

THE STUDY OF VARIATION IN SOME SMALLER FORAMINIFERA

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ABSTRACT—The paper embodies the results of the study of variation displayed by some smaller foraminifera, obtained from various localities. The variations in unit characters and in polymorphic generations are discussed and illustrated. It has been noticed that irregular growth in the arrangement of the last-formed chambers and in the over-all shape of the test may be produced in the attached forms. Attempt has been made to outline the difficulties encountered in establishing exact relationships in morphologically grading series.

THE SPECIES PROBLEM

IN his book "The origin of Species", Darwin (1859) made no attempt to define the term 'species'. Since then, numerous authors including Regan (1926), Dobzhansky (1937), Goldschmidt (1940) and Huxley (1948) have studied the biologic and taxonomic aspects of the species problem.

Regan (*op. cit.*) defined species as "a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name." Dobzhansky (*op. cit.*) seeks to define species as "that stage of the evolutionary process, at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separate arrays which are physiologically incapable of interbreeding." Although there are numerous other definitions of the term 'species', none of them is entirely satisfactory. According to Swinerton (1940) the term is still indefinable, and is "like x in mathematics, for it apparently represents something different in every problem."

The origin of species (speciation) has been ascribed to three different factors—the geographical, the ecological, and the genetic (Rensch, 1939). To these, a fourth factor—successional or transformation in geological time—has been added by Huxley (1948, p. 170).

Successional speciation in related organisms is produced by their separation in

time. The shifting of the peristome in *Micraster*, the sea-urchin, is a well known example. It may, however, be remarked that time, operating alone, can never produce speciation. Other factors like ecology and genetics also play a very important part. Successional speciation or changes in the characters of species through geological time, indicate the various stages in an evolutionary trend.

Geographical speciation is produced by the separation or isolation of forms in space. Closely related geographical species are distinguished by their tendency to adapt to general climates. On the other hand, ecological species are characterised by their tendency to adapt to special environments and mode of life.

Although there may not be general agreement among systematists regarding a reasonable definition of the term 'species' and the methods of speciation, there is broad agreement concerning the criteria that should be used for separating various species. According to Huxley (1948, p. 164) a species can be distinguished on the basis of the following criteria:—

(i) a geographical area consonant with a single origin;

(ii) a certain degree of constant morphological and presumed genetic differences from related groups;

(iii) absence of integradation with related groups."

The present trend, however, of giving names to different areal groups without

providing terms for continuous gradation, implies that arbitrary stages in grading series are uniform groups with rather definite distribution. The describers of such species, generally, do not state the number of specimens examined, and thereby lead one to an erroneous conclusion that the species is uniformly distributed throughout the assemblage. "Many modern descriptions of foraminifera contain not even definite qualitative indications of the intraspecific range of variation which in itself is an important taxonomic character" (Glaessner, 1948, p. 80).

It is a well known fact that no two individuals, even those belonging to the same species, are exactly identical. Though they have certain features in common, their shape, size and other characters vary considerably. Concerning variation in the foraminifera, Ovey (1938, p. 160) stated that "Specimens of a single genus from one sample of material have been found to vary not only outside the limits of a single species, but even outside those of a single genus." Thus, in view of the fact that certain foraminifera often adapt themselves to varying environmental conditions and show great variability and plasticity of characters, it becomes difficult to assign borderline species (morphological overlap) to an already named species. In such cases it becomes imperative to examine a large number of individuals in order to determine the true characters of a species and also to study the nature and range of variation from the typical form. The importance of statistical considerations in foraminiferal studies has been amply demonstrated, among others, by the works of Tan (1932) on *Cycloclypeus*, Cushman and Todd (1941) on *Bolivinas*, and Carter (1953) on *Operculina*.

ILLUSTRATIVE MATERIAL USED

Most of the material illustrated in this study was collected by the author from the localities mentioned in the text. The Oligocene material from Hermsdorf, Germany, was kindly sent by Dr. Herbert Hagn, Munich University, Germany; while the Miocene material from Beethovenausicht, Vienna Basin, Austria, was made available by Dr. C. Drooger, State University, Utrecht, Holland.

VARIATION IN UNIT CHARACTERS

On account of their minute size, abundance of material and world-wide distribution in the present and ancient seas, it is comparatively easier to undertake statistical studies in foraminifera, than probably in any other group of organisms. With greater number of specimens examined, it is possible to enumerate the variations in morphological features (unit characters). Swinnerton (1932) referred to the 'unit character' as the name for the simplest physical features which make up the body of an organism. The unit characters in foraminifera which are found to vary considerably, are:—

1. Shape of the test (including ratio of length and breadth).
2. Form of coiling
3. Number of chambers and shape of the septa.
4. Arrangement of the last-formed chambers.
5. Aperture.
6. Surface ornamentation.

1. *Shape of the test (including ratio of length and breadth).*—Although the shape of the foraminiferal test is not an important taxonomic character, considerable modifications and irregularities of growth are produced by the changes in salinity and other environmental conditions. In attached forms, the over-all shape of the test is dominantly controlled by the size and nature of the substratum. A very good example is provided by the well known species *Cibicides lobatulus* (Walker and Jacob) which is known to range from Eocene to Recent. Carter (1951, p. 246) studied the species from the Coralline Crag (Pliocene) of Sutton, England, and deduced that the abundance of the above species (along with *Planorbina mediterraneensis* d'Orbigny) is dominantly controlled by the distribution of the broad-froned algae, to which they were probably attached.

As the test of *C. lobatulus* adheres to algae by the dorsal side, the latter shows great variations in the degree of concavity as seen in the peripheral view. Figs. 1 a-g show something of the wide range of variation in the shape of this species. Since the

area of attachment varies from individual to individual, the degree of concavity of the dorsal side varies accordingly. This example shows that the external shape of the foraminiferal test often has some functional significance.

In the Coralline Crag, *C. lobatulus* is associated with another species—*C. refulgens* Montfort. The two species are closely related, except that the latter has a highly convex ventral side and slightly sigmoid sutures. According to Carter (personal communication) there appears to be a complete morphological transition between the two species. These may, therefore, represent two end members of a bioseries.

in the species. Fig. 2 a shows a stout conical form (of nearly equal length and breadth) without a biserial stage and probably represents a young form. Fig. 2 h shows an elongate form ($2\frac{1}{2}$ times as long as broad) with a well developed biserial stage.

Bulimina coprolithoides Andreae from the Hamstead Corbula beds (Rupelian), Isle of Wight, England, also shows considerable variation in the ratio of length and breadth during the various growth stages (figs. 3 a-e).

2. *Form of coiling*.—In planispirally coiled tests like *Peneroplis* and *Operculina*, the form of coiling shows considerable variation.

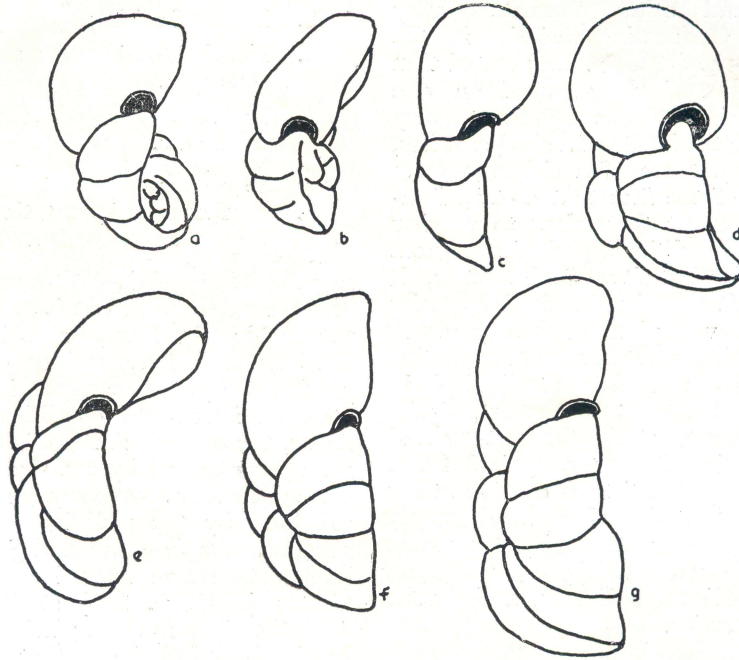


FIG. 1.—Peripheral views of *Cibicides lobatulus* (Walker and Jacob) from the Coralline Crag (Pliocene) of Sutton, England, showing variations in the degree of concavity of the dorsal side. $\times 52$.

Another good example is provided by *Karriella siphonella* (Reuss) from the Oligocene of Hermsdorf, near Berlin, Germany. In the initial nepionic stage, the test (which is finely arenaceous) is trochoid spiral with 3-5 chambers to a whorl. In the adult stage, the number of chambers is reduced to 2. Figs. 2 a-h indicate the extent of variation

Dreyer (1898, pp. 6-11) studied several species of *Peneroplis* and considered them to be synonyms of *P. pertusus* (Forskål). The species was found to show morphological gradation from a typically closely coiled or flaring test to an uncoiled test with the last whorl arranged in a rectilinear series (Fig. 4).

Similarly Ovey (1938, p. 161) found a complete sequence of grading series between *Cristellaria laevigata* d'Orbigny (closely coiled involute test) and *Marginulina* (earlier portion closely coiled, later uncoiled), from a single sample of Kimmeridge clay at Ely.

A well known species—*Amphistegina lessonii* d'Orbigny—may be taken as an example. In this species, from the Miocene of Beethovenaussicht, Vienna Basin, Austria, the number of chambers varies from 6 in the young forms to 20 in the adult (figs. 5 a-f).

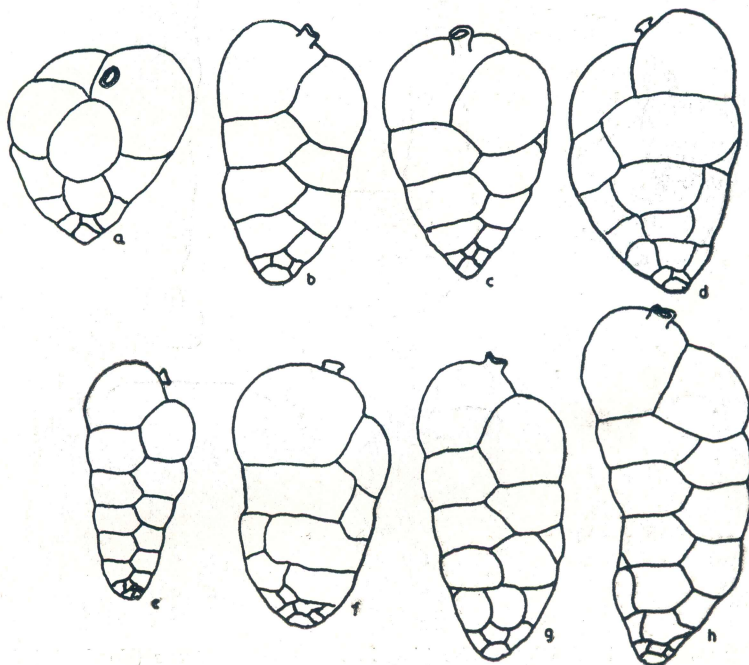


FIG. 2—*Kerrieriella siphonella* (Reuss) from the Oligocene of Hermsdorf, Germany, showing the extent of variation in the shape of the test. $\times 52$.

3. *Number of chambers and the shape of the septa.*—Systematists are often puzzled by the variations seen in the number of chambers in certain foraminifera. In some forms the number of chambers increases regularly from the juvenile to the adult

The shape of the septa in *A. lessonii* also shows changes during the growth of the individual. In young forms the dorsal side is somewhat evolute, and the septa are smooth and strongly curved (figs. 5 a-c). In the adult forms (figs. 5 d-f), the dorsal side

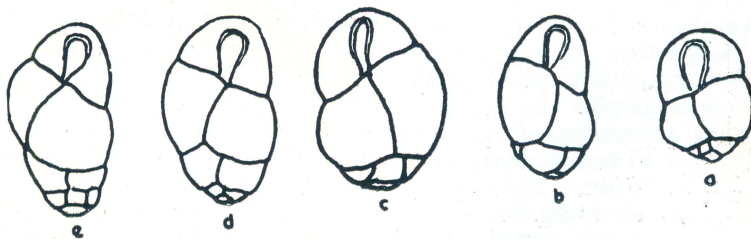


FIG. 3—*Bulimina coprolithoides* Andreae, from the Hamstead Corbula beds (Rupelian), Isle of Wight, England, showing the various growth stages and variation in the shape of the test. $\times 100$.

becomes completely involute, while the septa become undulating, subangular, with the outer portion strongly reflexed, and meeting the periphery at an acute angle.

normal *Cibicides* (*vide etiam* Galloway, 1933, p. 290). According to Glaessner (1948) irregular growth in size or shape of the foraminiferal chambers may be produced by

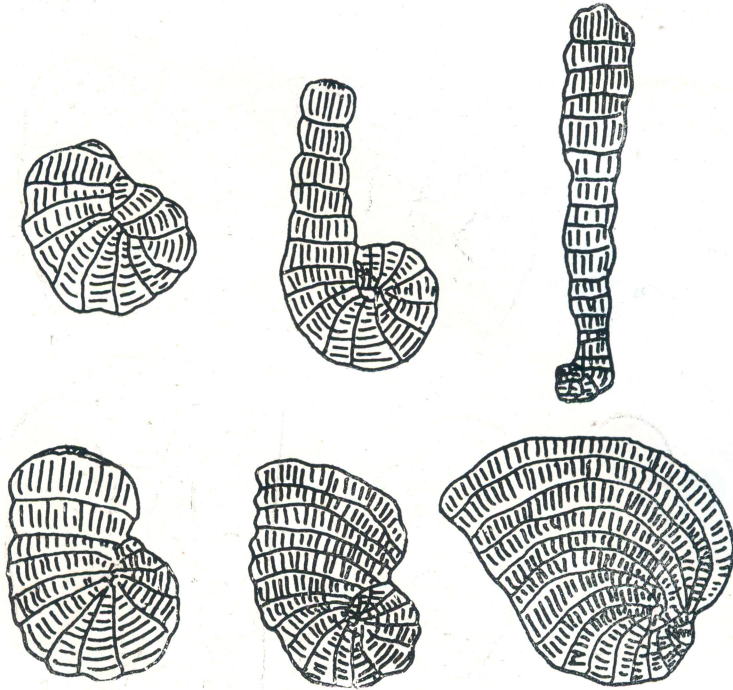


FIG. 4—Showing variation in the form of coiling in *Peneroplis pertusus* (Forskal) (after Dreyer).

4. *Arrangement of the last-formed chambers.*—In foraminifera the arrangement of the chambers, especially the last-formed chambers, varies considerably during the different stages of individual development. It has been a practice among taxonomists to regard such ontogenetic stages as features of taxonomic importance. These considerations have led to the creation of numerous species and even genera, based entirely on the arrangement of the last-formed chambers. The sub-family Cibicidiinae of the family Anomaliniidae (Cushman, 1948, pp. 335-339) may be quoted as an example. In this sub-family are included a number of genera which have evolved, or so to say, developed from the stable form *Cibicides*. The key to the various genera is shown in fig. 8.

It becomes quite obvious from the key mentioned, that most of these genera represent degenerate or gerontic forms of the

attached nature of an organism (*op. cit.*, p. 71) or as a result of variations in salinity (*op. cit.*, p. 191).

As referred to in the earlier pages, *Cibicides lobatulus* is one of the most common species in the Coralline Crag of Sutton, England. Besides showing a great variation in the shape of the test, the species also shows (in the same sample) both the normal forms and the gerontic forms in which the last-formed chambers depart from the normal form and grow irregularly (figs. 6 a-d). The latter forms have been referred to the genus *Cibicidella* Cushman. The palaeontologists would like to know whether the normal and the gerontic stages of a species, occurring within a uniform assemblage, should be referred to different genera or not. It would also be interesting to know from the taxonomic point of view, whether these variations produced during gerontism are

not passed on from one generation to the other, or whether these characters are heritable. This problem could only be solved by a detailed and careful study of the living species of the genus *Cibicides*.

5. *Aperture*.—The aperture is one of the most important taxonomic characters in foraminifera. However, its position and shape vary considerably, not only within families, but even within a single genus or species.

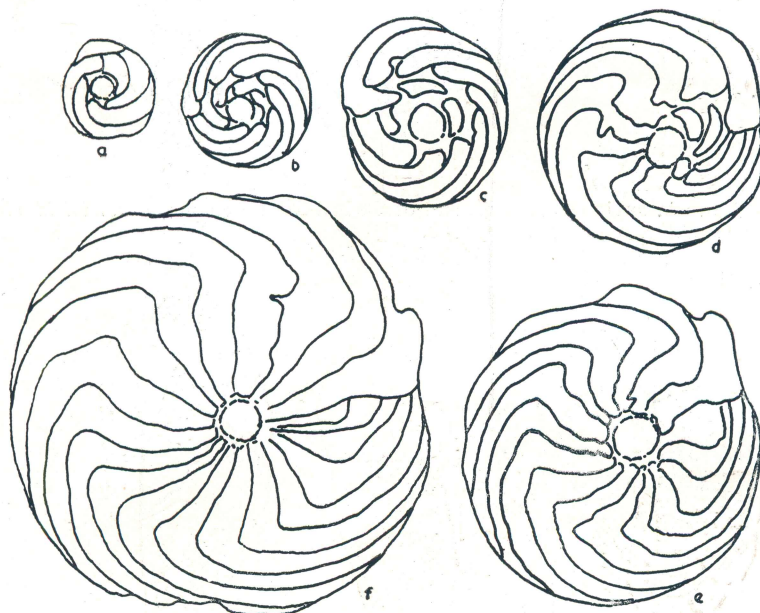


FIG. 5—*Amphistegina lessonii* d'Orbigny, from the Miocene of Beethovenausicht, Vienna Basin, Austria, showing the variation in the number of chambers and the shape of the septa. $\times 67$.

Another group showing variations in the arrangement of the last-formed chambers is the *Bolivina*—*Loxostomum* plexus. In a single sample from the Miocene of Beethovenausicht, it was found that *Loxostomum digitalis* (d'Orbigny) grades through intermediate forms into *Bolivina* (figs. 7 a-f). It is difficult to say whether one or two species are involved in this variation, since a complete morphological gradation exists between *Bolivina* and *Loxostomum* (at least in the Vienna Basin material). The author feels that the species should be referred to *Bolivina* instead of *Loxostomum*. As it is, it becomes very difficult to separate forms which grade into each other and especially when two different genera are involved. In such cases it is best to give priority to the older generic name of the series and let the other name lapse,

Although no suitable material was available for study, mention might be made of the variations shown by apertural characters in *Ataxogyroidina variabilis* (d'Orbigny) from the Upper Cretaceous of England (Figs. 9 a-e). Barnard (*vide* Barnard and Banner, 1953, pp. 205-206, fig. 7) studied the above species and found that the "amount of coiling, shape and overlap of the last chamber, position and shape of the aperture are all extremely variable. This variation is present in juvenile forms, but is more pronounced in the adults."

Similarly Arnold (1953, p. 24) found that the Miocene species of the genus *Uvigerina* show two types of apertures. A majority of the specimens had the *Uvigerina*-type of aperture. In some specimens, however, a lateral furrow cuts through the apertural rim

and appears to be close to the comma-shaped aperture of *Bulimina*. assumes varying and complex patterns, it is only of specific or varietal importance.

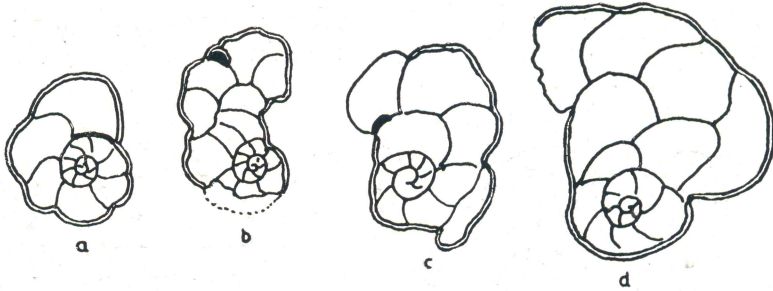


FIG. 6—Showing the variation in the arrangement of the last-formed chambers in *Cibicides lobatulus*, from the Pliocene of Sutton, England. $\times 50$.

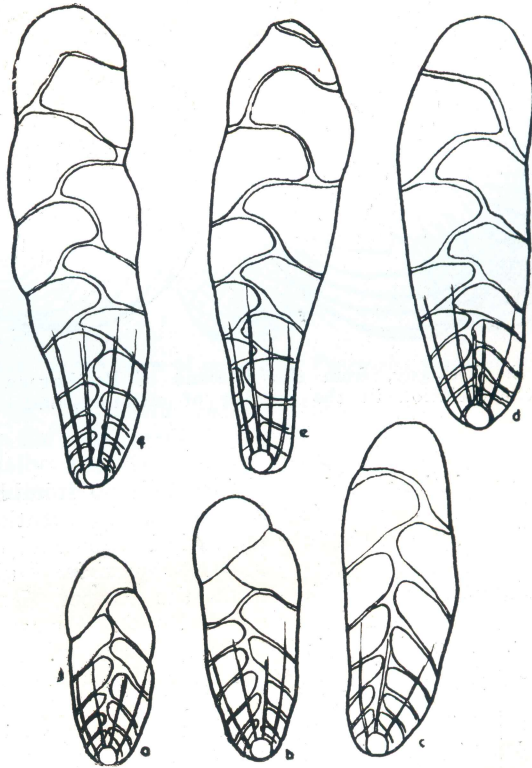


FIG. 7—Showing different individuals belonging to the *Bolivina-Loxostomum*-plexus, from the Miocene of Beethovenaussicht, Vienna Basin, Austria. $\times 47$.

6. *Surface ornamentation*.—In calcareous foraminifera the surface of the test is often highly ornamented. The surface ornamentation may vary from well defined raised costae to minute spines or raised meshwork. Though the surface ornamentation often

Cushman (1948, p. 221) stated that some of the species of *Lagena* (family Lagenidae) are “the most extravagantly ornamented of any of the foraminifera.” In *Lagena* cf. *sulcata* (Walker and Jacob) from the Coralline Crag of Sutton, England (Figs 10 a-f), the

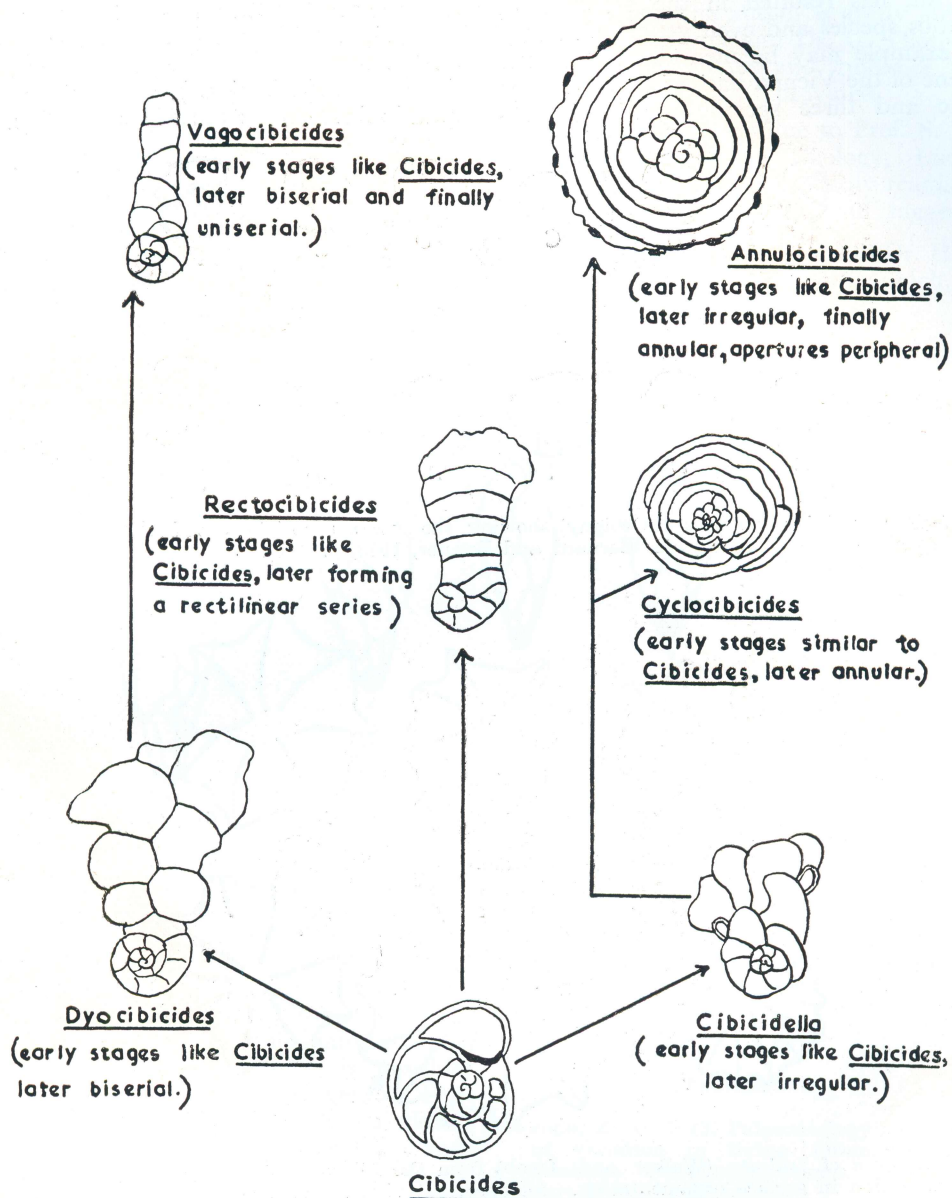


FIG. 8—Showing the relationships of the various genera of the subfamily Cibicidinae (partly after Cushman)

POLYMORPHISM AND VARIATION

The importance of dimorphism or polymorphism in foraminiferal studies has already been emphasised by numerous authors and it is not proposed to deal with this problem in any detail. It may, however, be remarked that failure to recognise poly-

morphism has resulted in the creation of numerous species and even genera. A very good example may be mentioned from the Miocene of the Vienna Basin, in which three generic and three specific names are in-

forms occur together and have similar ornamentation, Cushman (*op. cit.*) considers that all the specimens should be called *Marginulina aculeata* (d'Orbigny), as only the microspheric form shows the full characters.

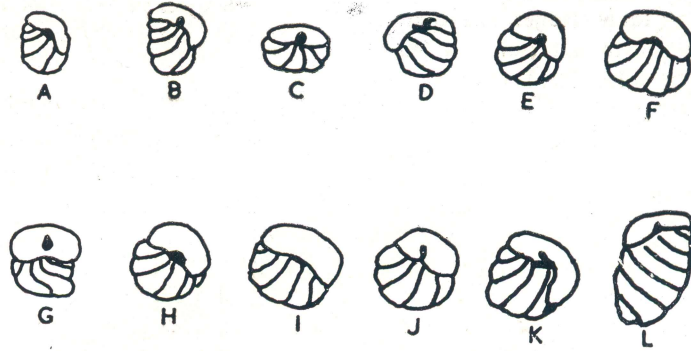


FIG. 9—*Ataxogyroidina variabilis* (d'Orbigny) showing the various positions and the shape of the aperture (after Barnard, *vide* Barnard and Banner, 1953, p. 206).

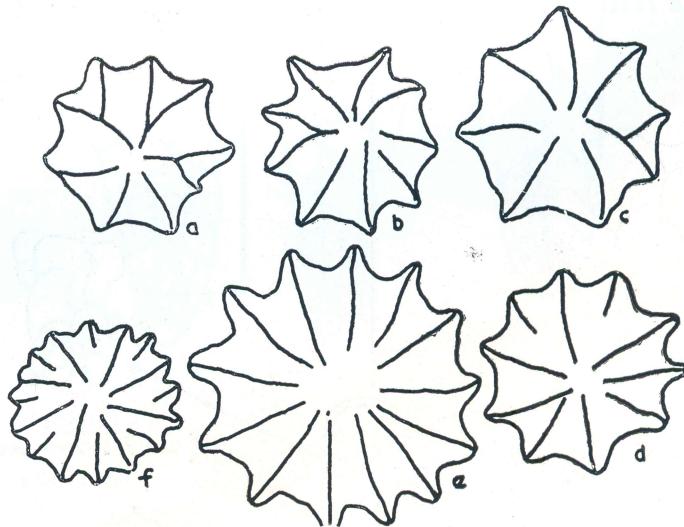


FIG. 10—*Lagena* cf. *sulcata* (Walker and Jacob) from the Pliocene of Sutton, England, showing variation in surface ornamentation. All apertural views. $\times 90$.

involved (Cushman, 1948, pp. 52-53). D'Orbigny named the three forms as —*Nodosaria aculeata* (with a large proloculum and chambers arranged in a straight line); *Dentalina floscula* (with comparatively small megalospheric proloculum and the chambers arranged in a curved axis); and *Marginulina hirsuta* (with microspheric) proloculum and the initial portion coiled). Since all these

From material obtained from the Hamstead Corbula Beds (Rupelian), Isle of Wight, England, the author found that the megalospheric and microspheric forms of *Virgulina schreibersiana* Czjzek, varied considerably in shape, size and the arrangement of the chambers (fig. 11). In the megalospheric forms (figs. 11 a-d), the test is $2-2\frac{1}{2}$ times as long as

broad, the chambers inflated, elongate, strongly embracing and extending down to the initial portion (at least in the young forms). With growth, however, the succeeding chambers are further removed from the base. The microspheric forms (fig. 11 *e*) are large and more elongate (3 times longer than broad). The chambers are numerous, comparatively stout, and less embracing, each succeeding one further removed from the initial portion.

logy, London. The author is greatly indebted to Mr. D. J. Carter and Dr. G. Thomas for the invaluable advice and guidance which they always willingly provided.

Grateful thanks are due to Prof. S. R. N. Rao, Department of Geology, Lucknow University, Lucknow, for kindly reading the manuscript and making useful suggestions.

The author is also indebted to Dr. Herbert Hagan, Munich University, Munich, Ger-

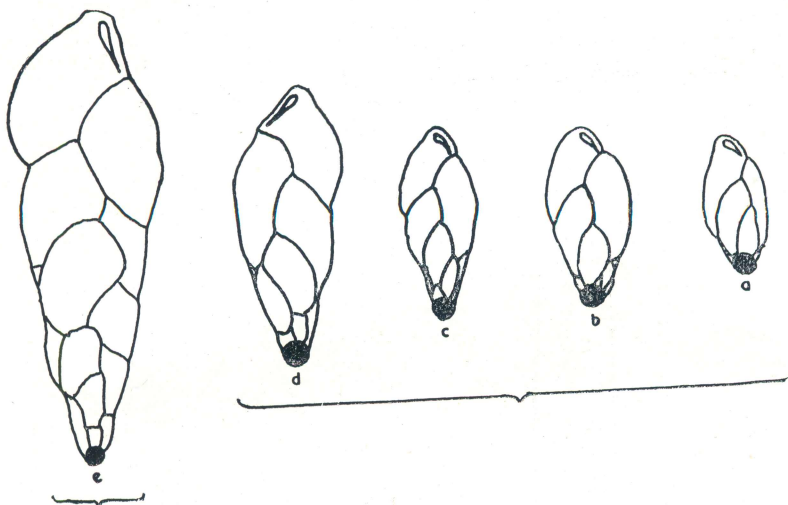


FIG. 11—*Virgulina schreibersiana* Czjzek, from the Oligocene of Isle of Wight, England, showing the variations in the dimorphic generations. $\times 82$.

CONCLUSIONS AND ACKNOWLEDGMENTS

In the preceding pages the author has attempted to outline some of the difficulties encountered in the study of foraminifera and the extent of variation which is possible within a single species or a genus. The author feels that there should be a closer understanding between biologists and palaeontologists in evaluating the taxonomic importance of various structural and morphological features exhibited in fossil foraminifera. Caution should be observed in creating new species and genera indiscriminately without providing reference to variation in the morphological features and in dimorphic generations.

The main outline of this paper was worked out during the post-graduate course at the Imperial College of Science and Techno-

many, and Dr. C. Drooger, State University, Utrecht, Holland, for the loan of some topotype material.

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