

Foraminiferid Architectural History; A review using the MinLOC and PI Methods

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ABSTRACT—Geometrical models of unit volume are used to examine the effects of differing rates of chamber or test volume expansion, growth plan, chamber shape and apertural form upon internal-external lines of communication within foraminiferid tests. The main quantitative measure is the minimum line of communication (MinLOC) from the back of the proloculus to the nearest aperture in contact with the external milieu. The Parsimony Index (PI) is a qualitative measure, here used to illustrate some basic changes in foraminiferid architecture through time. Three general trends from longer to shorter MinLOC are indicated, particularly in shallow water tropical carbonate facies, with climaxes in the Devonian, the Carboniferous to Permian and the Cretaceous to Recent.

INTRODUCTION

The aim of this paper is to outline some broad scale evolutionary changes in foraminiferid architecture, through the use of two methods of analysis: the MinLOC method (illustrated in detail by Brasier, 1982) and the Parsimony Index (given here for the first time). Together they suggest that internal-external lines of protoplasmic communication, or related factors such as test shape, test compactness and osmoregulation, deserve more study as factors in foraminiferid ecology and evolution.

A general tendency for increased constructional strength, from feeble non-septate tubes to compact multilocular coils, was postulated long ago by Rhumbler (1895) but the idea was contradicted by Galloway (1933), partly on the mistaken belief that foraminifera from the Malverns were Cambrian (Chapman, 1900; see Haynes, 1981, p. 72). Scepticism about adaptive morphology was also voiced in the works of D'Arcy Thompson (1942), Glaessner (1945) and Smout (1954). But more recent biological and ecological research has brought forward the question of test function (e.g. Marszalek *et al.*, 1969; Hottinger, 1978; Haynes, 1981), from which it seems that the test may serve to reduce biological, physical and chemical stresses, to enhance particular kinds of feeding and to regulate buoyancy. For example, Lipps (1975) suggests that different test shapes are adaptations to different feeding methods. Erect tubular and branched forms fixed to hard surfaces or embedded in sediment may be suspension feeders, with their pseudopodia in the water column (e.g. *Homotrema*). Active lenticular forms living on soft substrates and weed, or elongate forms feeding passively near the sediment/water interface may be detrital scavengers (e.g. *Elphidium*, miliolids, nodosariids, buliminids). Trochoid or flattened forms temporarily fixed, browsing

on algae or other substrates, are mostly herbivores, with pseudopodia streaming in all directions (e.g. *Cibicides*, *Discorbis*). Larger foraminifera tend to have high surface area to volume ratio plus other features adaptive for their endosymbiotic algae (Haynes, 1981, p. 55); discoidal forms may be attached to plants (e.g. *Marginopora*) or reclining on the sea bed (e.g. *Nummulites*, orbitoids); fusiform tests may be passive rollers in more turbulent conditions (e.g. fusulinids, alveolinids). A review of test form and habitat in recent Caribbean carbonate facies supports these generalisations (Brasier, 1975).

Much of the emphasis to date has therefore fallen upon external constraints on test form, such as hydrodynamic properties, substrate type and food source. Without dismissing the significance of these, it is the intention of this paper to focus upon an internal constraint: the lines of communication within the test. That communication may be an important factor in test form and foraminiferid evolution is suggested simply by the fact that they are unicellular. This means there will be constraints upon maximum size and upon the degree to which the protoplasm can be stretched out or partitioned by the skeletal elements. Myers (1936) noted that a ratio exists between the volume of test protoplasm and the number (or surface area) of nuclei. Mobility of the nuclei may therefore be especially important where there is much protoplasm and this is suggested by the relatively short lines of communication in larger foraminifera (Hottinger, 1978). These lines of communication must also affect the movement of other organelles, food vacuoles, osmotic vacuoles, symbionts and chemical signals around the test. To these internal factors may be added the external ones of physical and chemical stress: long lines of communication in the form of tubular chambers may help to keep these stresses away from sheltering protoplasm

(Marszalek *et al.*, 1969). Hence there may be a correlation between lines of communication and ecology or palaeoecology of foraminifera, as has already been suggested by Chamney (1976).

The hypothesis that lines of communication are factors in foraminiferid ecology and evolution deserves more cytological and ecological research, but the wide architectural range of fossil foraminifera provides ideal material for modelling lines of communication. This paradigm principle has been widely applied to macrofossils (e.g. Raup & Stanley, 1978) but less so in microfossils, though Berger (1969) has modelled the problems of ontogeny and buoyancy in planispiral planktonic foraminifera, and Scott (1974) has modelled the *Orbulina* lineage. Brasier (1980) modelled multilocular tests from the interaction between three variables during growth: the rate of growth translation (i.e. the net movement along the growth axis to the movement away from the growth axis), the rate of chamber volume expansion and the chamber shape. The aim of modelling here is to show that, for a fixed volume, lines of communication may vary with growth plan, apertural position and chamber shape.

MODELS AND THE MinLOC METHOD

The models in Figs. 1 and 2 illustrate, theoretically, a range of foraminiferid tests of identical volume but with varying growth plan, chamber shape, apertural position or rate of test volume expansion. These allow measurement of the minimum line of communication (MinLOC) from the most remote point of the proloculus to the nearest aperture in contact with the external milieu. Other comparative measurements discussed by Brasier (1982), such as the maximum line of communication (MaxLOC) from the most remote point of a distal chamber to its nearest aperture in contact with the external milieu, may be relevant to the number and placement of apertures but are not discussed in detail here.

The unit of MinLOC measurement in Figs. 1 and 2 is an arbitrary one, taken as the diameter of the proloculus. In each multilocular model the proloculus is assumed to be spherical with a single aperture, followed by six chambers of varying shape, but with a relatively high rate of chamber volume expansion E , where $E = 2.9$. This is calculated from the formula $E = V_n / V_{n-1}$ where V represents the volume of the n^{th} or $n - 1$ chamber. The chosen rate of expansion, $E = 2.9$, compares with that of *Hormosira globulifera* figured by Loeblich & Tappan (1964, fig. 128.4a). This was chosen as a model because the uniserial growth and sphaeroidal chambers allow easy calculation of test and chamber volume, while the relatively high rate of chamber volume expansion enhances the differences in MinLOC and MaxLOC found in the modified models. Fig. 1 shows how these parameters can be measured and compared. Models

were first drawn to a large scale on metric graph paper; simple geometry and arithmetic allowed the plotting of most architectural forms sketched in Fig. 2. The various apertural positions were then plotted and the MinLOC and MaxLOC were measured directly from the diagram with an opisometer, taking a reading for each chamber. In trochospiral models several elevations were plotted and the MinLOC calculated by simple geometry. The glomospiral growth of Fig. 2 (7) was modelled in plasticine and then dissected; whorl portions were then measured and the MinLOC was cumulatively plotted from these. The overall test volume is standard in all the models, allowing comparison between the other parameters.

Below is a review of the MinLOC in models of tests with continuous or septate growth, this being found in the majority of living and fossil foraminifera. It is assumed here that the aperture is the primary means of communication with the exterior and that mural pores, where present, are only used for osmoregulation, gas exchange and the passage of dissolved organic substances (Haynes, 1981, p. 51). Numbers in brackets refer to each of the models in Fig. 2.

Non-septate, continuous growth is shown in column 1 of Fig. 2 and clearly demonstrates how a greater rate of test (or chamber) volume expansion can shorten the MinLOC. Considerable reduction in this parameter is also achieved by meandering (2), planispiral (3), helical (4), zig-zag (5), tight helical (6) and, ultimately, by glomospiral (7) growth, demonstrated here in tubular chambers in which the width $W = 1$ unit. Such non-septate tests are seldom built with walls tapering at an apical angle of more than 10° , hence their MinLOC is long relative to many septate tests. Thus one function of the septum and aperture may therefore be to allow greater rates of volumetric expansion without exposing a larger area of protoplasm.

In septate tests of identical volume, great variation in the MinLOC may occur through changes in chamber shape and in apertural position (Figs. 1, 2) as well as through changes in the rate of chamber volume expansion. In uniserial tests, for example, flattening of the chambers towards the proloculus in the models (21), (25), (34) and (35) results in a great reduction in the MinLOC. Flattening and arching of the chambers to a flabelliform test (24) may assist adherence or endosymbiosis but the addition of many peripheral apertures (31) also greatly reduces the MinLOC.

Growth plan also modifies the MinLOC, as shown by comparing a simple uniserial test having sphaeroidal chambers and a terminal aperture (21) with comparable planispiral (22), trochospiral (23) and biserial (26) forms (see Fig. 1). Modification of chamber shape and aperture can reduce the MinLOC, as for example in biserial tests with the change from terminal (26) to basal (27) to a long basal slit (29) aperture, and in planispiral or trocho-

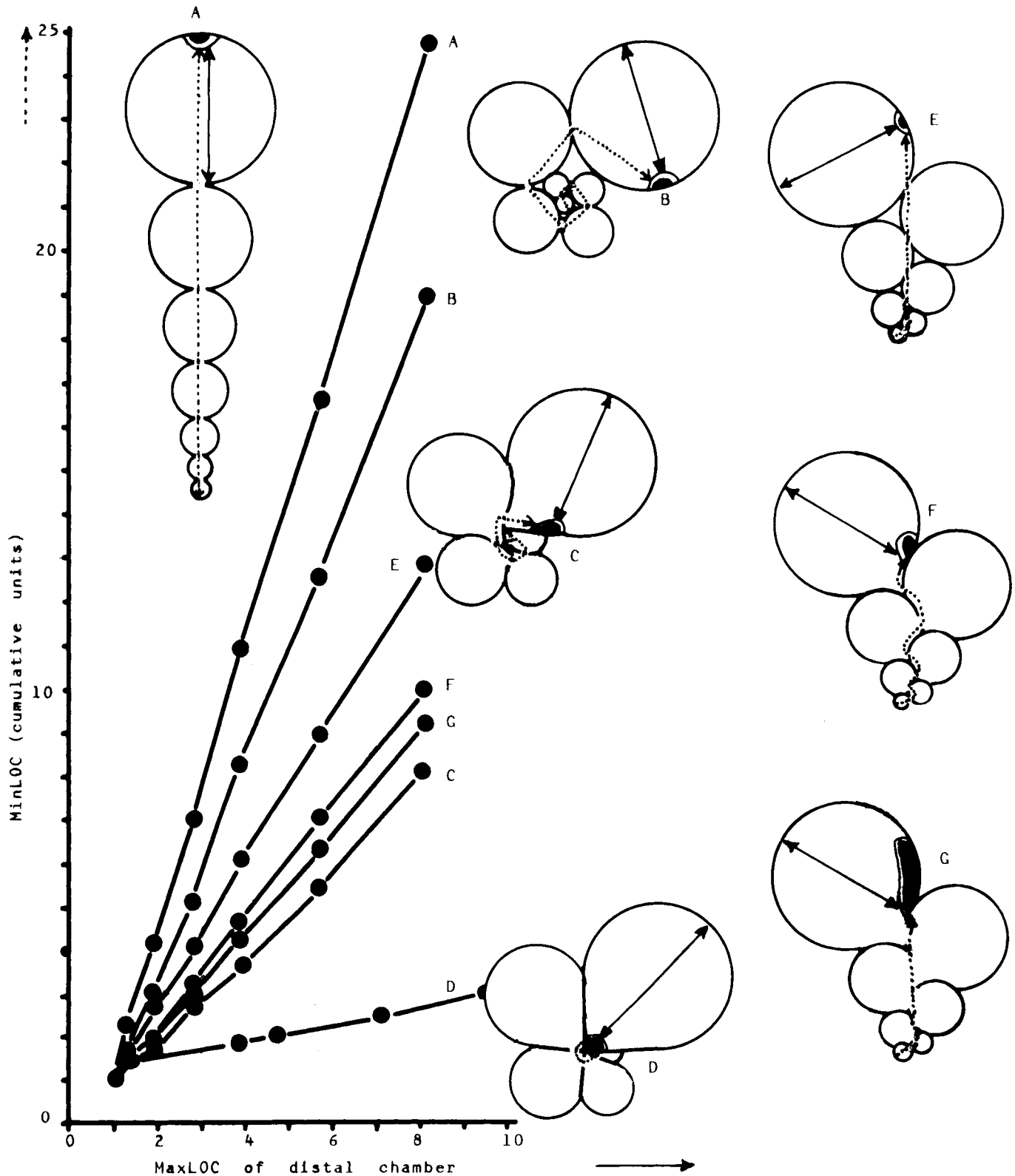


Fig. 1. Geometrical models of foraminifera with seven sphaeroidal chambers (including proloculus) and identical chamber volume and total volume. The growth plan and aperture have been varied to modulate the MinLOC parameter (vertical axis, dotted line on each model) and the MaxLOC of the distal chambers (horizontal axis, plain line on each model).

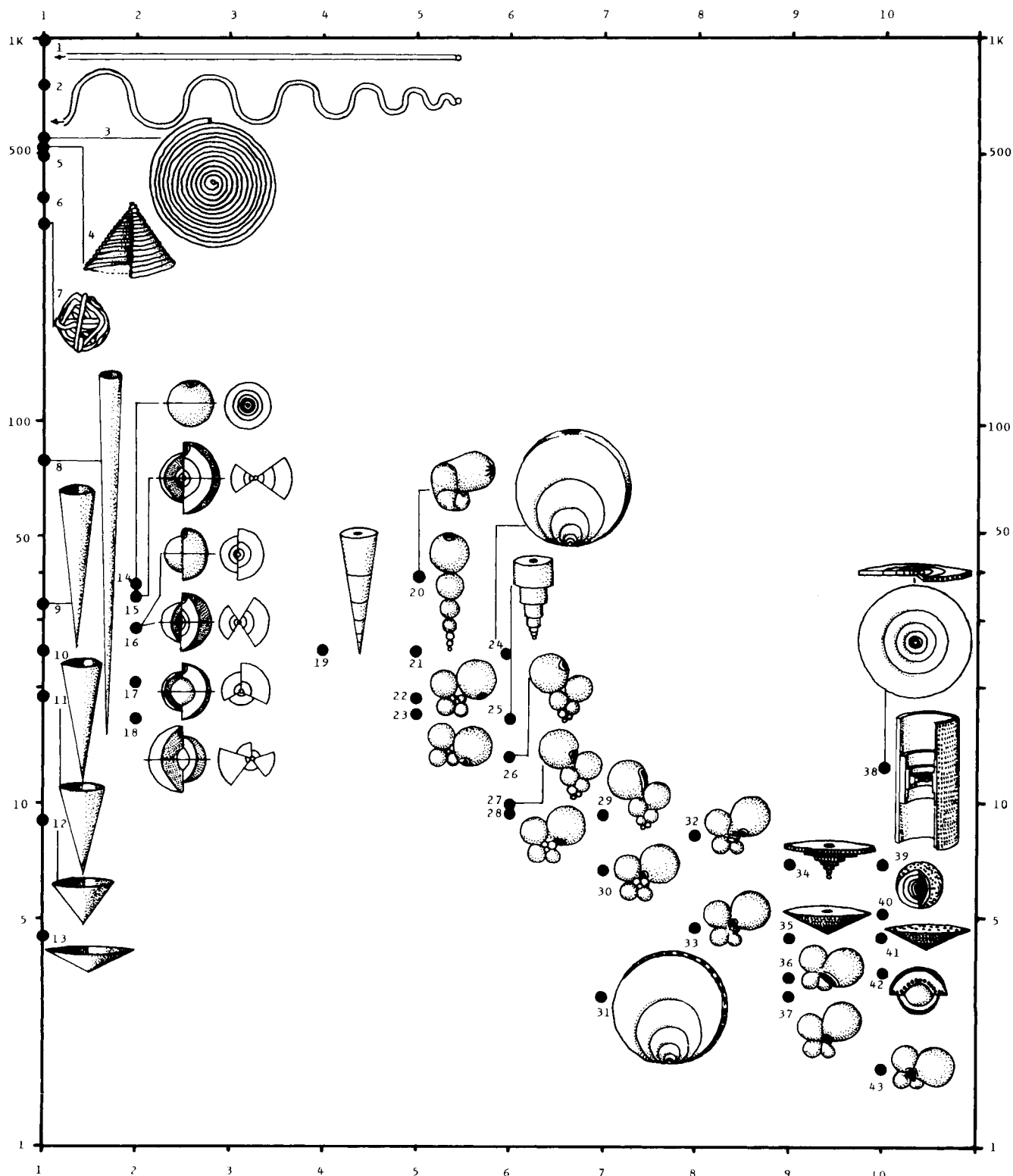


Fig. 2. Geometrical models of foraminifera with one, two or seven chambers (including proloculus) and identical chamber volume and total volume. The chamber shape, growth plan and aperture have been varied to modulate the quantitative MinLOC parameter (vertical axis, 1–1000) and the qualitative Parsimony Index (horizontal axis, 1–10).

spiral tests with the change from terminal (22) to basal (28, 30) apertures. Coiled tests may also take advantage of an involute chamber shape, which can greatly shorten the MinLOC if the aperture and foramina keep near to the umbilicus; e.g. from evolute (28) to semi-involute (32) to involute (33, 37). The shortest MinLOC is made possible by connecting each chamber directly with an open umbilicus (43).

The growth plans adopted by most larger foraminifera are relatively economical in their MinLOC values, as for example in discoidal annular (38), flaring annular (39), sphaeroidal annular (40), orbitoline conical (41) and fusiform planispiral (42) growth; multiple apertures are necessary in most of these to avoid the MaxLOC parameter exceeding the MinLOC.

A number of multilocular test types have relatively high MinLOC values; e.g. periloculine (14), biloculine and spiroloculine (15, 16), triloculine (17) and quinqueloculine (18) streptospiral growth of miliolids. *Lenticulina*, which is planispiral with a single, excentric aperture (cf. 20), also has a relatively high MinLOC value for its growth plan. Multiform tests that uncoil may also lengthen the MinLOC, though this is not necessarily the case since there may be a modification in chamber shape or apertures (Brasier, 1982, fig. 14).

PARSIMONY INDEX (PI) AND PI SPECTRUM

Studies of the ecological and evolutionary potential of this MinLOC spectrum should, ideally, begin with measurements of absolute test volume and MinLOC in living and fossil foraminiferid populations. But this is an immense labour and it is necessary to have a reconnaissance method. The Parsimony Index (PI) has therefore been devised to permit a rapid ranking of foraminiferid tests in rough proportion to their *potential* for shortened (parsimonious) MinLOC values, without reference to any absolute measurements (see Fig. 2, horizontal axis, columns 1–10). The PI of a foraminiferid test is the sum of separate point scores for growth plan, chamber shape and aperture; only one score can be achieved in each category. Multiform tests may have mean scores for each category. Foraminiferid populations can thus be separated into a PI spectrum ranging from 0 (unilocular spheres) to 10 (multilocular complex and others) as shown in Figs. 2 to 4. In these examples the PI was calculated as follows:

General growth plan

- 0 points: all non-septate tests (1–13) and streptospiral miliolid tests (14–18).
- 1 point: uniserial and rectilinear septate tests (19, 21, 24, 25, 31).
- 2 points: biserial (26, 27, 29), evolute planispiral (22, 28, 30), evolute trochospiral (23) and evolute plectogyral tests.
- 3 points: triserial, semi-involute planispiral (32, 33),

involute planispiral (20, 37, 43), involute trochospiral (36), involute plectogyral and polymorphinid tests.

- 4 points: annular or cyclic (38, 39), fusiform planispiral (42), sphaeroidal annular and orbitoline (40), orbitoline conical: uniserial, biserial or coiled (34, 35, 41) and all other forms with chamberlets.

Chamber shape

- 0 points: all non-septate unilocular or bilocular chambers (1–13).
- 1 point: septate chambers in which the diameter parallel to the MinLOC (length l of Brasier 1980, fig. 13.7 and Brasier, 1982) is greater than the width w (*op. cit.*). Such chambers are “longithalamous” (14–19).
- 2 points: septate chambers in which l and w are more or less equal; i.e. equant or sphaeroidal in shape (20, 21–23, 26–30, 33).
- 3 points: septate chambers in which the diameter parallel to the MinLOC, l , is smaller than the width w . Such chambers are “brevithalamous” (24, 25, 32, 34–42).

Aperture

- 0 points: non-septate tests without continuous growth, having a single, multiple or no aperture; coiled septate tests with a single excentric aperture (20).
- 1 point: non-septate tests with continuous growth, having terminal aperture at the open end of the tube (1–13); miliolid tests with an open end, dentate or labiate aperture (14–18); uniserial tests with open end or excentric aperture; biserial tests with excentric aperture; coiled septate tests with an areal, terminal pore (22, 23).
- 2 points: uniserial tests with a central terminal pore (19, 21, 24, 25, 34, 35) or slit; biserial tests with an areal, terminal pore (26) or basal slit (27); coiled septate tests with a basal equatorial (28, 32) or basal extra-umbilical aperture.
- 3 points: uniserial with a cribrate (31) or wide slit aperture; biserial tests with a cribrate, high slit or high arched aperture (29); coiled septate tests with a basal umbilical (30, 33, 36, 37) or cribrate (38, 42) aperture.
- 4 points: uniserial, biserial and coiled septate tests with supplementary sutural apertures or an open umbilicus in coiled forms (43).

PI MAXIMUM AND ARCHITECTURAL EVOLUTION

A general trend towards shortened MinLOC through the Palaeozoic has been inferred from the MinLOC models by Brasier (1982) but the PI method now allows a more graphic plot of foraminifera with the highest PI from each of eight suborders through time (Fig. 3). The classification adopted here follows Hohenegger & Piller (1975, 1977) in distinguishing hyaline Lagenina,

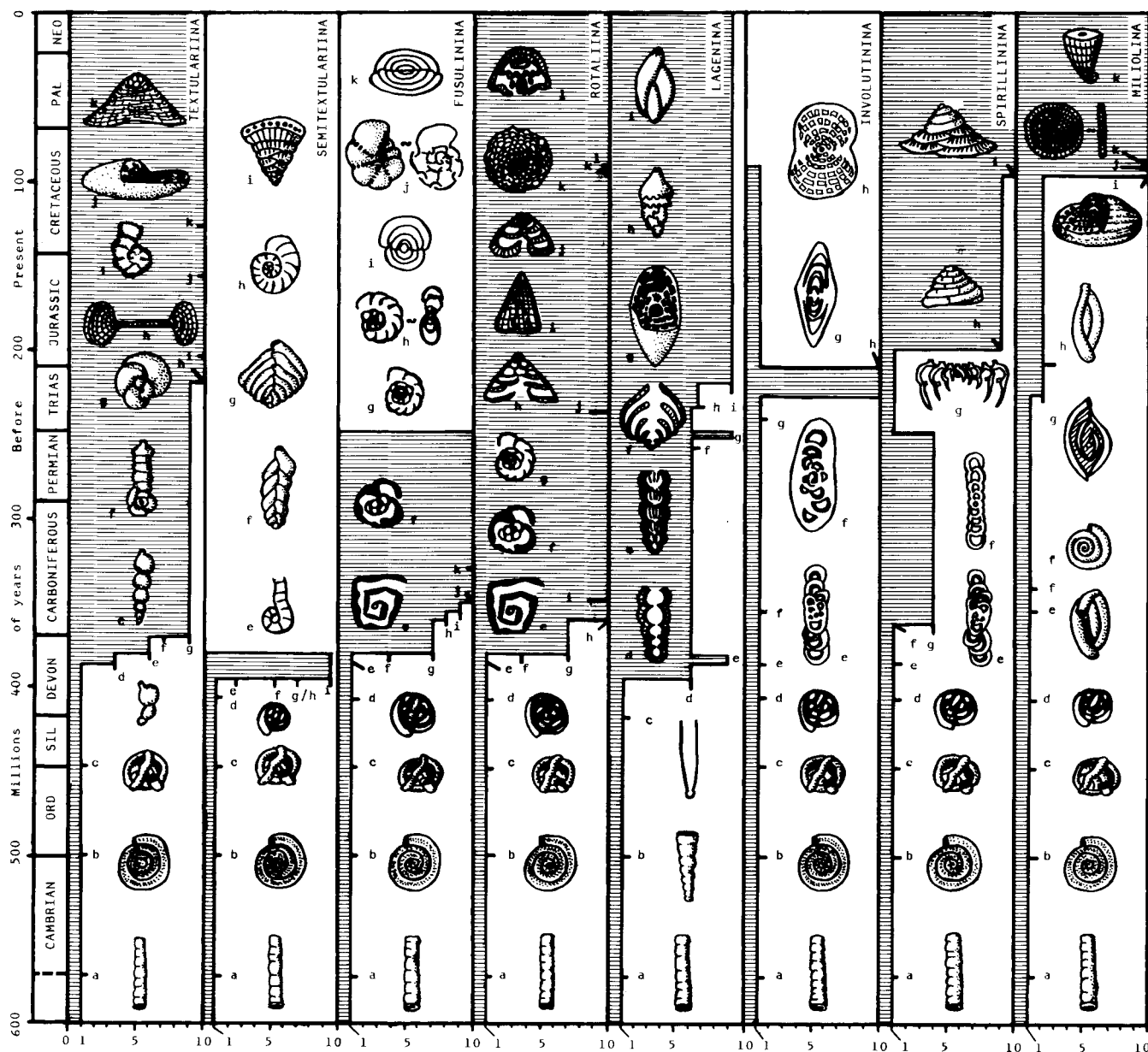


Fig. 3. The trend towards increasing maximum Parsimony Index for eight major foraminiferid lineages through time. All lineages: a, *Bathysiphon* (*Platysolenites*). All lineages except Lagenina: b, *Ammodiscus*; c, *Glomospira*. Textulariina: d, *Oxinoxis*; e, *Reophax*; f, *Ammobaculites*; g, *Trochammina*; h, *Orbitopsella*; i, *Pseudocyclammina*; j, *Paracyclammina*; k, *Orbitolina*. Semitextulariina: d, *Pseudoglomospira*; e, *Moravammina*; f, *Paratextularia*; g, *Pseudopalmula*; h, *Nanicella*; i, *Semitextularia*. Fusulinina: d, *Pseudoglomospira*; e, *Eotournayella*; f, *Septaglomopiranella*; g, *Quasiendothyra*; h, *Endothyra*; i, *Eostafella*; j, *Bradyina*; k, *Profusulinella* and *Fusulinacea*. Rotaliina: a–g as for Fusulinina; h, *Tetrataxis*; i, *Valvulinella*; j, *Oberhauserella*; k, *Archaeocyclus*; l, *Rotalia*. Lagenina: c, *Earlandia*; d, *Nodosinella* (*Eonodosaria*); e, *Multiseptida*; f, *Frondicularia*; g, *Colaniella*; h, *Sagoplecta*; i, *Eoguttulina*. Involutinina: d, *Pseudoglomospira*; e, *Brunsia*; f, *Archaeodiscus*; g, *Aulotortus*; h, *Triasina*. Spirillinina: d, *Pseudoglomospira*; e, *Brunsia*; f, *Spirillina*; g, *Lasiodiscus*; h, “*Placentula*”; i, *Patellina*. Miliolina: d, *Pseudoglomospira*; e, *Agathammina*; f, *Cornuspira*; g, *Ophthalmidium*; h, *Spiroloculina*; i, *Ovalveolina*; j, *Broeckina*; k, *Praerhapydionina*. Data from sources in Loeblich & Tappan (1964), Harland *et al.* (1967), Jenkins & Murray (1981), Haynes (1981) & Brasier (1982).

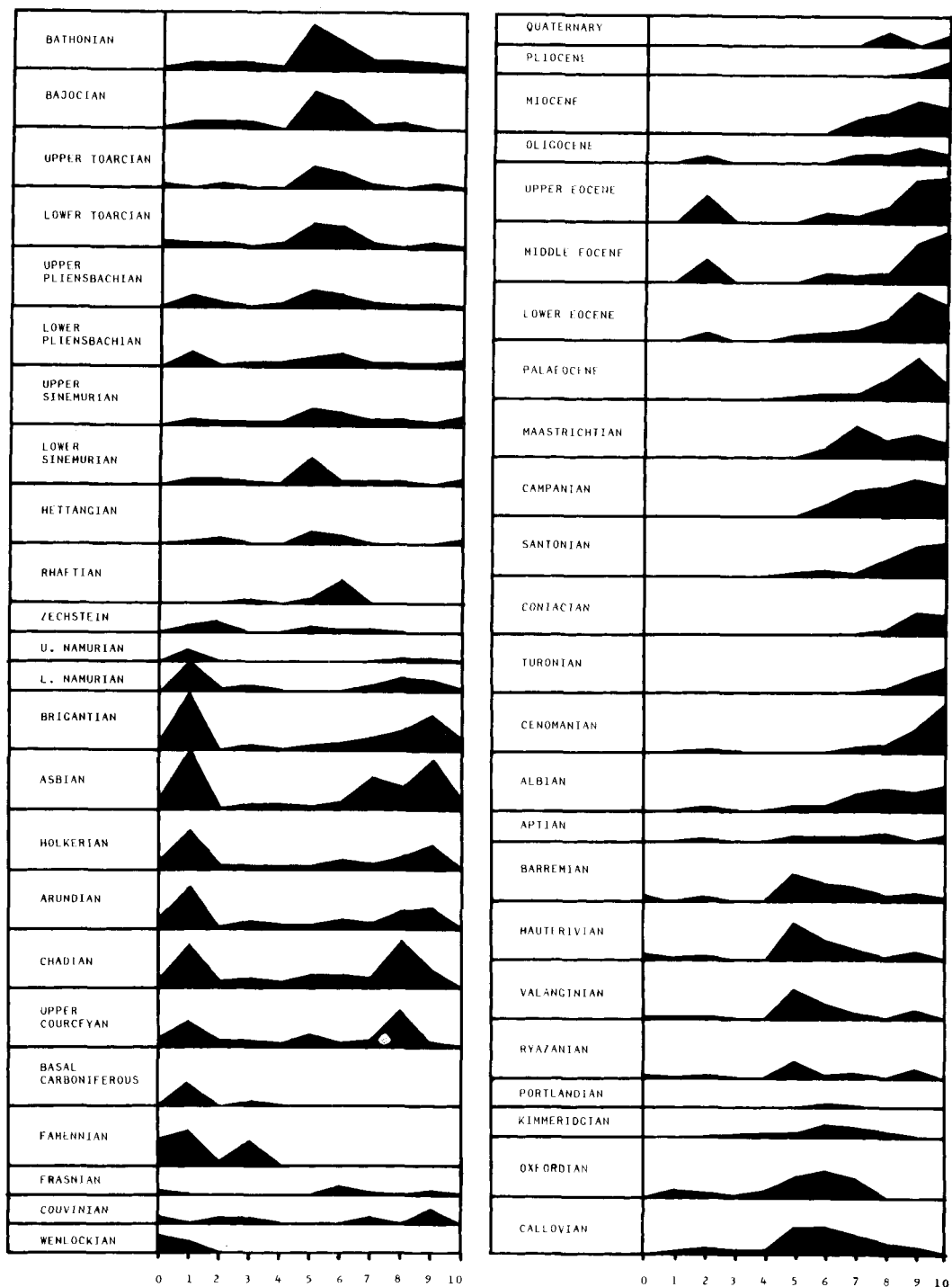


Fig. 4. Provisional plot of some temporal changes in the PI spectrum of foraminiferid species cited from stratigraphic units from Britain or comparable regions: Wenlockian of Oklahoma (Amsden *et al.*, 1980); type Couvinian of Belgium (Bultynk, 1970); Frasnian of North America (Toomey, 1972); Famennian to basal Carboniferous of West Germany (Eickhoff, 1979); Courceyan to Quaternary of the British Isles, from the data of Bailey, Coleman, Copestake, Curry, Fewtrell, Fletcher, Funnell, Hart, Haynes, Hughes, Jenkins, Johnson, King, Murray, Pattison, Price, Ramsbottom, Shipp, Strank and Swiecicki in Jenkins & Murray (1981). The vertical scale is 0–20 species, except in the smaller samples where it is 0–10 species.

Spirillinina and Involutinina from hyaline Rotaliina; it also follows Poyarkov (1979) in recognition of the distinct early history of the calcareous *Semitextularia*, *Nanicella* and relatives (here called *Semitextulariina*). This classification is believed to be more phylogenetic than that of Loeblich & Tappan (1964) or Haynes (1981) and interprets wall composition and ultrastructure as having evolved gradually through various similar grades in divergent stocks. It also places stronger emphasis on test architecture, particularly the change from non-septate tubes or coils to septate tests – a “Rubicon” that seems to have been crossed separately in each of the suborders shown in Figure 3, except for the Rotaliina. These may owe their septation to the Fusulinina, via Tetrataxidae, Duostominacea and Robertinacea (e.g. Loeblich & Tappan, 1974) or, less favoured, to the spirillinacean *Patellina* (e.g. Haynes, 1981).

In general, it can be seen from Fig. 2 that each presumed lineage has advanced from tubular forms with low PI to coiled forms with chamberlets or open umbilici and a high PI. But the rate of change and times of climax have not always coincided in these lineages.

The *Semitextulariina* rapidly reached a high PI in mid Devonian tropical carbonates but were eclipsed in the end Frasnian extinctions (e.g. Toomey & Mamet, 1978; Poyarkov, 1979). The Fusulinina developed rapidly in the late Devonian to early Carboniferous, of which the lineages leading to *Bradyina* (with open sutural apertures) and to the Fusulinacea (with a spindle shape and mural pores) appear to be classic examples of MinLOC shortening trends, connected perhaps with their increasing size. Hottinger (1978, fig. 11) has illustrated how the numerous short chambers and row of frontal foramina stretching from pole to pole may together give short lines of communication between the first and last shell compartments of fusiform tests. The iterative evolutionary trends to extend the biomass along the growth axis may also be seen as MinLOC shortening trends, since the length of the spiral canal is thereby shortened for a unit volume of protoplasm. These tropical carbonate foraminifera with high PI suffered extinction through the late Permian. Involutinina with low PI were common through the late Palaeozoic and Triassic and may be considered to have reached a climax in the Norian with the involute, septate, chamberlet-bearing *Triasina* (e.g. Piller, 1978). This reefal form did not survive the end of the Rhaetian, though simpler forms remained into the Jurassic and Cretaceous (*ibid.*) Rotaliine ancestors such as *Tetrataxis* appear to have survived the late Permian crisis and, through progressive changes in perforation, wall ultrastructure and composition, may have led ultimately to the canaliculate Rotaliacea and other larger foraminifera in the late Cretaceous and Cainozoic (e.g. Tappan, 1976). The canal system of the Rotaliacea may be a device for maintaining mobility of the test when the protoplasm has been withdrawn from the later chambers.

They are able to do this because the canals connect the protoplasm of the inner chambers with the ambient environment (Hottinger, 1978). The spiral canals in the marginal cord of nummulites and the radiating stolons of orbiotoids were also features that allowed for shorter MinLOC in larger discoidal foraminifera.

A late Cretaceous to Recent climax is also found in the imperforate Miliolina and less spectacularly in the perforate Spirillinina (*Patellina*). Extinctions of complex larger foraminifera in the late Cretaceous embraced the Textulariina, Rotaliina and Miliolina but these were not a great set back because Palaeocene tropical carbonates may contain complex larger foraminifera with high PI, such as *Discocyclina* and *Glomalveolina*.

Unlike the above groups, the fossil record suggests that the perforate Lagenina did not develop from coiled ancestors but from rectilinear ones (e.g. Hohenegger & Piller, 1975; Tappan, 1976) which, combined with their conservative retention of a single, often excentric aperture, may have discouraged the development of many new forms with high PI. *Pachyploia* and *Colaniella* of the late Permian may belong to this lineage, however, and some polymorphinids and glandulinids of Triassic to Recent times have comparatively high PI values.

PI SPECTRUM THROUGH TIME

The summary presented above is a great simplification, however, because it overlooks fluctuations that have taken place in the PI spectrum (and by implication, in the MinLOC) through time, as shown for example in Fig. 4. This has been compiled from the major foraminiferid – bearing stages of the British Isles or adjacent regions and it must be emphasised that it does not represent population studies or complete faunal lists but simply the number of cited taxa in each PI class, from the sources mentioned. But it does illustrate the pattern of architectural change in the British area, with three rather unequal cycles from low to high PI dominance: Wenlock to Frasnian; Famennian to Upper Namurian; Zechstein to Quaternary. And the high PI climaxes in the Couvinian to Frasnian, Carboniferous, and Albian to Recent noted in Fig. 3 are even more clearly illustrated. Some of the main foraminiferid changes are noted below, with PI subscores for growth plan, chamber shape and aperture.

The low PI of Wenlockian assemblages is typical for the Lower Palaeozoic foraminifera, with simple non-septate Textulariina such as *Thurammina* (000), *Hyperammina* (001) and *Ammodiscus* (001). The type Couvinian also has some high PI *Semitextulariina* such as *Nanicella* (232), *Pseudopalmula* (232) and *Semitextularia* (432½). The Frasnian assemblage has *Nanicella* and *Multiseptida* (432) which are absent from Famennian and basal Carboniferous assemblages; the latter contain *Septatourmayella* (1 ½ 1½) and *Paratikhinella* (111) plus simple forms such as *Hyperammina* and *Thurammina*.

The Carboniferous PI spectra are distinctly bimodal in Fig. 3, with numerous Archæodiscidae (001) and *Endothyra* sp. (332). A shift towards higher PI after the Chadian is related to the appearance of *Eostafella* (333), *Tetrataxis* (333), *Bradyina* (334), *Janichewskina* (334) and *Valvulinella* (433). Dwindling faunas in the Namurian may reflect the more brackish and regressive conditions, and Westphalian foraminifera are only simple ammodiscaceans (e.g. Calver, 1969). But the carbonate platforms of North America and Tethyan regions continued to support diverse assemblages in which the Courceyan to Brigantian pattern of Fig. 3 was sustained and developed (e.g. Toomey & Winland, 1973) culminating in the fusulinacean assemblages of Permian times.

The English Permian Zechstein foraminifera have a PI spectrum which more resembles the typical Mesozoic pattern with *Miliolina* (011) and *Nodosariacea* (PI mainly from 4 to 6). The Rhaetian to Barremian pattern is remarkably stable, slight shifts often reflecting the variety of forms such as uniserial *Dentalina* (111 to 131), *Lingulina* (122 to 132), *Nodosaria* (122 to 132), *Fronicularia* (132), *Citharina* (131), “uncoiled” *Astaculus*, *Saracenaria* and *Planularia* (23 $\frac{1}{2}$) and coiled *Lenticulina* (330). Although rotaliines such as *Rheinholdella* (333 to 334) and *Epistomina* (331 to 332) reach flood abundance in some facies at this time, they are not diverse in species.

Aptian microfaunas are sparse in Britain, but they may form the transition to the typically high PI spectra of Albion to Recent times. Characteristic taxa include *Bolivinoidea* (232), *Gavelinella* (333 to 334) and *Globotruncana* (332 to 334) and their relatives in the late Cretaceous, and *Cibicides* (333 to 334), *Elphidium* (332 to 333), *Globorotalia* (332 to 333), *Globigerina* (334) and their relatives in the Cainozoic.

While these PI spectra are suggestive of evolutionary change, they are an incomplete record since the data chosen may ignore some low PI taxa of little biostratigraphic interest; independent study of selected assemblages and discussions with foraminiferid workers specialising in different parts of the column confirm, however, that the pattern is quite representative. The PI spectra illustrate, at least, the value of the PI method for preliminary investigations and the potential of the MinLOC method for more accurate evolutionary research.

DISCUSSION

Although the emphasis has been placed on trends from longer to shorter MinLOC, there are certainly some counter-trends and some anomalies.

Firstly there is the question of survival in many ancient genera with relatively long MinLOC, such as *Bathysiphon*, *Ammodiscus* and *Nodosaria*. It might be thought that their longevity argues against any major functional

significance in the MinLOC, though there are several reasons to refute this. These survivals may be seen as the counterpart to the more rapid evolution and extinction of larger foraminifera, planktonics and others with shortened MinLOC; i.e. evolutionary rate, survival and lines of communication may be related in some way. They may also owe their survival to a shift from shallow to deeper or marginal marine habitats, where longer lines of communication are not disadvantageous. It is noteworthy that many of the forms evolving a short MinLOC have lived in shallow marine conditions, but any relationship between habitat and MinLOC, particularly of habitat shift in archaic forms, requires much more research.

A second problem concerns the interpretation of supposed MinLOC lengthening trends, such as the “uncoiling” of *Lenticulina* (Barnard, 1960). Various interpretations have been put on these uncoiling trends, ranging from adaptation to deposit feeding (e.g. Haynes, 1981), evolution in stable marine conditions (e.g. Chamney, 1976) to non functional explanations (e.g. Hofker, 1954). Related to this is the problem of dimorphism, in which the gamont and schizont generations of a species may have quite different architecture, and hence have MinLOC values which are different. Both uncoiling and dimorphism require more study, but the MinLOC method may give these trends new significance since they should throw further light on the adaptive and non-adaptive features of test architecture.

There is also the problem of the Saccamminidae (Cambrian to Recent) and other non-septate, non tubular rhizopods. These do not show a clear MinLOC shortening trend because they had relatively short internal-external lines of communication from the start, though the Saccamminidae declined in importance after the Silurian. Their displacement by foraminifera with septate growth is not hard to explain, since these gained the advantages of size increase, tests reinforced by spiral walls and septa, and novel architectural forms with a wider adaptive range. Even so, the Saccamminidae evolved from simple forms with no aperture, to forms with multiple apertures, stellate arms and labyrinthic walls, through the course of the early Palaeozoic (Brasier, 1982).

In summary, the MinLOC method provides another way of looking at foraminifera, from the inside. The MinLOC and PI methods can be used to study patterns of architecture through time (evolution) or in space (ecology) but these are likely to be the outcome of both internal factors (such as MinLOC and MaxLOC) and external factors (such as osmotic stress, substrate type, hydrodynamic properties and food source). The effects of these external factors could also be studied by modelling. But interpretation of the architectural patterns is a complex matter that will also involve further biological and ecological work.

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