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Chapter 1

OVERVIEW OF EOCENE PLANKTONIC FORAMINIFERAL TAXONOMY, PALEOECOLOGY, PHYLOGENY, AND BIOSTRATIGRAPHY

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INTRODUCTION

This monograph has been compiled by members of the Paleogene Planktonic Foraminifera Working Group (hereafter referred to as the Working Group) of the International Subcommission on Paleogene Stratigraphy, International Union of Geological Sciences. It is the second such work in a projected series of three, the first being the *Atlas of Paleocene Planktonic Foraminifera* published by Smithsonian Institution Press (Olsson and others, 1999). Here we extend that effort to encompass the full flowering of the adaptive radiation of planktonic foraminifera in the Eocene.

The atlas has its origins in 1987, when the Working Group was formed. At that time it was clear that a major revision of the Paleogene planktonic foraminifera was necessary in order to synthesize a highly dispersed body of literature and to develop new taxonomic concepts, based, as far as possible, on scanning electron microscopy (SEM). At the first formal meeting a decision was made to focus on the production of an initial Paleocene atlas. Since that work was sent to press in 1996, our efforts have been directed almost exclusively at unravelling the taxonomic complexities of the Eocene planktonic foraminifera. The Working Group's practice has been to meet once or twice a year to coordinate efforts, debate the latest proposals and discoveries, and set a series of tasks to be completed before the following meeting. Meanwhile, participants have continued to disseminate their own research through the open literature.

Most of the important species of Eocene planktonic foraminifera were described before the advent of the SEM (Fig. 1.1), often using illustrations that are inadequate by modern standards. Central to our approach has been to obtain new SEM micrographs of as many of the original type specimens as we can, in an effort coordinated by B.T. Huber at the U.S. National Museum. Because it is now possible to scan specimens without the need for conductive coating, we have been able to obtain images of the vast majority of the important type specimens, as well as those of less well-known species, many of which we have been able to confirm as synonyms of other taxa. Although this has led to the upsetting of some long-held opinions, it has proved extremely beneficial for the establishment of a well-founded taxonomy.

As was the case for the Paleocene atlas, we have continued to find the study of wall microstructures to be indispensable for establishing the higher-level taxonomy. This follows the approach applied to the Paleocene by Olsson and others (1992, 1999). For this it has been necessary to obtain well-preserved material. In particular, collection of new samples from Tanzania (by P.N. Pearson), New Jersey (by R.K. Olsson), the Adriatic (by V. Premec-Fucek), Mexico (by R.K. Olsson), Java (with thanks to Peter Lunt of Lundin Petroleum Co.) and the U.S. Gulf Coast (by various investigators) has allowed us to study very well-preserved examples of species that have previously been known only in a poorly preserved state. The study of wall textures has been coordinated by Ch. Hemleben at Tübingen University, in collaboration with R.K. Olsson.

HISTORY OF TAXONOMIC WORK

The first descriptions of Eocene planktonic foraminifera were made during nineteenth century geological exploration in Europe (e.g., Gümbel, 1868; Hantken, 1875; Terquem, 1882). However, for most of the nineteenth century it was widely held that foraminifera were "primitive" organisms, and consequently evolved only slowly, if at all (e.g., Huxley, 1868). This in turn led to the erroneous assumption that foraminifera would be useless for biostratigraphy. Eocene planktonic foraminiferal studies only began in earnest in the mid 1920s when their stratigraphic value in oil exploration first began to be recognized. The subsequent developments (Fig. 1.1) can be divided into three main phases:

Phase 1: Initial exploration, 1924-1950

Following the foundation of the Cushman Laboratory for Foraminiferal Research in 1923, the indefatigable J. Cushman and co-workers began describing foraminiferal assemblages from the Cretaceous to Recent strata of the United States, especially the oil-producing southern states. Comparable exploratory researches were undertaken by M. Glaessner, N.N. Subbotina, V.G. Morozova and others in the Former Soviet Union from the late 1930s, and at about the same time by H.J. Finlay in New Zealand. The Second World War slowed the pace of research, which only began to pick up again in the late 1940s. Although most of the common species of Eocene planktonic foraminifera were described during this initial phase of research, the descriptions are usually very brief and the illustrations are often poor by modern standards.

Phase 2: Comparative and synthetic studies, 1950-1967

Straightforward taxonomic works that include descriptions of Eocene planktonic foraminiferal assemblages from individual localities have of course continued to be published up to the present day. However by the 1950s, a sufficient body of knowledge regarding the diversity of Eocene species and their stratigraphic ranges had been accumulated for the first major synthetic works to be produced. For the first time, concerted attempts were made to recognize synonyms and develop phylogenetic hypotheses for the group. The three outstanding contributions from this period are those of Subbotina (1953), Loeblich and others (1957) and papers therein (especially those by H. Bolli); and Blow and Banner (1962). The standard of description and illustration in these works is far superior to anything that preceded them, hence there is generally much less difficulty for modern workers to place the various species, although ambiguities about wall texture often

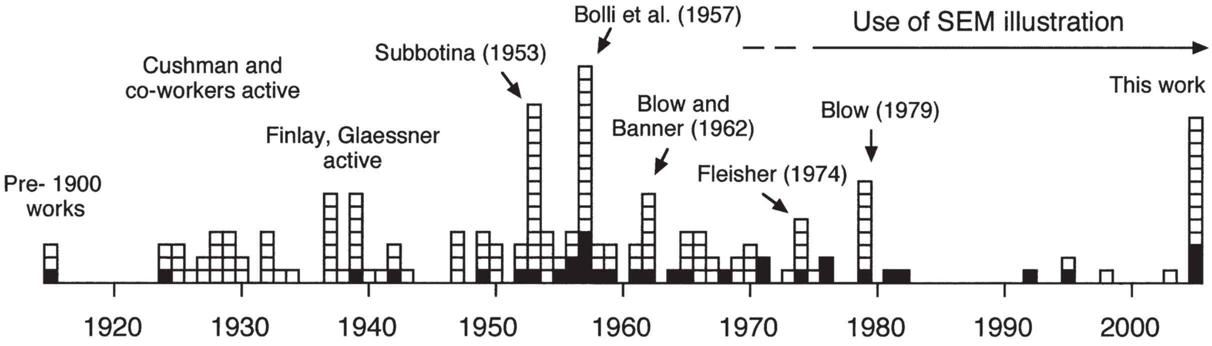

Figure 1.1. Diagram showing chronological development of Eocene planktonic foraminiferal taxonomy. Boxes indicate the date of first description of taxa that are recognized as valid in this work. Closed squares = genera; open squares = species.

remain. Happily these works describe foraminifera from different parts of the world, namely the Former Soviet Union, the Caribbean, and Tanzania, and among them they encompass most of the diversity in the group.

Phase 3: Deep sea drilling and SEM, 1969-present.

The most important innovation in taxonomic studies of foraminifera has been the SEM. Scanning electron micrographs provide undistorted and unembellished images of specimens at high magnification, and for the first time it became possible to use wall textures as a taxonomic feature. Among the first SEM micrographs of Eocene planktonic foraminifera to be published were those of Blow (1969) and Fleisher (1974). The SEM is now standard equipment in all well-equipped laboratories.

Another epochal development in the late 1960s was the advent of systematic ocean drilling, through the Deep Sea Drilling Project (DSDP) which first sailed in 1968, and has continued to this day through the Ocean Drilling Program (ODP) and Integrated Ocean Drilling Program (IODP). Planktonic foraminiferal biostratigraphy (which was originally developed from outcrop and oil well studies) immediately proved its worth in deep sea exploration. It was first employed at Site 1 of Leg 1 of the DSDP, which was drilled in the Gulf of Mexico (Blow, 1969; Berggren and others, 1969). The first Eocene planktonic foraminifera to be described were from also from Leg 1, at Site 5 in the Western North Atlantic Ocean, where they occurred as reworked contaminants in a younger sample (Blow, 1969, p.397). The first *in situ* Eocene assemblage was described from Leg 2, at Site 10, also in the western North Atlantic (Blow, 1970, p.358). By Leg 5, the DSDP drill-ship was in the Pacific Ocean, and again planktonic foraminifera were proving their worth (Olsson and Goll, 1970). It soon became evident that Eocene assemblages from the Pacific were "the same species assemblage and faunal succession as reported from other areas" (Krasheninnikov, 1971, p.1065-1066), and that consequently the regional studies of earlier workers were applicable on a global scale, at least within comparable climatic belts. Age-dating of sea floor sediments by planktonic foraminifera in these early days of ocean drilling played a significant part in the validation of plate tectonic theory. Many deep sea sites have now been drilled, and the focus of academic work on Eocene planktonic foraminifera has shifted to deep sea studies, notwithstanding their continuing utility in oil exploration and regional correlation.

Significant contributions to the synthetic taxonomy and biostratigraphy of the Eocene planktonic foraminifera were made by El Naggar (1966), Jenkins (1971), Postuma (1971), H. Luterbacher in Stainforth and others (1975) and Berggren (1977). However, without doubt the most important synthetic work to have appeared in this period, or any period, is that of W.H. Blow (1979). This was published posthumously, after Blow's untimely death in April, 1972, with editorial help of J. Van Couvering (see review by Berggren, 1981).

Blow's work is a great one; it is also somewhat idiosyncratic. Many of his taxonomic and phylogenetic hypotheses were adopted immediately by other workers, and most have stood the test of time. Some ideas, that for some reason were not followed by other workers (e.g., the polyphyletic origins of '*Pseudohastigerina*'), we have now found to be correct on closer inspection. However, the taxonomist must always be wary of Blow's work, not least because he adopted a strongly orthogenetic view of evolution and an unusual approach to stratigraphic correlation. For example, some of Blow's evolutionary sequences were described from individuals from the same sample (e.g., the transition from *Globigerina officinalis* to *angustiumbilicata*, and *yeguaensis* to *tripartita*, or the development of complex cribrate apertural system in *Cribrohantkenina*; see Blow and Banner, 1962). He was also fond of polyphyletic form-genera. Berggren (1981) remarked that a committee would be necessary to adequately review Blow's work. In a way, this has been the part of the function of this Working Group, and Blow's many hypotheses have usually been near the center of any major debate or discussion.

The last major synthesis to have appeared was by Toumarkine and Luterbacher (1985). That work is a very useful summary of taxonomic and biostratigraphic information up to that time, including a response to some of Blow's (1979) innovations, although it does not attempt to deal with the more obscure taxa. Since then relatively few studies have resulted in the naming of valid taxa. This in part reflects the maturity of taxonomic research on the Eocene planktonic foraminifera, which is probably rivalled by very few other fossil groups. The vast majority of obvious species have already been named, and most are well known across a substantial research community.

PALEOECOLOGY

Since the nineteenth century it has been appreciated that the foraminifera have planktonic and benthic representatives. Fortunately, the planktonic species are relatively easy to distinguish and there has been little confusion between planktonic and benthic taxonomy in the past (with the exception of some microperforate taxa and a few macroperforate forms like *Astrorotalia palmerae*). In the first phase of investigation, most Eocene species were assigned to the genera *Globigerina* (for forms with rounded chambers and an umbilical aperture) or *Globorotalia* (for more flattened forms with a more extraumbilical aperture and often a peripheral keel).

Emiliani (1954) suggested, on the basis of the oxygen isotope ratios of their shells, that modern tropical species are stratified in the water column, with some species preferring a warm surface mixed layer habitat through their life cycle and others sinking through the water column to the thermocline, where they add the adult chambers of the test. Much subsequent research (summarized by Hemleben and others, 1989) has revealed the complexities of modern planktonic foraminiferal life cycles, diet, symbiotic associations, and their varying preference for water temperature, depth, and productivity conditions.

Direct observation of Eocene species is impossible because they are all extinct. They were of comparable diversity and morphologic disparity to modern assemblages, however, and it seems probable that they occupied a similar range of life habitats. Deductions can be made about these species from their shell morphology (by analogy with modern species), by their distribution in marginal environments, and most importantly, by the geochemical composition of their shells.

The earliest geochemical studies of Paleocene and Eocene planktonic foraminifera were conducted in the late 1970s. Douglas and Savin (1978) analyzed a Paleocene assemblage and found that species of *Morozovella* had more negative δ^{18}O values than co-occurring *Subbotina*. Boersma and others (1979) published more data from the Paleocene that showed the isotopic ordering discovered in a single sample by Douglas and Savin (1978) was typical of other samples and other sites. They interpreted the morozovellids as shallow water forms on account of their negative δ^{18}O, indicating warm water growth, and the subbotinids as deep water forms. This generalization has stood the test of time (e.g., Boersma and others, 1987; Corfield and Cartlidge, 1991; Pearson and others, 1993, 2001; Lu and Keller, 1996; Bralower and others, 1995; Pearson, 1998b; Coxall and others, 2000), although it may be that subbotinids were more diverse in their habitats than has generally been accepted.

Carbon isotope ratios also yield important information on the life habits of extinct species, but the results are more difficult to interpret. Other factors being equal, shallow-water calcifiers ought to have more positive carbon isotope ratios than deeper forms, because there is generally an isotopic gradient in the water column caused by photosynthesis in the surface, which preferentially removes the light isotope, and remineralization at depth which returns it (Kroopnick, 1985). Such a relation was found in the pioneering studies of Douglas and Savin (1978), Boersma and others (1979, 1987), and Shackleton and others (1985), supporting the depth habitat inference from oxygen isotopes that Boersma and others (1979) first made with respect to the morozovellids, subbotinids and others.

Shackleton and others (1985) analyzed the isotopic variation of $\delta^{13}C$ with shell size and found that some muricate species display a pronounced trend towards more positive values as they grow larger. Pearson and others (1993) observed a similar carbon isotope enrichment with size fraction in Eocene morozovellids and acarininids and, arguing by analogy with the isotopic characteristics of modern species (e.g., Berger and others, 1978; Spero and Lea, 1993), suggested that they were symbiotic in life. Similar interpretations were made by D'Hondt and Zachos (1993), D'Hondt and others (1994), and Norris (1996) for Paleocene species. However, the presence of symbionts is not the only mechanism for producing a carbon isotope enrichment trends (e.g., Spero and Lea, 1996), so the inference should not be considered infallible.

In recent years an increasing number of species have been subjected to stable isotope analyses, but there are still many for which no data are yet available. For the most part, the available data are consistent between sites and studies. New methods such as boron isotope analysis, which reflects pH differences in the water column, are also becoming available (Pearson and Palmer, 1999) and have provided useful corroboration of the results obtained from oxygen and carbon isotopes. In most cases, related species within genera tend to have similar isotopic characteristics, indicating that most speciation occurs without major changes in habitat. In contrast, some groups such as the hantkeninids show a more interesting pattern that can be interpreted in terms of changing depth habitats during their evolutionary history (Coxall and others, 2000). In this atlas we have reviewed the available stable isotope data, species by species. We have also provided new data for certain microperforate species that have been little analyzed in the past (Huber and others, Chapter 16, this volume). We hope that workers will be motivated to fill in the gaps for species that have yet to be studied.

BIOSTRATIGRAPHY

The growth of taxonomic knowledge of the Eocene planktonic foraminifera has been accompanied by a similar growth of knowledge regarding their stratigraphic distributions and the geochronology of the Eocene epoch in general. There is not sufficient space here to review the long history of innovation and discovery with respect to the biostratigraphy of Eocene planktonic foraminifera; the reader is referred to Toumarkine and Luterbacher (1985), Berggren and Miller (1988) and Berggren and others (1995) for details.

The taxonomic revisions of the Working Group were accompanied by a review of the biostratigraphic occurrences of all the Eocene taxa. This revealed a number of inconsistencies and deficiencies in the most recent incarnation of the standard (sub)tropical Eocene zonation (the so-called P-Zones of Berggren and others, 1995). Accordingly, we developed a revised (sub)tropical zonation that, in order to be consistent with the Neogene zonal appellations of Berggren and others (1995), were renumbered using an 'E-for-Eocene' prefix (so-called E-Zones). This biostratigraphic scheme was published by Berggren and Pearson (2005). Similarly, revisions to the Antarctic Paleogene biozonation (that was originally introduced by Stott and Kennett, 1990) were deemed necessary, mainly because of new discoveries arising from recent drilling in the Southern Ocean. These are the so-called 'AP- for Antarctic Paleocene' and 'AE - for Anarctic Eocene' Zones of Huber and Quillévéré (2005). An abbreviated discussion of E-zone and AE-zonal schemes is given in Chapters 2 and 3.

TAXONOMIC AND PHYLOGENETIC PHILOSOPHY OF THIS WORK

During the gestation period of this work, a revolution in the understanding of the species-level biology of modern planktonic foraminifera has arisen through genetic sequencing studies of their ribosomal RNA genes (Darling and others, 1996, 1997, 2000, 2004), Huber and others (1997), De Vargas and Pawlowski (1998), De Vargas and others (1999, 2001, 2002). It has become apparent that many modern 'traditional' species-level taxa often encompass several distinct genetic variants that may represent cryptic genotypes with substantial divergence ages from one another (based on estimates of the molecular clock). Sometimes, when these genetic variants have been identified, it has then been possible to recognize subtle morphological or behavioral differences between them (Huber and others, 1997, De Vargas and others, 2001, Kucera and Darling, 2002). There is no reason to think that Eocene planktonic foraminifera would have been any different in this respect. We have therefore been forced to re-evaluate what is signified by the Linnean rank of species as employed in our paleontological taxonomy.

The taxa in this work are regarded strictly as morphotaxa, which are recognized using the primary criterion of morphological similarity to their respective holotypes, irrespective of the stratigraphic level in which they occur. This is necessary to avoid circular reasoning in biostratigraphy; it is also the practical outcome of applying the rules of the ICZN to the fossil record in the absence of behavioral information about the species in question. In making our taxonomy, we have aimed for morphological subdivision that is as fine as possible, provided that the differences between taxa must be readily communicable between workers and explicable using SEM plates and descriptions. When we have observed substantial variation within a species-level taxon, as is frequently the case, we have attempted to illustrate it by selecting representative specimens for the plates and describing the variability.

The species concept employed here can be envisioned using the concept of a notional multidimensional morphospace. Given a single sample or time plane, the species-level taxa are intended, as far as possible, to correspond to islands in morphospace that are separated from other such islands (i.e., other morphospecies) by empty space (Pearson, 1998a). We acknowledge that such taxa may contain substantial cryptic or semi-cryptic diversity that further studies, especially through biogeographic and morphometric work, may reveal. However we also note that many of our morphospecies have clear, well-defined extinction levels, with no apparent reduction in the degree of morphologic complexity in the immediately preceding horizons. This suggests that some of the cryptic genetic diversity that has been discovered in modern planktonic foraminifera may either be at the subspecies level or, in the long term, tend to become re-sorted and assimilated by hybridization. Thus the traditionally recognized 'lineages' of descent in planktonic foraminifera may still approximate to the 'evolutionary species' concept as classically understood (e.g., Simpson, 1953).

Given the dense fossil record and the wide geographic sampling that is available, paleobiologists are increasingly using planktonic foraminifera to investigate evolutionary patterns and processes. This has inevitably included studies of Eocene species (Banner and Lowry, 1985; Corfield and Granlund, 1988; Collins, 1989; Norris, 1996; Kelly, 1999; Kelly and others, 2001; Coxall and others, 2000, 2003; Norris and Nishi, 2001; Quillévéré and others, 2001, 2002). Morphometric studies have often revealed gradual transitions between morphospecies, such that although populations from different stratigraphic levels may be clearly distinct, at intervening levels a full intergradation between them can be observed. Even in cases that have at one time been regarded as exemplifying the punctuated equilibrium pattern of evolution, detailed study has revealed transitional forms at the appropriate stratigraphic level (Coxall and others, 2003). It is inevitable in such instances that the typological approach to taxonomy, which we must necessarily apply, will lead to the arbitrary subdivision of populations along the stratigraphic, or time, dimension.

This dilemma can be illustrated by taking, as an example, the middle and upper Eocene morphospecies *Turborotalia frontosa* and *T. cunialensis*, which are very different in general test morphology, but are observed to intergrade through *T. pomeroli*, *T. cerroazulensis* and *T. cocoaensis* (see Chapter 15, this volume). Other morphotaxa also intergrade with *T. pomeroli* in the middle Eocene, becoming subsequently more distinct in the upper Eocene and Oligocene, namely *T. altispiroides*, *T. increbescens* and *T. ampliapertura*. These various species have different well-defined extinction levels. Given this apparent gradual evolution among populations near the time of their origin, we cannot adopt a policy of synonymizing all species that are found to intergrade with one another at some or other level, or even regarding them as subspecies of one another (e.g., Toumarkine and Bolli, 1970). Taken to its extreme, if we had complete gradation and complete knowledge of the fossil record, such an approach would lead us to subsume all species into one!

A corollary of the typological species concept used here is that the chronostratigraphic range of a given morphospecies represents the total amount of time in which its sector of morphospace was occupied (Pearson 1998a). The first appearance of a morphospecies in the fossil record may represent an evolutionary branching event or a gradual transition (pseudospeciation) from an earlier form. Similarly a last occurrence datum may represent a true biological extinction or the pseudoextinction of a morphospecies by anagenesis (Pearson and Chaisson, 1997; Pearson, 1998a). These important distinctions in the underlying process are not made in the phylogenetic range-charts included in this volume, hence one cannot necessarily derive 'speciation rates', 'extinction rates' etc. from the data we present, although the data will of course be useful for deriving some of the major patterns of evolution in the group.

Since the 1950s, workers have striven to piece together the phylogeny of planktonic foraminifera by careful attention to stratigraphically ordered samples, in effect following the evolutionary lineages through the sediment record (see McGowran, 2005, for a review). This approach has been called stratophenetics (Gingerich, 1979), at least when it is backed up by quantitative morphometric data. It can, of course, lead to error, when species with similar morphologies are confounded with one another, and it is particularly liable to the criticism when 'back-of-the-envelope' phylogenies are presented with (seemingly) little objective data provided in their support. The approach does, however, play to the strengths of the planktonic foraminiferal record, which is a dense, stratigraphically ordered one showing an overwhelming preponderance of gradual evolution. Hypotheses of ancestry and descent, as are presented here in the many phylogenetic range-charts, can be falsified by new detailed study.

Some advocates of the cladistic method have been outspoken in their criticism of this approach (Padian and others, 1994). To the hard-line cladist, stratigraphic information contains no information of relevance in reconstructing phylogeny, which can only be achieved through application of strict phylogenetic systematic methods (generally parsimony) to matrices representing the distribution of characters among the set of taxa in question (Siddall, 1998). The phylogenetic efforts of micropaleontologists are sometimes represented as a lingering residue of old, pre-cladistic practice (McLeod, 1999). On the whole, however, we find that planktonic foraminifera are not optimal for cladistic analysis, inasmuch as their taxonomy is based on frustratingly few discrete, unlinked, and objectively recognizable morphocharacters, the number of species is quite large (especially if one does not restrict the analysis to certain time intervals) and homeomorphy is rampant. Cladistic analyses make no use of the large population sizes and time-ordered sequences that have traditionally been so useful in establishing lines of ancestry and descent (e.g., Subbotina, 1953; Bolli, 1957; Blow and Banner, 1962; Berggren, 1968; McGowran, 1968; Bolli, 1972, Blow, 1979, Premoli Silva and Boersma, 1989; Pearson, 1993, 1998c; Coxall and others, 2000, 2003). Many morphocharacters used in cladistic analysis of planktonic foraminifera are redundant in the sense that they express variations of the same feature; they can be little more than descriptions of various test features from different views, for instance of a chamber or coil. These subjective morphocharacters will often overly emphasize a single feature and skew the analysis to an erroneous conclusion. Furthermore, a single morphocharacter such as a spinose, nonspinose, or microperforate wall is enough by itself to separate distinctive groups of taxa, but is subsumed in cladistic analysis to relative obscurity. These are the practical reasons that we present non-cladistic phylogenies in this work.

With regard to the higher taxonomy, we have adopted the strict criterion that all taxa must be either monophyletic or paraphyletic according to our phylogeny. This excludes the use of polyphyletic morphotaxa (as used, for example, by Blow, 1979). In this way the higher taxa accord as closely as possible to natural groups. We acknowledge that the Family and Genus categories are intrinsically arbitrary, but can nevertheless be used to convey useful information. We have used the Family level to indicate groups that are united by possessing a particular wall structure. As is traditional in foraminiferal studies, the Genus is used to represent, as far as possible, groupings of species that are united by distinctive test architecture (e.g., a particular coiling geometry, apertural system, or prominent structure such as a keel), even if it is monospecific.

Our insistence that no higher taxon is polyphyletic has, in two instances, forced us to name new genera when, after careful study, a previously united group was found to have had more than one point of origin (these were the splitting of *Morozovelloides*, n. gen. from *Morozovella*, and *Planoglobanomalina*, n. gen. from *Pseudohastigerina*). Several of the genera in our taxonomy are monospecific. One genus (*Pseudoglobigerinella*, n. gen.) was named to recognize the distinctive planispiral test geometry of its only species, *P. bolivariana* and another pre-existing but rarely used genus (*Astrorotalia*) is used to recognize the distinctive keel-spines of its only species, *A. palmerae*.

We have tried hard to use existing names and concepts to represent the species we recognize, even if those names have in some instances been previously little used (e.g., *Subbotina jacksonensis*, *Globigerinatheka korotkovi*, *Clavigerinella caucasica*, *Hantkenina nanggulanensis*, *Morozovelloides bandyi*, *Turborotalia altispiroides*). However we have not shirked from the responsibility of naming new species where necessary. This has generally been for small, cold-water taxa, but we have also described some conspicuous forms that for some reason have simply been overlooked (*Planoglobanomalina pseudoalgeriana* n. sp., *Hantkenina singanoae* n. sp., *Acarinina mcgowrani* n. sp., *Acarinina pseudosubsphaerica* n. sp.). Parts of our taxonomy will be unfamiliar to experienced taxonomists, such as the novel treatment of the *Parasubbotina* - *Paragloborotalia* group, the derivation of *Turborotalia* from *Globanomalina*, and the recognition of genera previously thought characteristic of the Neogene, such as *Globoturborotalita* and *Turborotalita* in the Eocene for the first time. Taxonomic research will of course go on. In particular we are painfully aware that more work is needed on cold water / high productivity assemblages, more test dissections are desirable in some of the more complex groups such as the globigerinathekids, and more precise delimitation of all the main biostratigraphic horizons within astronomically constrained reference sections is needed. By making this work available in a web-based format, we hope to make it both more accessible and amenable to supplement as new knowledge accumulates.

SYNTHESIS OF PLANKTONIC FORAMINIFERAL EVOLUTION IN THE EOCENE

Phylogenetic range-charts for each group are presented and discussed individually in the chapters of this atlas. An overview of the phylogeny and biostratigraphy of the genera is presented in Figure 1.2. A species-level range-chart is given in Figure 1.3. These phylogenetic range-charts help capture the main features of evolution in the group in the Eocene.

By the beginning of the Eocene, the planktonic foraminifera had already enjoyed about 10 million years of evolutionary recovery from their near extinction at the end of the Cretaceous Period. From a few small survivor species in the earliest Paleocene, substantial diversity had evolved, as described in the *Atlas of Paleocene Planktonic Foraminifera* (Olsson and others, 1999). The upper sun-lit parts of the water column were dominated by morozovellids and acarininids, with rarer

Figure 1.2. Stratigraphic ranges and inferred phylogenetic relationships of Eocene genera discussed in this atlas.

Figure 1.3. Stratigraphic ranges of Eocene species discussed in this atlas (parts 1 to 3).

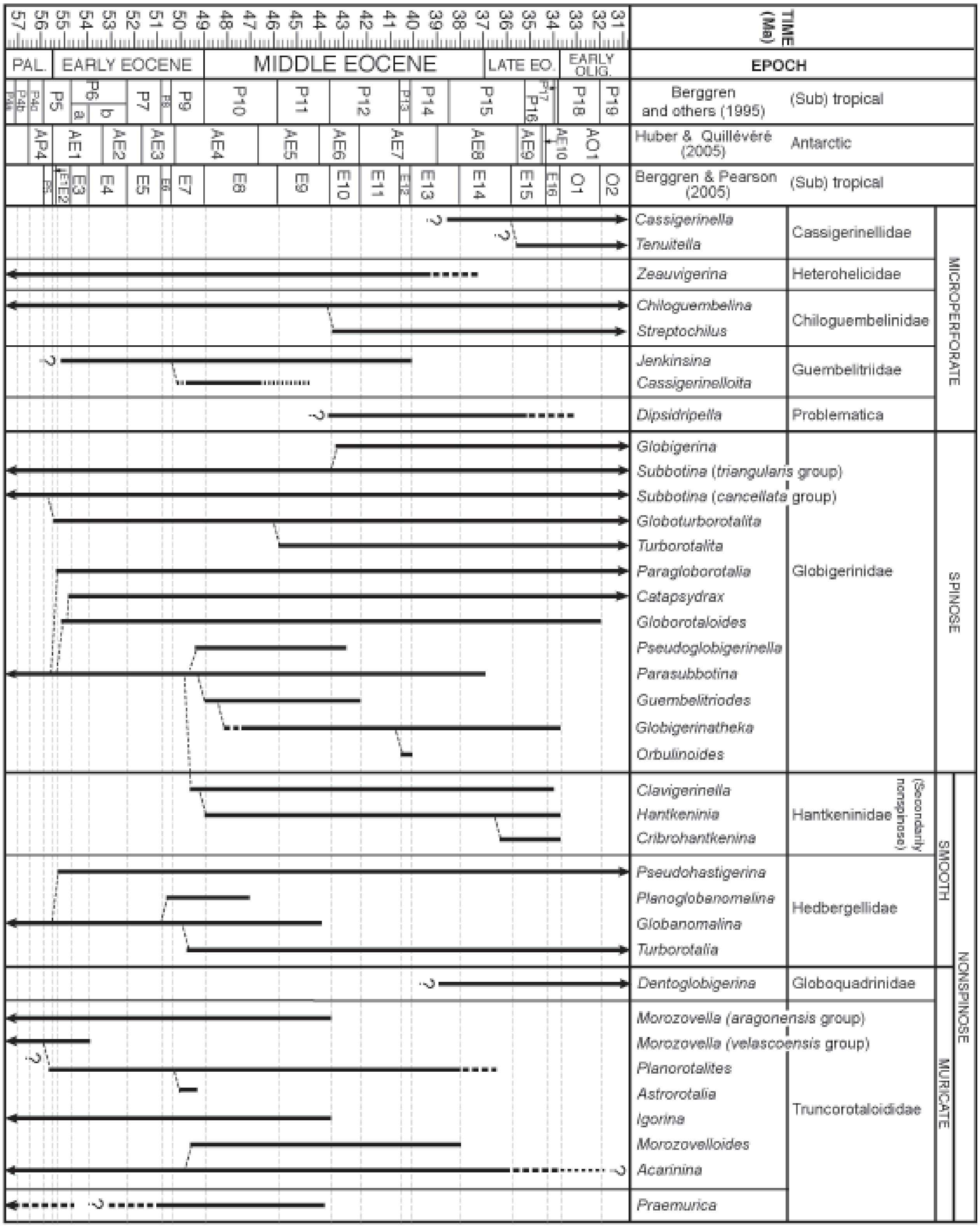
TIME (Ma)
57 56 55 54 53 52 51 50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31
EPOCH
PAL.
EARLY EOCENE
MIDDLE EOCENE
LATE EO.
EARLY OLIG.
P4a P4b P4c P5 P6 a b P7 P8 P9 P10 P11 P12 P13 P14 P15 P16 P17 P18 P19
Berggren and others (1995)
(Sub) tropical
AP4 AE1 AE2 AE3 AE4 AE5 AE6 AE7 AE8 AE9 AE10 AO1
Huber & Quillévéré (2005)
Antarctic
E1 E2 E3 E4 E5 E6 E7 E8 E9 E10 E11 E12 E13 E14 E15 E16 O1 O2
Berggren & Pearson (2005)
(Sub) tropical
Cassigerinella
Tenuitella
Cassigerinellidae
Zeauvigerina
Heterohelicidae
Chiloguembelina
Streptochilus
Chiloguembelinidae
Jenkinsina
Cassigerinelloita
Guembelitriidae
Dipsidripella
Problematica
MICROPERFORATE
Globigerina
Subbotina (triangularis group)
Subbotina (cancellata group)
Globoturborotalita
Turborotalita
Paragloborotalia
Catapsydrax
Globorotaloides
Pseudoglobigerinella
Parasubbotina
Guembelitriodes
Globigerinatheka
Orbulinoides
Globigerinidae
SPINOSE
Clavigerinella
Hantkeninia
Cribrohantkenina
Hantkeninidae
(Secondarily nonspinose)
Pseudohastigerina
Planoglobanomalina
Globanomalina
Turborotalia
Hedbergellidae
SMOOTH
Dentoglobigerina
Globoquadrinidae
NONSPINOSE
Morozovella (aragonensis group)
Morozovella (velascoensis group)
Planorotalites
Astrorotalia
Igorina
Morozovelloides
Acarinina
Truncorotaloididae
MURICATE
Praemurica
?

FIGURE 1.2

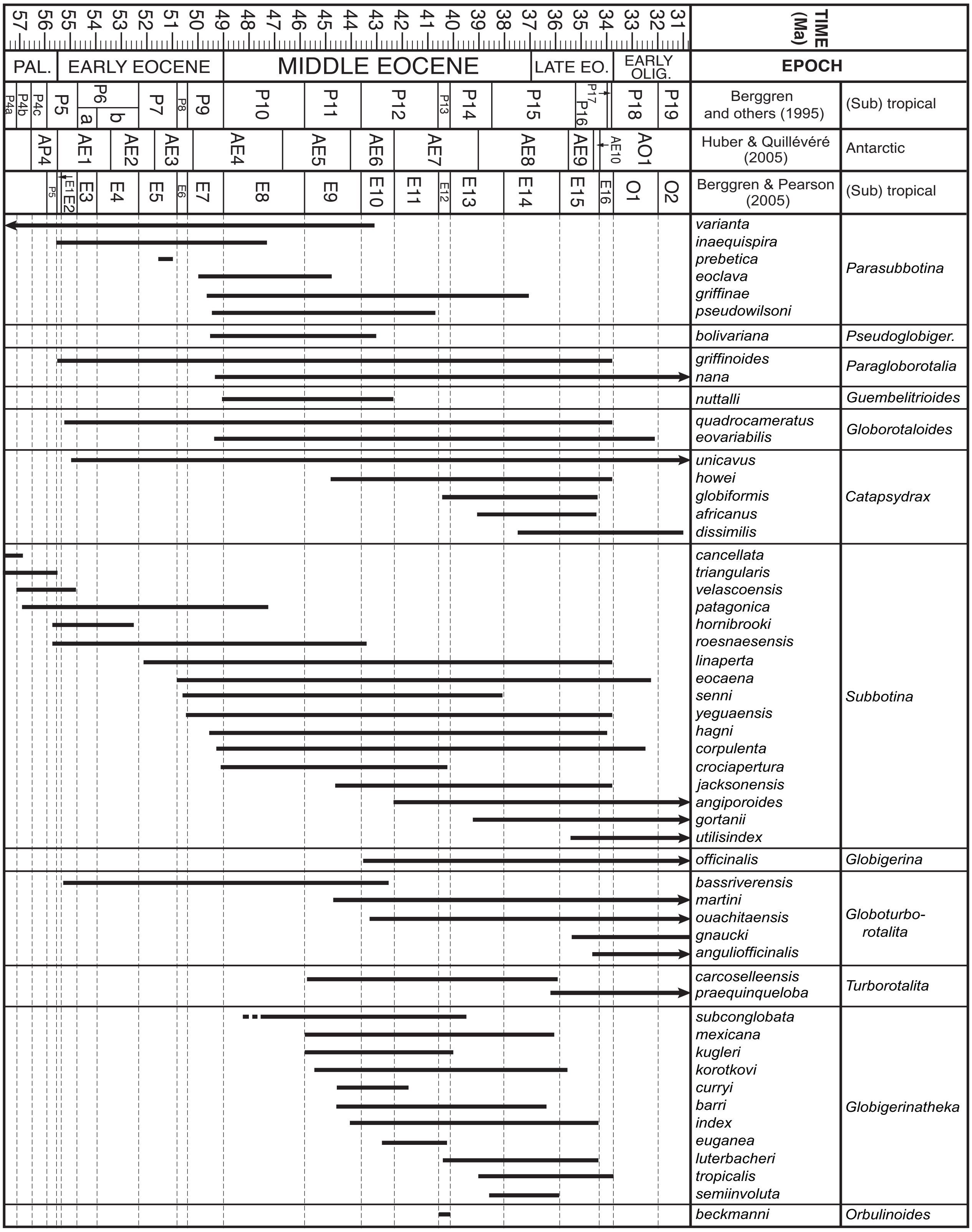

FIGURE 1.3 (PART 1)

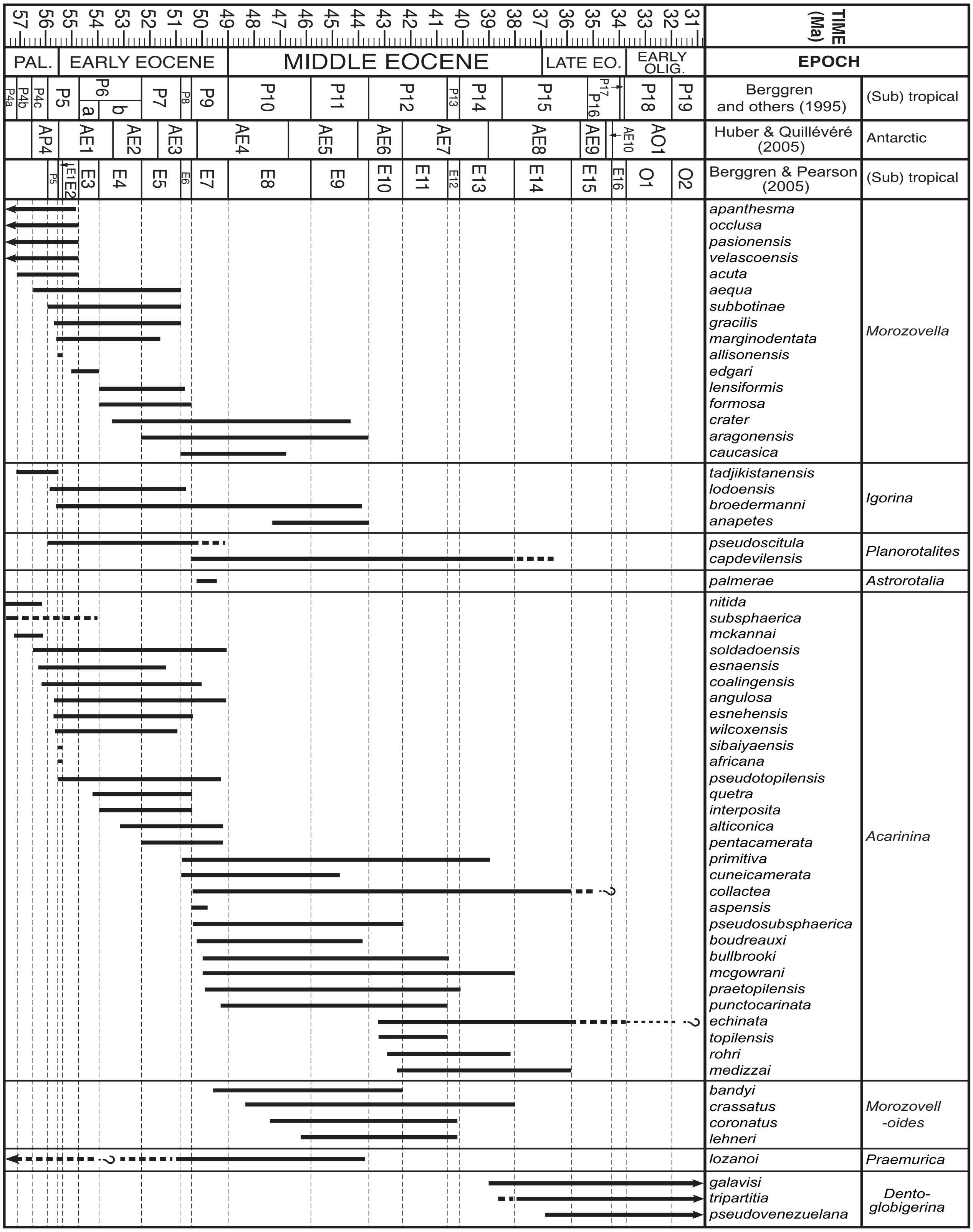

FIGURE 1.3 (PART 2)

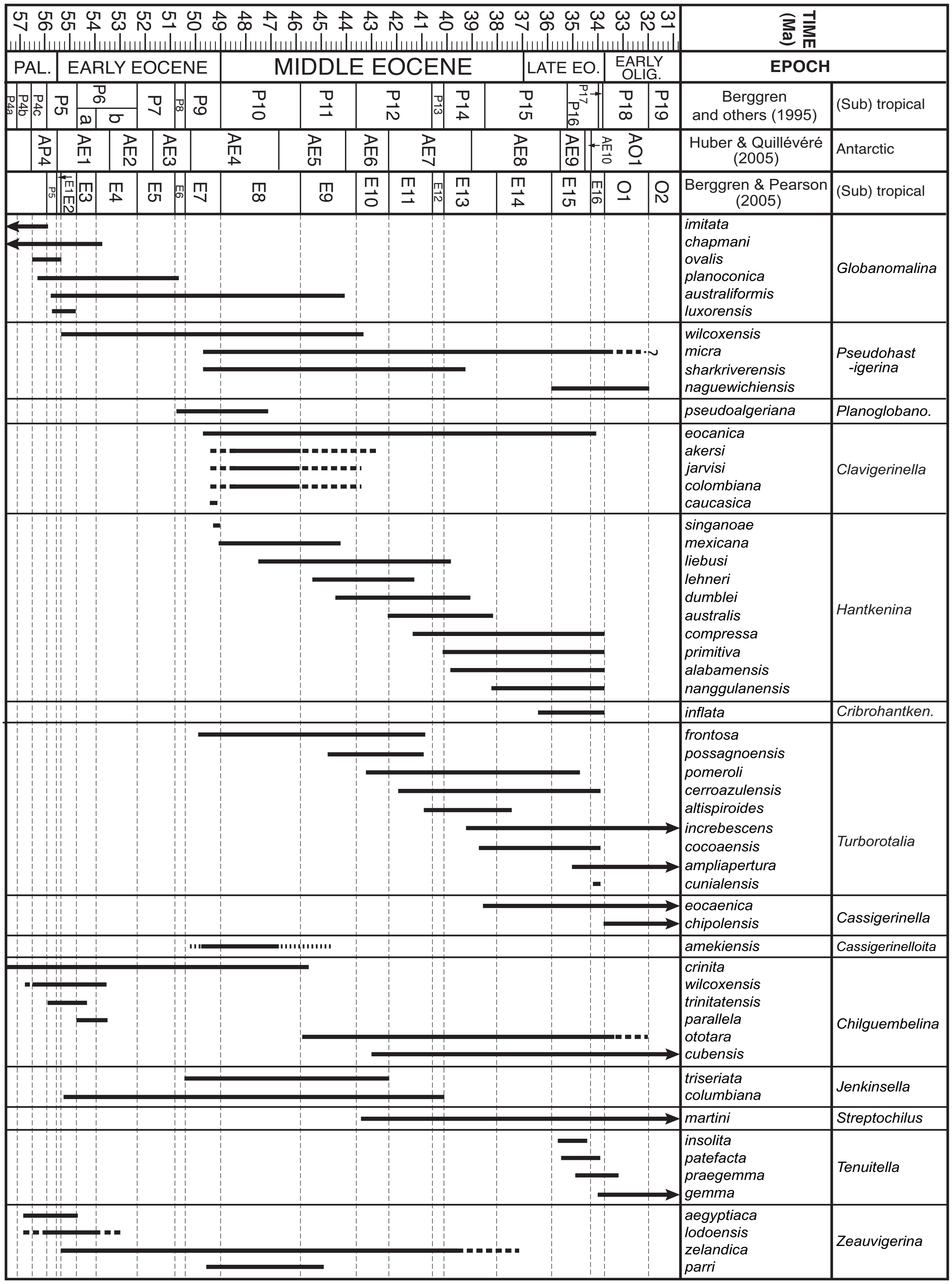

FIGURE 1.3 (PART 3)

igorinids, all of which probably lived in symbiotic association with photosynthetic dinoflagellates. The deeper thermocline environments hosted the subbotinids (a group with true spines) and the smooth-walled globanomalinids. Less common in oligotrophic settings, but diverse in more marginal and shelf environments, were various microperforate genera and the spinose parasubbotinids. The diversity of these late Paleocene assemblages does not rival the pre-extinction communities of the latest Cretaceous, but it is nevertheless substantial, and late Paleocene assemblages include some large and ornate species.

The Eocene Epoch, as now defined, began in a period of environmental crisis. According to the current state of understanding, the already warm, greenhouse world of the late Paleocene was suddenly and dramatically warmed further by the catastrophic release of large quantities of methane from sub-seafloor reservoirs (Dickens and others, 1995; Zachos and others, 2005). In response, the carbonate compensation depth in the ocean shoaled considerably, so that many sections across the Paleocene/Eocene boundary are condensed and dissolved. The disruption to the carbon cycle is witnessed everywhere by a sudden shift towards more negative carbon isotope ratios, which is used to correlate the Paleocene / Eocene boundary worldwide.

The abrupt changes in ocean circulation that occurred at the Paleocene / Eocene boundary seem to have caused the extinction of many species of benthic foraminifera. The plankton were also affected, but to a lesser extent. There were no major extinctions of pre-existing forms, but the event seems to have acted as a spur for evolutionary innovation, in both the short and long term. The event itself is characterized by the transient appearance and extinction of several short-lived 'excursion species' and the extra-tropical expansion of low latitude species into the high southern latitudes. In the longer term, it seems that several major groups appeared either during or shortly after the Paleocene / Eocene boundary event.

The planispiral pseudohastigerinids and the more inconspicuous (but later significant) globoturborotalitids make their first appearances in the earliest levels of the Eocene. There was also substantial diversification in the acarininids, parasubbotinids and other groups. The extinction of the abundant, large and ornate *Morozovella velascoensis* group (including the related species *M. acuta*, *M. apanthesma*, *M. pasionensis* and *M. occlusa*) occurred in the earliest Eocene, but other species in the genus evolved fairly rapidly thereafter. The burst of evolution in the morozovellids at the species level in the early Eocene makes them very useful for biostratigraphic correlation in that interval.

Despite these innovations, the diversity and morphological disparity of the early Eocene still did not match that of the latest Cretaceous. However, a second phase of Eocene diversification occurred in the latest part of the early Eocene (around Zone E7, about 49 to 50 million years ago), and subsequent assemblages certainly approached that mark. Around this time several genera first appeared, including *Turborotalia*, *Astrorotalia*, *Catapsydrax*, *Pseudoglobigerinella* n. gen., *Morozovelloides* n. gen., *Clavigerinella* and *Hantkenina*. Most of these genera are characterized by ornate and distinctive tests. Some of them are monospecific, but others continued to diversify throughout much of the Eocene. There was also substantial turnover at the species level in *Acarinina*, *Subbotina* and other genera at this time.

The peak of morphologic diversity in the group occurred in the early part of the middle Eocene, when the important genus *Globigerinatheka* evolved. The extinction of true *Morozovella* (i.e., the last surviving species, *M. aragonensis*) and *Igorina* at the end of biochron E9 were the first of several waves of extinctions by which many of these disparate elements were lost. From this point on, the major biostratigraphic events were predominantly extinctions rather than originations, although there are of course exceptions.

The highly diverse assemblages of the middle part of the middle Eocene illustrate a broad range of ecological adaptations comparable to that seen in modern communities. In the surface mixed layer of the oligotrophic oceans a variety of photosymbiotic groups were very abundant, including various morozovelloids, acarininids and igorinids, which were descendants of the surface dwellers of the Paleocene. Unlike the Paleocene, however, there were also abundant spinose forms in the surface ocean, namely the globigerinathekids and *Guembelitrioides*. These can be considered closely analogous to modern species of *Globigerinoides,* which occupy similar habitats today and have a very similar spinose wall texture. The deeper thermocline environments were dominated by the subbotinids, parasubbotinids, turborotaliids and hantkeninids, although the latter two groups seem to have evolved a shallower depth preference as the Eocene progressed.

The diversity of planktonic foraminifera was lower in the higher latitudes and in more eutrophic settings, as it is today. Upwelling environments seem to have been dominated by a few species of *Parasubbotina*, *Clavigerinella* and *Pseudoglobigerinella* n. gen. This distinctive upwelling assemblage has been recorded from coastal zones in the Americas and off Africa, above certain seamounts, and in the Pacific equatorial divergence.

Major groups to disappear in the middle and late Eocene include *Morozovelloides* n. gen., most *Acarinina*, *Planorotalites*, *Globigerinatheka*, *Clavigerinella*, *Parasubbotina*, the *Turborotalia cerroazulensis* lineage, and then, at the Eocene / Oligocene boundary itself, *Hantkenina* and *Cribrohantkenina*. This sequential diminution of diversity and disparity in planktonic foraminiferal assemblages may have been related to progressive global cooling that eventually led to the establishment of a permanent ice cap on Antarctica in the earliest Oligocene epoch (Keller and others, 1992). An alternative view is to consider the diversity history more as a random walk, with extinctions happening to predominate for a while, in the way that gambler might have a run of bad luck following a winning streak. Whatever view is nearer the truth, it is clear that Oligocene assemblages are less disparate, morphologically, than Eocene ones, and probably less diverse in terms of life habit as well, although renewed study is needed.

The middle and upper Eocene history of the group is not just a case of extinction, however. Several groups that were to be subsequently important made their first appearances at this time, but in a relatively inconspicuous way. These include *Globigerina*, *Dentoglobigerina, Turborotalita*, and the microperforate tenuitellids and related forms. By the early Oligocene, the stage was set for a new phase of evolution in the planktonic foraminifera. Fluctuations in ice volume, sea level and the frontal arrangement of the oceans began to exert more of an influence, leading to fragmentation of the habitats (Boersma and others, 1987). Surviving groups such as the dentoglobigerinids, globigerinids and globoturborotalitids diversified substantially, eventually leading to the direct ancestors of part of the modern biota. However, many of the major groups of the Oligocene were based on generalized (at least in comparison to the Eocene assemblages), globular test morphologies. The task of unravelling their complexities is deferred to a future *Atlas of Oligocene Planktonic Foraminifera*.

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