TULANE STUDIES IN GEOLOGY

Volume 6, Number 1 July 31, 1968

PHYLOGENETIC AND TAXONOMIC PROBLEMS OF SOME TERTIARY PLANKTONIC FORAMINIFERAL LINEAGES[1]

W. A. BERGGREN

WOODS HOLE OCEANOGRAPHIC INSTITUTION

CONTENTS

Page
ABSTRACT 1
I. INTRODUCTION 2
II. PHYLOGENETICS AND CLASSIFICATION 2
III. SOME PROBLEMS OF BIOSTRATIGRAPHY AND CHRONOSTRATIGRAPHY 5
IV. SOME TERTIARY PLANKTONIC FORAMINIFERAL LINEAGES 7
  Introductory remarks 7
  Lineage 1: *Globorotalia pseudobulloides-Globorotalia broedermanni* lineage 7
  Lineage 2: *Globorotalia pseudobulloides-Globorotalia pseudoscitula* lineage 8
  Lineage 3: *Globorotalia pseudobulloides-Globorotalia lehneri* lineage 9
  Lineage 4: *Globorotalia pseudobulloides*-Neogene-Recent globorotaliids 11
  Lineage 5: *Globorotalia pseudobulloides* and the origin and development of *Acarinina* and *Truncorotaloides* 12
V. SOME COMMENTS ON *ACARININA* AND *TRUNCOROTALOIDES* 16
  1. *Acarinina* 16
  2. *Truncorotaloides* 17
VI. SUMMARY 18
VII. ADDENDA 18
VIII. REFERENCES 20

ABSTRACT

Some basic principles of taxonomy and classification are considered in relationship to planktonic foraminifers, along with various problems which face the specialist in his attempts to arrive at a suitable and "natural" classification of this group.

The phylogenetic development of five major lineages of Tertiary planktonic foraminifers is discussed and the more important species illustrated. The definition of the genus *Globorotalia* includes keeled and non-keeled forms and its range is Danian to Recent. *Globorotalia pseudobulloides* (Plummer) is a highly polytypic species and the ancestral form of all later Tertiary members of the Globigerinacea with the exception of the Heterohelicidae, which had their own, separate evolutionary development. *Glo-*

---

[1] This paper originally appeared in Russian in the Memorial Volume commemorating the 70th birthday of Professor D. M. Rauzer-Chernousova, Head of the Section of Micropaleontology, Geological Institute, Academy of Sciences, USSR, Moscow, published as Vol. 10 of Voprosy Mikropaleontologii, p. 309-332.

Woods Hole Oceanographic Institution Contribution 1911.

bigerina daubjergensis Bronnimann (= *Globoconusa daubjergensis* Bronnimann) is classified in the Guembilitriinae; derivation from *Guembelitria* near the top of the Maestrichtian is suggested.

Four lineages within the genus *Globorotalia* include: 1) leading towards low-conical, keeled and non-keeled forms (*G. spiralis-pusilla-convexa-broedermanni*), extinct within the middle Eocene; 2) leading towards compressed, keeled and non-keeled forms (*G. compressa-pseudomenardii-chapmani-planoconica-pseudoscitula*), extinct at the top of the middle Eocene; 3) leading to low to high conical forms ("conical globorotaliids"), extinct at the top of the middle Eocene; and, 4) leading to the Neogene and Recent globorotaliids.

The acarininids, lineage 5, are characterized by species which are distinguished from *Subbotina* and *Globorotalia* by strongly spinose wall texture. Two, and possibly three, branches within this lineage lead independently, through parallel trends, to the development of the polytypic, but monophyletic, genus *Truncorotaloides*. In terms of normal criteria of divergence (gaps) and monophyly, the acarininids are recognized as a genus, emended to include primarily spinose forms. The genus *Truncorotaloides* is also accepted, although it seems unlikely that this genus warrants a separate subfamily. On the other hand, there is insufficient reason for the erection of new genera or subgenera for the various branches of globorotaliids in the Paleogene and Neogene. A conservative, relatively unspecialized stock, or "mainstream," leading through *Globorotalia wilsoni* (Cole) and *G. opima nana* Bolli in the Eocene survived the planktonic diminution at the close of the Eocene and was the source of further progression and splitting of various branches leading to the wide divergence of forms in the Neogene and, ultimately, to the globorotaliid faunas in the present day seas.

I. INTRODUCTION

The recent interest in planktonic foraminifers for stratigraphic and paleoecologic studies in the late Mesozoic and Tertiary continues unabated. Current studies on Recent faunas have aided considerably in our understanding of the variability and geographic distribution of various species. Micropaleontologists dealing with fossil faunas and reasoning by analogy would do well to heed the work done by these "neontologists" in their evaluations and interpretations of the variability of the so-called "paleospecies" ("successive species" of Imbrie). The present paper is divided into two sections: the first presents a general discussion of some principles of phylogenetics and classification which is designed to serve as frame of reference in which the discussion in part two is to be considered; the second section deals with this writer's interpretation (admittedly eclectic) of five planktonic foraminiferal lineages within the Tertiary.

Acknowledgments: The continuation of this research is being sponsored by the National Science Foundation, Grant GA 676. Discussions with various colleagues have played no small part in the formulation of the ideas expressed in this paper. Among those to whom I owe my gratitude are Dr. F. T. Barr and Dr. K. Gohrbandt, Tripoli, Libya; Dr. V. A. Krasheninnikov, Dr. V. G. Morozova and Dr. V. P. Alimarina, Moscow; and Dr. R. K. Olsson, Princeton, New Jersey.

II. PHYLOGENETICS AND CLASSIFICATION

A given taxon cannot be adequately denoted by reference to its type specimen (or specimens) alone. A number of specimens should be utilized to define the concept of a species (or other lower taxonomic category) and the term *hypodigm* was suggested by Simpson (1940) for those individuals chosen collectively from the original material which are considered representative of the population of the new taxon. Yet, all too often in past and current literature slight differences which a specimen (or a few specimens) has from the holotype of another species results in the "necessity" of erecting a new species. Such static, rigid concepts cannot be applied to highly variable members of an evolutionary continuum. Only by recourse to a number of individuals (the more the better) can the intrapopulation variation of a given taxon be determined with satisfactory accuracy. The decision as to whether a given species is conspecific with another is, in the last analysis, based on the inferred range of variation for the whole taxon as a result of studying adequate comparative material, not on the morphologic similarity to any given specimen (holotype, or other). The population inferences drawn from it, not the holotype specimen itself, must serve as ultimate criteria of identification and classification of a taxon. The typological approach is inextricably linked with philosophical idealism, as Simpson (1961) has pointed out, and as such has no place in modern paleontologic thought.

Today, classification should be based upon phylogeny. Simpson (1961) listed several criteria of strictly Darwinian taxonomy which should be utilized in attempts to erect a classification founded on phylogeny.

1. Taxonomic groups are the results of descent with modification, or phylogeny.
2. Each valid taxon has a common ancestry.
3. The fundamental, but not sole, criterion for ranking of taxa is propinquity of descent.

The characters chosen to define the taxa are interpreted as showing evidence of phylogenetic affinities and are ranked in accordance with their probable bearing on nearness of descent.

Populations, not individuals, are classified. The individual is merely referred, by inference, to a population of which it is a small (in the case of planktonic foraminifers an infinitessimal) part. The variation which is observed in populations of different species is an inherent part of their nature and definition. Types serve merely as the legislative requirement of nomenclature. Observations of individual morphology and other somatic attributes of the species will aid in determining whether the evolutionary definition is met by a given population.

Even in instances where a strict application of quantitative data is not made, the fundamental approach of taxonomic studies is statistical in nature. This is because the observations on populations in nature can, at best, provide only partial information on the taxon of which it is a member. It is not the characters and general similarity between individuals which are of primary significance in determining membership in a given taxonomic category, but rather the *relationships* these characters express which are of main importance. These relationships are evolutionary; in short, they are phylogenetic.

Supraspecific taxa are delimited on the principle of monophyly—all members of a taxon having a single phylogenetic origin. The pragmatic criterion of monophyly is derivation from an ancestral taxon of the same, or lower, rank (see Simpson, 1961)

The genus makes the characters, it has been said. In the study of the characters of the planktonic foraminifers, specialists and non-specialists alike have found it difficult to agree on the relative rank of distinctive characters in these deceivingly "simple" organisms which can be used in classification. Let us briefly survey some of the types of evidence available and some of the problems which still challenge the imagination.

It should be apparent that the whole organism—the *holomorph*—is to be studied, not merely a part. And yet the surface has only been scratched in regard to description of the *total morphology of the total organism* in the planktonic foraminifers. Detailed wall-structure studies offer a fertile field for investigation by such methods as the recently refined bioden peel-replica method (Honjo, 1964) and the recent advances in electron microscopy (Hay, Towe and Wright, 1963; Krinsley and Bé, 1965). Although it has been recognized for some time that there are two distinct groups of globigerinids in the Tertiary—the reticulate, or cancellate, typified by *Globigerina triloculinoides*, and the spinose, typified by *G. bulloides*—only recently were these distinctions made clear by detailed observations on surface structures by Brotzen and Pożaryska (1962). Additional studies of the nature mentioned above will aid in defining more accurately the various lineages grouped under *Globorotalia* and may help to determine whether the group known as the acarininids possess a unifying morphologic and phylogenetic continuity which warrants their recognition as a taxonomic entity (see discussions in Subbotina, 1953; Hillebrandt, 1962; Gohrbandt, 1963; Berggren, 1965).

Consider again the difference in material available to the specialist working on Recent faunas and the paleontologist working with fossil forms. Where the former has access through accurately collected plankton tow material and ocean bottom sediment cores to a suite of specimens representing all variations of morphologic development from genesis through gerontism, the paleontologist is limited to death assemblages—thanatocoenoses. Thus, where the Recent plankton specialist has an advantage in making observations on living populations and drawing the most logical inferences with regard to the taxonomic composition of Recent faunas, he is at a distinct disadvantage in utilizing these observations as the foundation of a coherent, logically founded classification due to the lack of the time element in his studies. The planktonic foraminiferal species in the present day oceans are the result of a long sequence of phylogenetic events in the Tertiary, and, as classification is to be based upon phylogeny, only by taking cognizance of these events can a satisfactory classification of these organisms be formulated. Thus, in an interesting study, Bé (1965) suggests that *Sphaeroidinella dehiscens* is a deep-water, terminal (gerontic) form of *Globigerinoides sacculifer.* The thick calcite crust which covers the test of *Sphaeroidinella dehiscens* is interpreted as a secondary deposit which forms at depths generally greater than 500 meters. But stratigraphic evidence does not bear out these conclusions and Bé recognized this. Only rare transitional specimens were observed by Bé in the water column in the present day seas. This example points out the need for closer cooperation between Recent and fossil specialists in attempts to formulate a meaningful classification of planktonic foraminifers.

Zoogeographical data are of further importance in providing information on taxonomy and classification. The geographic distribution of various Recent planktonic foraminiferal species has been delineated by several authors (Bé, 1959, 1960; Bradshaw, 1959; Parker, 1962, among others). Similar studies on the latitudinal distribution and composition of fossil faunas is a fertile field for investigation. Bandy (1960) has discussed the distribution of keeled and non-keeled globorotaliids in the Tertiary as an index to surface water isotherms. Observations by this writer would suggest that the acarininids in general have a much wider latitudinal distribution than the globorotaliids, an indication perhaps of their taxonomic validity. The "globigerinids" (reticulate and spinose alike) have an even broader latitudinal distribution in the Tertiary which is similar to conditions in the present day seas. Studies also are needed to formulate a zonation for Tertiary strata in northern regions (north of 40° Latitude, roughly) which can be correlated with already established zones in the circum-equatorial regions. Ecologic and paleoecologic data may provide criteria whereby the difficult problem of distinguishing between convergence (which implies similar ecologic conditions among forms of unrelated phylogenies) and parallelism (which refers to the independent acquisition of similar structure in forms having a common genetic origin) may be resolved. Thus, in the various lineages and branches of globorotaliids described below (see figs. 1-3), this writer considers the development of a keeled periphery as evidence of parallel development. The development of subangular to acute peripheries, strongly depressed sutures and the acquisition of rudimentary spinose keels in some acarininids is considered, on the contrary, as evidence of a convergent trend towards some conical globorotaliids of the Paleogene.

Populations, not the characters observable on the individual forms, are the things classified. The same character may in one group characterize a genus or a family, whereas in another, a species or a subspecies. These characters are not *a priori* determinable but their rank must be ascertained as a result of experience. Successive planktonic foraminiferal species should be defined so that the morphologic differences between them are at least as great as sequential differences among contemporaneous species of the same, or closely allied, groups.

In the elucidation of characters distinctive of a given specific or subspecific taxon, geographic variation in the character—the *geographic cline* concept—may provide a clue to the nature and limits of variation within that taxon. It is primarily an evolutionary and not a taxonomic concept. Some suggested examples of geographic clines in Paleogene planktonic species include: a) the modification of the umbilicus and umbilical collar within a given species and between successive species of conical globorotaliids (chronocline); b) the variation in surficial ornament from dense, spinose or hispid ornament to sporadic hispidity on an otherwise smooth, finely perforate test observed on some conical globorotaliids (geocline). The most obvious example of an Upper Cretaceous geocline is the marked difference in surface ornament in *Rugoglobigerina* from spinose or hispid in northern latitudes to meridionally oriented rugosities in southern latitudes.

An evolutionary classification should be interpreted as being consistent with phylogeny. This point has been stressed by Simpson in discussions in various works and is repeated here. One of the main problems of morphologic classification based on phylogeny is the selection of characters which are homologous or parallel in nature, not convergent. The writer hopes that the discussion below of five lineages of planktonic foraminifers in the Tertiary will aid in an understanding of their phylogenetic development and provide some criteria for a future classification of these forms within the superfamily Globigerinacea.

III. Some Problems of Biostratigraphy and Chronostratigraphy

The relationship between the planktonic foraminiferal zones discussed in this paper and internationally recognized chronostratigraphic boundaries (Stage, Epoch) is still a matter of controversy in some instances. A thorough discussion of these controversies is beyond the scope of the present paper; however, mention is made of some of the problems which should receive the attention of biostratigraphers insofar as they apply to subdividing the Tertiary into recognizable chronostratigraphic units operable on a mondial scale.

In the figures accompanying this article (1, 2, 4), a comparison is presented of the Paleogene planktonic foraminiferal zones used in the Soviet Union (Subbotina, 1953, 1960; Leonov and Alimarina, 1961; Alimarina, 1963) and the Caribbean and Central American region (Bolli, 1957a,c; in this connection see also Berggren, 1965b). Among the more pertinent of these problems are the following:

1. The uncertainty of the relationship of planktonic foraminiferal zones to the lower-middle Eocene boundary.

   Discussion: Bolli (1957c) drew the top of the lower Eocene at the top of his *Globorotalia palmerae* Zone. This zone, the overlying *Hantkenina aragonensis* Zone and at least the lower part of the the *Globigerapsis kugleri* Zone, correspond to the *Acarinina crassaformis* Zone of Subbotina (1953, 1960). In a recent study of Paleogene nannofossil assemblages from the northern Caucasus and Crimea, Wade, Mohler and Hay (1964) observed *Discoaster lodensis* present but *Marthasterites tribrachiatus* absent at the top of the *Assilina placentula* Zone and in the *Acarinina rotundimarginata* Zone of the Bodraksian Stage of the Crimea, indicating a Cuisian (upper lower Eocene) age for the top of the Bakchisaraian, Simferopolskian and Bodraksian Stages. At Cherkessk (North Caucasus, Kuban River) they recorded *Discoaster lodoensis* in the *Acarinina crassaformis* Zone of the Simferopolskian Stage, "confirming its Cuisian age," and observed that "a Lutetian nannofossil assemblage was not encountered." This writer suggests that there is an overlap in the concepts of Cuisian (upper part of the lower Eocene and recognized by some stratigraphers as distinct and younger than the Ypresian) and Lutetian as they are generally defined by most stratigraphers. The *Acarinina rotundimarginata* Zone corresponds roughly to the upper part of the *Globigerapsis kugleri* Zone and the *Globorotalia lehneri* Zone of Bolli (1957a,c) and contains, *i. al., A. rotundimarginata* [= *A. spinuloinflata* Bolli, *non* Bandy], *Globorotalia lehneri, G. pseudoscitula* [= *G. renzi*], *Hantkenina dumblei* [= *H. liebusi*], *H. lehneri* [= *H. aragonensis* (?)], *Globigerapsis kugleri, G. index, Subbotina pseudoeocaena, S. frontosa* and *Truncorotaloides topilensis.* These species would place it within the time-stratigraphic limits of the middle Eocene (Lutetian) as defined by most stratigraphers.

2. The probability that *Globorotalia palmerae* Cushman and Bermúdez is not a planktonic foraminifer.

   Discussion: Globorotalia palmerae, guide form of the lower Eocene zone of this name, is probably not a planktonic foraminifer. Its rarity, or total absence, in strata of this age containing normal planktonic faunas and the peculiar morphology of the test tends to raise doubt of its assignation to the genus *Globorotalia.* Indeed, it was described by Cushman and Bermúdez as one of several closely related species assigned to the genus *Rotalia.* Some of the new species placed in this genus at the time were: *R. capdevilensis, R. peñonensis, R. primitiva, R. havanensis* and *R. madrugaensis.* Among these *R. palmerae* shows a close morphologic similarity to *R. capdevilensis* and *R. peñonensis.* The strongly overlapping chambers and spinose projections at the peripheral margins and (apparently) closed umbilicus (by a plug) indicates that these species are more correctly assigned to the genus *Pararotalia.* The apparently areal aperture on the type figures of *R. palmerae* and *R. peñonensis* support this determination. In view of these morphologic characters *R. palmerae* should be restudied and its generic status clarified; it is almost certainly not a planktonic foraminifer. Its usage as a planktonic zonal indicator should also be abandoned in future studies. It is possible to suggest another name for this biostratigraphic interval, or to utilize the *A. crassaformis* Zone as defined and applied by Subbotina (1947, 1953, 1960; cf. Berggren, 1965b). In the figures accompanying this paper a question mark is placed in the *"Globorotalia" palmerae* Zone.

3. The division of Bolli's (1957c) upper Eocene *G. cocoaensis* Zone into two distinct planktonic zones by Blow and Banner *in* Eames, *et al.* (1962).

Discussion: In the charts accompanying this paper the two new upper Eocene zones of Blow and Banner (1962) are not distinguished. Recognition of these zones in other parts of the world has not been adequately demonstrated to date; this writer has not been able to recognize them in the upper Eocene of North Africa where continuous planktonic facies exist across the Eocene-Oligocene boundary.

4. The age of the *Orbulina*-datum and the relationship of the planktonic zones to Miocene stage boundaries.

Discussion: The conflicting data of Drooger (1956), Blow (1957, 1959), Blow and Banner *in* Eames *et al.* (1962), Saito (1962b), Takayanagi and Saito (1962), Papp (1963) and Wade (1964) on the age of the *Orbulina*-datum continue to cause considerable difficulty to stratigraphers working in the Neogene. The recent study by Papp (1963) appears to indicate that the *Orbulina*-datum is somewhat younger than suggested by Blow (1957). Jenkins (1964) has recently suggested that *Orbulina* must have appeared in post-Burdigalian times, and Wade's (1964) data seem to support this.

A consideration of the conflicting data presented by various authors is beyond the scope of this paper. However, the *Globorotalia fohsi* Zone *s.l.* of Bolli (1957b) and Blow (1959) occupies a relatively small time-stratigraphic interval. This interval may represent but part of one of the stages involved in this controversy—the Burdigalian, Helvetian or Tortonian—since the exact time-stratigraphic limits of these zones do not appear to be known in any given vertical sequence. The failure (or inability) to define and recognize the time-stratigraphic limits of the successive stages of the Miocene has hindered definite dating of the *Orbulina*-datum. The evidence to date appears to indicate that the Tortonian of the Vienna Basin includes strata older than the type Tortonian of Italy. Whether this older Tortonian in the Vienna Basin can be correlated in part with the type Helvetian is still a moot point. In figure 3 the *Orbulina*-datum is placed at the boundary between the Burdigalian and Helvetian, the *G. fohsi barisanensis* Zone is correlated with the Helvetian, and the Helvetian-Tortonian boundary is placed at the base of the *G. fohsi fohsi* Zone.

5. Recognition and Zonation of the Pliocene-Pleistocene by planktonic foraminifers.

Discussion: On the basis of the appearance of *Globorotalia crassaformis* in the Pliocene it is suggested that this species serve as guide form to sediments of Pliocene Age. The characteristic *G. truncatulinoides,* which may be a descendant of *G. crassaformis,* may serve appropriately as a guide form for Pleistocene-Recent sediments (see fig. 3).

IV. SOME TERTIARY PLANKTONIC FORAMINIFERAL LINEAGES

Introductory Remarks

Cicero once observed (nearly two thousand years ago) that "the beginnings of all things are small." It is unlikely that he had planktonic foraminifers in mind, let alone the origin of the Tertiary planktonic Foraminifera at the base of the Danian Stage. Yet the fundamental thesis of the discussion below is that the beginnings of the Tertiary planktonic foraminiferal fauna were, indeed, small. At the base of the Danian only two species of planktonic foraminifers have been observed: *Globigerina pseudobulloides* Plummer and *Globigerina daubjergensis* Bronnimann. In this paper *G. daubjergensis* is interpreted as belonging to *Globoconusa* and to the subfamily Guembilitriinae (family Heterohelicidae). A relationship with the genus *Guembelitria* appears to exist in the upper Maestrichtian of North Africa; this relationship was suggested to this writer by Dr. R. K. Olsson in 1961 and, again, only recently by Dr. F. T. Barr. *Globoconusa daubjergensis,* although commonly classified with the Globigerinidae (this writer knows of no exception among modern classifications of planktonic foraminifers), would appear to have no relationship with *G. pseudobulloides* (at the base of the Danian) or any other of the late Cretaceous genera which became extinct at the top of the Maestrichtian. *G. daubjergensis* starts its development as a small, trochoid form with an indistinct, restricted aperture. Through convergence the test of this species became quite similar to globigerinid tests, but this form should be excluded from the family Globigerinidae. The main difference between *G. daubjergensis* and *Guembelitria* is the more rapid development of larger and more globular chambers. The problem of the origin of *G. daubjergensis* is under further study by Dr. Barr and this writer.

The earliest and most primitive member of the Globigerinidae in the Tertiary is *G. pseudobulloides,* here considered a globorotaliid.* *G. pseudobulloides* (or *G. eobulloides*) appears to be descended from *Hedbergella monmouthensis* (Olsson) (Berggren, 1962a,b), the most primitive and least specialized genus of the Cretaceous stock of the Globigerinacea. According to this writer's interpretation, then, the origin, progression and divergence of the various lineages of Tertiary planktonic foraminifers, exclusive of the Heterohelicidae, can be traced to a single, unspecialized form at the base of the Danian, *Globorotalia pseudobulloides,* itself probably derived from a relatively unspecialized form in the Maestrichtian, *Hedbergella monmouthensis.*

Several evolutionary trends within the Globigerinacea during the Tertiary have been described by Subbotina (1953), Bolli (1950, 1957a,b,c), Blow (1956, 1959), Banner and Blow (1959, 1960), Blow and Banner (1962), Saito (1959, 1962a,b, 1963), Hillebrandt (1962, 1964), Leonov and Alimarina (1961), Alimarina (1963) and Berggren (1962a,b, 1963, 1965b), among others. In this section the writer will attempt to present a synthesis of the views expressed by these various authors as well as his own interpretations of the development of some Tertiary planktonic foraminiferal lineages.

Lineage 1: *Globorotalia pseudobulloides-broedermanni* lineage

Evolutionary trends: Development in early stages of globular chambers, low-moderately high trochoid test and low interiomarginal, umbilical aperture (*G. spiralis*); subsequent development of low-conical test with inflated spiral side and subacute periphery (*G. pusilla pusilla*); acquisition of peripheral keel (*G. pusilla laevigata*); increase in surface spinosity, modifications of sutures, subrounded to subacute periphery (*G. convexa*); further modification of chambers, sutures and periphery, nearly flat spiral side (*G. broedermanni*).

In the *Globorotalia uncinata* Zone of Trinidad a small, strongly involute, moderately high trochoid form with globular chambers has been described by Bolli (1957a, p. 70) as *Globigerina spiralis.* Its

---

* This writer includes in his concept of *G. pseudobulloides* Morozova's (1959) *Globigerina* (*Eoglobigerina*) *eobulloides,* the smooth-walled, finely perforate form in the lower Danian of the Crimea, Denmark and other localities. Loeblich and Tappan (1964, p. C671) placed this form in *Globorotaloides.* The distinction between the two is one of degree, not kind, and immaterial to the present discussion.

evolution into *Globorotalia pusilla pusilla* as postulated by Bolli (1957a, fig. 12) has been corroborated in several studies. However, its origin has remained problematic, as it was to Bolli (*loc. cit.*) who suggested questionable derivation from *G. daubjergensis*. However, *G. daubjergensis*, with its unique high trochoid spire and supplementary sutural apertures on the spiral side and highly spinose test, is unrelated to *G. spiralis*. Rather the origin is to be sought in small forms intermediate between *G. pseudobulloides* and *G. imitata* Subbotina which have been observed in the lower part of the Wills Point Formation of Texas (Midway Group), among other places. Such a form, transitional between these two species has been illustrated by Loeblich and Tappan (1957, pl. 44, figs. 3a-c) as *G. imitata* from the Wills Point Formation (see "*G.* aff. *imitata*" in fig. 1). Both *G. spiralis* and *G. imitata* have been observed in the Wills Point, but distinction is difficult in the lower part where the separation of these two forms into distinct taxonomic entities occurs. Classification of *G. spiralis* in the genus *Globigerina* again points out the extremely artificial and rather weak foundation on which the taxonomy of planktonic Foraminifera is still based. Intermediate between *G. pseudobulloides* and *G. pusilla pusilla, G. spiralis* is hardly to be classified with *Globigerina,* unless *G. pseudobulloides* is also to be considered a *Globigerina.*

Bolli (1957a, fig. 12) considered that extinction of *G. pusilla laevigata* at the top of the *Globorotalia pseudomenardii* Zone represented the end of this lineage. However, this writer would interpret *G. convexa* as a descendant of *G. pusilla laevigata.* At the base of the *Globorotalia rex* (*G. subbotinae*) Zone it is suggested that *G. broedermanni* developed from *G. convexa* on the basis of close morphologic similarities and stratigraphic overlap (cf. Bolli, 1957a, p. 80, where the origin of *G. broedermanni* was considered an enigma due to a probable stratigraphic hiatus between the *G. velascoensis* and *G. rex* Zones). This lineage apparently became extinct in the middle Eocene (Lutetian) (see fig. 1), although it may be possible to distinguish a descendant (?subspecies) of *G. broedermanni* in the lower part of the middle Eocene (see Mallory, 1959, pl. 23, figs. 3a-c).

Lineage 2: *Globorotalia pseudobulloides*-*Globorotalia pseudoscitula* lineage

Evolutionary trends: Development of compressed test, acute periphery (*G. compressa*); acquisition of incipient keel (*G. ehrenbergi*); development of keeled periphery and strongly curved sutures on spiral side (*G. pseudomenardii*); progression of small oval-shaped form with acute to weakly keeled periphery (*G. planoconica*); development of gross pseudomorph of *G. pseudomenardii,* the low-trochoid, nearly circular form *G. pseudoscitula;* a side branch of *G. pseudomenardii* led through the finely perforate, globular chambered *G. chapmani* to the planispiral *Pseudohastigerina* at the base of the *G. rex* Zone and the development of the Hantkenininae (see Berggren, 1963).

The evolution of this lineage through *G. pseudomenardii* has been amply described by Bolli (1957a), Hillebrandt (1964), and Berggren (1962b) and needs no further discussion here. *G. haunsbergensis* Gohrbandt is included in this writer's concept of *G. ehrenbergi. Globorotalia chapmani* Parr, which appears to be the correct name for *G. elongata* of Bolli, Loeblich and Tappan, and others (*non* Glaessner) probably branched off from *G. pseudomenardii;* it ranges into the basal part of the *G. rex* Zone where the overlap with *Pseudohastigerina* can be seen (cf. Bolli, 1957a, fig. 12, where its extinction near the top of the *G. velascoensis* Zone is shown). This would seem to reaffirm Bolli's conviction that a hiatus separated the upper Paleocene and lower Eocene in Trinidad.

In the *Globorotalia velascoensis* Zone and ranging upwards into the *G. aragonensis* Zone there is a small, oval-shaped form with an acute- to weakly-keeled periphery described by Subbotina (1953, p. 210, pl. 17, figs. 4a-6c) as *Globorotalia planoconica.* This form has probably been mistaken for *G. pseudomenardii* in the past and may account for anomalous records of that species above its zone. This form evolved into *Globorotalia pseudoscitula* in the *G. aragonensis* Zone. The occurrence of *G. pseudoscitula* as low as the *G. aragonensis* Zone (as well as the fact that it is a senior synonym of *G. renzi* Bolli) was first pointed out to this writer by Dr. K. Gohrbandt, although this writer observed earlier that *G. renzi* did appear to extend down into the lower Eocene in Nigeria (Berggren, 1960c). This occurrence is considerably lower than that shown by Bolli (1957c, fig. 26) who placed its first occurrence at the base of the *Hantkenina aragonensis* Zone. Subbotina's (1953, tab. 3) long range for *G. pseudoscitula* ("Danian" to upper Eocene) may include more than one species. References to the Paleocene forms may include both *G. pusilla pusilla* and *G. pusilla laevigata*. This writer suggested elsewhere (1965b) that all of Loeblich and Tappan's (1957) illustrations of *G. pseudoscitula* (with the exception of pl. 46, figs. 4a-c from the Coal Bluff Marl Formation) from the *G. pseudomenardii* Zone are referable to *G. pusilla laevigata*.

Some workers suggest a new genus for forms in the *G. compressa-pseudomenardii-planoconica-pseudoscitula* lineage. Indeed, Morozova (1957, p. 1110) proposed the genus *Planorotalia* (type species: *Planulina membranacea* Ehrenberg) for compressed non-keeled globorotaliids of the "Maestrichtian-Danian and Paleocene." The choice of the type species is unfortunate, however, because of the controversial nature of *P. membranacea*. Originally recorded from the Weisser Kalkstein in Syria and Cattolica, Sicily, the type locality is in the Pliocene, not Maestrichtian (see Hay, 1962, p. 1393; Loeblich and Tappan, 1964, p. C668). The species, generally referred by authors to *Globorotalia membranacea* is the Paleocene *G. pseudomenardii*, or a polymorphic variant or closely related form, as *G. ehrenbergi*, which are keeled. Morozova (1957, p. 1112) erected the genus *Planorotalites* (type species: *Globorotalia pseudoscitula* Glaessner) and distinguished it from *Globorotalia* by its small size, thin wall, and slight hispidity and from *Planorotalia* by the presence of a keel. She later (Morozova, 1961, p. 16, pl. 2, fig. 3) described a new species, *Planorotalites tauricus*, from the lower Paleocene of the Crimea and northern Caucasus which is considered a synonym of *G. pusilla pusilla* by this writer. Species of the genera *Planorotalia* and *Planorotalites* belong to the same phyletic lineage (see lineage 2 in fig. 1) and demonstrate the artificiality of genera which are not supported by, nor consistent with, phylogenetic data.

Lineage 3: *Globorotalia pseudobulloides-Globorotalia lehneri* lineage

Evolutionary trends: Development of keel and compressed and angulo-conical tests in several, separate (parallel) branches; later trends involve development of low-conical tests.

The general outline of this evolutionary lineage was suggested by Subbotina (1953, p. 151, fig. 7; and 1960). Bolli (1957a) discussed the phylogeny of this group, and further remarks are to be found in the publications of Hillebrandt (1962), Gohrbandt (1963) and Berggren (1965a,b), Leonov and Alimarina, 1961; Alimarina (1963), among others.

The major evolutionary trends which characterize this lineage are the development of an umbilico-convex test and moderately to strongly keeled periphery. Various branches have developed low-conical tests and broad, thick keels (*G. subbotinae marginodentata*) or high-conical tests with strongly ornamented umbilical collars (*G. velascoensis* group). The derivation of this lineage from *Globorotalia pseudobulloides* can be traced clearly within the *Globorotalia uncinata* Zone (which is approximately equivalent to the *Globigerina inconstans* Zone as defined in Soviet literature) where the separation and truncation of chambers along the distal margins and incipient angularity of the test can be seen in *Globorotalia inconstans* (Subbotina). This form evolved rapidly into *Globorotalia uncinata* Bolli within the *G. uncinata* Zone. The further development of angulo-conical chambers, more strongly curved sutures on the umbilical and spiral sides and the acquisition of a keeled periphery lead to *G. angulata angulata* White. The high conical, multichambered descendant of *G. angulata angulata* described by Bolli (1957a) as *G. angulata abundocamerata* should be considered a synonym of *G. conicotruncata* Subbotina.

Several branches developed from *G. angulata angulata* (see fig. 2). Thus, *Globorotalia velascoensis* evolved from *G. angulata* near the top of the *G. pusilla pusilla* zone. Contrary to Bolli's (1957a, fig. 12) belief, *G. velascoensis* ranges into the basal part of the *G. rex* Zone. The writer observed the overlap of *G. velascoensis, G. rex, G. chapmani* and *Globanomalina wilcoxensis* (= *Pseudohastigerina eocenica*) in the basal part of the *G. rex* Zone in the Esna Shale Formation at Luxor, Egypt, and in the Lodo Formation of California, among other places.

Several closely allied forms occur together with *G. velascoensis* through a part or all of its stratigraphic range: *G. velascoensis acuta* (considered by Bolli, 1957a, a synonym of *G. velascoensis,* but as a separate species by Loeblich and Tappan, 1957, and a subspecies by Hillebrandt, 1962, 1964, and Gohrbandt, 1963); *G. velascoensis parva* (based on Berggren's studies of near topotype material from the Farafra Oasis, Egypt, a synonym of *Globorotalia simulatilis* (Schwager); recorded by Loeblich and Tappan, 1957, pl. 60, figs. 1a-c, as *Globorotalia rex*); and *Globorotalia velascoensis occlusa* (a synonym of *Globorotalia colligera* (Schwager) from the Paleocene of Farafra Oasis; also, *G. crosswickensis* Olsson is interpreted as a junior synonym). Hillebrandt (1962, 1964) has suggested that these forms are best interpreted as races or biologic subspecies of *Globorotalia velascoensis.* (Similar problems exist in the *G. menardii* branch in the late Neogene.) The *G. velascoensis* branch led to an evolutionary dead end, however.

Through *Globorotalia aequa* this lineage progressed further (see fig. 2). At the base of the Eocene, the *Pseudohastigerina* (= *Globanomalina*) datum of Berggren (1964, 1965a,b), rapid diversification into a rich and varied fauna of low- and moderately high-conical globorotaliids with peripheral keels varying from thin to extremely broad, thick and spinose occurred. Separation into distinct taxa and recognition of these forms is difficult for planktonic specialists. It is doubtful that any two specialists will agree on just how many lower Eocene species there are in this group, or to what species given specimens should be assigned. Based on Berggren's studies, *Globorotalia rex* is a junior synonym of *G. subbotinae* and *G. marginodentata* is very closely related, but distinguished primarily by its compressed test and thick, and on many tests, spinose keel. However, morphologic gradation can be observed between these two forms in large populations and this writer considers *G. marginodentata* a subspecies of *subbotinae. G. marginodentata* has more restricted geographic distribution than *G. subbotinae.* Another offshoot from *G. aequa* (at the base of the *G. rex* (= *subbotinae*) Zone) is the *G. formosa* branch. Again, *G. formosa gracilis* is similar to *G. subbotinae marginodentata.* However, based on slight morphologic differences and different phylogenetic relationships, the two forms are retained as distinct taxa.

The further development of this lineage can be traced to *Globorotalia aragonensis* via *G. lensiformis,* a high-conical form intermediate between *G. subbotinae* and *G. aragonensis* which is found in the *G. formosa formosa* Zone. The further eversion of the umbilical collar and the development of a more acute peripheral margin leads to *G. aragonensis caucasica* which is a gross pseudomorph of the Paleocene *G. velascoensis velascoensis.*

This lineage persists through the middle Eocene but its decline is evident. *G. aragonensis caucasica* becomes extinct in the lower part of the middle Eocene. *G. aragonensis* ranges somewhat higher and is replaced by *G. spinulosa* through compression of the test. Characters intermediate between *G. aragonensis* and *G. spinulosa* are shown on the form identified by Saito (1962a, pl. 33, fig. 9) as *G. spinulosa.* Further compression of the test and the development of a thick, spinose keel (which, in some individuals borders on the bizarre) led to *G. lehneri.* The evolution of this lineage would appear to have completed its course at this stage and it became extinct at the top of the middle Eocene. Hillebrandt (1964, fig. 3 and p. 197) suggested that *G. spinulosa* and *G. lehneri,* together with *G. topilensis,* are the last members of the acarininids (and related in an unspecified way to *G. bullbrooki* and *G. soldadoensis*). This writer would consider the interpretation presented above more consistent with phylogenetic data; the trend toward an acute periphery and the development of incipient, coarsely spinose keels in some acarininids is interpreted by this writer as the result of convergence between two previously divergent types.

Some investigators have the opinion that this group of conical globorotaliids should be given generic (or subgeneric) status to distinguish them from the keeled globorotaliids of the Neogene. Here again we are faced with the problem of phylogenetic continuity of *Globorotalia* s.l. This writer would interpret the three lineages described above as offshoots of the mainstream of a single taxon.

As discussed previously, classification is an art and can be no more accurate than the observations and conclusions made by (fallible) individuals. Evolutionary classification must be consistent with phylogeny with attention to similarity and dissimilarity in homologous and parallel characters. Criteria of relative monophyly and degree of divergence must be defined. Some planktonic foraminiferal genera appear to exhibit extreme diversity (polytypy), but this diversity is an inherent aspect of prolific numbers and rapid evolution. By lowering the criteria of divergence *Globorotalia* might be split into several, less diverse, genera or subgenera. However, prior to further diagnostic work on wall structure and ontogenetic studies of ancestor-descendant species within the various lineages and branches, splitting of this taxon may lead to more problems than it hopes to solve.

Lineage 4: *Globorotalia pseudobulloides*-Neogene-Recent Globorotaliids

Evolutionary trends: Several divergent branches from the mainstream of this lineage (fig. 3) led to repetitive development of forms with a more acute and, finally, keeled periphery. Development of angulo-conical chambers and umbilico-convex test in some late Neogene forms is reminiscent of branching trends within the Paleogene in the same group.

Bolli (1950) and Blow (1959, p. 95f) discussed the phylogeny of the Neogene keeled globorotaliids. Blow (1959, p. 97) and Blow and Banner *in* Eames *et al.* (1962, p. 131, fig. 12a) suggested that *Globorotalia opima nana* is the ancestor of *Globorotalia mayeri* (= *G. siakensis* in this paper) as well as of *G. opima opima.*

This writer (see fig. 4) essentially agrees with these authors in regard to the evolution of *G. siakensis,* the *G. praescitula-scitula* and *G. menardii* branches. However, *G. opima opima* is suggested here as the ancestor of *G. siakensis.* If the phylogeny of this lineage as presented is valid, the essential continuity of this group through the Tertiary will have been demonstrated.

In the examples given above (and, indeed, for all lineages that could have been discussed) *Globorotalia pseudobulloides* is interpreted as the progenitor. In the *Globorotalia uncinata* Zone a form bearing a strong resemblance to *G. pseudobulloides* branches off. This is *G. varianta* Subbotina, considered by some (Gohrbandt, 1963) a subspecies of *G. pseudobulloides.* It is distinguished by its more compressed test, normal development of four chambers in the final whorl and the low, narrow apertural slit at the base of the last chamber. This species ranges through the Paleocene and into the lower part of the "Zone of conical globorotaliids" in the Soviet Union. It is a common form in the *G. rex* and (?) *G. formosa formosa* Zones of the Esna Shale Formation at Luxor, Egypt, in the *G. rex* Zone of the Lodo Formation in California, and in the *G. marginodentata* Subzone of the Zone of compressed globorotaliids (Subbotina, 1953) from the North Caucasus, as well as in somewhat higher strata attributable to the Zone of conical globorotaliids. It is suggested here that *G. varianta* evolved into *G. prolata* Bolli in the *G. formosa formosa* Zone. This writer has been unable to reconcile Bolli's (1957a, p. 72, pl. 15, figs. 21-23) identification of "*Globigerina collactea* Finlay" with topotypes in his collections. They are markedly different. The form illustrated by Bolli may prove to be involved in the phylogenetic species complex under discussion, but in the absence of other criteria *G. varianta* is suggested as a suitable ancestor. *G. varianta* is one of the longest ranging Paleogene globorotaliids.

In the uppermost part of the lower Eocene (Cuisian of some authors) and lower part of the middle Eocene (Lutetian) *G. prolata* appears to have evolved into *Globorotalia wilsoni* (Cole), classified as *G. bolivariana* by Bolli (1957a). Study of the holotype and paratype of *G. bolivariana* (Berggren, 1961) confirmed its synonymy. This middle Eocene species is distinguished by its strongly involute spire, ovate chambers and low interiomarginal, umbilical-extraumbilical aperture which extends to the spiral side on some individuals. It evolved into *G. opima nana* in the upper part of the middle Eocene and thus provides the link between the older Paleogene and younger Neogene forms of this lineage.* The *G. centralis, G. cerro-*

---

* cf. Blow, 1959, p. 94, where it is suggested that the sole species of *Globorotalia* which persisted into the lower Oligocene was *G. opima* Bolli. Blow and Banner, 1962, p. 131, 132, have since modified this opinion slightly, but the essential features of this lineage at the critical Eocene-Oligocene boundary remain the same.

azulensis and *G. pseudoampliapertura* branch evolved from *G. wilsoni,* beginning somewhat lower in the middle Eocene than the *G. opima* branch. Although transitional forms between *G. wilsoni* and *G. centralis* have not been observed, the relationship is suggested as depicted on the basis of stratigraphic overlap. *Globorotalia pseudomayeri,* which appears at the base of the *Hantkenina aragonensis* Zone, actually is morphologically more similar to *G. centralis* than to *G. wilsoni,* but their stratigraphic ranges are not known to overlap.

The type species of the higher taxon *Turborotalia* is *G. centralis* Cushman and Bermúdez. The characteristics of the *G. centralis-cerro-azulensis* branch, development of subangular chambers and more acute periphery, are repeated several times within the Neogene as various branches developed keeled forms. These characteristics are interpreted here as "stages" in phylogenetic branching through which various species groups, or gens, have gone. As such, they are not considered satisfactory criteria for divergence upon which definition of higher taxa (subgeneric or generic rank) can be based. Thus, *Turborotalia* is not used in this paper.

The origin of *Globorotalia kugleri* Bolli in the lower Miocene (Aquitanian) has been an enigma for many years. However, the full spectral range of transition between *G. siakensis* and *G. kugleri* is observed in samples from the *G. kugleri* Zone of Trinidad and *G. siakensis* is postulated as the ancestor of *G. kugleri* (see fig. 3). *G. barisanensis* developed at the top of the *G. kugleri* Zone and continued for a considerable stratigraphic interval giving rise to the *G. fohsi—G. lobata* branch a short distance above the *Orbulina* datum.

Globorotalia praescitula branched off from *G. barisanensis* in the lower part of the *G. stainforthi* Zone. Morphologic changes included development of a more acute axial periphery and a more lobulate test with strongly curved to sinuous sutures on the spiral side. The *G. praescitula-scitula* branch is ancestral to several of the globorotaliids found in the present seas (see fig. 3): *G. puncticulata, G. inflata, G. crassaformis* and *G. truncatulinoides,* as well as *G. hirsuta.* Forms transitional to *G. puncticulata* are present in the *Sphaeroidinellopsis seminulina* Zone in North Africa which is considered uppermost Tortonian or lowermost Sarmatian. Bandy (1964, p. 10, fig. 6), on the basis of data from AGIP Mineraria (1957), records *G. puncticulata* in the lower Pliocene; Banner and Blow (1960, p. 17) record it from the Pleistocene of Sicily and "deposits from the same locality which may be Pliocene, as well as having seen it in collections from the recent seas." The evolutionary trend suggested here involved flaring of the aperture and development of a broader (less acute) periphery (*G. puncticulata*), rounded to subangular periphery and flaring extraumbilical aperture (*G. inflata*), evolute, subangular to sharply angular to keeled periphery, high umbilico-convex test and slightly curved to radial sutures on spiral side (*G. crassaformis* (Galloway and Wissler) = *G.* (*T.*) *oceanica* Cushman and Bermúdez) to high umbilico-convex test with strongly keeled periphery and straight, radial sutures on spiral side and highly variable (but generally small) umbilicus and low extraumbilical aperture (*G. truncatulinoides*). Although *G. truncatulinoides* and *G. velascoensis* may be considered grossly pseudomorphous, the evolutionary trends leading to these two forms were quite dissimilar when the different species involved in the respective gens are considered.

Similarly, the *Globorotalia menardii* branch can be traced from the *G. praescitula* branch. Several "subspecies" have been erected by various authors (Bolli, 1957b; Blow, 1959; Jenkins, 1960), but some of these forms may be polytypic variants within species or subspecies of this branch, attesting to polymorphism within a given taxon rather than to a high rate of evolutionary development in lower taxonomic units.

Several other branches shown in fig. 3 are not discussed here. They have been discussed adequately by Blow (1959).

Lineage 5: *Globorotalia pseudobulloides* and the origin and development of *Acarinina* and *Truncorotaloides*

Evolutionary trends: Development of inflated chambers, spinose tests; separate branches developed parallel tendencies towards subacute peripheries, incipient keels; two (perhaps three) branches led to forms which develop "supplementary" apertures on the spiral side.

The phylogenetic development of this group and its taxonomic validity are complex and puzzling and led to considerable discussion in recent literature (Bolli, Loeblich and Tappan, 1957; Banner and Blow, 1959, Hillebrandt, 1962, 1964; Gohrbandt, 1963; Berggren, 1965b). As originally defined by Subbotina (1953), *Acarinina* (type species: *A. acarinata* Subbotina) was interpreted as exhibiting features intermediate between *Globigerina* and *Globorotalia,* but subsequent authors have varied widely. Bolli, Loeblich and Tappan (1957), Banner and Blow (1959) and Loeblich and Tappan (1964) considered *Acarinina* a synonym of *Turborotalia* (Subbotina originally included *G. centralis,* type species of *Turborotalia,* in *Acarinina*). Hillebrandt (1962, 1964) considered *Acarinina* a subgenus of *Globorotalia* and suggested restricting it to spinose forms such as *G. mckannai, G. primitiva, G. pentacamerata, G. soldadoensis, G. quetra* and *G. pseudotopilensis.* Gohrbandt (1963), on the other hand, included these forms under *Turborotalia,* although he included *G. gravelli* (= *G. pentacamerata*) and *G. mckannai,* in *Globigerina.* (He has modified his views on this group somewhat in later discussions.) In fig. 4 the origin and development of the acarininids and *Truncorotaloides* are presented. The essential characters serve to demonstrate the phylogenetic homogeneity of this group and may serve as criteria of divergence and monophyly sufficient to justify definition of *Acarinina* as a higher taxonomic category. Classification of various species in *Acarinina* would then be consistent with phylogeny.

Once again the derivation of this lineage is found in *Globorotalia pseudobulloides.* In the lower Danian transitional forms from the typical four-chambered *G. pseudobulloides* grade into typically three-chambered "*Globigerina triloculinoides* Plummer." This may support the suggestion by Parker (1962, p. 221) that "Tertiary species as "*Globigerina*" *triloculinoides* Plummer (including all the species put in the synonymy of this form by Loeblich and Tappan, 1957b) probably will be found to be more closely related to the *Globoquadrina* group than to the globigerinids, and hence are members of the Globorotaliidae." (see Parker, 1962, p. 234, 235 for further discussion). In this connection, the recent distinction of Brotzen and Pożaryska (1962) between *Globigerina* (spinose test) and *Subbotina* (reticulate, or cancellate, test), may be considered. The latter is common in the Paleogene, but is not represented in late Neogene or Recent. This group is "closely related" to *Globoquadrina;* indeed, it may be ancestral to *Globoquadrina. Globigerina* may also be a descendant of *Subbotina* originating in the late Eocene-Oligocene. If *Globigerina* is limited to forms with a hispid globigerine stage in their ontogeny, the writer would disagree with Parker (1962, p. 22) that "*Globigerina* appears to be the most primitive genus of the family," as *G. pseudobulloides* (and *G. eobulloides*) and *G. triloculinoides*, the oldest forms in the Tertiary, are closely related and both might be considered species of *Subbotina* under this definition. In the absence of diagnostic studies, further discussion is hypothetical. *Subbotina* is used here to denote the Paleogene reticulate "globigerinids," whose phylogenetic development places them closer to *Globorotalia* (as used in this paper) than *Globigerina.*

Migration of the aperture and the peripheral compression of the test led to the origin of *Subbotina velascoensis* at the base of the *Globorotalia pseudomenardii* Zone. At this point rapid diversification occurred. Several branches have been discerned and will be discussed in the reverse order shown in fig. 4. One branch led towards the robust, spinose form recorded in the literature variously as *Globigerina primitiva* (Finlay) or *Acarinina triplex* Subbotina, both of which probably are junior synonyms of *Globigerina coalingensis* Cushman and Hanna.

The exact nature of the phylogenetic diversification of the earliest members of this lineage is not clear. There is general similarity (fig. 4) to the scheme suggested by Bolli (1957a, fig. 12) and somewhat less to those proposed by Subbotina (1953, fig. 8; 1960, fig. 3); some of the species names have been changed as a result of comparative studies. *A. primitiva* (? = *G. coalingensis*) has been observed together with *A. mckannai* in the *G. pseudomenardii* Zone in many areas, and perhaps best preserved and exemplified in specimens from Nigeria (West Africa) (Berggren, 1960c). The type species of *Acarinina, A. acarinata,* a junior synonym of *A. nitida* (Martin), develops at about the same level. It is shown as the ancestor of *A. mckannai* in fig. 4, although in some localities transition from *A. primitiva* to *A. mckannai* occurs. Comparison of type material by this writer and studies by Shutskaya (1956, p. 91, pl. 3, figs. 1a-c; 1958, p. 89, pl. 2, figs. 6-14, pl. 3, figs. 1-21) show that *A. mckannai* has been recorded as *A. subsphaerica* (Subbotina) in Soviet literature. Some of the four chambered specimens of *A. acarinata* illustrated by Subbotina (1953, pl. 22, figs. 7-9) appear to be intermediate between *S. velascoensis* and *A. primitiva,* and one form (pl. 22, fig. 9) is very close to *A. primitiva.* The primary difference is surface ornament. One of the main evolutionary trends in the acarininids is development of a dense, hispid to strongly spinose wall texture. *A. acarinata* lies intermediate between the cancellate surface characteristic of *Subbotina* and the spinosity characteristic of *Acarinina.* Using this distinct feature of the wall texture as a criterion of divergence, the boundary separating the two groups is drawn between *S. velascoensis* and *A. acarinata;* in a similar manner the boundary is drawn between *S. velascoensis* and *A. intermedia* (= *A. esnaensis*), a separate branch of this lineage.

The form mentioned above (Subbotina, 1953, pl. 22, fig. 9) was described from the Zone of compressed globorotaliids (Paleocene) of Mangyshlak. It illustrates the trend towards developing spinosity of the test, increase in size and greater inflation of chambers. On the other hand, the holotype of this species (Subbotina, 1953, pl. 22, fig. 4) is a five chambered form similar to *A. mckannai*, differing mainly in surface ornament and size, and for this reason the phylogenetic development of *A. mckannai* from *A. acarinata* is as shown in fig. 4.

One branch (branch 4) led from *A. primitiva* to *A. soldadoensis* at the top of the *G. pseudomenardii* Zone. In the lower Eocene (*G. rex* Zone) *A. gravelli* branched off from *A. soldadoensis* from which it is distinguished by its globular chambers and subangular to subrounded periphery and, on many individuals, by a slight angular circum-umbilical reflection of the chambers (thus the walls of the chambers slope steeply inwards towards the umbilicus). A great number of taxonomic problems have been associated with this species. *Globorotalia pentacamerata* Subbotina (1947, p. 128, pl. 7, figs. 12-17; pl. 9, figs. 24-26) was described from the lower and middle Eocene of the northern Caucasus (Kuban river region). The holotype (pl. 7, figs. 15-17) is a tightly coiled, six chambered form described from the *Globorotalia crassaformis* Zone (uppermost lower Eocene to lowermost middle Eocene age) approximately equivalent to the *G. palmerae, H. aragonensis* and the lower part of the *G. kugleri* Zones of Bolli (1957a,c). The illustrated specimen is somewhat reminiscent of *Globigerina aspensis* Colom (1954). The two paratypes (Subbotina, 1947, pl. 7, figs. 12-14; pl. 9, figs. 24-26) were described from the *Globorotalia velascoensis* Zone (later named the "Zone of conical globorotaliids," Subbotina, 1953) which corresponds roughly to a part of the *G. formosa formosa* Zone, the *G. aragonensis* Zone and a part of the *G. palmerae* Zone (Berggren, 1965b). The paratype figured on pl. 7, figs. 12-14 is similar to Subbotina's subsequent identification of *G. pentacamerata* (1953, pl. 23, fig. 8; pl. 24, figs. 1-5), but the specimen figured on pl. 9, figs. 24-26, is almost identical in its characters with Bolli's (1957c, pl. 35, figs. 8a-c) illustration of *Globigerina soldadoensis angulosa.* Subbotina (1947) recognized from the beginning the close similarity which this species bore to *G. mckannai* but retained them as separate species. Berggren (1960a) placed them in synonymy. Bolli and Cita (1962) and Gohrbandt (1963) have maintained, on the contrary, that these two forms can be distinguished, and this writer is now in agreement based on his study in 1962 of specimens illustrated by Subbotina (1953) from the northern Caucasus in the collections at VNIGRI, as well as on material collected from localities in the northern Caucasus. The specimens illustrated on Subbotina's pl. 24, figs. 1-5 (VNIGRI numbers 4142-4146) agree well with Bolli's (1957a, pl. 16, figs. 1-3) illustration of *G. gravelli,* as well as with Bronnimann's (1952, pl. 1, figs. 16-18) holotype illustration. The species has been used by most workers in this sense and it should be used this way if the species is to have any value in stratigraphic and phylogenetic studies. The specimen illustrated by Subbotina (1953, pl. 23, fig. 8) is somewhat closer to Bolli's (1957a, pl. 16, figs. 7-9) illustration of *Globigerina soldadoensis.* The illustration of Subbotina (1953, pl. 24, fig. 6; VNIGRI 4147) from the *G. crassata* Subzone of the Zone of compressed globorotaliids of Mangyshlak probably should be included in *A. mckannai* and the two smaller forms (pl. 24, figs. 7, 8; VNIGRI 4148, 4149) from the same stratigraphic level may be young forms of *A. mckannai.* The specimen figured on pl. 24, fig. 9 clearly is related to *A. gravelli* and may be merely an aberrant form with an unusually large number of chambers. *A. pentacamerata* evolved into the globular, multichambered *A. aspensis* at or near the top of the *G. aragonensis* Zone. This branch (branch 3) ended its development in the lower part of the Lutetian (see fig. 4).

Branch 4 continued through *A. soldadoensis angulosa* to *A. densa* through the development of a more angular periphery and involute spire. This species has been recorded in Soviet literature as *Globorotalia crassaformis* Galloway and Wissler and as *Globorotalia bullbrooki* by Bolli (1957c). The middle Eocene *G. densa* and the Pliocene-Recent *G. crassaformis* are distinctly different, have distinctly different stratigraphic ranges, and are products of distinctly different phylogenetic lineages; in fact they probably do not belong to the same genus. Where pseudomorphy between forms having widely different stratigraphic distributions is involved and where phylogenetic relationships can be demonstrated to be distinctly different, different species names should be applied to the two (or more) forms involved. By further development of an acute periphery, and densely spinose ornament, flattening of the top and spiral side of the test and the development of "supplementary" apertures in the form of a space between chamber margins on the spiral side, *Truncorotaloides topilensis* developed. (As will be shown below the genus *Truncorotaloides* appears to have developed independently in two and perhaps three different branches within the group of acarininids.)

Another branch (branch 2, fig. 4) is interpreted as having developed from *A. acarinata* to *A. rotundimarginata* Subbotina. As shown elsewhere (Berggren, 1960b, p. 76; 1965b; Bandy, 1964), *Globorotalia spinuloinflata* Bandy, 1949, is conspecific with, and a senior synonym of, *G. bullbrooki* Bolli. Both are apparently predated by Cushman's *Globorotalia densa* which Pessagno (1961) has verified as a senior synonym of *G. bullbrooki. G. spinuloinflata* Bolli is interpreted as a junior synonym of *Acarinina rotundimarginata* Subbotina (1953, p. 234, pl. 25, figs. 1 (holotype), 2, 3). A second truncorotaloid developed as an end form of this branch, *T. pseudodubia* (Bandy). This form is a senior synonym of *Truncorotaloides rohri* Bronnimann and Bermúdez (see Bandy, 1964, p. 6).* *Acarinina rugosoaculeata* Subbotina is also interpreted as a junior synonym of *T. rohri.*

A final branch (branch 1, fig. 4) of this lineage has its origin in *Acarinina esnaensis* (Leroy) (of which *A. intermedia* Subbotina is a junior synonym). Small, four chambered forms similar to those illustrated by Subbotina (1953, pl. 20, figs. 14-16) are common in the *G. pseudomenardii* Zone and have been recorded elsewhere as *Globigerina stonei* Weiss, *Globorotalia whitei* (Bolli, 1957a), *Globorotalia irrorata* Loeblich and Tappan, among other names. The development of a larger test and subangular periphery led to *A. wilcoxensis* in the lower Eocene *G. rex* Zone. Separation of these two species is difficult in the lowermost lower Eocene where this transition occurs. Bolli (1957a, fig. 12) suggested derivation of the robust *A. quetra* directly from *A. wilcoxensis* within the *G. rex* Zone. He mentioned (1957a, p. 80) that transitional forms were observed in the *G. rex* Zone, but this writer believes these forms are referable to *A. pseudotopilensis* Subbotina. *A. pseudotopilensis* is intermediate between *A. wilcoxensis* and *A. quetra* in the development of a subtruncate periphery, and the cuneate or trapezoidal shape of the last two chambers. *A. quetra* has a sharply angular periphery, strongly incised, curved sutures on the umbilical side and shows the development of a keel (confluence of spines along the peripheral margin) on the chambers of the last two whorls (see Bolli, 1957a, pl. 19, figs. 1-6; cf. Subbotina,

---

* It is unfortunate that Bandy placed this species in *Globigerinoides* with which it has no relationship. The development of *Globigerinoides* from *Globigerina* within the *G. kugleri* Zone has been demonstrated by Blow and Banner *in* Eames *et al.* (1962) and observed by Berggren at equivalent stratigraphic levels in North Africa.

1953, whose illustration on pl. 21, fig. 5, of "*A. crassaformis*" from the Zone of acarininids is referable to *A. quetra*). On the other hand *A. pseudotopilensis* was described from the Paleocene and lower Eocene of the northern Caucasus (Subbotina, 1953, p. 227). It was shown to range (1953, p. 29, tab. 3, p. 153, fig. 8) from the Zone of compressed globorotaliids *into, not through,* the Zone of conical globorotaliids. In her phylogenetic chart Subbotina (p. 153, fig. 8) suggested derivation of *A. pseudotopilensis* from *A. crassaformis* at the base of the *G. crassata-A. intermedia* Subzone of the Zone of the compressed globorotaliids. This is approximately equivalent to the *G. pseudomenardii* Zone. All illustrated specimens of this species, including the holotype on pl. 21, fig. 8, were from the Zone of conical globorotaliids of the lower Eocene. In a subsequent work Subbotina (1960, fig. 3) suggested derivation of *A. pseudotopilensis* from *A. intermedia.*

Additional problems regarding the origin of *A. pseudotopilensis* remain. In some features this species appears transitional between *A. wilcoxensis* and *A. quetra.* However, it differs strongly from both forms in the consistently subacute, or subtruncate peripheral margin; there is, however, no tendency toward the development of a peripheral keel. In this respect *A. pseudotopilensis* is morphologically very close to *A. esnaensis. A. wilcoxensis* displays the tendency to develop a spinose, keeled periphery in the final chamber, or last two chambers of the test. Thus, on strictly phylogenetic grounds it appears that *A. quetra* developed from *A. wilcoxensis* through *acceleration* (a mode of *gerontomorphism,* see De Beer, 1958) of a morphologic character (spinose keel) which in the ancestral form appeared late in ontogeny and in the descendant form *A. quetra* appeared earlier in ontogeny. Important here is the stratigraphic distribution of *A. pseudotopilensis* which appears to have its main development in the lower Eocene, although Subbotina (1953, 1960) recorded its origin in the Paleocene. Loeblich and Tappan (1957, pl. 60, fig. 2) illustrated a form which conforms to *A. pseudotopilensis* from the mid-Paleocene Nanafalia Formation (*G. pseudomenardii* Zone). Reyment (1960, pl. 15, figs. 14-17) illustrated forms of this species from the Paleocene and lower Eocene of Nigeria which agree very well with topotype material in Berggren's collection. Hillebrandt (1962) and Gohrbandt (1963) recorded this species from the lower Eocene only and failed to identify it in the Paleocene part of their respective sections. D. Graham Jenkins (personal communication) has observed *A. pseudotopilensis* in the Paleocene of New Zealand with supplementary apertures, suggesting that it, too, is a truncorotaloid.

V. SOME COMMENTS ON *ACARININA* AND *TRUNCOROTALOIDES*

1. *Acarinina*

The original definition of the genus *Acarinina* by Subbotina (1953, p. 219) with the exception of *A. centralis, A. conicotruncata* (= *Globorotalia angulata conicotruncata*) and *A. rugosoaculeata* (= *Truncorotaloides pseudodubia*) describes a group of planktonic foraminifers distinct from the globigerinids and globorotaliids as customarily defined. Subsequent broadening of the concept of the genus *Acarinina* to include forms which appear to be phylogenetically distinct from it (Morozova, 1957, 1961; Leonov and Alimarina, 1961; Alimarina, 1963) has lessened the likelihood of its acceptance as a valid taxonomic unit.

For example, Hillebrandt's (1962, 1964) usage of *Acarinina* is somewhat inconsistent. In 1962 he interpreted it as a subgenus of *Globorotalia* (see Berggren 1965b). In a later paper (1964) he interprets *Acarinina* as a "stage" through which various forms have developed. Thus, he suggests (1964, fig. 3) a *Globigerina-Acarinina* stage followed by an *Acarinina-Globorotalia-Truncorotalia* stage followed by a *Truncorotalia* stage followed by a *Truncorotaloides* stage. However, it is not clear to which genera he would assign the various species in this lineage; indeed all forms in fig. 3 are prefixed by "*G*," apparently a reference to *Globorotalia.* This is a highly artificial usage of the category genus. In fact, his suggestion that forms which can be referred to *Globorotalia* (*G. spinulosa*) appear in the Cuisian, would make *Globorotalia* polyphyletic at both the generic and specific level.

The acarininids may be interpreted in yet another way, as a chronologic superspecies in the sense of Sylvester-Bradley (1951, 1954). Here the superspecies is applied to a taxon which is part of a branching phylogeny larger than a species but smaller than a genus (or subgenus). It may be that Hillebrandt (1964) tried to use *Acarinina* in this sense; uncertain of its categoric rank, he wants to utilize the name *Acarinina* as a supraspecific taxonomic category.

In attempting to arrive at criteria by which acarininids may be defined, Huxley's concept of *grade* taxa is useful: groups of organisms similar in general levels of organization. Various branches (*clades*) of this lineage may be arranged into steps, or grades. Grades are based upon parallelism within related organisms and grade genera are monophyletic at the generic level and are based upon evolutionary patterns of development. In this way, phylogenetic patterns may be discerned in the branches of the acarininids which may aid in the definition of the lineage (*i.e.,* the genus) itself. These concepts are to be used solely in the interpretation of evolutionary phenomena and classification and not as a substitute for normal lineage classification.

If taxonomy is primarily concerned with the definition and formalization of relationships between organisms, then the origin and basis of these relationships must be evolutionary. As a basis for recognizing higher categories (genus and higher) monophyly and gaps (degree of divergence) have been suggested as definitive (Mayr, Linsley and Usinger, 1953). The acarininids fit the criterion of monophyly by all standards if their origin occurred in the lower part of the Paleocene from the reticulate globigerinids, *Subbotina.* Considered as an homogeneous unit (*i.e.,* forms included in the genus in this paper) a definite gap exists between typical acarininid morphology and the "*typical*" globigerinid (*Subbotina*) or globorotaliid (*Globorotalia*) morphology. On the basis of the present discussion the acarininids are an homogeneous group which possess a taxonomic unity of their own and which warrants their recognition at the generic level.

The classification and stratigraphic range of *Acarinina* are a final consideration. As the genus is defined, recognized and delimited in this paper the acarininid lineage ends within the middle Eocene, two of the branches evolving into species of the genus *Truncorotaloides.* Subbotina (1953, p. 219) originally defined *Acarinina* as a genus of the Globorotaliidae; she later (1959, p. 302) included it in the subfamily Rugoglobigerininae Subbotina, subfam. nov., of the Globorotaliidae. This interpretation is invalid as *Acarinina* bears no phylogenetic relationship of magnitude to the rugoglobigerinids of the Upper Cretaceous. *Acarinina* is more properly classified as a genus within the Globorotaliinae (Globigerinidae), together with *Globorotalia* (in the sense used in this paper) and *Truncorotaloides.* As Parker (1962, p. 221) has observed, it may be that *Subbotina* and *Globoquadrina* are more properly classified in the Globorotaliidae (Globorotaliinae of this writer). Because of the close relationships between the globigerinids and globorotaliids this writer would hesitate to distinguish between them at the family level.

Certain late Eocene, Oligocene and early Miocene species such as *Globigerina tripartita* and *G. sellii* and related forms bear a close resemblance to some Paleogene acarininids, *A. primitiva* for instance. Here is an example where understanding of phylogenetic relationships illustrates the principle that classification should be based upon phylogeny. *G. tripartita* and *G. sellii* are members of a late Eocene-Oligocene divergence from *Globigerina yeguaensis* (a species which probably should be included under *Subbotina*) which led to the origin of *Globoquadrina.* In the last analysis in evolutionary classification the taxa are either made consistent with a conceptualized reconstruction of phylogeny or with the phylogenetic process which probably produced the taxa.

2. *Truncorotaloides*

The development of "supplementary" apertures in the forms assigned to *Truncorotaloides* does not seem to be regular by any definition of the word. In many individuals the "supplementary" apertures do not develop and where they do, they appear as "spaces" formed by separation along the margins of adjacent chambers. This type of supplementary aperture is hardly the same as the type developed during the course of ontogeny in *Globigerapsis* and *Globigerinoides,* and in similar forms.

If the degree of divergence (gaps) which a branch of a lineage displays is a criterion for the recognition of higher taxa, then the size or degree of separation between the ancestral-descendant forms must be evaluated and the level of (or degree of) monophyly must be specified. If the level of monophyly is determined by the category of lowest ranking taxon immediately ancestral to the taxon under consideration and the level of polyphyly by the category of the highest ranking taxa of which two or more were immediately ancestral to the given taxon, then the definition of the nature of the phylogeny of the genus is clear. Thus, in the example cited above of two, and perhaps three, branches leading through parallel trends to forms assignable to *Truncorotaloides,* the genus *Truncorotaloides* would be considered monophyletic at the generic level but polyphyletic at the specific level (see Simpson, 1961, chapter 4).

The pattern of parallel development within a single (monophyletic) lineage leading to similar end forms has all the characteristics of Huxley's *clade* concept. The separation of the various species groups (branches) by gradual, but recognizable, gaps or *grades* (to use Huxley's term) leading to end forms of similar levels of organization also helps to understand and explain the phylogenetic development of the acarininids and truncorotaloidids. But, with repetitive branching and interconnection between homology, parallelism, divergence and convergence, grades and clades become difficult to distinguish (and this is certainly true in the acarininids) and the use of these concepts here is made strictly for descriptive purposes (as an aid to understanding and evaluating evolutionary relationships within the group) not as a substitute for normal lineage classification. On the basis of the discussion presented here *Truncorotaloides* is considered a valid genus, but the writer would tentatively disagree with those who would include it in its own family or subfamily (cf. Loeblich and Tappan, 1964).

VI. SUMMARY

A discussion has been presented of the phylogenetic trends within five major lineages of planktonic foraminifers in the Tertiary. The origin of these lineages (and, indeed, all others within the Globigerinacea with the exception of the Heterohelicidae) is in a single, polytypic species *Globorotalia pseudobulloides.* In the Danian and Dano-Montian Stages relatively rapid divergence of the principal stock of the Tertiary Globigerinacea occurred as adaptive radiation in an environment in which the planktonic microfauna had been decimated by the radical changes at the end of the Cretaceous. The opportunity for rapid deployment and evolution was available and the planktonic foraminifers availed themselves of it. Although some lineages terminated within the Paleogene, the overall development is one of continued progression and divergence, a gradual but definitely noticeable elimination of various branches in the late Eocene, and a second, gradual radiation of planktonic forms in the Oligo-Miocene.

The evidence points to the suggestion that, indeed, the beginnings of the Tertiary planktonic foraminifers were small.

VII. ADDENDA

Addendum 1

Shortly after the completion of this paper, Dr. D. Graham Jenkins of the New Zealand Geological Survey sent this writer a manuscript draft of a paper entitled "A re-examination of the type material of *Globorotalia collactea* Finlay, 1939." Jenkins (1965) placed this species in *Truncorotaloides* on the basis of discrete supplementary apertures on the spiral side of *some* individuals. A stratigraphic range of lower Eocene-lower upper Eocene was given for the species in New Zealand. Comparison of several specimens from the type section (sample 354, Hampden Section, New Zealand, Porawagan Stage (?)) which Dr. Jenkins kindly sent has shown that *T. collactea* is conspecific with *Acarinina rotundimarginata* Subbotina and *Globorotalia spinuloinflata* Bolli (*non* Bandy). The stratigraphic ranges given by these two authors correspond with Jenkins's. This writer would agree further with Jenkins that *T. collactea* and *T. rohri* are related; here it is suggested that *T. rohri* (= *T. pseudodubia*) is a direct lineal descendant of *A. rotundimarginata* (= *T. collactea*). *T. collactea* does not appear to be related to any of the globorotaliid branches distinguished in this paper and offers additional evidence that a phylogenetic approach in paleontology aids in the recognition of similar, but unrelated, forms and their assignation to different higher taxa.

Addendum 2

The original version of this paper was prepared in the winter of 1963-1964. Some modification was made during 1965. To bring the English version up to date an addendum is added here to include modifications in concepts and statements occasioned by recent data.

1) The uncertainty of the relationship of planktonic foraminiferal zones to the lower/middle Eocene boundary was discussed (p. 312, 313 in original version; p. 5 this volume). Bolli (1957c) had drawn the lower/middle Eocene boundary at the *base* of his *Hantkenina aragonensis* Zone (top *G. palmerae* Zone). In the Soviet Union (N. Caucasus) the lower/middle Eocene boundary is customarily placed at the base of the Cherkessk Group (which is approximately the base of the *Globorotalia aragonensis* Zone).

Wade, Mohler and Hay (1964) recorded a lower Eocene-Cuisian-nannofossil assemblage from the Simferopolskian Stage in the Caucasus. They also recorded a Cuisian assemblage in the *Acarinina rotundimarginata* Zone of the Bodrakskian Stage of the Crimea. However, this zone corresponds approximately to the *Globorotalia lehneri* Zone of Bolli, and perhaps a part of the *Globigerapsis kugleri* Zone. On the basis of these data the question of overlap in the concept of Cuisian and Lutetian by various workers was raised.

The lower/middle Eocene boundary was provisionally drawn at a level correlative with the *Globigerapsis kugleri* Zone. If the *A. rotundimarginata* Zone were included wholly within the Cuisian, there would be little room left for middle Eocene in the southwestern part of the Soviet Union. Indeed, Schaub (1964, Mém. Bur. Rech. Géol. et Min., no. 28, p. 939; 1966, Voprosy Mikropalentologii, vol. 10, p. 300) has suggested that on the evidence of the nummulites the middle Eocene is missing in the Crimea. The *N. distans-planulatus-polygyratus* zones (which Soviet paleontologists generally correlate with lower Eocene to upper part of middle Eocene) are all placed by Schaub in the lower Eocene. The beds with *N. incrassatus* above are placed in the upper Eocene.

This writer has re-examined a series of samples collected in 1962 in the Crimea and North Caucasus. A summary of the results is presented here. In the Crimea a biostratigraphic zonation of Paleocene-Eocene is difficult to make on the basis of planktonic Foraminifera. The acarininids are common in the Paleocene-lower Eocene; keeled globorotaliids are scarce except at certain levels near the Paleocene-Eocene boundary (*G. velascoensis*—*G. subbotinae* zones). Lower Eocene was recognized on the basis of the acarininid assemblages. In the region of Bakchissaray some samples of the *Lyrolepis* marls contain *A. densa, A. rotundimarginata, A. aspensis,* and various small globigerinids, *Globigerapsis kugleri* and *G. index.* This fauna correlates approximately with the *G. kugleri-lehneri* zones of Bolli.

In the North Caucasus (Kuban River section) the Novogeorgisk Group is overlain by the Cherkessk Group. The boundary lies approximately at the base of the *Globorotalia aragonensis* Zone. Samples from the upper part of the Cherkessk Group have yielded a fauna containing *i. al., A. coalingensis* (= *A. primitiva* = *A. triplex*), *A. pentacamerata-aspensis* group, *A. densa-Truncorotaloides topilensis* transition, *Globorotalia aragonensis, G. pseudoscitula, Pseudohastigerina micra,* and *Globigerina frontosa* (= *G. boweri*). Significant here is the transition from *A. densa* to *T. topilensis* for this occurs within the upper part of the *G. kugleri* Zone in the Caribbean. The upper part of the Cherkessk Group is generally equated with the *A. crassaformis* Zone of Subbotina (which is approximately equivalent to the *H. aragonensis* Zone and a part of the *G. kugleri* Zone (at least). The Kumsk Group above contains the *Lyrolepis* Marl with a relatively poor planktonic fauna among which are, *i. al.*; *A. rotundimarginata, Truncorotaloides topilensis* and *Pseudohastigerina micra.* The association suggests that this level is not younger than the *P. mexicana* Zone of Bolli. The fauna is still middle Eocene in its affinities. The Beloglin clays above contain a rich and variegated globigerinid and globigerapsid microfauna which correlates well with the upper Eocene.

Thus, although a sharp sequential, biostratigraphic zonation of the Crimean and Caucasus sections is difficult, the presence of middle Eocene is quite apparent. What is more likely is that the correlation between nummulitic and planktonic foraminiferal zones is still unsatisfactory. The exact level at which *Nummulitis incrassatus* occurs is important as well as the possibility that it has been misidentified (see Bolli and Cita, 1960, Int. Geol. Congress, pt. 5, p. 158-160, where an association of nummulites identified by Vialli as middle-upper Eocene was found to occur with a planktonic fauna of *Hantkenina aragonensis* Zone age).

This writer would place the lower/middle Eocene boundary at the top of the *G. densa* (= *G. bullbrooki*) Zone (which is approximately equivalent to the *G. palmerae* Zone of Bolli.

2) The name *Acarinina densa* Zone or *A. bullbrooki* Zone is best used for the *G. palmerae* Zone of Bolli. This zone is defined then by the concurrent-range of *Acarinina densa* and *Globorotalia aragonensis* prior to the first evolutionary appearance of *Hantkenina aragonensis.*

3) Recent data on the age of the *Orbulina*-datum and the relationship between planktonic zones to Miocene stage boundaries suggest that the Aquitanian and Burdigalian Stages are older than the *Orbulina*-datum, that the Helvetian stratotype is closer in age to the Burdigalian than the Tortonian, and that a considerable time-stratigraphic interval is represented between top Burdigalian and base Tortonian. This interval corresponds approximately to the extent of the Langhian Stage in northern Italy. The *Orbulina*-datum occurs near the base of the Langhian.

4) Much additional work has appeared recently regarding the subdivision of the Pliocene-Pleistocene which may eventually modify the development of *G. crassaformis-G. truncatulinoides* suggested in this paper.

5) *G. chapmani* (*G. elongata* auct.), probably evolved directly from a non-keeled globorotaliid such as *G. ehrenbergi-haunsbergensis,* rather than from *G. pseudomenardii* through loss of the keel.

6) Evidence cited in the text by Jenkins (1965) and investigations by this writer on samples from the upper Eocene of Denmark have shown that the genus *Acarinina* (*A. collactea*) ranges into the upper Eocene.

VIII. References

Agip Mineraria, 1957, Foraminiferi padani (Terziario e Quaternario); Atlante iconografico e distribuzione stratigrafica, 52 pls., Milan.

Alimarina, V. P., 1963, Nekotorye osobennosti razvitiya planktonykh foraminifer v svyazi s zonalanym raschleneniem nizhnego paleogena Severnogo Kavkaza. Akad. Nauk SSSR, Voprosy Mikropal., vol. 7, p. 158-195, 1 text fig., 1 tab. (Oct. 30).

Bandy, O. L., 1964, Cenozoic planktonic foraminiferal correlation. Micropaleontology, vol. 10, no. 1, p. 1-17, 6 text figs.

Banner, F. T. and W. H. Blow, 1959, Classification and stratigraphical distribution of the Globigerinaceae. Palaeontology, vol. 2, pt. 1, p. 1-17, pls. 1-3.

Banner, F. T. and W. H. Blow, 1960, Some primary types of species belonging to the superfamily Globigerinaceae. Cushman Found. Foram. Res., Contr., vol. 19, pt. 1, p. 1-41, 8 pls.

Bé, A. W. H., 1959, Ecology of Recent planktonic Foraminifera: Part 1, areal distribution in the western North Atlantic. Micropaleontology, vol. 5, no. 1, p. 77-100, 1 pl., 52 text figs., 2 tabs.

Bé, A. W. H., 1960, Ecology of Recent planktonic Foraminifera; Part 2, bathymetric and seasonal distributions in the Sargasso Sea off Bermuda. Micropaleontology, vol. 6, no. 4, p. 373-392.

Bé, A. W. H., 1965, The influence of depth on shell growth in *Globigerinoides sacculifer* (Brady). Micropaleontology, vol. 11, no. 1, p. 81-97, pls. 1-2.

Berggren, W. A., 1960a, Some planktonic Foraminifera from the lower Eocene (Ypresian) of Denmark and northwestern Germany. Stockholm Contr. Geol., vol. 5, no. 3, p. 41-108, 13 pls.

Berggren, W. A., 1960b, Paleogene biostratigraphy and planktonic Foraminifera of the SW Soviet Union: An analysis of recent Soviet publications. Stockholm Contr. Geol., vol. 6, no. 5, p. 63-125, 8 tabs.

Berggren, W. A., 1960c, Paleogene biostratigraphy and planktonic Foraminifera of Nigeria (West Africa). XXI Int. Geol. Congr., Proc. Sect. 6, p. 41-45, 1 text pl.

Berggren, W. A., 1962a, Some planktonic Foraminifera from the Maestrichtian and type Danian stages of southern Scandinavia. Stockholm Contr. Geol., vol. 9, no. 1, p. 1-106, 14 pls.

Berggren, W. A., 1962b, Stratigraphic and taxonomic-phylogenetic studies of Upper Cretaceous and Paleocene planktonic Foraminifera. Stockholm Contr. Geol., vol. 9, no. 2, p. 107-129, 3 text figs.

Berggren, W. A., 1964, Paleocene-Lower Eocene biostratigraphy of Luxor and nearby western desert. Petrol Expl. Soc. Libya, 6th Annual Field Conf., p. 149-176, 2 pls., 8 figs., 5 tables, 1 chart, Amsterdam.

Berggren, W. A., 1965a, The recognition of the *Globorotalia uncinata* Zone (Lower Paleocene) in the Gulf Coast. Micropaleontology, vol. 11, no. 1, p. 111-113.

Berggren, W. A., 1965b, Some problems of Paleocene-Lower Eocene planktonic foraminiferal correlations. Micropaleontology, vol. 11, no. 3, p. 278-300, 1 pl.

Blow, W. H., 1956, Origin and evolution of the foraminiferal genus *Orbulina* d'Orbigny. Micropaleontology, vol. 2, no. 1, p. 57-70, 4 text-figs. (Jan.).

Bolli, H. M., 1950, The direction of coiling in the evolution of some Globorotaliidae. Cushman Found. Foram. Res., Contr., vol. 1, pts. 3-4, p. 82-89, pl. 15.

Bolli, H. M., 1957a, The genera *Globigerina* and *Globorotalia* in the Paleocene-Lower Eocene. Lizard Springs Formation of Trinidad, B.W.I. U.S. Natl. Mus. Bull. 215, p. 61-81, pls. 15-20.

Bolli, H. M., 1957b, Planktonic Foraminifera from the Oligocene-Miocene Cipero and Lengua formations of Trinidad, B.W.I. U.S. Natl. Mus. Bull. 215, p. 97-123, pls. 22-29, text-figs. 17-21.

Bolli, H. M., 1957c, Planktonic Foraminifera from the Eocene Navet and San Fernando formations of Trinidad, B.W.I. U.S. Natl. Mus. Bull. 215, p. 155-172, pls. 35-39.

Bolli, H. M. and M. B. Cita, 1960, Globigerine e Globoratalie del paleocene di Paderno d'Addo (Italia). Riv. Ital. Paleont., vol. 66, no. 3, p. 361-402, 3 pls., Milan.

Bolli, H. M., A. R. Loeblich and Helen Tappan, 1957, Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae. U.S. Natl. Mus. Bull. 215, p. 3-50, pls. 1-11.

Bradshaw, J. S., 1959, Ecology of living planktonic Foraminifera of the north and equatorial Pacific Ocean. Cushman Found. Foram. Res., Contr., vol. 10, pt. 2, p. 25-64.

Bronnimann, Paul, 1952, Trinidad Paleocene and Lower Eocene Globigerinidae. Bull. Am. Paleontology, vol. 34, no. 134, p. 1-34, pls. 1-3.

Brotzen, Fritz, and K. Pożaryska, 1962, Foraminifères du Paleocene et de l'Éocène inférieur en Pologne septentrionale remarques paleógeógraphiques. Rev. Micropal., vol. 4, no. 3, p. 155-166, 4 pls.

Colom, Guillermo, 1954, Estudio de las biozonas con foraminiferos del Terciario de Alicante. Inst. Geol. Min. España, Bol., vol. 66, p. 1.279.

De Beer, G. K., 1958, Embryos and ancestors, 197 p., 19 text-figs., Oxford Univ. Press, London (3rd ed.)

Drooger, C. W., 1956, Transatlantic correlation of the Oligo-Miocene by means of Foraminifera. Micropaleontology, vol. 2, no. 2, p. 183-192.

Eames, F. E., *et al.*, 1962, Fundamentals of mid-Tertiary stratigraphical correlation, 163 p., 17 pls., Cambridge Univ. Press.

Gohrbandt, Klaus, 1963, Zur Gliederung des Paläogen im Helvetikum nördlich Salzburg nach planktonischen Foraminiferen. Erste Teil: Paleozän und tiefstes Untereozän mit Beitragën von Adolf Papp (Grossforaminiferen) und Herbert Stradner (Nannofloren). Mitt. Geol. Ges., Wein, Band 55, Heft. 1, 116 p., 11 pls., 1 chart.

Hay, W. W., 1962, The type level of some of Ehrenberg's Foraminifera. Jour. Paleontology, vol. 36, no. 6, p. 1392, 1393.

Hay, W. W., K. M. Towe and R. C. Wright, 1963, Ultra-microstructure of some foraminiferal tests. Micropaleontology, vol. 9, no. 2, p. 171-195 (April).

Hillebrandt, A. V., 1964, Zur Entwicklung der planktonischen Foraminiferen im Alttertiär und ihre stratigraphische Bedeutung. Paläont. Z., Bd. 38, no. 3/4, p. 189-206, 4 text-figs. (Sept.).

Jenkins, D. G., 1960, Planktonic Foraminifera from the Lakes Entrance oil shaft, Victoria, Australia. Micropaleontology, vol. 6, no. 4, p. 345-371, pls. 1-5, text-figs. 1-10 (October).

Jenkins, D. Graham, 1964, Preliminary account of the type Aquitanian-Burdigalian planktonic Foraminifera. Cushman Found. Foram. Res., Contr., vol. 15, pt. 1, no. 277, p. 28, 29, 1 tab. (January).

Jenkins, D. Graham, 1965, A re-examination of *Globorotalia collactea,* Finlay, 1939. New Zealand, Jour. Geol., Geophys. (*in press*).

Krinsley, David, and A. W. H. Bé, 1965, Electron microscopy of internal structures of foraminifera: *in* Handbook of paleontological techniques (B. Kummel, D. M. Raup, eds.), p. 335-343, Paleont. Soc., W. H. Freeman & Co., San Francisco, Calif.

Leonov, G. P., and V. P. Alimarina, 1961, Problema V. Granitsa melovoi i paleogenovoi sistem. Sb. trudov geol. fak. MGU, p. 29-60, 7 pls., Moscow.

Loeblich, A. R., Jr., and Helen Tappan, 1957, Planktonic Foraminifera of Paleocene and early Eocene age from the Gulf and Atlantic Coastal Plains. U.S. Natl. Mus. Bull. 215, p. 173-198, pls. 40-64.

Loeblich, A. R., Jr., and Helen Tappan, 1964, Treatise on Invertebrate Paleontology. (ed. R. C. Moore), Part C: Protista 2—chiefly "Thecamoebians" and Foraminiferida, 2 vols., xxxi + 900 p., 653 text-figs. (5311 figs.) Geol. Soc. America and Univ. Kansas Press.

Mallory, V. S., 1959, Tertiary biostratigraphy of the California Coast Ranges. Am. Assoc. Petrol. Geol., spec. publ., 416 p., 42 pls.

Mayr, Ernst, E. G. Linsley, and R. L. Usinger, 1953, Methods and principles of systematic zoology, McGraw-Hill, N.Y.

Morozova, V. G., 1957, Nadsemeistvo foraminifer Globigerinidea superfam. nova i nekotori yevo predstaviteli. Doklad. Akad. Nauk SSSR, t. 114, no. 5, p. 1109-1112, fig. 1, Moscow.

Morozova, V. G., 1959, Stratigrafiya datsko-montskikh otlozhenii Krima po foraminiferam. Doklad. Akad. Nauk SSSR, t. 124, no. 5, p. 1113-1116, 1 chart, 1 fig., Moscow.

Morozova, V. G., 1961, Datsko-montskie planktonniye foraminiferii yuga SSSR. Akad. Nauk SSSR, Paleont. Zhurnal, no. 2, p. 8-19, 2 pls.

Parker, F. L., 1962, Planktonic foraminiferal species in Pacific sediments. Micropaleontology, vol. 8, no. 2, p. 219-254, pls. 1-10 (April).

Papp, Adolf von, 1963, Die biostratigraphische Gliederung des Neogens im Wiener Becken. Mitt. Geol. Ges. Wein, Bd. 56, H. 1, p. 225-317, 14 pls.

PESSAGNO, E. A., JR., 1961, The micropaleontology and biostratigraphy of the Middle Eocene Jacaquas group, Puerto Rico. Micropaleontology, vol. 7, no. 5, p. 351-358, 1 pl. (July).

REYMENT, R. A., 1960, Some Globigerinidae, Globotruncanidae and Globorotaliidae from the Upper Cretaceous and Lower Tertiary of Nigeria. Rep. Geol. Surv. Nigeria (1957), no. 6, p. 68-86, pls. 15-17 (March 4).

SAITO, TSUNEMASA, 1959, Tertiary stratigraphy of the Kakegawa district, Central Japan and its planktonic Foraminifera. Tohoku Univ., Inst. Geol. Pal., Contr., 51, 45 p., pls. 1-6, text-figs. 1-6, 2 tabs., 7 charts.

SAITO, TSUNEMASA, 1962a, Eocene planktonic Foraminifera from Hahajima (Hillsborough Island). Trans. Proc. Paleont. Soc. Japan, n.s., no. 45, p. 209-224, pls. 32-34 (April 10).

SAITO, TSUNEMASA, 1962b, Notes on *Globigerina nepenthes* Todd, 1957. Trans. Proc. Paleont. Soc. Japan, n.s., no. 48, p. 331-342, pls. 51, 52 (Nov. 30).

SAITO, TSUNEMASA, 1963, Miocene planktonic Foraminifera from Honshu, Japan. Sci. Rep. Tohoku Univ., Sendai, spec. ser. (Geology), vol. 35, no. 2, p. 123-209, pls. 53-56 (Nov. 20).

SHUTSKAYA, E. K., 1956, Stratigrafiya nizhnikh gorizontov paleogena tsentral'nogo predkavkaz'ya po foraminiferam. Akad. Nauk SSSR, Tr. Inst. Geol. Nauk, vol. 164, p. 3-119, 5 pls.

SHUTSKAYA, E. K., 1958, Izmenchivost nekotorykh nizhnepaleogenovykh planktonnykh foraminifer Severnogo Kavkaza. Akad. Nauk SSSR, Voprosy Mikropal., vol. 2, p. 84-90, 3 pls.

SIMPSON, G. G., 1961, Principles of animal taxonomy, 247 p., 30 text-figs., Columbia Univ. Press, N.Y.

SUBBOTINA, H. H., 1947, Foraminifery datskikh i paleogenovykh otlozhenii Severnogo Kavkaza: *in* mikrofauna neftyanykh mestorozhdenii Kavkaza, Emby i Srednii Azii. VNIGRI, p. 39-160, 9 pls., Lengostoptekhizdat, Leningrad.

SUBBOTINA, N. N., 1953, Fossil Foraminifera of the USSR: Globigerinidae, Hantkeninidae and Globorotaliidae Tr. Vses, Neft., Naukno-Issled. Geol.-Razved. Inst. (VNIGRI), vol. 76, p. 1-296.

SUBBOTINA, N. N., 1959, *in* Rauzer-Chernousova, D. M. and Fursenko, A. V., Osnovy Paleontologii, Obshchii chast, Prosteishie, p. 296-304.

SUBBOTINA, N. N., 1960, Pelagicheskie foraminiferi paleogenovikh otlozhenii yuga SSSR. Akad. Nauk SSSR, p. 24-36, 1 tab., 3 figs., Moscow.

SYLVESTER-BRADLEY, P. C., 1951, The subspecies in paleontology. Geol. Mag., vol. 88, p. 88-102.

SYLVESTER-BRADLEY, P. C., 1954, The superspecies. Systematic Zoology, vol. 3, p. 145, 146, 173.

TAKAYANAGI, YOKICHI, and TSUNEMASA SAITO, 1962, Planktonic Foraminifera from the Nobori Formation, Shikoku, Japan. Sci. Rep. Tohoku Univ., Sendai, Japan, spec. ser. (Geology), spec. vol., no. 5 (Kon'no mem. vol.), p. 67–106, pls. 24–28 (March).

WADE, MARY, 1964, Application of the lineage concept to biostratigraphic zoning based on planktonic Foraminifera. Micropaleontology, vol. 10, no. 3, p. 273-290, 2 pls. (Jan.).

WADE, MARY, HANSPETER MOHLER, and W. W. HAY, 1964, Paleogene nannofossils from the Crimea and Caucasus. Geol. Soc. America, Progr. 1964, p. 215 (abstr.).

REVIEW

ALGAE AND MAN

HUBERT C. SKINNER
TULANE UNIVERSITY

ALGAE AND MAN, edited by Daniel F. Jackson. Published by Plenum Press, New York, 1964, x + 434 pp., illus., $14.50

This volume is the proceedings of the Advanced Study Institute held July 22 through August 11, 1962, at the University of Louisville and sponsored by the Scientific Affairs Division of NATO. The purpose of the Institute was to examine current concepts concerning the biology of algae and to discuss the effects of algae, beneficial and detrimental, on the human organism.

The articles summarize recent independent work by the twenty prominent authors from many nations, in the fields of taxonomy, cytogenetics, culturing, physiology and ecology of algae, including algal toxins and the possible role of algae as gas exchangers in space vehicles.