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ANALYSIS OF THE TAXONOMIC, BIOSTRATIGRAPHIC AND EVOLUTIONARY RELATIONSHIPS OF SPECIES OF THE CALCAREOUS NANNOFOSSIL GENUS *CYCLICARGOLITHUS* (BUKRY, 1971) FROM THE UPPER EOCENE AND OLIGOCENE OF THE NORTH ATLANTIC

CONTENTS

Key words: Biometrics, calcareous nannofossils, Cyclicargolithus, evolution, biostratigraphy, Eocene, Oligocene, North Atlantic.

ABSTRACT

The taxonomic status, evolution, and biostratigraphic utility of the calcareous nannofossil genus *Cyclicargolithus* was studied using biometric and multivariate analyses of sample populations from a wide geographic distribution in upper Eocene to Oligocene sediments from six DSDP/ODP sites in the North Atlantic. No significant morphologic changes occur between sample populations of varying size, age, and geographic distribution. Furthermore, no cladogenetic event was recognized within this genus, nor was any directional phyletic trend seen. Significant overlaps in morphological parameters, and a lack of clear distinguishing features between various species of *Cyclicargolithus* indicate that, within the upper Eocene to Oligocene, this genus consists of only one morphologically variable species. A general increase in abundance of larger forms of *Cyclicargolithus* through the Oligocene does not correlate closely over wide geographic distances, nor does it correlate with the first occurrence of *Sphenolithus ciperoensis* in any sections studied. The nature of evolutionary development of *Cyclicargolithus* through the Oligocene can be explained simply as a pattern of increased variance in overall size.

RIASSUNTO

Tassonomia, evoluzione e valore biostratigrafico dei nannofossili calcarei appartenenti al genere *Cyclicargolithus* sono stati studiati mediante analisi biometriche e multivariate su campioni di popolazioni di ampia distribuzione geografica in sedimenti dall'Eocene superiore all'Oligocene di sei località DSDP/ODP nell'Atlantico settentrionale. Non si verificano cambiamenti morfologici significativi fra campioni di popolazioni diversificate per dimensione, età e distribuzione geografica. Inoltre, all'interno di questo genere non è

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stato evidenziato nessun evento cladogenetico, né tendenze filetiche orientate. Consistenti sovrapposizioni dei parametri morfologici e mancanza di chiari caratteri distintivi fra le varie specie di *Cyclicargolithus* indicano che nell'Eocene superiore-Oligocene questo genere consiste di una sola specie morfologicamente variabile. Un generale aumento di forme grandi di *Cyclicargolithus* durante l'Oligocene non è strettamente correlabile su ampie distanze geografiche e non si correla in nessuna delle sezioni studiate con la prima comparsa di *Sphenolithus ciperoensis*. La natura dello sviluppo evolutivo di *Cyclicargolithus* nell'Oligocene può essere spiegata semplicemente nell'ambito di un alto grado di variabilità morfologica delle dimensioni.

INTRODUCTION

The concept of a fossil species is a subjective idea based on the particular need or use of the paleontologist that erects it (SHAW, 1969; BLUEFORD, 1984). The basis for recognition of fossil species is morphology. Primarily from the range of variation of morphologic features and their stratigraphic and paleogeographic distributions, inferences are made concerning fossils' systematic status, paleobiology, paleoecology, evolutionary development, and diversity. How morphologic features are synthesized into a species concept can affect the other inferences (SHAW, 1969) as well as be affected by them (BLUEFORD, 1984). Biological information from studies of living organisms is also important in determining species, however such information is not always available for or directly applicable to the study of fossil organisms.

In calcareous nannofossils, a single structural plan based on the crystallographic orientation and number of cycles of crystallites can display a wide range of forms based on differences in features such as length, width, thickness, roundness, size of central hole, and number of rays, to name a few. In other words, these forms are variations on a structural theme, and do not represent ultrastructural changes, as would be seen between genera or higher taxonomic levels. Common practice among nannofossil paleontologists is to elevate many of these forms to species status mainly because they appear to have distinct biostratigraphic ranges. The genera *Nannoconus, Reticulofenestra,* and *Cyclicargolithus* are examples of this (PERCH-NIELSEN, 1985a, b). In many cases an assessment of intra-and interspecific variability, ecophenotypic and evolutionary change has not been adequately made.

Furthermore, distinctions between species are often not stated as clear lines of separation, but are based instead on degrees of variation, such as 'larger than', 'rounder than', or 'has a smaller hole'. HAQ and BERGGREN (1978, p. 1190) provide an example of how a 'biostratigraphic' species concept may develop. They recognized three "clearly distinct" varieties of *Reticulofenestra pseudoumbilicus*, based on "larger form", "smaller central opening", "narrower collar", etc. They suggested that one variety "may prove to be a distinct species" because it has a slightly different range than the other varieties in just one out of eight cores studied. The lack of clarity in taxonomic distinctions between closely similar 'biostratigraphic' species can negatively affect their biostratigraphic utility, as well as hamper the study of nannofossil evolutionary mode and tempo, diversity, and paleoecology. BLUEFORD (1984), however, in discussing the effects of different possible reproductive modes on radiolarian evolution and taxonomy, suggested that maximum information from a species can be derived if "the characters that define the species reflect biological systems, environmental conditions, and biostratigraphic variations". Likewise, LAZARUS (1983) stated that "micropaleontologists need to place a greater emphasis on paleobiogeographic analysis, on taxonomic analysis and the quantification of morphologic change, and on the collection of species-specific paleoecologic information" in order to test biological models of evolution.

One commonly used method for gaining such an understanding of paleobiological relationships is to biometrically analyze lineages of fossil populations. This approach has been used effectively to address taxonomic, biostratigraphic and evolutionary questions in microfossil groups such as planktonic foraminifers (ARNOLD, 1983; MALMGREN *et al.,* 1983; NEDERBRAGT and VAN HINTE, 1987; HUNTER *et al.,* 1988), conodonts (MURPHY and SPRINGER, 1989), radiolarians (LAZARUS, 1983, 1986; KELLOGG, 1976, 1980, 1983), and calcareous nannofossils (BACKMAN, 1980; BACKMAN and HERMELIN, 1986). Until recently, this approach has not been commonly used in the study of calcareous nannofossils, possibly because of their extremely small size (roughly an order of magnitude smaller than adult planktonic foraminifers). Also, such studies have mainly concentrated on stratigraphic changes in fossil morphologies, and have had limited geographical coverage.

I have attempted in this paper to document the temporal and spatial variations in morphology of coccoliths from the genus *Cyclicargolithus*. This group has several attractions as the subject of a biometric study: it has a relatively simple and easy to measure morphology; it is abundant, geographically widespread and long-ranged within upper Paleogene marine sediments; it has at present six species assigned to it whose taxonomic distinctions, biostratigraphic ranges, and evolutionary relationships are not clear (see discussion below); it provides an opportunity to study the mode of evolution of a group of nannofossils. One limiting factor on the last point is that coccoliths represent only parts of the coccosphere of a coccolithophore, as compared to the entire test of a planktonic foraminifer. Thus, without studies of entire coccospheres, conclusions on modes of evolution must be limited. Nevertheless, the analysis of individual coccoliths is a necessary starting point.

It is also necessary to state my own concepts of species and speciation, in order to make my conclusions more clear. They are not based simply on the biostratigraphic value of a form, but rather follow the usage of LAZARUS (1983), who in turn followed the definitions of SIMPSON (1961) and ELDREDGE and CRACRAFT (1980). To summarize, a species is a morphologically continuous, separately evolved lineage, which can be distinguished from other morphologic clusters, has a continuous geographic and stratigraphic range, and displays a cladogenetic origin.

The objectives of this study were to: (1) quantitatively delineate the morphologic boundaries and range of variation of the genus and its constituent species, (2) determine whether the species display separate morphologic clusters and phyletic or cladogenetic changes, (3) assess the taxonomic validity of the species based on the results of the first two objectives, (4) tie the results to chronostratigraphy as much as possible, in order to test the biostratigraphic utility of the genus, and (5) determine the extent of ecophenotypic variations through time, and its affect on taxonomy, biostratigraphy, and evolutionary patterns.

Cyclicargolithus is most abundant in calcareous nannofossil assemblages of Oligocene age. Therefore this study concentrates mainly on Oligocene populations from the North Atlantic. However, additional samples of upper Eocene and Miocene age, samples of type material from outside the North Atlantic, and published photo and electron micrographs of holotype and paratype specimens were also analyzed. A synopsis of the genus and its constituent species is found below.

DESCRIPTION OF THE GENUS *CYCLICARGOLITHUS*

Cyclicargolithus (BUKRY, 1971) includes circular to subcircular placoliths with shields connected by a central tube that surrounds a central hole, and whose distal shield, in plan view, is birefringent under cross-polarized light. It was erected to distinguish such placoliths from those whose distal shields are non-birefringent under cross-polarized light (*Calcidiscus, Coccolithus*). BUKRY (1971) stated that the central tube may or may not be open. He did not state in what way the tube may be closed-whether the collar (wall) of elements (crystallites) constricts to close the central hole, or whether the central hole is filled with a structure, such as a grill or plug. The distinction between *Cyclicargolithus* and the related genus *Reticulofenestra* is made primarily on the lack of a central grill in the former and the presence of such in the latter (PERCH-NIELSEN, 1985b), as well as larger relative hole sizes in *Reticulofenestra* (OLAFSSON, 1989). Although some authors do not recognize these features as generic level distinctions, for the purpose of this study I regard the lack of a central grill (an ultrastructural difference) as a generic distinction, and therefore use *Cyclicargolithus*.

A summary of the ultrastructure of *Cyclicargolithus* can be obtained from the descriptions and electron micrographs of several species now assigned to the genus. The wall consists of broad, lath-shaped or plate-like elements forming a collar around the central hole (BLACK, 1964; WISE, 1973). The distal shield consists of narrow, slightly imbricate elements whose sutures extend outward in a radial pattern, and which may gyre slightly in a counterclockwise direction. The smaller proximal shield has roughly the same number of elements as the distal, with radial sutures except near the center where they bend sharply towards the pore (BLACK, 1964; ROTH and HAY in HAY *et al.*, 1967). A graphical representation of the ultrastructure of *Cyclicargolithus* and related genera can be seen in YOUNG (1989).

Six species are presently assigned to *Cyclicargolithus*, and are listed below in chronological order of description, along with their distinguishing features.

Cyclicargolithus pseudogammation (BOUCHÉ, 1962) BUKRY (1973) encompasses small (5-7 μm) subcircular to slightly elliptical placoliths. One shield is smaller and thicker than the other. A distinct swastika pattern under crossed nicols makes it similar to ?*Toweius gammation*, though often the pattern is not as distinct as in the latter species. It differs from ?*T. gammation* by being less circular, and by having two shields of unequal size (Bouché, 1962). *C. pseudogammation* was described from the lower Lutetian (lower middle Eocene).

Cyclicargolithus marismontium (Black, 1964) Perch-Nielsen (1985b) is elliptical to nearly circular, with a central pore that is broadly elliptical in shape. The size range of the type material is from 5.0-8.0 µm, and hole size ranges from 1.2-2.5 µm. The number of shield elements ranges from 38-65. *C. marismontium* was described from the middle Eocene.

Cyclicargolithus hesslandii (Haq, 1966) Gheta (1982) is subcircular to circular with three(?) concentric rings of crystal rays. It has a small central opening, and varies from 3.5 to 9.1 µm in size. According to Perch-Nielsen (1985b, p. 509) it is "difficult to distinguish from *Cyclicargolithus floridanus*, which is generally more subcircular and has a smaller, empty central opening". *C. hesslandii* was described from the upper Eocene.

Cyclicargolithus floridanus (Roth and Hay in Hay *et al.*, 1967) Bukry (1971), the type species for the genus, is broadly elliptical, with a subcircular central hole about one fifth the shorter dimension of the coccolith. The size range is from 3.6-5.0 µm. The number of shield elements ranges from 40-41. According to Roth and Hay (in Hay *et al.*, 1967, p. 445) this species differs from *C. marismontium* by being "more strongly elliptical and (having) a much smaller central hole". *C. floridanus* was described from the Oligocene.

Cyclicargolithus abisectus (Müller, 1970) Wise (1973) is subcircular or broadly elliptical with a simple round opening. The size range is from 8.8-10.6 µm, and the number of shield elements ranges from 50-55. It differs from *Cyclococcolithus neogammation* (junior synonym of *C. floridanus*) by having a large central opening (Müller, 1970). *C. abisectus* was described from the Oligocene.

Cyclicargolithus bukryi Wise (1973) is distinctly subcircular with a "moderate to wide central area covered or partially covered by lath-shaped plates on the distal side" (Wise, 1973). The size range is from 6.0-8.0 µm, and the number of elements in the shields ranges from 48-54. It differs from *C. floridanus* by "having a distinctly subcircular outline with an eccentricity greater than 1.1" (Wise, 1973, p. 594). *C. bukryi* was described from the lower Miocene.

It is apparent from the descriptions that there are no clear morphologic distinctions between the various species. They are all round to subelliptical, broadly elliptical, or subround, and have round to subround or elliptical central holes. The number of shield elements in each species is similar, with that of *C. marismontium* encompassing them all. The only differences claimed by the authors relate to the eccentricity of the placolith, or the relative size of the central hole. The reported size ranges for the type of each species overlap greatly. Calcareous nannofossils may also be distinguished by their birefringent patterns under cross-polarized light. This optical phenomenon, however, is determined by the ultrastructure and morphology of the nannofossils. Distinctions between the species of *Cyclicargolithus* based on birefringent patterns will be discussed in the taxonomic section below.

The names *C. marismontium* and *C. bukryi* are rarely, if ever used in biostratigraphic studies. Both *C. pseudogammation* and *C. floridanus* have been used to designate forms in the lower to middle Eocene (Barron *et al.*, 1984, Monechi and Thierstein, 1985, and Valentine, 1987, for the former name; Proto Decima *et al.*, 1978, Siesser, 1983, and Nocchi *et al.*, 1988, for the latter name). In the upper Eocene to Miocene, both *C. floridanus* and *C. hesslandii* have commonly been used to designate forms up to about 9 µm in size. Forms larger than this are commonly assigned to *C. abisectus*, although the basis for distinction of this form by some workers may also rest in its extinction pattern under cross-polarized light. This last species is reported to have a first occurrence datum which approximates the first occurrence of *Sphenolithus ciperoensis* (Martini and Müller, 1986), a nannofossil datum which occurs near the base of the upper Oligocene (Berggren *et al.*, 1985). However, other reports show *C. abisectus* to occur well below the other datum level (Roth, 1970; Parker *et al.*, 1985; Firth, 1989).

STUDY MATERIAL

DSDP Sites 366, 549, 558, and 563, and ODP Sites 628 and 647 were selected for this study in order to obtain broad latitudinal and longitudinal coverage of the North Atlantic (Fig. 1). A list of samples analyzed in this study is found in Table 1. Age control on samples is based upon linear interpolation between magnetostratigraphic reversal boundaries and/or upon best-fit lines between integrated biostratigraphic datums (Fig. 2, Tab. 2).

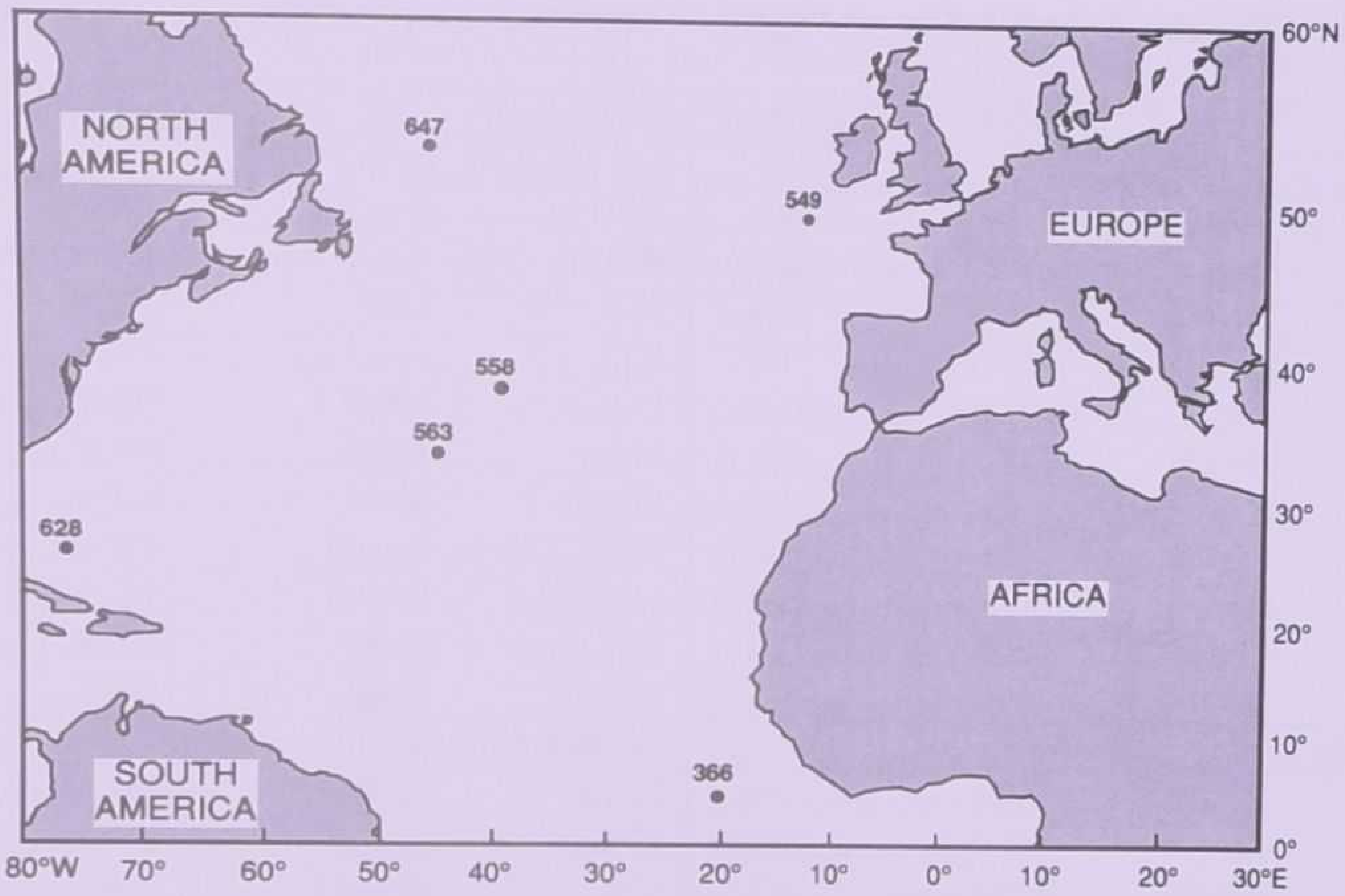

FIG. 1 - Map of North Atlantic Ocean showing location of Sites 647, 549, 558, 563, 628, and 366.

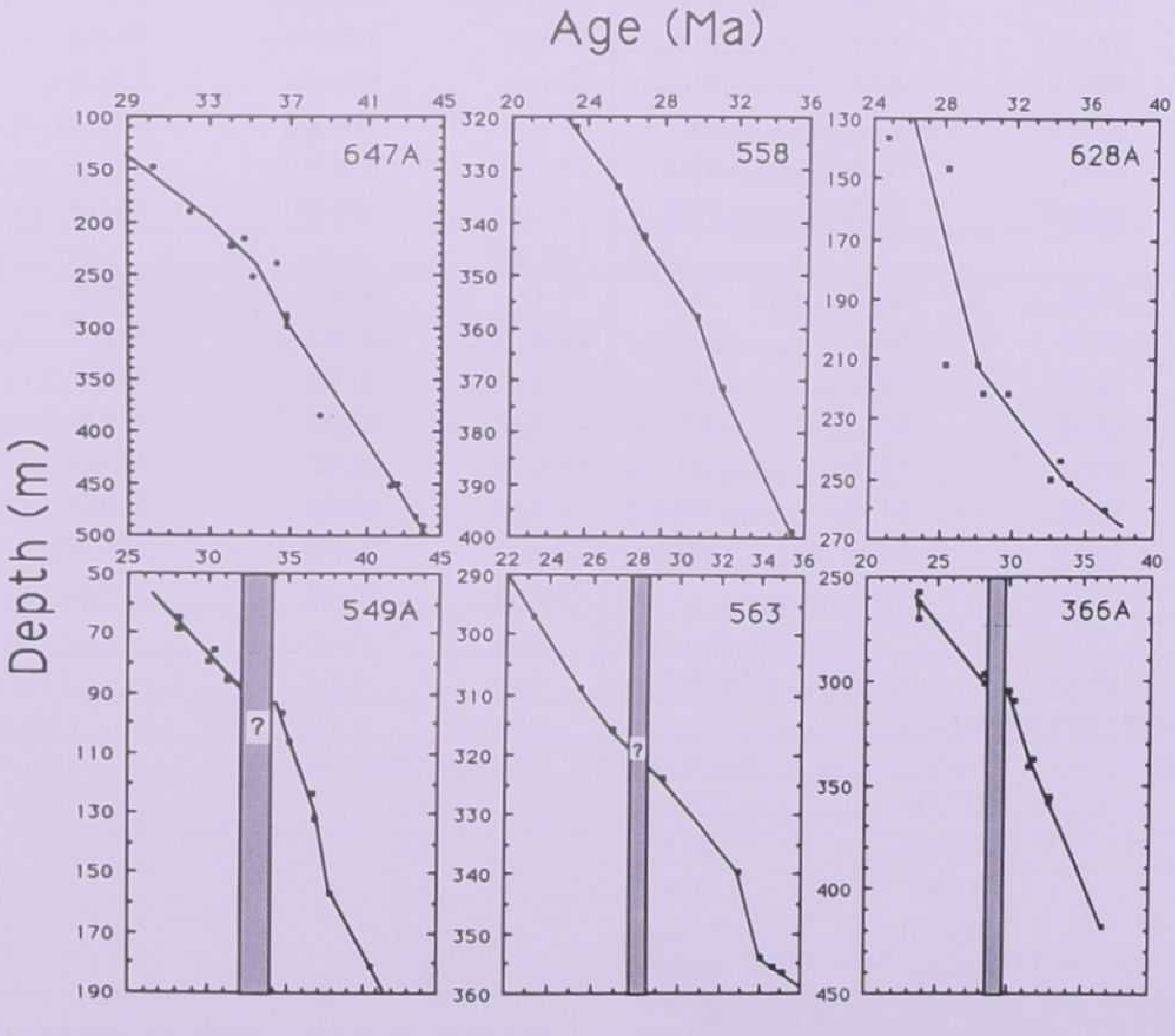

FIG. 2 - Age/depth plots of Holes 647A, 549A, 558, 563, 628A, and 366A. Datums used are listed in Table 2. Shaded regions represent hiatuses or possible hiatuses in the sections.

Table 1 - List of samples, sample depths, and ages of samples analyzed for biometric study of *Cyclicargolithus*

Core-Section,	cm	Depth (m)	Age (Ma)	Core-Section,	cm	Depth (m)	Age (Ma)
Site 647, Hole 647A				Site 366, Hole 366A			
15-1,	68-70	136.1	29.0	28-1,	110-111	255.6	23.4
16-2,	54-59	147.2	29.7	29-1,	114-115	263.6	24.3
17-1,	107-112	155.9	30.4	30-1,	93-94	272.9	25.1
18-1,	70-75	164.8	31.1	31-2,	99-100	284.0	26.3
19-1,	96-100	174.8	31.6	33-2,	100-101	303.0	29.9
20-1,	106-108	184.6	32.5	34-1,	121-122	311.2	30.3
21-1,	13-16	193.2	33.1	35-2,	90-91	321.9	30.8
25-5,	107-110	238.6	35.2	36-2,	99-100	331.5	31.2
27-1,	51-53	250.9	35.6	37-3,	99-100	342.5	31.7
28-1,	105-108	261.2	35.8	38-1,	79-80	348.8	32.1
39-1,	75-77	366.9	39.5	39-1,	79-80	358.3	32.7
Site 549, Hole 549A				Site 628, Hole 628A			
7-1,	100-101	56.5	26.5	16-1,	98-99	137.6	26.2
8-1,	100-101	66.0	28.1	17-1,	99-100	147.1	26.7
9-1,	100-101	75.5	29.7	18-1,	100-101	156.7	27.2
10-1,	100-101	85.0	31.3	19-1,	98-99	166.2	27.7
10-4,	100-101	89.5	32.0	21-1,	98-99	184.2	28.6
11-1,	100-101	94.5	32.6	22-1,	100-101	193.7	29.1
12-1,	100-101	104.0	35.0	23-1,	100-101	203.3	29.6
13-1,	100-101	107.0	35.3	24-1,	100-101	212.9	30.1
14-1,	100-101	112.0	35.6	25-1,	100-101	222.5	31.0
15-1,	100-101	117.0	36.1	26-1,	100-101	232.4	32.5
16-1,	100-101	120.5	36.3	27-1,	100-101	242.0	34.0
24-1,	80-81	132.8	37.2	28-1,	100-101	251.6	35.5
34-1,	100-101	156.5	38.9	29-1,	100-101	261.2	36.9
Site 563				Site 558			
16-1,	52-54	299.5	24.1	19-1,	60-62	329.6	24.8
17-1,	70-72	309.2	25.5	20-3,	60-62	342.1	26.8
18-1,	69-71	318.7	28.0	21-1,	60-62	348.6	28.0
19-1,	66-68	328.2	30.3	22-1,	60-62	359.6	29.9
20-1,	60-62	337.6	32.5	23-1,	30-32	367.3	30.8
21-1,	80-82	347.3	33.9	24-3,	40-42	379.9	32.5
22-1,	50-52	356.0	34.9	25-3,	97-99	390.0	34.0
				26-2,	16-18	397.2	35.0
Site 178							
54-2,	28-29	743.8	NN3-NN4				

Samples of small *Cyclicargolithus*

Site-Core-Sect.,	cm	Depth (m)	Age (Ma)
647A-25-5,	107-110	238.6	35.2
549A-10-1,	100-101	85.0	31.3
563-16-1,	52-54	299.5	24.1
628A-24-2	100-101	214.4	30.3
366A-38-1	79-80	348.8	32.1

Samples from Cipero Section, Trinidad, West Indies

(Bolli, 1957)	(Bramlette & Wilcoxon, 1967)	Zone
Bo. 187;	178888	*G. insueta* (NN4)
J.S. 20;	193265	*G. opima* (NP23-24)

Table 2 - Magnetostratigraphic and biostratigraphic datums compiled from Bukry (1978), Krasheninnikov and Pflaumann (1978), Johnson (1978), and Miller *et al.*, (1989) for Site 366; Snyder and Pflaumann (1978), and Miller *et al.*, (1989) for Site 366; Snyder and Waters (1985), and Müller,(1985) for Site 549; Miller *et al.* (1985), and Parker *et al.* (1985) for Sites 558 and 563; Austin *et al.* (1986), and Moran and Watkins (1988) for Site 628; and Srivistava *et al.* (1987), Firth (1989), and Baldauf and Monjanel (1989) for Site 647. These were correlated to the Berggren *et al.* (1985) time scale, and used to construct age/depth plots and calculate ages of samples analyzed in this study

647A

Datum	Depth (m)	Age (Ma)
FO *S. ciperoensis* (N)	147.0	30.3
LO *G. angiporoides* (F)	190.0	32.0
LO *R. umbilicus* (N)	215.0	34.6
LO *C. reticulata* (D)	222.0	34.0
FO *C. reticulata* (D)	239.0	36.2
LO *E. formosa* (N)	251.0	35.1
LO *D. saipanensis* (N)	289.0	36.7
LO *G. linaperta* (F)	291.0	36.7
LO *T. cerroazulensis* (F)	299.0	36.7
LO *N. truempyi* (F)	385.0	38.5
Base Anomaly 18 (M)	451.0	42.8
LO *C. solitus* (N)	453.0	42.3
Top Anomaly 19 (M)	481.5	43.6
Base Anomaly 19 (M)	490.5	44.1

558

Datum	Depth (m)	Age (Ma)
Top Anomaly 6c (M)	322.0	23.3
Top Anomaly 7 (M)	333.0	25.5
Top Anomaly 8 (M)	342.5	26.9
Top Anomaly 10 (M)	358.0	29.7
Top Anomaly 11 (M)	371.5	31.2
Top Anomaly 13 (M)	399.0	35.3

628A

Datum	Depth (m)	Age (Ma)
Top Zone P22 (F)	136.5	24.8
Base Zone P22 (F)	212.0	28.2
Top Zone NP24 (N)	146.5	28.2
Base Zone NP24 (N)	221.5	30.3
Top Zone P21a (F)	212.0	30.0
Base Zone P21a (F)	221.5	31.6
LO *R. umbilicus* (N)	243.5	34.6
Base Zone P19 (F)	250.5	34.0
LO *E. formosa* (N)	251.5	35.1
Top Zone P16 (N)	260.2	37.2

549A

Datum	Depth (m)	Age (Ma)
LO *S. distentus* (N)	65.0	28.2
LO *G. opima opima* (F)	68.5	28.2
FO *S. ciperoensis* (N)	75.5	30.3
LO *C. cubensis* (F)	79.6	30.0
FO *G. angulisuturalis* (F)	85.9	31.2
LO *R. umbilicus* (N)	96.5	34.6
LO *E. formosa* (N)	106.0	35.1
LO *G. cerroazulensis* (F)	123.4	36.6
LO *D. saipanensis* (N)	132.1	36.7
FO *I. recurvus* (N)	156.5	37.8
LO *Truncorotaloides* (F)	181.2	40.6

563.0

Datum	Depth (m)	Age (Ma)
Top Anomaly 6c (M)	297.0	23.3
Top Anomaly 7 (M)	309.0	25.5
Top Anomaly 8 (M)	316.0	26.9
Base Anomaly 9 (M)	324.0	29.2
Base Anomaly 12 (M)	339.5	32.9
LO *Pseudohastigerina* (F)	354.0	34.0
LO *R. umbilicus* (N)	355.5	34.6
LO *E. formosa* (N)	356.5	35.1

366A

Datum	Depth (m)	Age (Ma)
LO *S. ciperoensis* (N)	263.0	23.7
LO *S. ciperoensis* (N)	270.0	23.7
FO *G. ciperoensis* (F)	301.0	28.2
FO *S. ciperoensis* (N)	309.0	30.3
FO *D. ateuchus* (R)	341.0	31.2
FO *P. opima* (F)	358.5	32.7
LO *D. saipanensis* (N)	418.0	36.6
FO *G. kugleri* (F)	257.1	23.6
LO *P. opima opima* (F)	297.0	28.2
LO *Chiloguembelina* (F)	305.1	30.0
FO *G. angulisuturalis* (F)	337.6	31.6
LO G. *ampliapertura*	356.0	32.8

METHODS

Population counts of each sample were made by light microscope study of smear slides at 1250X magnification before the biometric study was begun. In these counts, specimens of *Cyclicargolithus* were separated into three size categories: <5µm (small), 5-9 µm (medium), and >9µm (large). In many samples, the assemblages are flooded by a large number of specimens <5µm. Because most species descriptions encompass specimens >5µm in size, and because the biostratigraphic use of *C. abisectus* includes the largest specimens, this study focused mainly on the >5µm size fraction. Therefore, specimens >5µm were sampled separately from specimens <5µm, in order to obtain a sufficient number of the larger forms. Five geographically widespread samples of specimens <5µm were also measured in order to compare their morphologies with the larger forms (Tab. 1). For each sample analyzed, the first 50 best-preserved, horizontal and uncovered specimens encountered along a straight transect across a smear slide were chosen for measurement. Each specimen was photographed using a Sony UP-811 screen printer connected to a video camera mounted on a Zeiss Photomicroscope III. The high quality prints were measured using a digitizer. Seven variables were measured on each specimen: length, width, length of the inner collar, width of the collar, length of the central hole, width of the hole, and thickness of the collar (Fig. 3).

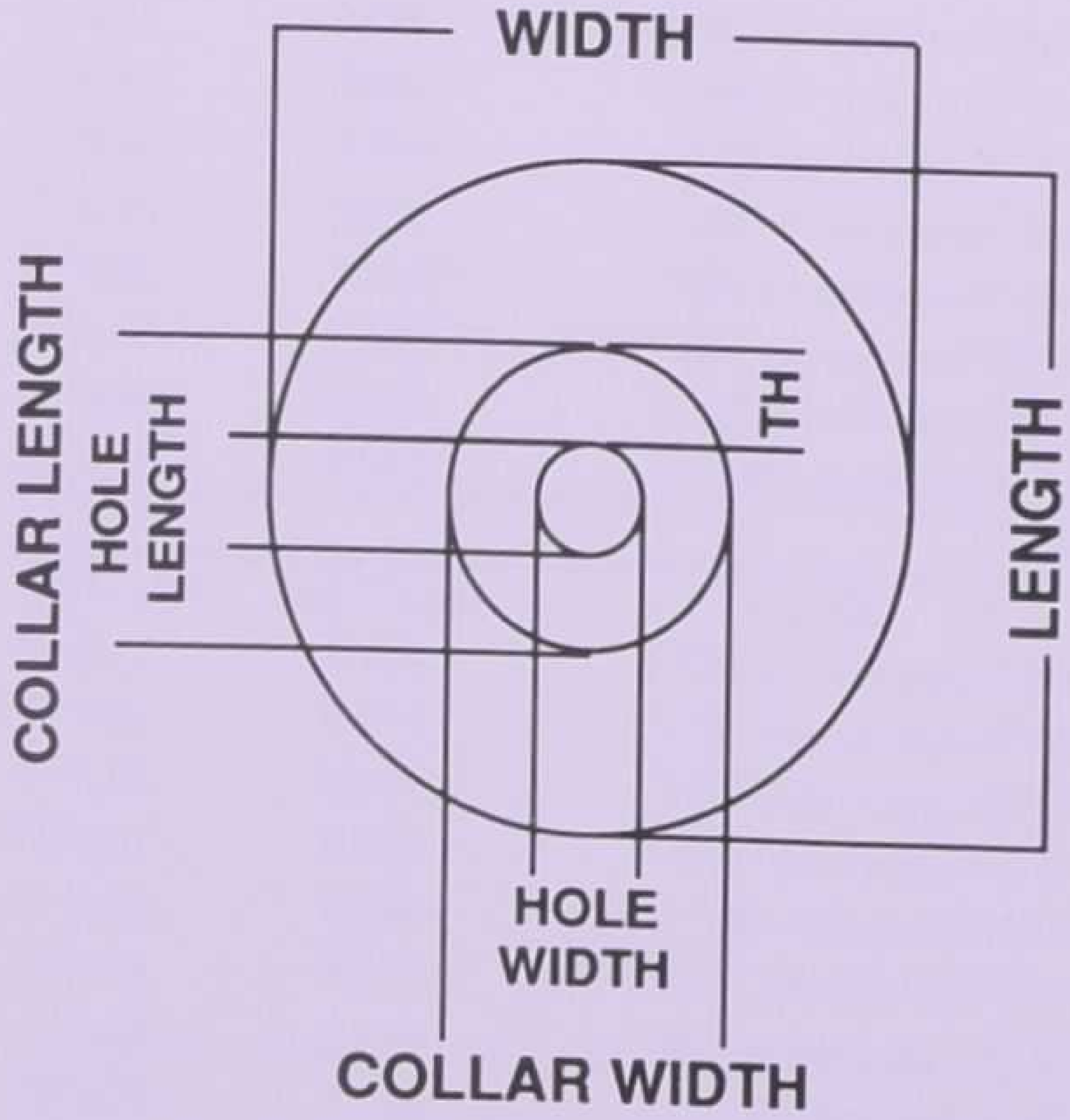

Fig. 3 - Diagram of distal view of *Cyclicargolithus*, showing measurements made for biometric analysis.

MULTIVARIATE ANALYSIS

An initial survey was made of samples from Sites 647 and 563. An R-mode principal components analysis (PCA, using the BMDP program BMDP4M) was used to determine the relationships between the seven measured variables. Each site was analyzed separately. In both cases, all seven variables were reduced to one principal

Table 3 - Results of PCA of specimens from Site 647 and 563, using both size variables and ratio (shape) variables

Site 647		Site 563	
Principal Component:	1	Principal Component:	1
Proportion of Variance		Proportion of Variance	
In Data space	In P.C. space	In Data space	In P.C. space
0.794	1.000	0.752	1.000
Rotated Loadings:		Rotated Loadings:	
Length:	0.937	Length:	0.904
Width:	0.933	Width:	0.900
Collar Length:	0.972	Collar Length:	0.953
Collar Width:	0.953	Collar Width:	0.947
Hole Length:	0.848	Hole Length:	0.842
Hole Width:	0.843	Hole Width:	0.860
Thickness:	0.724	Thickness:	0.616
Site		Site	
Principal Component:	1	Principal Component:	1
Proportion of Variance		Proportion of Variance	
In Data space	In P.C. space	In Data space	In P.C. space
0.544	1.000	0.521	1.000
Rotated Loadings:		Rotated Loadings:	
R1 (L/W)	0.293	R1 (L/W)	0.302
R2 (L/LC)	0.886	R2 (L/LC)	0.867
R3 (L/LH)	0.872	R3 (L/LH)	0.849

Table 4 - Results of DFA of young versus old samples at Sites 647, 563, and 366. Overlap represents the percentage of overlap of values of specimens from each group

Site 647

Variable	F to Remove
R2 (L/LC)	17.44

Jackknifed Classification Matrix

Group	% Correct	Young	Old
Young	70	35	15
Old	70	15	35
Total	70	50	50

Overlap = 91%

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R2	1
Constant	-10.232

Site 563

Variable	F to Remove
none	

Site 366

Variable	F to Remove
none	

component, with large loadings for each variable (Tab. 3). Three ratio variables were then constructed to define the shapes of the specimens: length/width (R1), length/collar length (R2), and length/hole length (R3). A PCA was again run on each site separately, and the ratio variables were also reduced to only one principal component (Tab. 3), with high loadings for R2 and R3. These results indicate a strong correlation between all size variables, while relative hole size and relative collar size are also strongly correlated to each other.

Discriminant function analysis (DFA, using the BMDP program BMDP7M) was also used in order to determine whether different groups of *Cyclicargolithus* could be distinguished from each other. The shape ratios R1, R2, and R3 were selected as variables in the DFA's.

Age was used as a grouping criteria to test for differences in shape between younger and older forms. Samples 136.1 (young) and 261.2 (old) from Site 647, 299.5 (young) and 356.0 (old) from Site 563, and 263.6 (young) and 342.5 (old) from Site 366 were paired and analyzed in three separate DFA's (Tab. 4). At Site 647, only variable R2 was used, with a classification rate of 70% (in comparison, a random classification between two groups should produce a 50% classification

TABLE 5 - Results of DFA of low versus middle versus high latitude samples taken from three time intervals within the Oligocene. Overlap represents the percentage of overlap of values of specimens from each group

24 Ma

Variable	F to Remove
R2 (L/LC)	22.213
R1 (L/W)	8.206
R3 (L/LH)	5.948

Jackknifed Classification Matrix

Group (Sample #)	% Correct	Low	Middle
Low (263.6)	78	39	11
Middle (299.5)	72	14	36
Total	75	53	47

Overlap = 80%

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R1	0.508
R2	-0.688
R3	-0.488
Constant	0.589

31.5-32.5 Ma

Variable	F to Remove
R3	41.154
R2	12.705
R1	7.590

Jackknifed Classification Matrix

Group (Sample #)	% Correct	Low	Middle	High
Low (342.5)	58	29	7	14
Middle (337.6)	66	8	33	9
High (184.6)	68	11	5	34
Total	64	48	45	57

Overlap = 78%

Standard. Coeff. for Canonical Variables

	Can. Var. 1	Can. Var. 2
R1	0.175	0.824
R2	-0.567	0.427
R3	-0.666	-0.372
Constant	6.175	-17.353

35 Ma

Variable	F to Remove
R2	78.644

Jackknifed Classification Matrix

Group (Sample #)	% Correct	Middle	High
Middle (356.0)	78	39	11
High (238.6)	84	8	42
Total	81	47	53

Overlap = 65%

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R2	1.000
Constant	-8.377

31.5-32.5

Variable	F to Remove
R2	45.508
R1	8.864

Jackknifed Classification Matrix

Group (Sample #)	% Correct	Low	High
Low (342.5, 348.8)	62.6	62	37
High (174.8, 184.6)	76	24	76
Total	69.3	86	113

Overlap = 93%

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R1	0.454
R2	0.789
Constant	-15.631

rate). At Sites 563 and 366, no discriminant function was constructed.

Table 6 - Results of DFA of <6μm (Group 1), 6-9 μm (Group 2), and >9μm (Group 3) specimens from Sites 647 and 563. Overlap represents the percentage of overlap of values of specimens from each group

Site 647

Variable	F to Remove
R2	13.411
R3	6.465

Jackknifed Classification Matrix

Group	% Correct	Group 1	Group 2	Group 3
1	54.5	79	29	37
2	39.2	105	120	81
3	44.9	8	19	22
Total	44.2	192	168	140

Overlap = 91%

Standard. Coeff. for Canonical Variables

	Can. Var. 1	Can. Var. 2
R2	-1.079	0.611
R3	0.147	-1.232
Constant	10.217	0.635

Site 563

Variable	F to Remove
R1	16.748

Jackknifed Classification Matrix

Group	% Correct	Group 1	Group 2	Group 3
1	7.3	9	55	60
2	54.6	25	113	69
3	52.6	4	5	10
Total	37.7	38	173	139

Overlap = 100%

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R1	-1.000
Constant	16.748

A second grouping based on latitudinal differences (low, middle, and high) was tested. Three separate DFA's were run for three time intervals (Tab. 5). The first and second analyses (approximately 24 Ma and 31.5-32.5 Ma) used all three variables, with 75.0% and 64.0% classification rates, respectively. The third analysis (approximately 35 Ma), using variable R2, achieved an 81% classification rate, although the amount of overlap between the groups was still 65%.

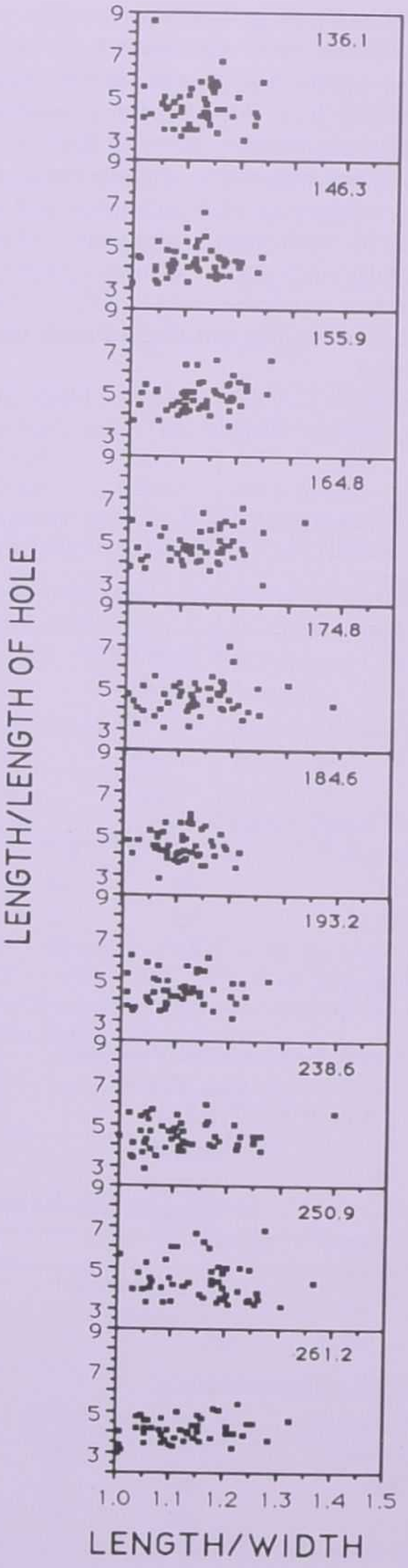

Fig. 4 - Length/width versus length/length of hole for ten Oligocene samples from Site 647.

This author and Parker *et al.* (1965) both observed moderate to heavy overgrowth of nannofossils throughout the middle latitude Oligocene section at Site 563. The poorer preservation of *Cyclicargolithus* at this site may have affected the discrimination of shapes between sites. Another DFA, grouping two low latitude versus two high latitude samples at approximately 31.5-32.5 Ma (Tab. 1), used variables R1 and R2 with a 69.3% classification rate (Tab. 5).

Overall size was used as a third basis for grouping. For the ten Oligocene samples at Site 647 and seven Oligocene samples at Site 563, the >5μm size fraction was divided into three size groups: 5-6 μm (Group 1), 6-9 μm (Group 2), and >9μm (Group 3). A DFA was run on each site separately. The resulting discriminant functions used different variables at each site, with very low classification rates (Tab. 6).

Five samples of small (<5μm) *Cyclicargolithus* (Tab. 1) were measured and the ratio variables R1, R2, and R3 constructed. A PCA of these samples produced one principal component with relatively high loadings for each variable (Tab. 7). A DFA with each sample representing a separate group from a different locality used R2 and R3, and had a classification rate of 34.6% (Tab 8). One final comparison between small (<5μm) specimens and larger (>5μm) specimens was tested. For Sites 366, 563, and 647, samples of small specimens were paired with a sample of larger specimens of comparable age from the same site. A DFA was run on each pair of samples. For Sites 366, 563, and 647, the variables used in each DFA and their classification rates are R3, 60.6%; R1 and R2, 63.0%; and R1, 59.8%, respectively (Tab. 9).

Table 7 - Results of PCA Of <5μm *Cyclicargolithus* from Sites 647, 628, 563, 549, and 366. Variables are length/width (R1), length/collar length (R2), and length/hole length (R3)

Small (<5 μm) *Cyclicarg.*	
Principal Component: 1	
Proportion of Variance In Data space	Proportion of Variance In P.C. space
0.560	1.000
Rotated Loadings:	
R1 (L/W)	0.605
R2 (L/LC)	0.855
R3 (L/LH)	0.763

The PCA and DFA analyses show a lack of significant differences in shape between *Cyclicargolithus* assemblages of different age, latitude, or size, within the Oligocene of the North Atlantic. Plots of the eccentricity (R1) versus the relative hole size (R2) for samples at Sites 647 and 563 also show relatively stable distributions of placolith shapes through time (Figs. 4 and 5). Eccentricity

Table 8 - Results of DFA of five geographically widespread samples of <5μm *Cyclicargolithus*

Small (<5μm) *Cyglicargolithus*

Variable	F to Remove
R2	12.702
R3	4.741

Jackknifed Classification Matrix

Group	% Correct	238.6	85.0	299.5	214.4	348.8
238.6	66	31	4	1	8	3
85.0	18	15	9	15	6	5
299.5	46	2	8	23	11	6
214.4	32	12	4	15	16	3
348.8	12.2	16	11	13	3	6
Total	34.6	76	36	67	44	23

Standard. Coeff. for Canonical Variables

	Can. Var. 1	Can. Var. 2
R2	-0.682	-0.866
R3	-0.498	0.984
Constant	8.81	1.984

TABLE 9 - Results of DFA between samples of >5µm and <5 µm *Cyclicargolithus* from Sites 647, 563, and 366

Site 366

Variable	F to Remove
R3	4.874

Jackknifed Classification Matrix

Group	% Correct	Small	Large
Small	53.1	26	23
Large	68.0	16	34
Total	60.6	42	57

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R3	-1.000
Constant	-5.957

Site 563

Variable	F to Remove
R1	7.139
R2	5.167

Jackknifed Classification Matrix

Group	% Correct	Small	Large
Small	66.0	33	17
Large	60.0	20	30
Total	63.0	53	47

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R1	-0.932
R2	0.688
Constant	9.110

Site 647

Variable	F to Remove
R1	6.988

Jackknifed Classification Matrix

Group	% Correct	Small	Large
Small	51.1	24	23
Large	68.0	16	34
Total	59.8	40	57

Standard. Coeff. for Canonical Variables

	Can. Var. 1
R1	-1.000
Constant	12.742

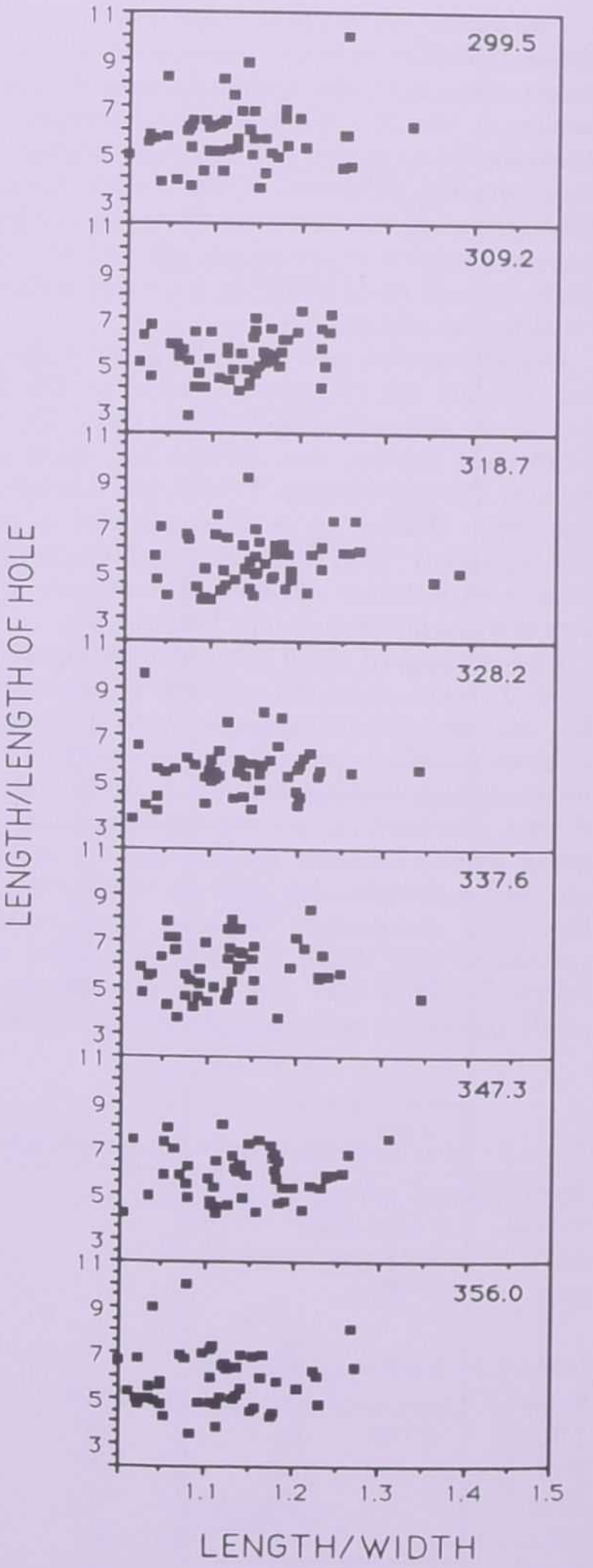

FIG. 5 - Length/width versus length/length of hole for seven Oligocene samples from Site 563.

values vary between 1 (circular) and 1.4 (elliptical), with over 98% being less than 1.3. Only a small percentage of specimens measured were completely circular (R1=1). Relative hole sizes vary from 1/3 to 1/10 the size of the placoliths (R2 = 3 to 10), with 98% falling between 1/3 and 1/8. Fluctuations in the range of relative hole sizes can be seen at each site, but do not show any overall directional change through time. Within this range of shape variation, no distinct subclusters are seen, and none were detected using multivariate analyses. The sample populations of *Cyclicargolithus* analyzed display no evidence of directional phyletic change, no polymodality which would suggest cladogenesis, and no morphologic basis for subdivision into more than one species.

UNIVARIATE ANALYSIS

The remaining samples from Sites 366, 549, 558, 628, and 647 were analyzed with only overall length measured for the >5µm specimens. A plot of the percentage of the >8µm, >9µm, >10µm and >11µm size fractions in all six sites examined shows that the first occurrences of the larger forms of *Cyclicargolithus* and their relative abundance peaks are asynchronous, and do not correspond to or approximate the first occurrence of *Sphenolithus ciperoensis* (Fig. 6). At all sites, the >9µm fraction first becomes common in Zone NP23 (Martini and Müller, 1986), between the last occurrence of *Reticulofenestra umbilicus* and the first occurrence of *Sphenolithus ciperoensis*. However, rare specimens of this size fraction occur as old as the late Eocene in Sites 647 and 549.

Overall size of 200 specimens/sample, including both small (<5µm) and large (>5µm) specimens, was measured in selected lower and upper Oligocene samples at all sites (Fig. 7). A unimodal size distribution is seen in all samples, with a skew towards the smaller sizes. The larger specimens form thin, continuous tails off the central size groups, and are more abundant in the upper Oligocene samples than the lower Oligocene samples. Similar size distributions are seen in upper Oligocene and Miocene samples from the Atlantic and Indian Oceans (Olafsson, this volume).

ANALYSIS OF TYPE MATERIAL

Published photomicrographs of the holotype and paratype specimens of all species of *Cyclicargolithus* (except for the holotype of *C. floridanus*, which is a coccosphere, and whose individual coc-

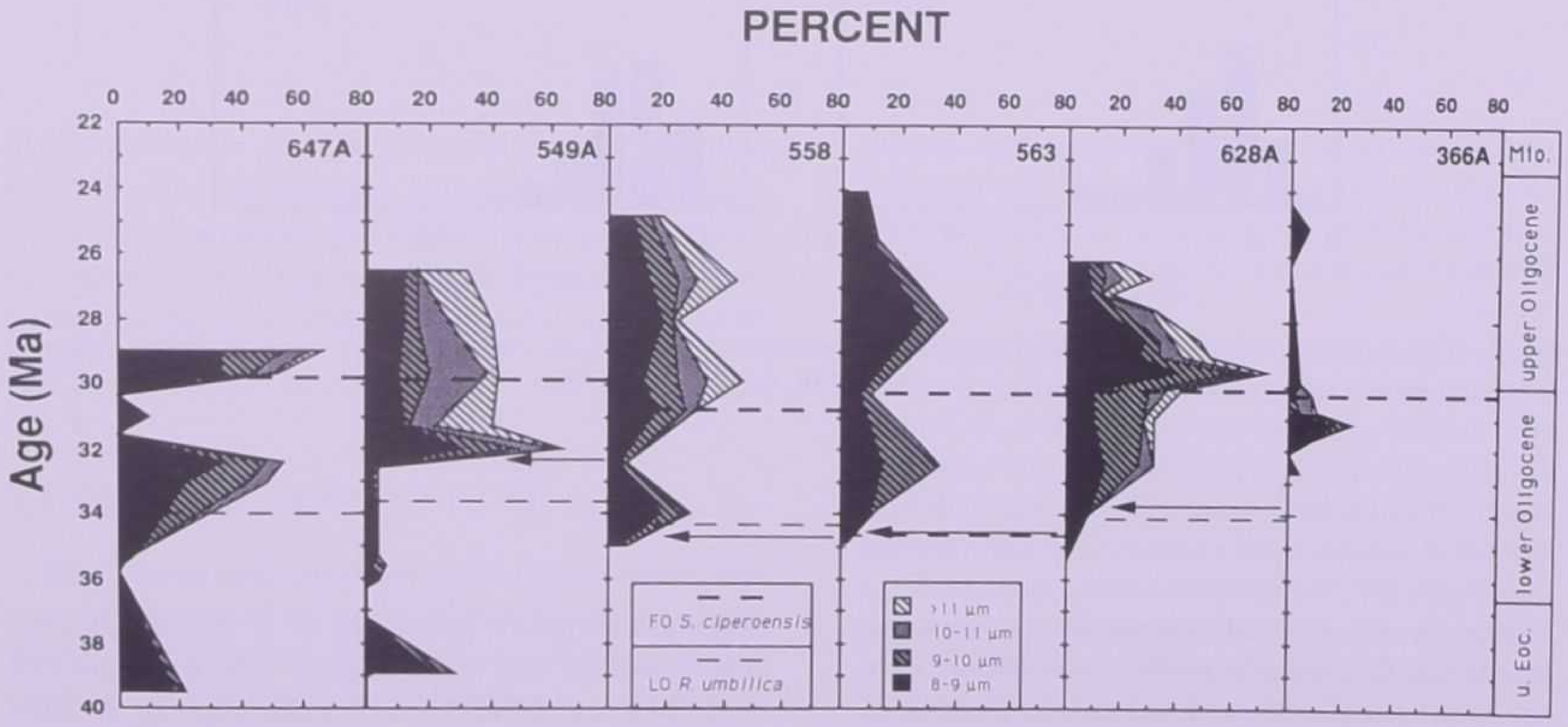

Fig. 6 - Relative abundances of the 8-9 µm, 9-10 µm, 10-11 µm, and >11 µm size fractions of *Cyclicargolithus* out of 50 specimens measured per sample from Holes 647A, 549A, 558, 563, 628A, and 366A. Arrows mark the first occurrence of *C. abisectus* as reported by Müller, (1985; Hole 549A), Parker *et al.* (1985; Hole 558), Miller *et al.* (1985; Hole 563), and Moran and Watkins (1988; Hole 628A). The first occurrences of *Sphenolithus ciperoensis* and the last occurrences of *Reticulofenestra umbilicus* are included for comparison.

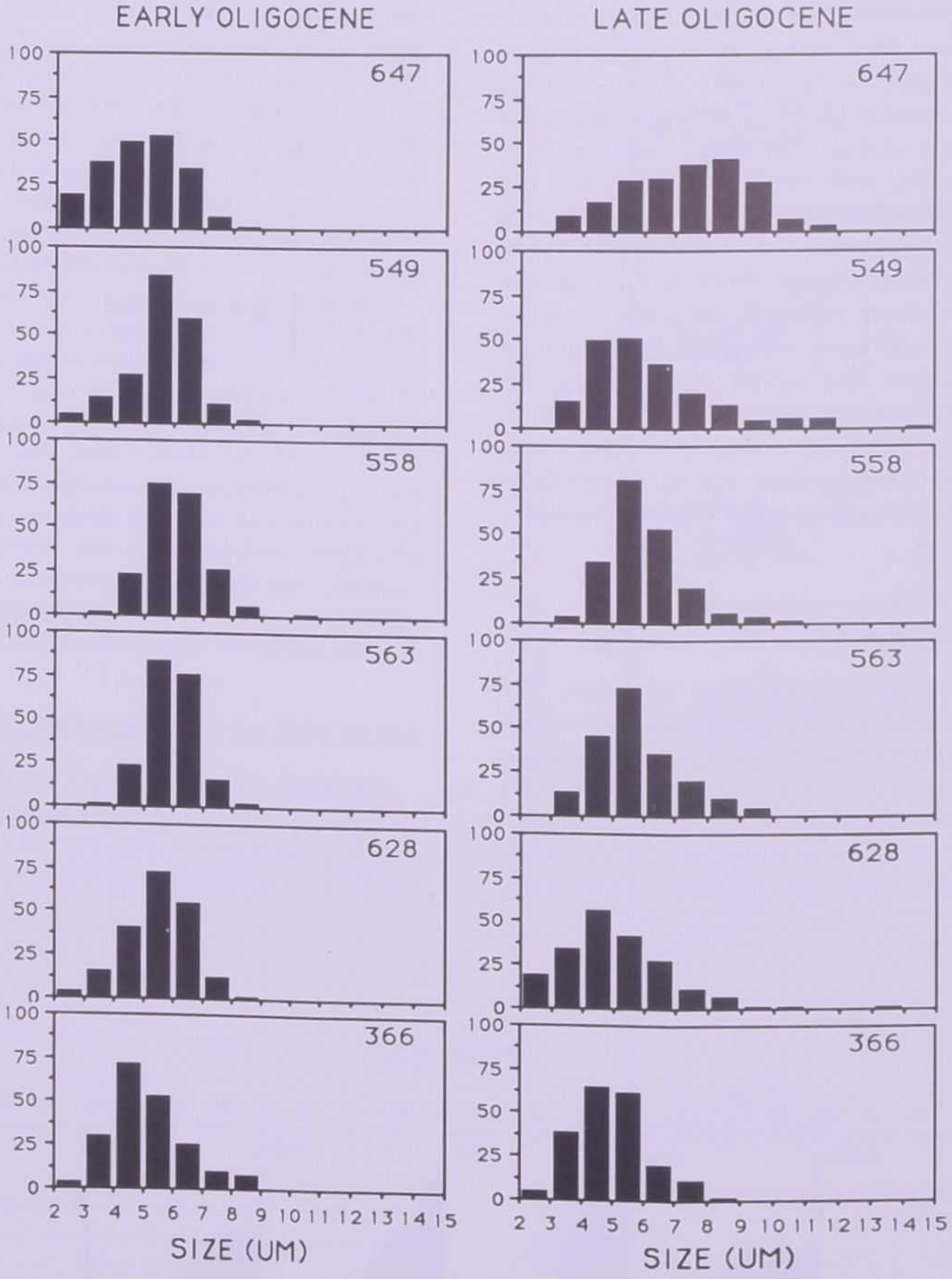

FIG. 7 - Histograms of overall size of *Cyclicargolithus* specimens, out of 200 measured per sample, from selected lower and upper Oligocene samples from Sites 647, 549, 558, 563, 628, and 366.

coliths are not oriented horizontally) were measured, and their length/width (eccentricity) versus length/length of hole values are plotted in Figure 8. A similar plot shows the distribution of values for photomicrographs of *C. floridanus* and *C. hesslandii* from HAQ and LOHMANN (1976), and for the mean values of sample populations from the type *C. bukryi* material, the type *C. neogammation* (junior synonym of *C. floridanus*) locality, and of five samples of <5µm specimens from different DSDP/ODP sites (Fig. 8). A comparison with similar plots for samples measured at Site 647 (Fig. 4) and Site 563 (Fig. 5) shows that the values of all the species' holotypes and paratypes, as well as the other samples listed above, fall within the range of variability of the

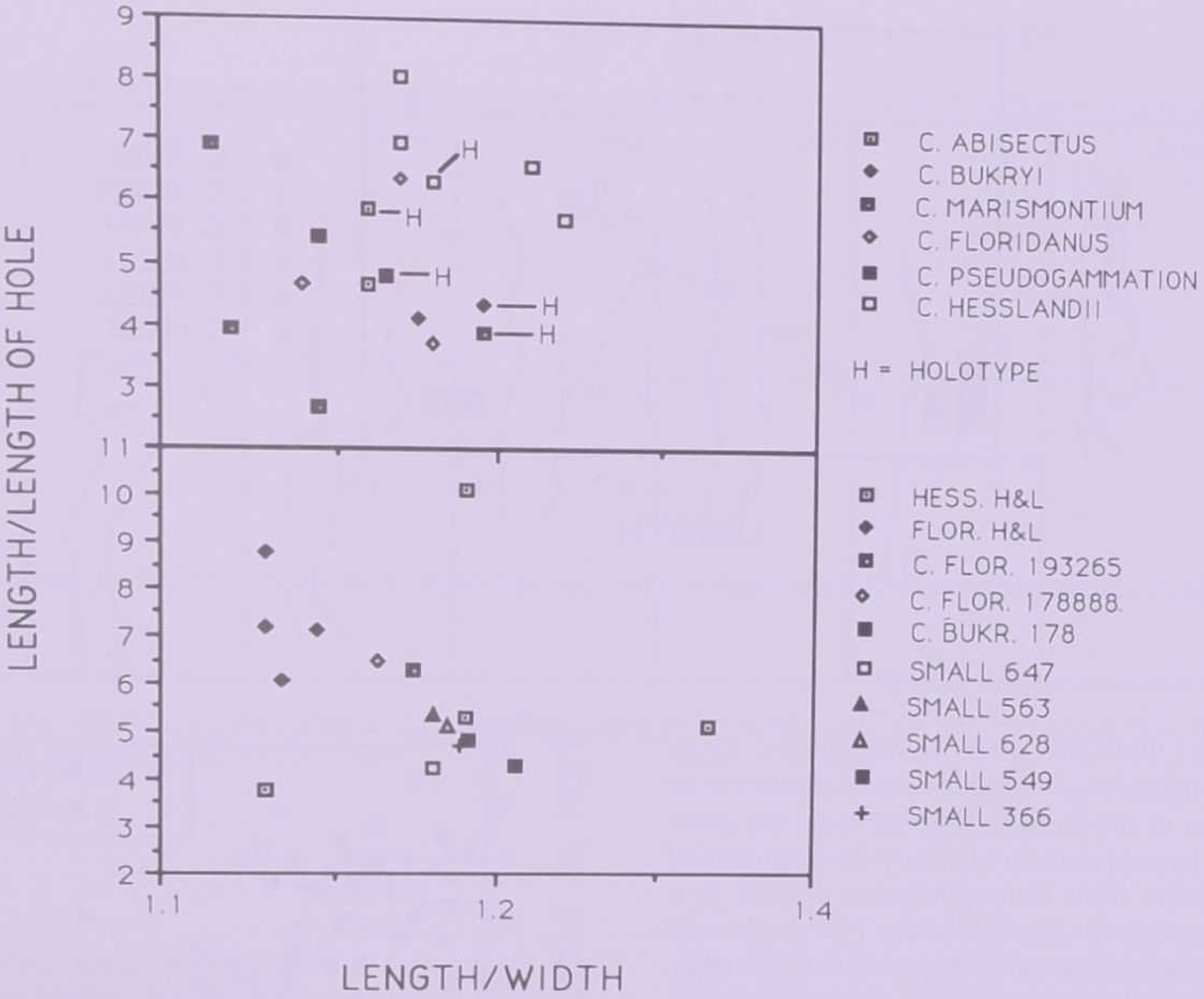

FIG. 8 - Length/width versus length/length of hole of the holotype and paratype specimens of six species of *Cyclicargolithus* (top). Similar plot of *C. hesslandii* (HESS. H & L) and *C. floridanus* (FLOR. H & L) pictured in HAQ and LOHMANN (1976), and of the mean values of samples of *C. floridanus* from Trinidad (178888 and 193265), of *C. bukryi* from the type section at DSDP Site 178 (C. BUKR. 178), and of samples of small (<5 μm) specimens from five geographically widespread sites in the North Atlantic.

Cyclicargolithus sample populations at Sites 647 and 563. The differences in eccentricity and relative hole size stated by several of the authors to distinguish their species do not appear to be sufficient to separate the populations into different species.

TAXONOMIC IMPLICATIONS

The taxonomic concepts of various authors can now be evaluated in light of this biometric study. ROTH (1970) pictured specimens which he attributed to *Reticulofenestra hesslandii*, and which contained grills in the central holes. However, the type description of *C. hesslandii* did not mention any grill in the central holes (HAQ, 1966), nor did the photographs of the holotype and paratypes show any grills. Also, HAQ and LOHMANN (1976) discuss and recombine *C. hesslandii* and do not mention any central grill. Therefore, the distinction which ROTH (1970) made between *C. hesslandii* and *C. floridanus* does not appear to be valid.

HAQ and LOHMANN (1976) stated that *C. floridanus* is larger and has a more prominent hole than *C. hesslandii*, but otherwise has similar construction. In contrast, PERCH-NIELSEN (1985b) said that they are difficult to distinguish from one another, but *C. floridanus* has a smaller hole than *C. hesslandii*. Measurements of the respective holotypes and paratypes show that the size range of *C. hesslandii* encompasses that of *C. floridanus* (Fig. 9), and that the holotype of the former is very close in eccentricity and relative hole size to one of the paratypes of the latter (Fig. 8). Therefore, the distinctions which HAQ and LOHMANN (1976) and PERCH-NIELSEN (1985b) made between the two species do not appear to be valid.

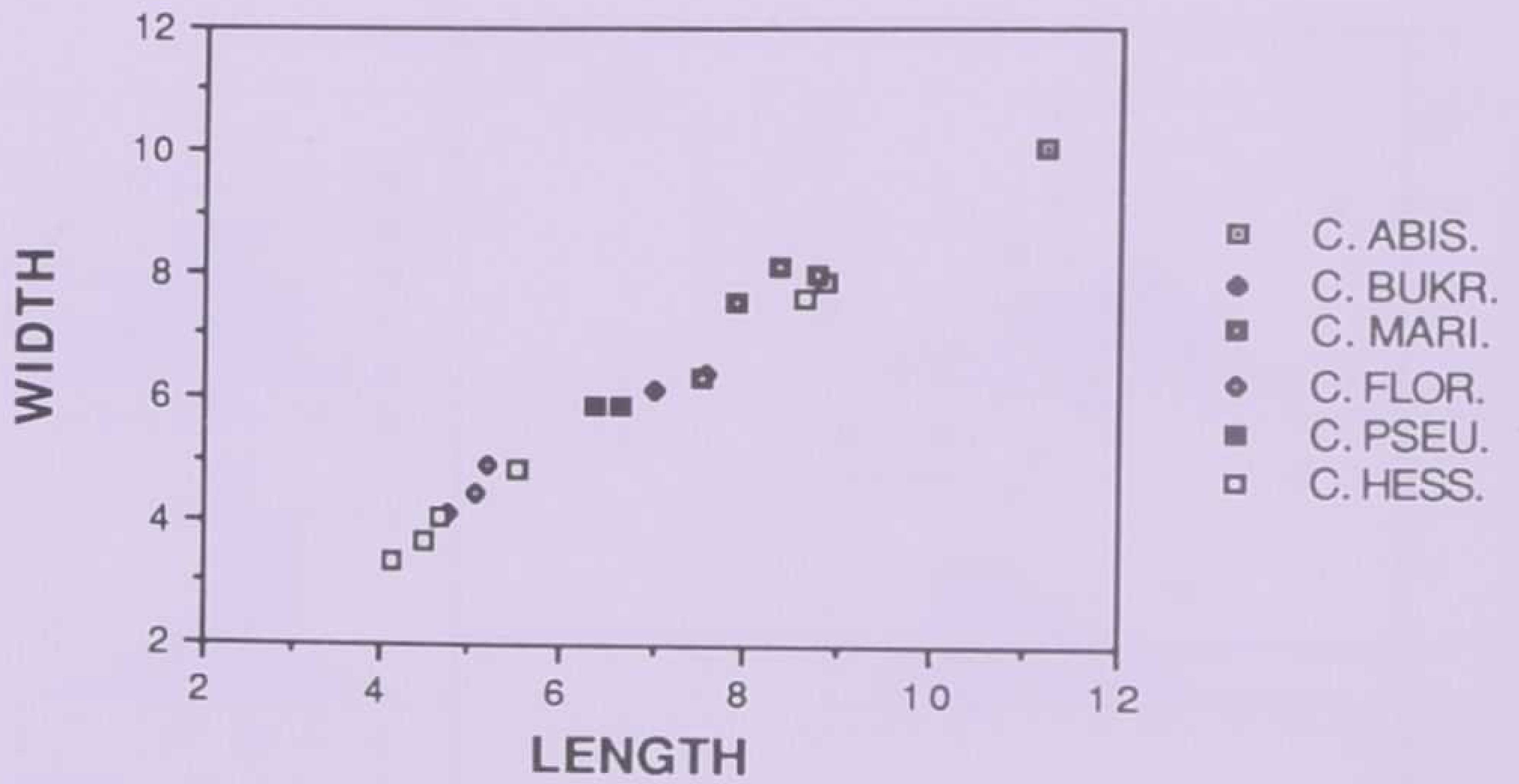

FIG. 9 - Length versus width of the holotype and paratype specimens of six species of *Cyclicargolithus*.

PUJOS (1987) presented the stratigraphic range of *C. hesslandii* as having its lowest occurrence at the base of the Miocene. Furthermore, she presents a hypothetical evolutionary development of this species from *Reticulofenestra daviesii* near the Oligocene-Miocene boundary. Her conclusions are based on three reliable records (in her opinion) of the distribution of this species. However, she did not include as reliable the type description and occurrence of this species by HAQ (1966) from the upper Eocene, nor did she include HAQ and LOHMANN's (1976) study documenting its occurrence from the upper Eocene through the Oligocene. PUJOS' (1987) stratigraphic and evolutionary conclusions do not appear to be valid. She does correctly distinguish this species from *Dictyococcites scrippsae*, which according to BUKRY and PERCIVAL (1971) is similar to *Reticulofenestra bisecta*.

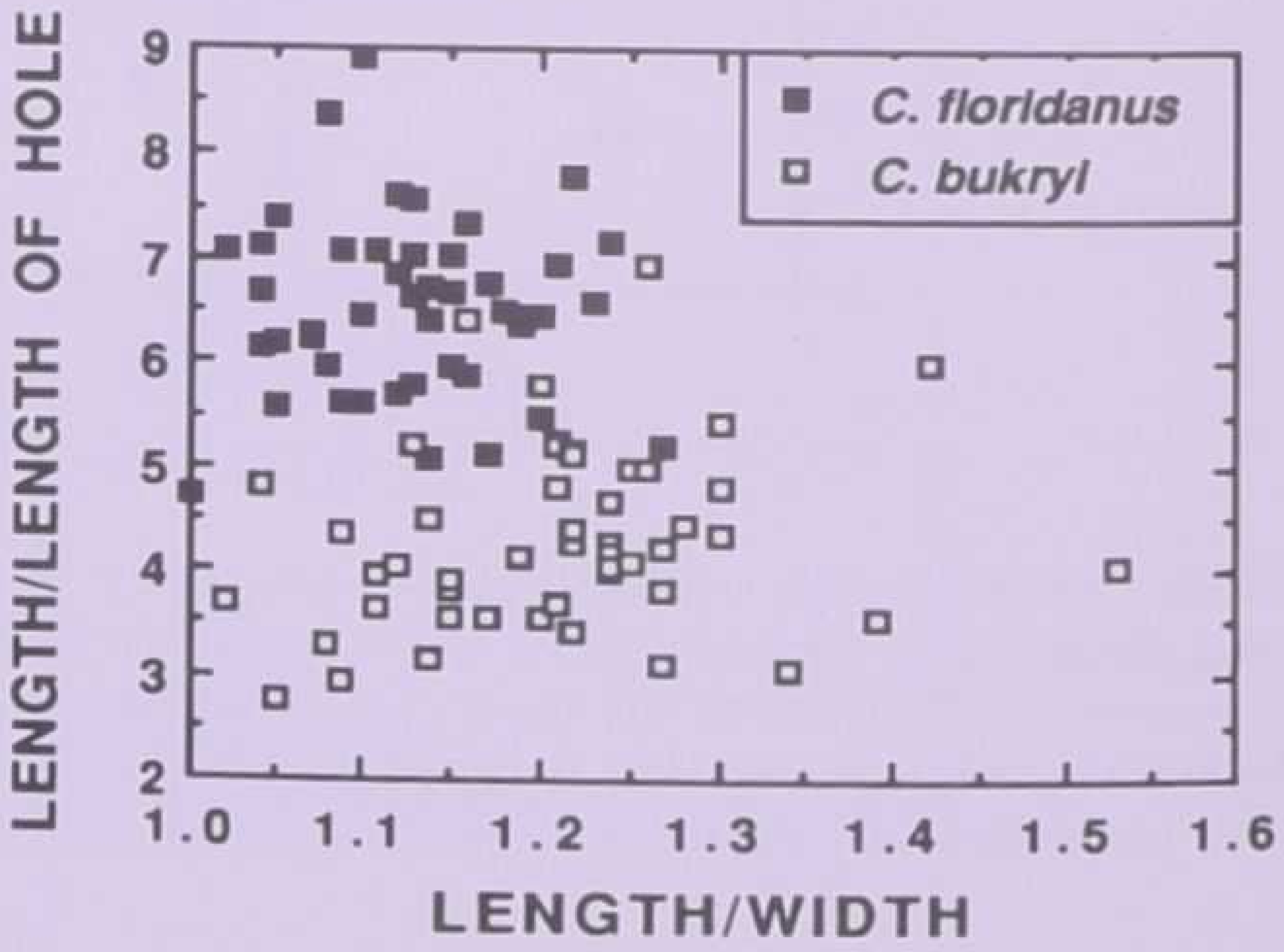

FIG. 10 - Length/width versus length/length of hole for sample 178888 (*C. floridanus*) and for sample 178-54-2, 28-29 cm (*C. bukryi*), showing separation of samples based mainly on relative hole size.

WISE (1973) stated that *C. bukryi* differed from *C. floridanus* by having an eccentricity >1.1 and by having a larger central area. However, the paratypes of *C. floridanus* also have an eccentricity greater than 1.1, and have a range of variation in relative hole size which encompasses the range of relative hole size in the holotype and paratype of *C. bukryi* (Fig. 8). The mean of 50 specimens measured from the topotype sample of *C. bukryi* falls within the range of relative hole size of the paratypes of *C. floridanus*. The eccentricity verus relative hole size of a Miocene sample of *C. floridanus* from Trinidad and the Miocene topotype sample of *C. bukryi* shows clear separation according to relative hole size, with the latter having generally larger holes (Fig. 10). However, both samples fall within the range of variation seen in Oligocene samples from Sites 647 and 563 (Figs. 4 and 5). Further analysis of Miocene populations is needed to evaluate the nature and extent of this separation.

BUKRY and PERCIVAL (1971) refer to *C. abisectus* as a subround form derived from *R. bisecta*. They reported its size range as 12-16 μm, and its stratigraphic range as no lower than the *Sphenolithus distentus* (NP 24) Zone. Their reported size range, however, is larger than the size range of the type specimens (MÜLLER, 1970). ROTH (1970) reports the range of *C. abisectus* from several sections in Italy as extending into the *Sphenolithus predistentus* (NP23) Zone. Figure 11

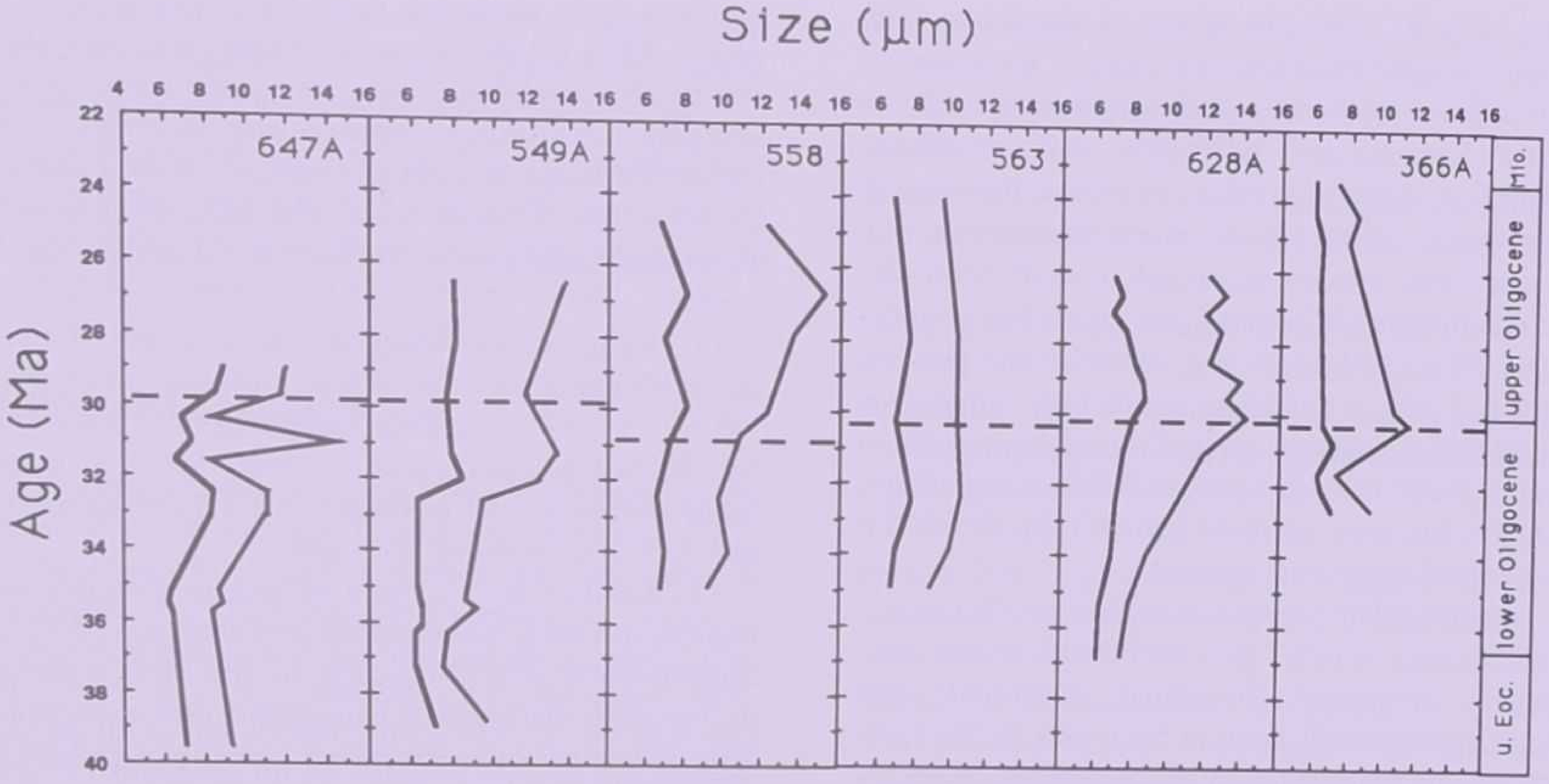

FIG. 11 - Maximum and mean sizes of *Cyclicargolithus* from Holes 647A, 549A, 558, 563, 628A, and 366A. Minimum sizes in all samples are less than 5 µm.

shows that specimens 12 µm or larger were encountered below NP24 at Sites 647, 549, and 628, while Figure 6 shows specimens >9µm occurring in the upper Eocene at Sites 647 and 549. XU and WISE (in press) also report *C. abisectus* from the upper Eocene. The last common occurrence of *C. abisectus* was used to define the top of Subzone CN1a by OKADA and BUKRY (1980). However, I (unpublished data) and XU and WISE (in press) observe common to abundant *C. abisectus* occurring along with *C. floridanus* up to the latter's extinction level in the middle Miocene in the Bonin/Mariana forearc basin. Large forms of *Cyclicargolithus* may be biostratigraphically useful in a general sense for indicating roughly a 'middle' Oligocene (NP23) to middle Miocene (NN5) age, based on their relative abundance in nannofossil assemblages through this interval (XU and WISE, in press), however different reported ranges by various authors make the first and last occurrences of *C. abisectus* of little value as a biostratigraphic datum over wide geographic regions.

The birefringent pattern of *C. abisectus* differs from *C. floridanus* (PERCH-NIELSEN, 1985b). The extinction gyres between the inner collar and the outer shield are typically disjunct, while the overall birefringence color of the collar and shield is commonly a first order yellow-white. *C. floridanus* has, instead, distinct curving gyres across the collar and shield, and shows a first order white color. Increasing birefringence can be attributed to either a change in crystallographic orientation or to increasing thickness, which is a function of size. Comparison of electron micrographs of *C. abisectus* and *C. floridanus* (HAY *et al.*, 1967; MÜLLER, 1970; PERCH-NIELSEN, 1985b) do not show evidence for crystallographic reorientation. In Figure 6, the first observed occurrence of *C. abisectus* by four different authors at four sites closely matches the first common occurrence of >9µm forms, which points to a close correlation between birefringence and size (see Pl. 1). Thus, the change in birefringence and extinction pattern of *Cyclicargolithus* can be better explained as a direct function of size, and does not alone constitute a valid criteria, in my opinion, for separation of evolutionary species.

ROTH and HAY (in HAY *et al.*, 1967) describe *C. floridanus* as being more strongly elliptical and having a smaller hole than *C. marismontium*. However, the range in eccentricity and in relative hole size of the holotype/ paratypes of *C. marismontium* encompasses the range of respective values of *C. floridanus* (Fig. 8). Therefore, the distinction between these two species does not appear to be valid.

The range in variation in size, relative hole size and eccentricity of *C. marismontium* and *C. floridanus* also encompasses that of *C. pseudogamma-*

tion (Fig. 8). The size range of the latter falls within the middle of the spectrum of sizes, and of the relative hole sizes and eccentricities of the other five species' holotypes and paratypes. Therefore, there is no clear distinction between *C. pseudogammation* and *C. marismontium* or any of the other species discussed here. Further detailed analyses of Eocene *Cyclicargolithus* populations are needed. However, based on the present results, I believe that there needs to be conclusive quantitative evidence that *C. pseudogammation* and *C. floridanus* are distinguishable morphologic and evolutionary entities, before they should be considered as separate species.

Gould (1988) presented arguments that many evolutionary 'trends', usually interpreted as anagenesis (a general directional movement), are more appropriately seen as increases in the variance of the characteristics studied. When the origination point is located near one end of a spectrum of possible values, the only pathway open for expansion or movement is towards the other extreme. If the original end-value remains the same, and the modal values remain relatively constant, then no anagenetic trend occurs. Rather, an increase in variance explains the changes in the populations. This can be applied to the populations of *Cyclicargolithus* studied here. The minimum size of specimens of *Cyclicargolithus* remains the same through the upper Eocene to Oligocene - less than 5 μm. The mean size increases and fluctuates mainly because of the increase in maximum size through time (Fig. 11). The modal size of *Cyclicargolithus* is relatively constant (Fig. 7) at between 5-7 μm. Therefore, the population change can be characterized simply as an increase in the variance of the overall size, rather than a directional change in the population as a whole. *Cyclicargolithus*, therefore, remains basically unaltered from the upper Eocene through the Oligocene, except for the addition of larger specimens through the Oligocene.

CONCLUSIONS

The ubiquitous distribution and simple morphologic plan of the calcareous nannofossil genus *Cyclicargolithus* provided a relatively easy group to study biometrically on a large scale. Those same characteristics, on the other hand, may be the reason why there seems to be relatively little going on, in terms of evolutionary development, ecophenotypic changes, and diversity of species. A cosmopolitan organism, adapted to a wide range of environmental conditions, might be expected to show little variation over large geographic regions. Also, a simple morphology does not allow for much variability - one must add features that increase morphologic complexity in order to increase the range of possible variations of a particular structure. Despite this, the following conclusions and suggestions for further research can be made:

1) The genus *Cyclicargolithus* consists of circular to elliptical placoliths (eccentricity varies from 1.0 to 1.5) with variable hole sizes (1/3 to 1/10 the overall placolith size). About 98% of specimens measured fall between 1.0-1.3 (eccentricity) and 1/3-1/8 (relative hole size).

2) Multivariate analysis of geographically and stratigraphically widespread assemblages of *Cyclicargolithus* in the Oligocene of the North Atlantic failed to distinguish consistent and significant differences in shape between sample populations of varying size, latitude, or age. No separation of populations into morphologic clusters is seen, and no evidence exists that cladogenesis occurred. Univariate analysis reveals unimodal population distributions with a consistent dominance of small to medium size specimens, and an increase in the relative percentage of larger sized specimens due to an increase in variance of size, through the Oligocene. No evidence was found for directional phyletic change in the populations.

3) Analysis of the published photomicrographs of the type specimens of all species of *Cyclicargolithus* shows an overlap in morphologies, all of which fall within the range of variability of *Cyclicargolithus* populations from the North Atlantic. No valid morphologic separation of the various described species can be made.

4) Biostratigraphic datums and correlations based on the first occurrence of larger specimens are asynchronous and not useful over a wide geographic region. The genus may be biostratigraphically useful in a general sense because of the common occurrence of larger specimens (>9μm) in sediments of "middle" Oligocene to middle Miocene age.

5) Taxonomically, the six species of *Cyclicargolithus* appear to all belong to one variable species which adds larger forms through the Oligocene but otherwise remains the same from the upper Eocene to Oligocene.

6) Some further analyses of Miocene populations would be profitable to determine the extent of the differences in relative hole sizes between low and high latitude populations, and what taxonomic, evolutionary or paleoenvironmental significance this would have. Likewise, analyses of Eocene populations may determine whether there

is a phyletic or cladogenetic change within the Eocene that would be biostratigraphically useful and/or sufficient for species level distinctions.

7) A less cosmopolitan and more morphologically complex nannofossil group may be expected to show different evolutionary, paleoecologic, and taxonomic results than the present study.

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EXPLANATION OF PLATE I

Specimens of *Cyclicargolithus*.

FIGS. 1-4, 6, 10, 15, 16 - Sample 628A - 16-5, 98-99 cm (upper Oligocene; NP25).

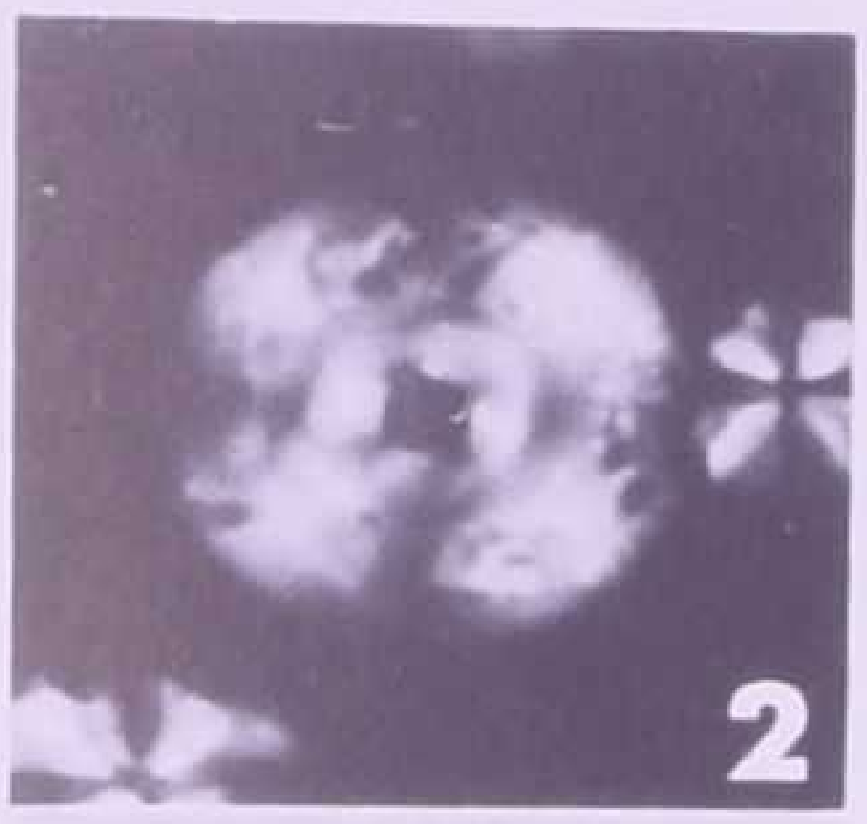
FIGS. 5, 7-9, 11-14 - Sample 647A - 20-1, 106-108 cm (lower Oligocene; NP23).

Specimens arranged in order of increasing size from bottom row to top and from left to right in each row. All specimens 2000X magnification.

J.V. FIRTH - *Analysis of the taxonomic, biostratigraphic and evolutionary relationships of species of the calcareous nannofossil genus* Cyclicargolithus *(Bukry, 1971) from the upper Eocene and Oligocene of the North Atlantic*

PLATE I


1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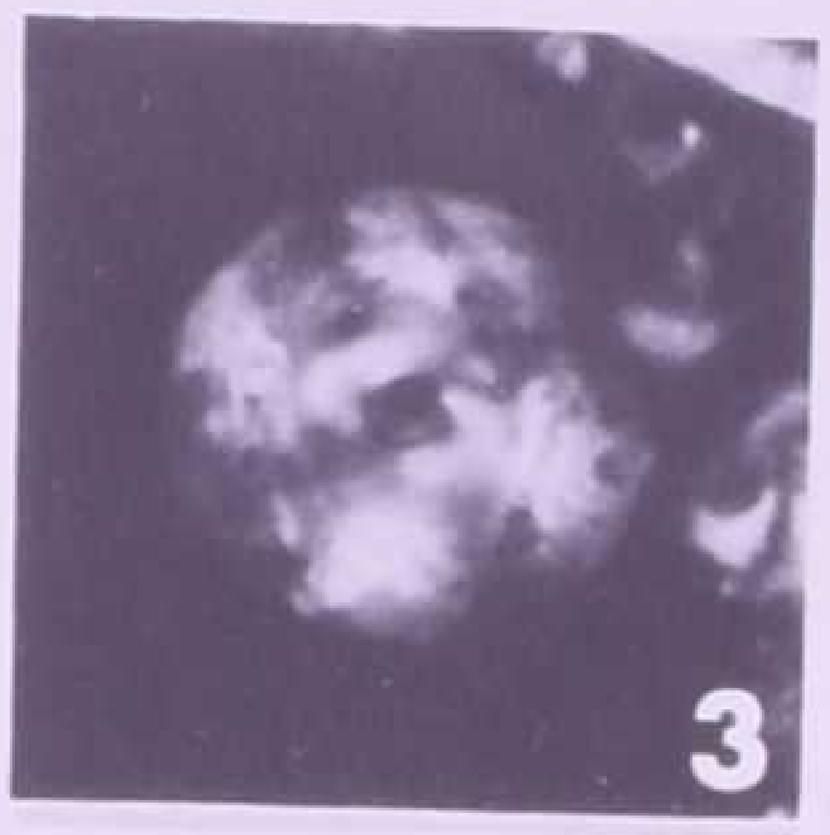
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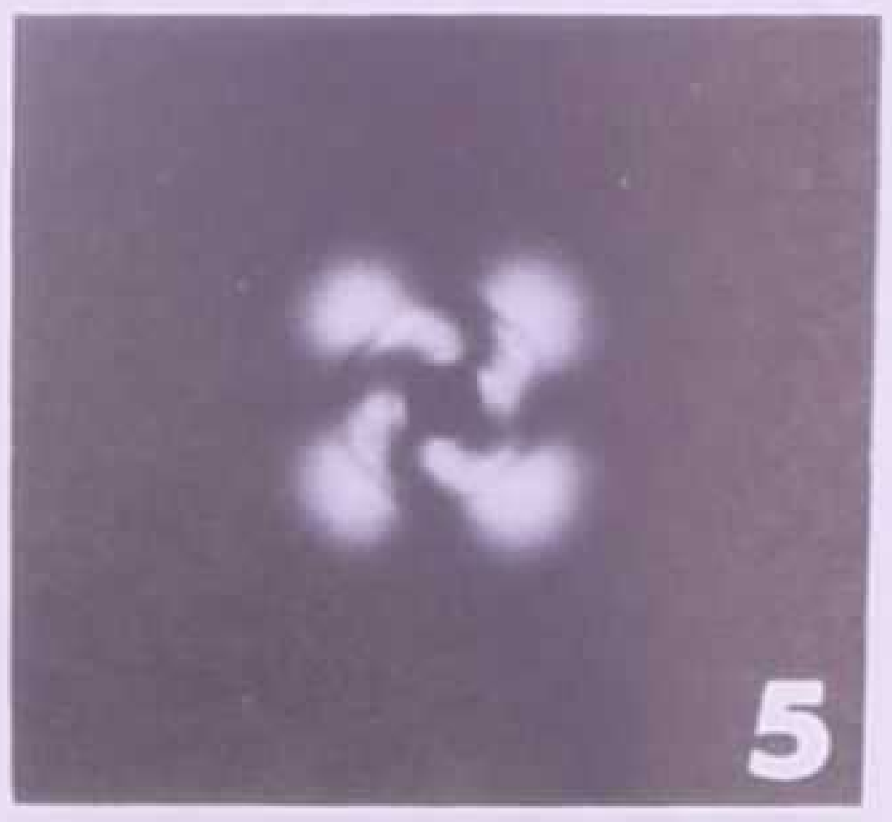
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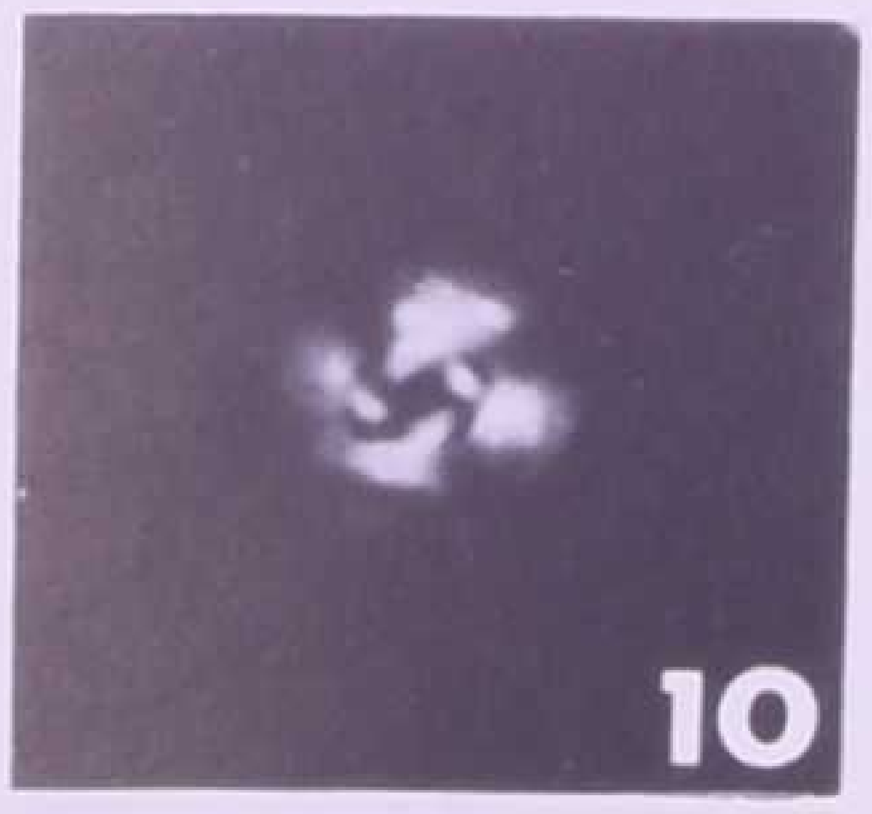
6


7


8


9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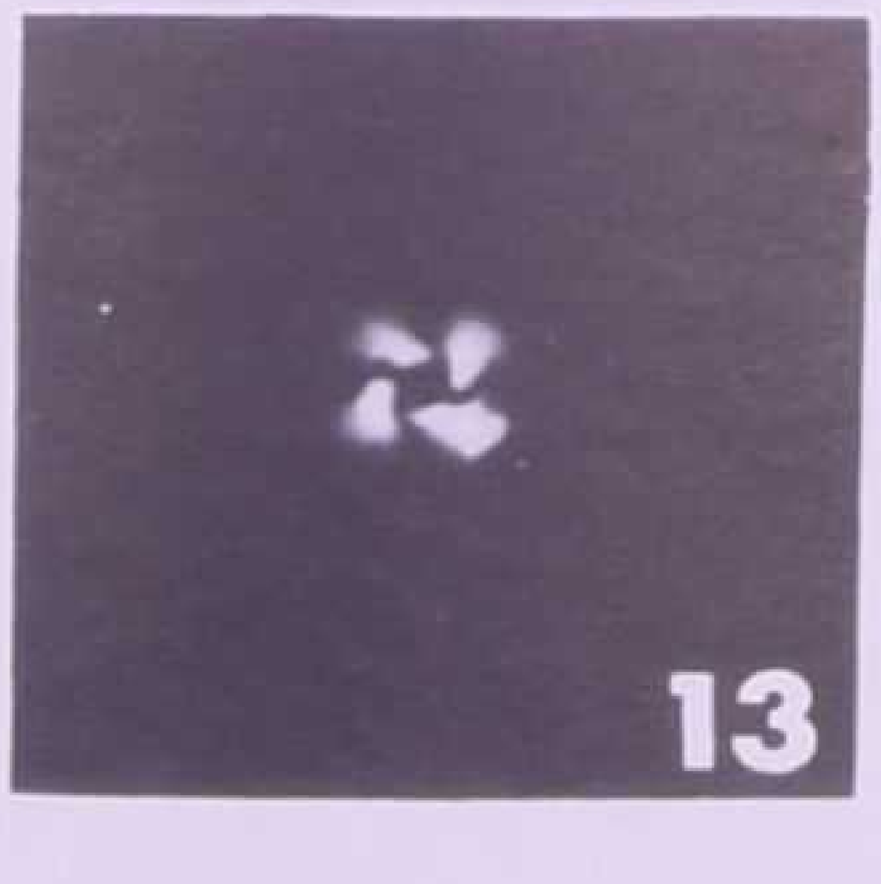
11


12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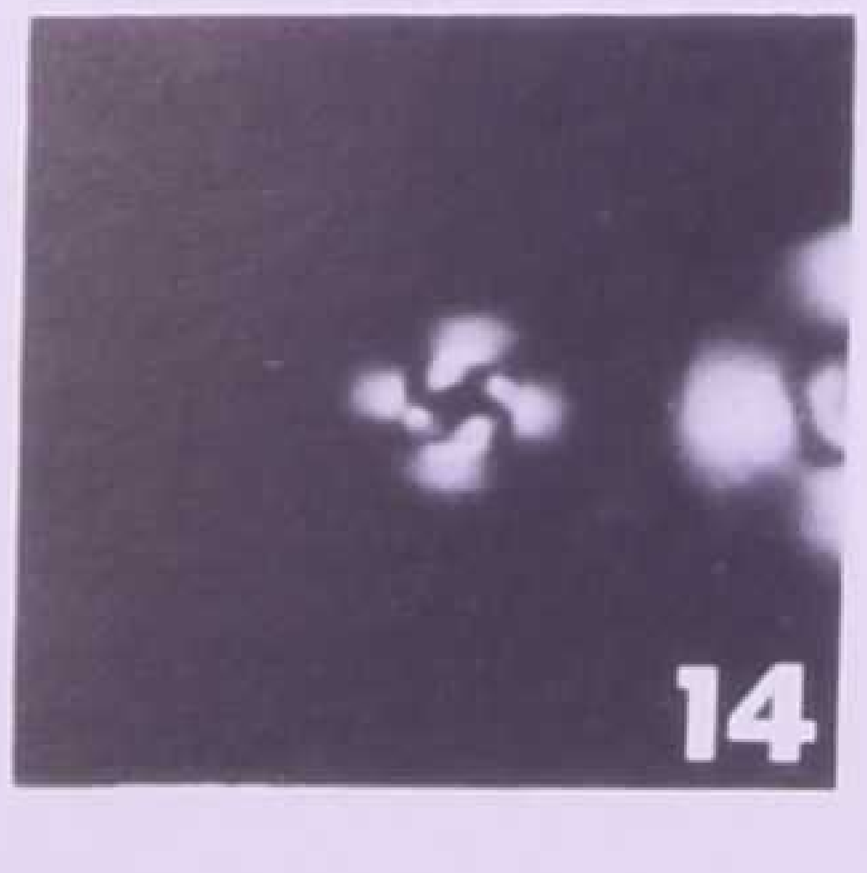
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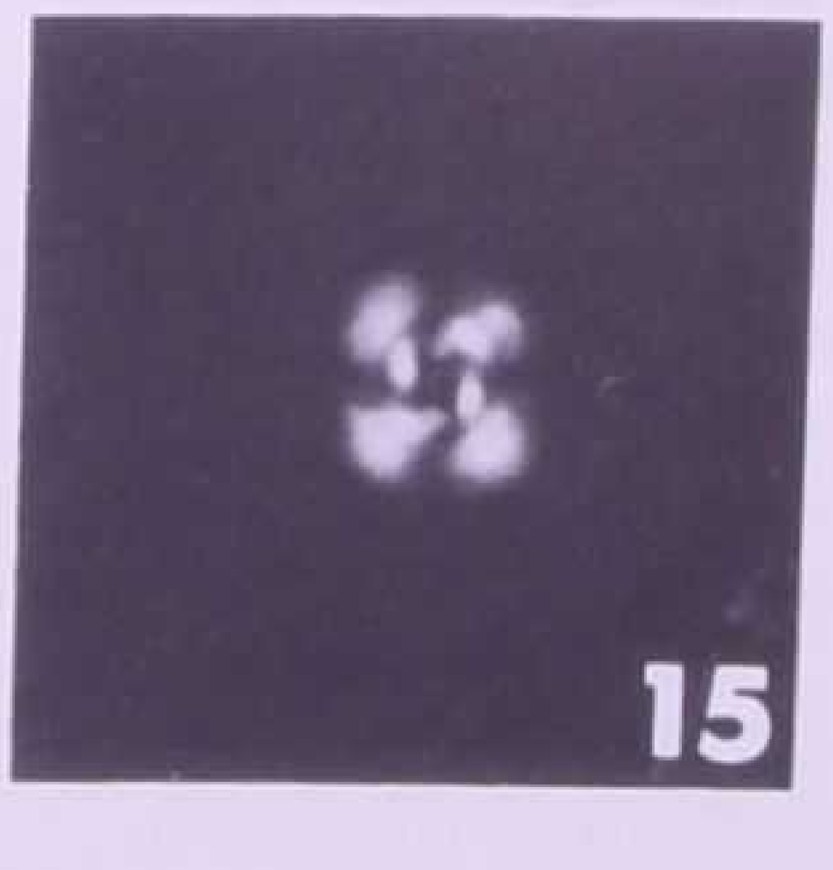
15


16