schizogony are haploid; LEUTENEGGER (1977) has observed that megalospheric specimens of the Peneroplid genera *Amphisorus* and *Sorites* are plurinucleate, the implication being that they are diploid, a situation which could occur if meiosis failed to occur prior to asexual reproduction of the microspheric parent. This is not documented by chromosome counts and Leutenegger's paper is therefore inconclusive. Megalospheric schizonts of *Heterostegina depressa* are uninucleate (lit. in LEUTENEGGER, 1977, p. 34 and HOTTINGER, 1977, p. 108); in this species the predominating form would be considered to be haploid by all authors.

Sorites, Amphisorus and *Marginopora* have the same type of morphology as *Cycloclypeus,* but they belong to an entirely different family. They represent three different stages of nepionic reduction, *Marginopora,* which is the most advanced, representing the ultimate stage of nepionic reduction. Nothing is known about the rate of evolution in these forms. Since, however, sexual recombination is considered to be an almost absolute necessity for evolution (e.g. Monod in AYALA & DOBZHANSKY, 1974, p.364), the trend towards extreme reduction of the sexual phase through repeated schizogonic reproduction in animals that clearly have had a complex evolutionary history, becomes the more mysterious. ROSS (1972, p.190) suggests that this reduction of the sexual phase is 'in keeping with the strong physical environment of their reef habitat where asexual reproduction is also commonly dominant in lower invertebrates'. But that is an equilibrium consideration which does not take into account the required dynamics of sustained change. Nor can random genetic drift due to the reduced numbers of sexual individuals account for the sustained gradualism of nepionic reduction. One would then rather expect evolution to proceed in spurts and at a much higher rate, with occasional reversals towards nepionic retardation.

We will therefore have to consider three main problems with regard to the evolution of larger foraminifera.

The first problem, then, is that of the apparent gradualism of nepionic reduction, a problem to me because I think that gradualism is rare, and particularly to Eldredge and Gould who believe that it occurs 'hardly ever'. Hence their statement (GOULD & ELDREDGE, 1977, p. 134): 'perhaps they (*i.e.* tiny sustained evolutionary rates) constitute a fundamental mystery worthy of our serious thought and attention.'

The second problem is that of parallel evolution, *i.e.* the curious fact that the same type of phylomorphogenesis has been followed in the same manner by unrelated groups of foraminifera. The *Cycloclypeus*-type of phylomorphogenesis is a particularly striking example. This type of structure-pattern is found in at least four different families, in each of which it must have been acquired by the same evolutionary pathways. The evidence is still insufficient or even lacking in several cases, but there is little doubt that it will be found to conform to expectation. Furthermore there is ample evidence that *Heterostegina* originated several times out of *Operculina* (Mac Gillavry in TAN, 1939; PAPP, 1963; DROOGER, 1960, p. 328) and *Cycloclypeus* or Cycloclypeus-like forms *(Heterocyclina)* more than once out of *Heterostegina* (HOTTINGER, 1977; MEULENKAMP, 1977).

The third problem is why this type of evolution should occur at all.

Let us begin with this last problem. TAN (1932) considers nepionic reduction to be autonomous in the sense that the 'stimulative causes of the genotypic shifts are inhaerent in their very genotypic constitution'. His conclusion is based on the polymodal frequency distributions of his samples, on the coincidence of his modes in successive populations, and on his observation that a mode appears before the preceding mode has attained its maximum relative frequency in time. He furthermore notes (p. 95) that the evolution proceeds irrespective of lithological facies, thus suggesting that environmental influences did not exert the determinative and, by implication, selective influence. Actually Tan's idea of genotypic shifts occasioned by causes or limitations inhearent in their very genotypic constitution would fall within the category of what WHYTE (1965) calls internal factors of a non-Darwinian nature. Nowadays such factors as meant by Whyte are easily regarded as subject to natural selection at a low level in the organic hierarchy of the animal (Campbell in AYALA & DOBZHANSKY, p. 142); I do not think, however, that there would be many selectionists who would consider this type of internal selection as a sufficient cause for the observed nepionic reduction: usually one would also assume some phenotypic selection to be operative at a higher level. In the case of haploid foraminifera such selection would be uncommonly severe.

In 1956 I calculated that, if Tan's modes had any reality, such evolution could occur at the observed rate by differential mutation pressure in a sequence of multiple alleles. This idea was criticized from a theoretical point of view by VAN VALEN (1969, p. 201). Nor would it be considered very plausible from a purely statistical point of view. A statistician would wish to see such a situation documented by samples of far greater size. The entire matter furthermore hinges upon the situation in the primitive lineage of *Cycloclypeus koolhoveni*. At higher stratigraphic levels the issue is confused by the coexistence of a mixture of lineages. Later investigations did not confirm the reality of Tan's tops, but they all dealt with different lineages or else with mixtures of lineages. Note, however, that coexistence of different lineages in the same locality does not differ in principle from coexistence of modes within one species, for the latter, if real, presupposes lack of genetic flow or at least restricted flow between modes.

An important point is the apparent irreversibility of nepionic reduction; hence everybody's interest in this process because of its potential use in biostratigraphic correlation. Soon, however, it was found that nepionic reduction cannot be used as a simple yardstick, since it was established that there often are lineages with different rates of evolution. A

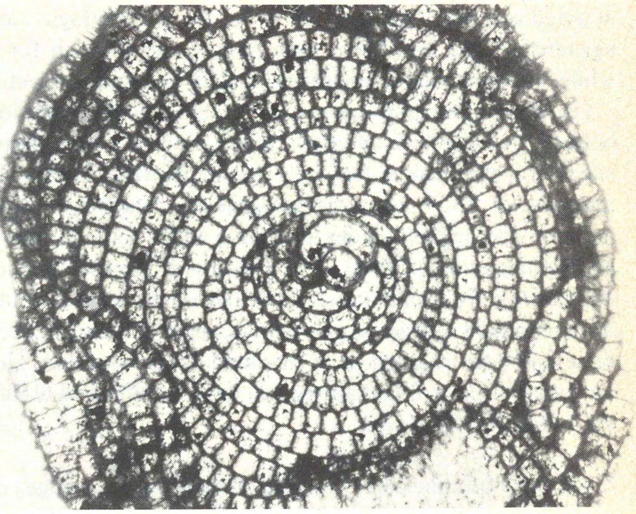

Fig 6
Cycloclypeus sp., Tji Kadu, South Preanger, Java. Magnification 26x. Specimen with three regenerated lesions of approximately equal size and semi-circular shape, possibly due to bites by a predator.

first example of this kind had already been found by Tan in the case of the Kali Lawak population (Tegal, Java: TAN, 1932, p.123), and a second in the case of *Katacycloclypeus* (TAN, 1936-b, p. 119). Considerable numbers of different lineages have been established for the Miogypsinidae (DROOGER in various papers, *e.g.*, 1956, 1963) and for *Cycloclypeus* (MAC GILLAVRY, 1962). Sometimes there are side-branches with different rates of nepionic reduction coexisting in the same region or even in the same sample. Some lineages of the same morphogenus may even have originated independently from the same type of ancestor, either more or less synchronous or even at different times.

Still, this irreversibility is so generally true, that when one encounters an apparent reversal or apparent nepionic retardation, one may wonder whether this is not yet another instance of a lineage being succeeded by a more primitive lineage derived from elsewhere (cf. RAJU, 1974, p. 101). As a result nepionic reduction can still be used for biostratigraphic correlation and is in fact so used, as long as one stays within one lineage.

To DROOGER (1956, p. 466) this irreversibility suggests directional pull by natural selection towards increasing adaptation to the zone of turbulent shallow water to which zone these animals would be confined because of their symbiosis with commensal algae. Drooger considers the advantages of nepionic reduction to be: first that it increases the early attainment of radial symmetry; secondly that it increases the size of the shell (in combination with the increase of the number of buddings) which would be of advantage against burial and transportation; thirdly that it leads to a framework of many small chambers and thus to increased strength of the test. VAN HINTE (1965) furthermore suggests that it enables the nucleus to take up a more strategic central position. VAN HINTE (1965), DROOGER & RAJU (1973) and DROOGER (1974) have further expanded this line of thought, taking into account also the size increase of the protoconch and the formation of lateral chambers.

I cannot give here a fuller account of Drooger's ideas nor do them full justice. But let us look at some of the factors mentioned.

The advantage of the strengthening of the test is irrefutable for this strengthening is certainly needed to support these gigantic shells. It is not a strengthening against breakage for these animals have an almost unlimited regeneration potential. Moreover, lesion would often appear to be due to little bites by predators (Fig. 6; LUTZE ET AL., 1971, p. 25) rather than to mechanical causes, and no amount of strengthening will be protection against such predation.

Danger of burial is more problematic for it has been observed that *Marginopora* can work its way to the surface of two centimeters of sediment overnight (ROSS, 1972, p. 189). Thus, such burial as is likely to occur in shallow water would hardly be a bother to them.

Next, take the problem of transportability which is a more complex problem. It is certainly clear that the shells of larger foraminifera can be transported to deeper water and out of their biotope, for they are frequently found at the base of deep-water turbidites; some beds deposited by grain-flow may even consist entirely of these shells. But these occurrences are not really relevant, for one peculiarity of foraminiferal shell assemblages is that they may not be death assemblages: when a foraminifer reproduces, whether in schizogony or in gamogony, the protoplasm leaves the shell and the discarded empty shell stays behind (cf. LE CALVEZ, 1938, p. 307, footnote). Thus, when a fauna, as is often the case, consists entirely of adult tests, then it may simply represent an accumulation of empty shells discarded at reproduction; the individuals which formerly occupied these tests have not been taken out of circulation by accidental death. Such empty shells may then be transported and reworked, but this has no relevance to the transportability of the living animal and it is this transportability of the living animal that we have to consider.

With regard to this transportability of the living animal, or rather the lack of it, we have the following observations: that larger foraminifera often take up a vertical or oblique position, sticking partly out of the sediment, thus giving purchase to the currents (HOTTINGER, 1977, p. 78; LUTZE ET AL, 1971, p. 25; ROSS, 1972, p. 189); that *Operculina* and *Heterostegina* tend to crawl up on elevated and thus most exposed parts of the substrate (LUTZE ET AL, 1971, p. 25); that larger and other forminifera can bind the upper several centimeters of the substrate into a loosely adhesive aggregate (ROSS, 1972, p. 181); and that *Marginopora* can attach itself with a force of up to 12,000 dynes/cm^2 (ROSS, 1972, p. 189).

Finally let us consider the larger encrusting foraminifera. Several of these forms follow the type of phylomorphogenesis which is characterized by retrovert apertures and secondary chambers (Type-II *sensu* MAC GILLAVRY, 1963). Some of these become radially symmetric, but others are more irregular in form; they may become very large, but the initial spiral part may not be in the centre. Here, then, this type of phylomorphogenesis is followed by forms which may not tend towards radial symmetry; forms, moreover, which are protected against transportation by their encrusting nature except when the object or plant to which they are attached is being transported. According to HOTTINGER (1977, p. 70, 74) such transportation of attached forms indeed occurs, but along the coast, thus not taking these forms out of their biotope range.

But let us turn to the first and second problems. How does one explain the slow and steady rate at which nepionic reduction proceeds; and why should it happen that side-lineages with a greater rate of nepionic reduction often die out while the lineage with a slower rate of evolution lives on? Finally, why should several unrelated forms follow the same evolutionary pathway with the same succession of innovations and the same elaboration of their effects by nepionic reduction?

With regard to the slow and steady rate at which nepionic reduction proceeds, I am inclined to agree with ELDREDGE & GOULD (1972, p. 97, 112) in their criticism of orthoselection by directional pull of the physical environment. In 1968 I observed that sustained directional change is rare among marine invertebrates and that it appears to be associated with low faunal diversity; thus it would be characteristic for exceptional environments in which synecologic conditions are chiefly determined by the coexistence of members of the same taxonomic group. This means that the entire group of coexisting related forms can react as one species to the physical environment and to the conditions of food and predators; competition, however, would occur between genetically isolated subgroups. This could lead to a kind of bootstrap evolution, not in the sense of a species pulling itself up by the bootstraps, but rather in the sense of a group of species each pulling the others up by the bootstraps. This idea is akin to Gould and Eldredge's clone selection (GOULD & ELDREDGE, 1977), but at various taxonomic levels: between clones, between demes with restricted gene flow, between species, lineages or genera; it could even be extended to members of different taxonomic groups as long as they have the same habits.

In assemblages of great diversity, the open market (αγορα) of the neritic zone, this situation does not exist. Here, as shown by observation, a species can maintain itself in a temporary equilibrium by sticking to the form and habits by which it has been able to spread and to establish itself, up to the time when it can no longer cope with a new change of equilibrium in the ever changing synecologic environment. This is the view institutionalized by ELDREDGE & GOULD (1972; or GOULD & ELDREDGE, 1977) as the theory of punctuated equilibria.

There has been considerable discussion as to what kind of evolution can take place in a constant environment; in my opinion there is no such thing as a constant environment. Even the above-meant equilibria are oscillating, fluctuating and ultimately unstable. One of the few exceptions to these statements may be the biotope of *Lingula*. In its exceptional environment *Lingula* has been able to thrive for some three hundred million years, but it is the only one that has been able to do so. Accordingly it is only subject to intraspecific selection, but as it is already fully adapted to its hermitage it does not need to change.

My hypothesis of gradualism in communities of related forms and low synecologic diversity explains why we find coexistence between *Heterostegina* and the primitive species *Cycloclypeus koolhoveni*, between *Pararotalia* and primitive *Miogypsinoides*, coexistence between the Soritid genera *Sorites* and *Amphisorus*, coexistence of various lineages of the same genus, and possibly coexistence of different statistic modes within a species. In the last case we are back to TAN's principle of coexistence of elementary species (1932, p. 113), but with the added factor of phenotypic selection between competing subunits. In this connection it is sobering to compare Gould and Eldredge's figure 9, illustrating their concept of pseudo-gradualism by clone-selection, with Tan's figure (p. 116) illustrating his hypothesis of autonomous evolution of coexisting elementary species and lineages: the two figures are practically identical.

The idea of clone selection could explain the slow and steady rate at which nepionic reduction appears to proceed; however, would it be applicable to populations of haplonts which would be genetically segregated and vulnerable to selective influences? Secondly we still have not explained Tan's observation that a new mode appears before the preceding mode attains its maximum relative frequency in time; of course this does not need to be explained if the modes have no reality. Thirdly, there are many cases where there is only one evolving lineage without any evidence of coexistence of genetically isolated subgroups; how would one be able to test the idea of clone selection in such a situation?

So I am still uneasy about this answer.

Entirely unexplained as yet is the problem why various unrelated forms should follow almost identical evolutionary pathways. In this connection it may be noted that the selective advantages, suggested to explain why this type of evolution should occur at all, are conceptual. With this I mean that, as Drooger observes, radial symmetry can be achieved by diverse means. Therefore, if it is achieved by the same succession of means in different groups, then an additional explanation is needed. Here I think that we must consider yet another factor, namely the possible existence of severe internal or rather structural limitations (cf. SIMPSON, 1955, p. 271; RAUP, 1972). What I have in mind is that perhaps only a few pathways of change are structurally possible at all. This then would be a real 'internal' factor, but not of a kind that can be regarded as subject to low-level selection: for that which cannot occur cannot be selected, and that which has no immediate alternative cannot be selected against.

An argument in favour of this line of thought is the observation that, as far as is known, the *Cycloclypeus*-type of phylomorphogenesis is followed by forms derived from planispiral ancestors, whereas the different varieties of phylomorphogenesis Type-II (with retrovert apertures and secondary chambers) appear to be followed by forms derived from trochoid ancestors (MAC GILLAVRY, 1963, p. 146). If this is found to be of general validity we would here have a determinative historical-phylogenetic factor *sensu* Seilacher (RAUP, 1972).

An argument against this idea is that my terms such as retrovert aperture are also conceptual: a retrovert aperture in one family need not be structurally homologous to a retrovert aperture in another family.

So back we must go to nature with the offerings of a student in our hands. For still I am not satisfied. What is the use of all these speculations unless we can test them? This is best done by experimenting with living forms, taking into account that the culturing may affect the outcome (FØYN, 1936, 1937; RÖTTGER, 1972). In the case of fossil forms we may try to get answers by the application of statistical methods. This I am trying to do by comparing the relative variability of juvenile versus adult features. In this way it will be possible to see whether there has been any differential mortality. In order to do so one must have species in which the adult form can be distinguished, such as the Soritidae with their brood chambers in the adult (LACROIX, 1941; HOFKER, 1964, 1976). In the second place we can compare the relative variability of haplonts with that of the diplonts of the same species. This will make it possible to see whether there is any selective difference acting upon these two generations. Of course, we must then be certain as to the haploid status of the forms studied.

For this program, it was found, we needed first to develop new statistical methods. These new statistical tools have now been forged to some extent.

So I will have work to do for another fifty years or so.

APPENDIX A

In *Cycloclypeus* the appearance of additional apertures in the frontal wall of spiral chambers leads to the partitioning of subsequent chambers into chamberlets. This is not the case in all forms which follow the *Cycloclypeus*-type of phylomorphogenesis. Partitioning is incomplete in Recent heterostegines of the Indo-Pacific region; no partitioning occurs in *Peneroplis* or in *Cycloloculina* (Fig. 3).

The appearance of the retrovert aperture does not necessarily lead to retrovert overlap in the next chamber to be formed: after its appearance chambers may continue to be added in normal spiral succession but without external spiral wall. Retrovert overlap is therefore not a direct consequence of the appearance of the retrovert aperture.

In *Cycloclypeus* the spiral wall is terminated at the introduction of the retrovert aperture. In the Type-II of phylomorphogenesis this is not necessarily the case: retrovert aperture and the addition of retrovert secondary chambers may take place within a continuing spiral wall which may continue up to the adult stage (e.g. *Helicolepidina, Helicorbitoides*), or terminate after a while *(Helicocyclina)*.

When, as in *Cycloclypeus*, the first retrovert aperture also terminates the spiral wall so that retrovert growth can take place outside the spiral wall of the preceding whorl, one might expect that this will automatically lead to cyclical growth. This is not so: in some Soritids, for instance, there is no coalescence of the opisthogyrate (=retrovert) and prosogyrate flaps. In *Cycloclypeus*, as suggested by some preliminary graphs, there seems to be a narrower correlation between number of pre-cyclic chambers and number of chambers without retrovert aperture, than between number of pre-cyclic chambers and number of chambers preceding first retrovert overlap; here, accordingly, there would also not be a mechanical connection between onset of retrovert overlap and the attainment of cyclic growth.

APPENDIX B

Most of my studies of larger foraminifera during my stay in Indonesia dealt with the Miogypsinidae.

I came to the conclusion that the primitive *Miogypsinoides* of Indonesia evolved independently from those of the western hemisphere. This conclusion was based upon a difference in the relationship between the number of uniapertural chambers and the number of primary chambers, and the much earlier appearance of lateral chambers in the American forms (DROOGER, 1963, p. 345). A comparable statement is found in DROOGER & RAJU (1973, p. 207), quote: "Although the central *Miogypsinoides-Miogypsina* lineage occurs in all three provinces, its development is different in detail from one province to the other. This suggests that evolution along this general path was at least in part independent in each of these larger regions" (America, Indo-Pacific and Mediterranean). An independent evolution and even independent origin would not be surprising, as *Miogypsinoides* has been observed to originate out of *Pararotalia* in at least two of these regions. A veritable nomenclatural revolution will have to follow if these ideas are further substantiated.

I agree with DROOGER & RAJU (1973, p. 207) and with VAN VESSEM (1977) that *excentrica* and *thecideaeformis* belong to different lineages, the *thecideaeformis-polymorpha* lineage being characterized by an evolutionary increase in size of the first auxiliary chamber and an increase in the number of chambers surrounding it. The *excentrica*-lineage with its precocious appearance of adauxiliary chambers soon became extinct. In South Sumatra *excentrica* and *thecideaeformis* coexist with *'kotoi'* in quiet water behind the limestone belt; as far as I have been able to ascertain they just postdate the disappearance of *Spiroclypeus*. The different stages of *'kotoi'* (TAN, 1937) are also found in the limestone belt. If *thecideaeformis* originated out of a *'kotoi'*-like ancestor, this must have been an older form than the *'kotoi'* with which it coexists. *Lepidosemicyclina thecideaeformis* left no descendants in south Sumatra; the younger species *polymorpha* coexists in east Kalimantan with *bifida*-like forms and with *Katacycloclypeus annulatus*.

The origin of *Orbulina* out of its precursors can be well observed in the south Sumatra section at a stratigraphic level much higher than the top *Spiroclypeus*. Occurrences in South Sumatra of *Miogypsina 'indonesiensis'* postdate the *Orbulina* datum plane.

APPENDIX C

A few notes on the marine Tertiary of south Sumatra are needed to place the preceding notes in a stratigraphic framework.

The oldest part of the marine Tertiary is well exposed along the Sungei Samuhun, West of Baturadja, which was surveyed by G. J. H. Molengraaff and me before the war. Our results differ markedly from the description by R. W. van Bemmelen (Geological map of Sumatra, sheet 10, Baturadja, 1932). An older, probably terrestrial formation of unknown age, which consists of sandstones and volcanics, is transgressively covered by a thin limestone bed. This basal bed of the marine Tertiary contains primitive *Miogypsinoides* with a slightly trochoid centre. The basal bed is followed by a section of marine dark-coloured shales which are unfossiliferous or nearly so; only at the base just above the limestone we found a fauna of thin and flat *Heterostegina* and *Cycloclypeus,* which therefore lived in a muddy environment of low energy. From well-information it is known that this section of dark unfossiliferous shales was deposited in a narrow north-south trending subsiding trough, probably under anaerobic conditions (high gamma-ray values). Higher up the section again becomes aerated with, in the centre of the trough, a rich fauna with pelagics and large benthonic foraminifera *(Vaginulina, Vulvulina,* etc.). Towards the east this part of the section is flanked by a limestone belt with *Spiroclypeus*. The subsidence pattern changed at the end of the Tertiary-e, and a much wider subsidence basin was formed with a different shape. In this basin the 'Telisa'-shales were deposited with an enormous thickness in the centre of the basin, but a much thinner section in the east. A limestone belt at the base of the 'Telisa' coincides near Baturadja with the preceding limestone; here, accordingly, a continuous limestone interval is present with *Spiroclypeus* in the lower part, but not in the upper part. Sandstones deposited behind this limestone contain the Miogypsinid fauna mentioned in Appendix B (*'kotoi', excentrica* and *thecideaeformis)*.

The 'Telisa'-section can be subdivided into three parts. In one well we penetrated 800 meters of the lower third, without getting the whole of it. The middle third is predominantly pelagic. *Orbulina* is observed to originate out of its precursors at or near the base of the upper third part.

The 'Telisa' shales are followed by the 'Lower Palembang' formation which becomes more sandy and which contains some beds with *Miogypsina 'indonesiensis'* and *Lepidocyclina* cf. *martini*.

Thereafter the section grades into the non-marine Middle Palembang beds. The transition is marked by an impoverished fauna of a few small multispinose *Rotalia*. A characteristic tuff of idiomorphic biotite with corrosion embayments occurs in the Middle Palembang and has been used as a marker bed; however it is not always one single bed, so that it can only be used as an approximate marker.

Folding postdates the Middle Palembang formation.

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