

## 42. CENOZOIC SILICOFLAGELLATES AND EBRIDIANS FROM ODP LEG 113: BIOSTRATIGRAPHY AND NOTES ON MORPHOLOGIC VARIABILITY<sup>1</sup>

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### ABSTRACT

Silicoflagellates are present at ODP 113 Sites 689, 690, 693, 695, 696, and 697. These are generally Neogene in age except for Oligocene and Eocene silicoflagellates and ebridiens at Sites 689, 690, and 693, and Lower Cretaceous (Albian) silicoflagellates at Site 693 (the latter are described in McCartney, et al., this volume). The uppermost Miocene-lowermost Pliocene of most sites contains an interesting assemblage of *Distephanus speculum speculum* that lack apical rings (the "pseudofibula plexus"). These co-occur with the youngest ice-rafted sediments deposited during the late Miocene-early Pliocene West Antarctic glaciations and are discussed in detail to show the variability within this group. We believe that these variations resulted from environmental stress, the precise nature of which is still undetermined. The "pseudofibulid" condition has developed at several different times during the Cenozoic within the *Distephanus speculum* lineage to produce such ecophenotypes. One new form from the "pseudofibula plexus," *D. s. speculum f. pseudopentagonus*, is described.

### INTRODUCTION

Ocean Drilling Program Leg 113 was the first drilling leg to explore the Weddell Sea (Figs. 1, 2). This complemented the inaugural leg to the high latitudes of the Antarctic Ocean, Leg 28 to the Ross Sea, which recovered the first extensive sequences of silicoflagellates from this region. Most of the six other legs that followed to the Southern Ocean were to the subantarctic region (Table 1).

During Leg 113, silicoflagellates were recovered from the Neogene at eight sites, the Paleogene (Oligocene-Eocene) at three sites, and the Lower Cretaceous at one site (Table 2). They were commingled with carbonate pelagic sediments throughout most of Sites 689 and 690 on Maud Rise and with biosiliceous and siliclastic sediments at the others. At all sites they were seldom abundant, except at certain intervals in the Pliocene and Pleistocene, and their diversities were also generally low. For the Maud Rise sites, low abundances and diversities can be attributed to low phytoplankton productivity, as indicated by the low sedimentation rates recorded at these sites (Barker, Kennett, et al., 1988). They were more abundant there, however, than at comparable water depths on the adjacent Antarctic margin (Site 693), where the section was considerably diluted by siliclastics. The accumulation of biosiliceous material was high in the middle Miocene to Pliocene at most other nonabyssal sites, but drilling problems precluded recovery in some holes, particularly at Site 696. In general, abundances and diversities of silicoflagellates at the Leg 113 sites were far lower than at subantarctic sites to the north, which are located closer to zones of upwelling along boundaries between major water masses (present and past), such as the Polar Front Zone.

An interesting phenomenon noted in silicoflagellate assemblages from two intervals is exceptional intraspecific variability or morphologic plasticity. This was expressed consistently at all sites among the lower Pliocene representatives of *Distephanus speculum speculum*, an assemblage we refer to as the "pseudofibula plexus."

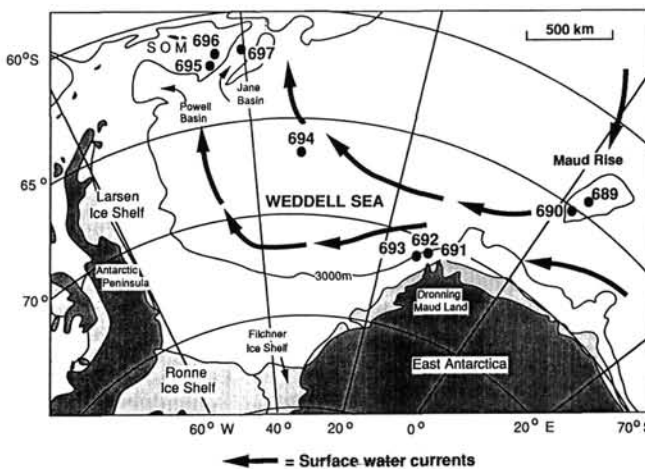


Figure 1. Location of sites drilled on ODP Leg 113; arrows indicate the surface current regimes prevalent during the late Neogene.

*bula plexus.*" We speculate in this paper that the morphologic plasticity within this plexus might be attributable to environmental stress. Exceptional variability was also seen in a much older Lower Cretaceous (lower Albian) assemblage from Site 693 where the cause is more likely purely genetic. We discuss the Pliocene case in some detail in this paper and the Lower Cretaceous occurrence in a companion paper (McCartney et al., this volume).

In addition to silicoflagellates, we chronicle here occurrences of ebridiens, which were locally abundant at Site 689. Notable there is an assemblage near the Eocene/Oligocene boundary which contains exceptionally large and complicated forms previously known only from middle Eocene piston cores taken on the Falkland Plateau to the north.

### SAMPLE PREPARATION, METHODS OF STUDY, AND ZONATION

For Holes 689B and 690B, in which there was an abundance of calcareous material, raw samples were placed in 100 mL beakers and a small amount of 30% hydrogen peroxide added. After 2-4 hr the beaker was placed in an ultrasonic cleaner and distilled water was added to approximately the 25 mL level. HCl

<sup>1</sup> Barker, P. F., Kennett, J. P., et al., 1990. *Proc. ODP, Sci. Results*, 113: College Station, TX (Ocean Drilling Program).

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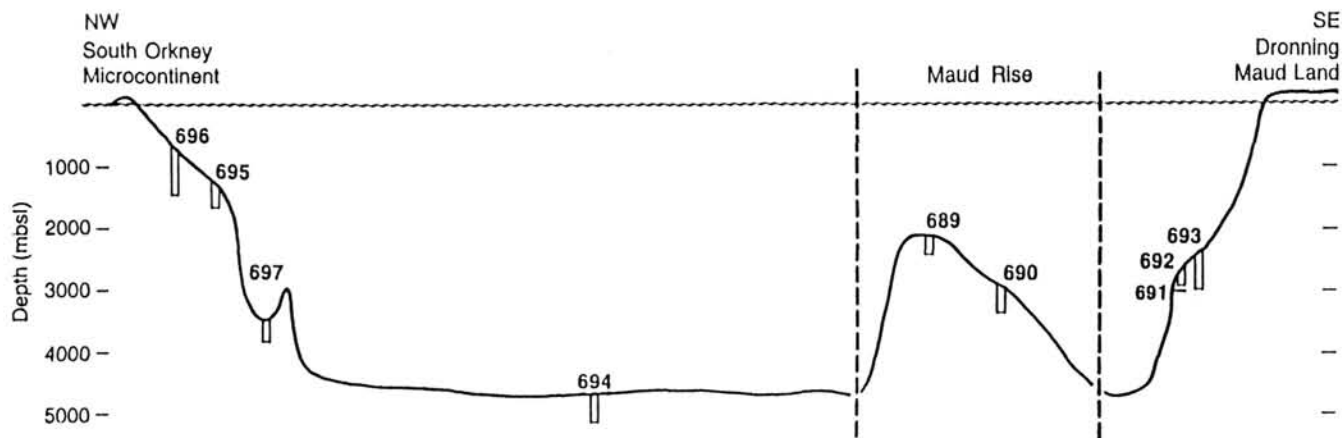


Figure 2. Cross section showing ocean bottom profile and water depth of holes drilled during Leg 113.

**Table 1. Silicoflagellate and ebridian studies from southern ocean sites (>45°S). All publications listed here, unless stated otherwise, include charts showing relative abundances. X = present throughout the series; U, M, or L = subseries.**

Leg (Sites)	Pleistocene	Pliocene	Miocene	Oligocene	Eocene	Paleocene	Pleistocene	Reference
28 (265-271)				X				Bukry (1975a) Ciesielski (1975)
	X	X	X	X				
29 (275, 278, 280)	X	X	X	X	U, M		U	Bukry (1975c) Hajos (1975)
	X	X	X	X	U		U	Perch-Nielsen (1975a, b)
35 (322-323)	(no abundance charts)							Bukry (1976b) Haq and Riley (1976) Hajos (1976)
		X	X		U			
36 (326-329)	X	X	U			U		Bukry (1976a)
	X	U	X	X	U, L	U		Busen and Wise (1977)
38 (336-346)			M, L	L	M?, U			Bukry (1976c)
71 (511-514)	X	X	X	X				Shaw and Ciesielski (1983)
90 (594)	X	X	X					Locker and Martini (1986)

**Table 2. Occurrence of Cenozoic silicoflagellates in Leg 113 cores.**

Hole	Latitude	Longitude	Water depth (m)	Number of cores	Recovery (%)	Silicoflagellate occurrence
689A	64°31.01'S	03°05.99'E	2080	1	98.4	Pleistocene-Pliocene
689B	64°31.01'S	03°05.99'E	2080	33	77.2	Pleistocene-upper Eocene
689C	64°31.01'S	03°06.03'E	2080	3	75.8	Pleistocene-Miocene
689D	64°31.01'S	03°06.03'E	2080	12	101.4	Pliocene-upper Eocene
690A	65°09.63'S	01°12.30'E	2914	1	128.0	Pleistocene-Pliocene
690B	65°09.63'S	01°12.30'E	2914	25	100.5	Pleistocene-Oligocene
690C	65°09.62'S	01°12.29'E	2914	24	88.3	Pleistocene-Oligocene
693A	70°49.89'S	14°34.41'W	2359	51	44.1	Pleistocene-Oligocene; Lower Cretaceous
693B	70°49.89'S	14°34.46'W	2539	19	55.1	Miocene-Oligocene; Lower Cretaceous
694A	66°50.83'S	33°26.80'W	4653	1	100.0	Pleistocene-Pliocene
694B	66°50.84'S	33°26.83'W	4653	25	34	Pleistocene-Miocene
694C	66°50.82'S	33°26.76'W	4653	23	33.7	Miocene
695A	62°23.48'S	43°27.10'W	1305	42	73.7	Pleistocene-Pliocene
696A	61°50.95'S	42°55.98'W	650	12	55.0	Pleistocene-Pliocene
696B	61°50.96'S	42°56.00'W	650	62	27.5	Pliocene-Miocene
697A	61°48.63'S	40°17.73'W	3481	3	94.7	Pleistocene
697B	61°48.63'S	40°17.73'W	3483	32	61.7	Pleistocene-lower Pliocene

was added and the beaker heated for 30 min. Samples were then centrifuged and decanted twice and washed once before making strewn slides. For similar methods of slide preparation, see Bukry (1983) and Busen and Wise (1977). For Sites 693 to 697, in which there was little calcareous material, strewn slides were made directly from the raw sediment.

A major goal of this study has been to provide quantitative information on the assemblages. Although a general practice is to count 300 specimens per slide, the silicoflagellate abundance in this study area was often not sufficient to allow such counts without a prohibitive investment of time. Except where the silicoflagellates were extremely abundant, all specimens on a slide

(under a 22 × 40 mm coverslip) were counted. Where the silicoflagellates were abundant, a second and even third slide might be counted. Fragments representing more than half of the original skeleton were included in the counts.

The desire to quantify the assemblage data necessarily meant that less emphasis could be placed on tracing out rare zonal markers, which was the goal during the shipboard studies. More detailed applications of zonal schemes applied to core catcher samples have been published in Barker, Kennett, et al. (1988). These qualitative biostratigraphic data from the shipboard work are included in the text of the present paper but are not always indicated on the range charts. Ages given on the range charts reflect the consensus ages provided by all of the microfossil groups plus the paleomagnetic data and are not derived solely from the silicoflagellate biostratigraphy. Where conflicts exist, the ages provided by the radiolarian stratigraphy are given (Lazarus, this volume).

While a number of high-latitude silicoflagellate zonation schemes are available in the literature (Bukry, 1975c; Ciesielski, 1975; Martini and Muller, 1976), the one by Bukry combined with a modification of the Pliocene scheme of Ciesielski was the most applicable to our quantitative study (Table 3). Alternate zonations that could be applied for a given section are discussed in the text. The silicoflagellate biostratigraphy of Leg 113 is shown in Table 4 and discussed in more detail below.

### SITE SUMMARIES

The locations and water depths of holes considered in this study are given in Table 2. Some of these holes were not examined in detail for silicoflagellates either because the core recovery was very low, they overlapped other holes at the same site, or the silicoflagellates were very rare.

#### Site 689 (Table 5)

Both the diversity and the abundance of silicoflagellates are higher at Hole 689B than elsewhere for ODP Leg 113. Silicoflagellates are well represented in the Pliocene and lower Oligo-

cene at Hole 689B, but are less common through most of the Miocene except at selected intervals. These can be zoned using the zonation of Bukry (1975c).

Cores from Section 113-689B-1H-1 to Section 113-689B-2H-5 are dated by radiolarian biostratigraphy as lower Pliocene in age (Shipboard Scientific Party, 1988a), and they contain large numbers of specimens that sometimes comprise veritable silicoflagellate oozes. These are strongly dominated by *Distephanus speculum speculum* down to Section 113-689B-2H-2 and by *D. boliviensis* below that. Sections 113-689B-2H-6 to 113-689B-3H-5 are dominated by forms of *D. speculum speculum* that are referred to here as the "pseudofibula plexus." These cores belong to the *Bachmannocena diodon* Subzone. Small numbers of the *pseudofibula* plexus occur in Sections 113-689B-2H-4 and 113-689B-2H-5. We assume that these are reworked above a discontinuity between Sections 113-689B-2H-5 and 113-689B-2H-6 indicated by the diatom stratigraphy (Gersonde and Burckle, this volume). The relatively high abundance of *Distephanus boliviensis* just above the *pseudofibula* plexus found at Hole 689B is similar to that found by Ciesielski (1974, 1975).

Hole 689B was unusual among those drilled during Leg 113 in that both members of the *pseudofibula* plexus and the *Bachmannocena* species *B. diodon* co-occur in large numbers. Large *Bachmannocena* specimens are rare or absent at the other Leg 113 sites. These have been used as zonal indicators (Ciesielski, 1975; Martini and Muller, 1976; Busen and Wise, 1977), but *B. diodon* is used here only as a subzonal marker because the occurrences of this and the other Miocene/Pliocene *Bachmannocena* species are generally sporadic, in part due to hiatuses. Neither *B. circulus* nor *B. diodon* occurs in many samples of Hole 689B, but where present they are abundant. According to the zonation of Ciesielski (1975), the high concentration of *B. circulus* in Sample 113-689B-6H-2, 29–31 cm, would indicate his upper Miocene *B. circulus* Zone. This core, however, is dated as middle Miocene by combined radiolarian, diatom, and magnetostratigraphic analysis (Shipboard Scientific Party, 1988a, p. 126, 127, and 143). This indicates that abundant *B. circulus* appears in the Southern Ocean earlier than previously documented, which is more in accordance with its range recorded elsewhere in the world (e.g., McCartney and Wise, 1987).

A hiatus at approximately 21 mbsf (Core 113-689B-3H), which separates lower Pliocene from upper Pliocene sediments, has been inferred from radiolarian and paleomagnetic data (Shipboard Scientific Party, 1988a, p. 123; Gersonde et al., this volume). This hiatus seems to be corroborated by the silicoflagellate stratigraphy in that *B. diodon* is absent below 21 m. Such a hiatus would also explain the absence of the *B. diodon/B. circulus* Zone of Busen and Wise (1977) at this site.

The Miocene is not zoned here in detail, although it may be possible to recognize the extinction of *Corbisema triacantha* in Section 113-689B-7H-5 based on a very small number of specimens. There is an acme of multiwindowed *Distephanus speculum hemisphaericus* in Sections 113-689B-7H-2 to 113-689B-8H-5, but the authors believe this to be due to environmental reasons. Thus we do not use this abundance to describe a new biostratigraphic zone, although this is done elsewhere (see Ciesielski et al., 1989). The multiwindowed forms are not as abundant at other Leg 113 sites.

There appears to be a hiatus between Sections 113-689B-8H-2 and 113-689B-8H-5 where the uppermost Oligocene sediments have been removed, as *Naviculopsis biapiculata* was not found (see also Shipboard Scientific Party, 1988a, p. 123). Sections 113-689B-8H-5 to 113-689B-14H-5 are characterized by *Bachmannocena apiculata*, *Distephanus crux*, and *Dictyocha frenguelli* in the upper part. Much of the interval can be assigned to the *Dictyocha deflandrei* Zone of Bukry (1975c). The *Dictyocha frenguelli* Subzone extends downhole to Section 113-689B-12H-2,

Table 3. Silicoflagellate zonation used for Leg 113.

Age	Silicoflagellate zones and subzones	Guide species	
Pleistocene	<i>Distephanus speculum speculum</i>		
Pliocene	"pseudofibula plexus"	<i>Distephanus</i> s. s. f. <i>notabilis</i>	<i>pseudofibula</i> assemblage <sup>†</sup>
		<i>Bachmannocena diodon</i>	<i>Bachmannocena diodon</i> <sup>†</sup>
Miocene	<i>Distephanus longispinus</i>	<i>pseudofibula</i> assemblage*	
	<i>Corbisema triacantha</i>	<i>Corbisema triacantha</i> <sup>†</sup>	
	<i>Naviculopsis quadratum</i>	<i>Corbisema triacantha</i> A*	
	<i>Distephanus speculum pentagonus</i>	<i>Naviculopsis quadratum</i> *	
	<i>Naviculopsis biapiculata</i>	<i>Naviculopsis biapiculata</i> <sup>†</sup>	
	<i>Naviculopsis biapiculata</i>	<i>Naviculopsis biapiculata</i> *	
Oligocene	<i>Dictyocha deflandrei</i>	<i>Dictyocha frenguelli</i>	<i>Dictyocha frenguelli</i> *
		<i>Bachmannocena apiculata</i>	<i>Bachmannocena apiculata</i> A*
		<i>Naviculopsis trispinosa</i>	
Eocene			

\* = First appearance.

† = Last appearance.

**Table 4. Silicoflagellate zones found in sections shown from Leg 113.**

Silicoflagellate zone or subzone		Hole 689B	Hole 690B	Hole 693A	Hole 694B	Hole 695A	Hole 696A	Hole 696B	Hole 697B
<i>Distephanus speculum speculum</i>		1H-1 to 2H-5	2H-1 to 3H-3	6R-2 to 12R-7		3H-2 to 30X-2	1X-2 to 9X-2	2R-1 to 3R-5	11H-3 to 32X-3
"pseudofibula plexus"	<i>Distephanus s. s. f. notabilis</i>		3H-4 to 3H-5	13R-1 to 18R-2	14H-1	32X-2 to 35X-2		5R-2 to 10R-1	32X-5
	<i>Bachmannocena diodon</i>	2H-6 to 3H-5							
<i>Distephanus longispinus</i>		3H-6 to 7H-2	3H-6 to 6H-2						
<i>Corbisema triacantha</i>			6H-5						
<i>Naviculopsis quadratum</i>									
<i>Distephanus speculum pentagonus</i>									
<i>Naviculopsis biapiculata</i>									
<i>Dictyochoa deflandrei</i>	<i>Dictyochoa frenguelli</i>	8H-5 to 12H-2	7H-2 to 10H-2	38R-1 to 40-1					
	<i>Bachmannocena apiculata</i>	12H-5 to 15H-2							
	<i>Naviculopsis trispinosa</i>								

based on the first occurrence of the nominative species. The boundary between the lower two subzones of the *D. deflandrei* Zone, however, cannot be drawn because *Bachmannocena apiculata* continues downhole to the disconformity at the base of the Oligocene section. There is a sharp abundance peak (acme) of *Naviculopsis trispinosa* in Section 113-689B-13H-2, however, which may coincide with the extinction of this taxon. Slightly lower in the section in Hole 689D, Core 113-689D-10H yielded a diverse assemblage, which includes *Distephanus crux*, *Bachmannocena apiculata*, and *B. occidentalis*. The upper Eocene Section 113-689D-12H, CC, contains well preserved *Dictyochoa quadria* (not shown on range chart).

Ebridians are unusually abundant in Sections 113-689B-14H-5 to 113-689B-15-2. A very unusual assemblage of large ebridians was found in Sample 113-689B-14H-5, 30-32 cm. A similar assemblage has been described previously by Gombos (1982) from the middle Eocene of the Falkland Plateau. The co-occurring silicoflagellates, however, indicate that these samples are still part of the *Dictyochoa deflandrei* Zone and thus are late Eocene or Oligocene in age. The ebridians *Adonnadonna* and *Triskeilion* (Pl. 7) appear to range above the middle Eocene, assuming that the specimens are not reworked.

#### Site 690 (Table 6)

The silicoflagellate stratigraphy at this site is similar to that at the shallower Site 689, except that abundances are lower in the Miocene and Oligocene. Silicoflagellates are well represented in the Pliocene at Site 690, where silicoflagellate-diatom oozes are dominated by *Distephanus speculum* from Sections 113-690B-2H-1 to 113-690B-3H-2. The last appearance datum of *Distephanus boliviensis* is in Section 113-690B-2H-7, below which this taxon alternates in dominance with *D. speculum* downsection to Section 113-690B-3H-4 and 113-690B-3H-5. As at Site 689, a wide diversity of six-sided morphologies without apical rings (the *pseudofibula* plexus) is very abundant in a relatively short interval from Section 113-690B-3H-4 to -3H-5. Unlike the situation at Site 689, however, *Bachmannocena diodon* is not present in this interval due to a disconformity within Section

113-690B-3H-5, whereby the lowermost Pliocene is missing (including the radiolarian lower Tau Zone (Lazarus, this volume)). This disconformity between 18.0 and 19.5 mbsf is recorded in all siliceous microfossil groups (Gersonde et al., this volume). The interval containing the *pseudofibula* plexus, therefore, is assigned to the *Distephanus s. speculum f. notabilis* Subzone. This subzone appears to be bounded above as well as below by disconformities, hence the abrupt changes in the abundances of the *pseudofibula* plexus. There might be a slight discrepancy between the diatom and silicoflagellate stratigraphies, however, in the placement of the disconformity shown in Table 6 between 15.0 and 16.5 mbsf (see Gersonde et al., this volume).

At this site, the *Distephanus longispinus* Zone includes an exceptional abundance of five-sided *Distephanus speculum*. The Miocene *Corbisema triacantha* Zone may be represented by Sample 113-690B-6H-5, 28-30 cm. Much of the Miocene and Oligocene, however, appears to be absent due to hiatuses (see Tables 4, 6). Among the lower Miocene and upper Oligocene zones that are missing are the *Naviculopsis biapiculata* Zone and the *N. trispinosa* Subzone of the *Dictyochoa deflandrei* Zone. *Bachmannocena apiculata* and *Dictyochoa deflandrei* co-occur in Section 113-690A-9H-02, indicating an early Oligocene age, but the silicoflagellate abundances are very low. The *Naviculopsis trispinosa* acme noted at Site 689 is missing due to the hiatus between the Miocene and Oligocene.

#### Site 693 (Table 7)

The silicoflagellate biostratigraphy at Site 693 on the Antarctic margin is very similar to that found at Site 690. The Pleistocene section is barren of silicoflagellates, whereas *Distephanus speculum speculum* is present in Sections 113-693A-6R-2 to 113-693A-12R-2, but the abundances are much less than that in comparable cores from Holes 689B and 690A. *Distephanus boliviensis* is abundant in Section 113-693A-12R-7, which is immediately above the *pseudofibula* plexus. This abundance of *D. boliviensis* above the *pseudofibula* plexus is also found in Hole 689B and in DSDP Leg 28, and this interval could be assigned to the *D. boliviensis* Zone of Ciesielski (1975). The *pseudofi-*

*bula* plexus occurs over a relatively large interval, spanning Sections 113-693A-13R-1 to 113-693A-15R-2 and perhaps extending to 113-693A-18R-2.

Although not shown in detail on the range chart, a number of important datums marked by rare to few *Bachmannocena* were noted in core-catcher samples. The last appearance datum (LAD) of *B. diodon* indicated by rare specimens in Section 113-693A-17R, CC, marks the lower Pliocene top of the *B. diodon* Zone of Ciesielski (1975) (or of the *B. diodon* Subzone of this study), which straddles the Pliocene/Miocene boundary. The top of the subjacent *B. circulus*-*B. diodon* Zone of Busen and Wise (1977) can probably be placed at Section 113-693A-22R, CC (uppermost Miocene), which contains rare *B. circulus* var. *dumitrica*. The Pliocene/Miocene boundary on the range chart is that given by the Shipboard Scientific Party (1988b). Silicoflagellates are infrequent throughout the remainder of the Miocene section, and it is not possible to zone this interval.

No range chart was prepared for Hole 693B, but the following observations were made on core-catcher samples from that hole. The lowermost(?) Miocene Section 113-693B-9X, CC, contains one nearly complete specimen of *Corbisema inermis crenulata*, which has only been reported from the Paleocene and is presumed to have been reworked into this section from sediments higher upslope on the margin of Antarctica.

Core 113-693B-11X (316.1–325.8 mbsf) contains *Bachmannocena apiculata apiculata* and *Distephanus crux darwinii*. On the Falkland Plateau, the latter taxon has been reported only from the upper Oligocene (Busen and Wise, 1977). Upper Oligocene Cores 113-693B-12X and 113-693B-13X contain *D. crux* and *Naviculopsis biapiculata*.

In the Oligocene of Hole 693A, the occurrence of *Bachmannocena apiculata*, *Dictyocha deflandrei*, and *Dictyocha frenguelli* in Sections 113-693A-38H-1 to 113-693A-40H-1 indicates that this interval belongs to the *Dictyocha frenguelli* Subzone of the *Dictyocha deflandrei* Zone, which is near the lower Oligocene/upper Oligocene boundary. Silicoflagellates are well preserved, and ebridians are also found in this interval. The lower Oligocene *Naviculopsis trispinosa* acme observed at Site 689 was not noted at Site 693. This indicates that, due to a hiatus, the lowermost Oligocene was not cored at this site. The ebridian *Ammodoichium ampulla* is common at the base of the sequence.

The Cretaceous diatomaceous sediments from Lithostratigraphic Unit 6 contain no members of the diverse silicoflagellate assemblage described from the Maestrichtian siliceous ooze at DSDP Site 275 on the Campbell Plateau (Hajos, 1975). Conspicuously absent at Site 693 are Upper Cretaceous taxa reported from Site 275 and elsewhere such as *Corbisema geometrica*, and species of *Lyrarmula*. This negative evidence indicates that the diatomaceous sediments recovered at Site 693 are older than Santonian or Campanian in age. According to the coccolith and palynomorph dates on the underlying "black shales," however, they can be no older than late Aptian in age (Mutterlose and Wise, this volume; Mohr, this volume, chapter 29), and Mohr (this volume, chapter 29) suggests an early Albian age for the deposit. These richly diatomaceous sediments do contain a rich assemblage of what appears to be an ancestral silicoflagellate stock, which McCartney et al. (this volume, chapter 27) discuss in some detail.

#### Site 694 (no range chart)

Silicoflagellates were largely absent at this deep water site, and no zonation is attempted. Members of the *pseudofibula* plexus are present, however, in a very narrow interval that includes Section 113-694B-14H-1, 67–69 cm. This is just below the thick sequence of sand turbidites of Lithostratigraphic Unit II. This occurrence supports an age near the Miocene/Pliocene

boundary (Gensonde et al., this volume). The sands are interpreted as the products of high-energy turbidity currents (see Barker, Kennett, et al., 1988). It is interesting to note that at the three sites drilled to the north of Site 694 (see summaries for Sites 695–697 below), *pseudofibula* plexus is present in several cores immediately above a prominent interval of ice-rafted debris attributed to late Miocene-early Pliocene glaciation.

#### Site 695 (Table 8)

Silicoflagellates are generally present but are of low diversity in Sections 113-695A-1H to 113-695A-35X-2 (Lithostratigraphic Units I and II), and are absent in the clays and glacial marine sediments of Lithostratigraphic Unit III (Cores 113-695A-37X to 113-695A-41X). Overall, silicoflagellates are most common and well preserved where diatoms are well preserved and are absent or present mostly as fragments where diatom preservation is only moderate or poor. As a group, the silicoflagellates appear to be more sensitive to dissolution than the diatoms (Schradler, 1972).

The Pliocene interval of Site 695 is much longer than in the previous Leg 113 sites. Short-spined *Distephanus speculum speculum* dominate the assemblages from Cores 113-695A-3H to 113-695A-7H. This interval can be assigned to the *D. speculum speculum* Zone of Bukry (1975c) or, alternatively, to *D. speculum* B of Ciesielski (1975) and Ciesielski and Weaver (1983). Silicoflagellates are absent in Cores 113-695A-8H to 113-695A-12H where diatom preservation is poor. *Distephanus speculum* and *D. boliviensis* co-occur in Sections 113-695A-12H, CC (not on range chart) to 113-695A-20X-2, but *D. boliviensis* dominates from 113-695A-22X-2 to 113-695A-29X-2, although its abundance is low. This interval, where *D. boliviensis* is dominant, is zoned here as part of the *Distephanus speculum speculum* Zone (Bukry, 1975c) but can alternatively be assigned to the *Distephanus boliviensis* Zone of Ciesielski (1974, 1975). The zonation of Bukry is preferred by the authors because the two *Distephanus* taxa sometimes appear to intergrade and because the *pygmaea* and *pumila* variants of *Dictyocha* (see Ciesielski, 1975; Ciesielski and Weaver, 1983) are absent throughout the Leg 113 samples.

Sections 113-695A-32X-4 to 113-695A-35X-2 are dominated by members of the *pseudofibula* plexus. Shaw and Ciesielski (1983) place the *pseudofibula* acme in the middle Gilbert. This corresponds well to the radiolarian assignment for these cores (upper portion of the lower Tau; see Lazarus, this volume). Core-catcher samples below Core 113-695A-35X were barren.

#### Site 696 (Tables 9 and 10)

Holes 696A and 696B present a biostratigraphy similar to that found in previous Leg 113 sites, but only down to the middle Miocene. *Distephanus speculum* dominates through Hole 696A except for the deepest sample studied. At Hole 696B, *Distephanus boliviensis* is dominant in Section 113-693B-3R-5. Aboard ship an attempt was made to apply the zonation of Ciesielski (1975) to the sequence with the following results (Shipboard Scientific Party, 1988c): Core 113-696A-1H contained *Distephanus speculum speculum* and *D. septenarius*, and is assigned to the *D. speculum* A Zone of Ciesielski (1975). Short-spined *D. speculum* dominate Cores 113-696A-2H to 113-696A-6H, and these are assigned to the *D. speculum* B Zone. The *Distephanus boliviensis* Zone extends from 55 to 101 mbsf, with an acme in the numbers of silicoflagellates in Cores 113-696A-11X and 113-696A-12X as well as in Core 113-696B-3R. This sequence could not be discerned at all sites, however, and is not indicated on the range charts. The *pseudofibula* plexus occurs from Sections 113-696B-5R-2 to 113-696B-12R, CC (not on range chart), which is a thick interval similar to that found at Hole 693A. The silicoflagellate-

**Table 5. Abundance of silicoflagellates and ebridians in selected samples from Hole 689B. Species (in alphabetical order) are recorded as total number of specimens found in slides examined.**

Litho-stratigraphic unit	Age	Silicoflagellate zone or subzone		Core, section, interval (cm)	Depth (mbsf)	Number of slides examined	Silicoflagellates																				
							<i>Bachmannocena apiculata</i>	<i>B. circularis</i>	<i>B. diodon</i>	<i>B. occidentalis</i>	<i>Corbisema apiculata</i>	<i>D. geometrica</i>	<i>C. hastata</i>	<i>C. inermis inermis</i>	<i>C. triacantha</i>	<i>Dictyocha aspera</i> (s. amph.)	<i>D. byronalis</i>	<i>D. calida</i>	<i>D. deflandrei</i>	<i>D. frenguelli</i>	<i>D. fibula</i> (s. amph.)	<i>D. spinosa</i>					
I	Pliocene	<i>Distephanus speculum speculum</i>		1H-1, 29-31	0.3	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
				1H-4, 29-31	4.8	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
				2H-2, 33-35	7.1	0.9	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				2H-4, 29-31	10.1	0.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				2H-5, 29-31	10.6	0.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				2H-6, 30-32	12.1	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
IIA	Miocene	<i>Distephanus longispinus</i>		3H-2, 30-32	16.6	0.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
				3H-5, 29-31	21.1	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
				3H-6, 29-31	22.6	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				4H-1, 30-31	24.6	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				4H-2, 29-31	26.1	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				4H-5, 30-32	30.6	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
IIA	Miocene	<i>Corbisema triacantha</i>		5H-2, 30-32	35.6	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
				5H-5, 29-31	39.1	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
				6H-2, 29-31	45.1	1.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				6H-5, 29-31	49.6	2.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				7H-2, 29-31	54.7	2.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				7H-5, 29-31	59.3	2.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
IIB	Oligocene	<i>Dictyocha deflandrei</i>		8H-5, 30-32	68.8	2.0	65	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
				9H-2, 29-31	73.9	2.0	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				9H-5, 29-31	78.4	2.0	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				10H-2, 29-31	83.5	2.0	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				10H-5, 29-31	88.0	2.0	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				11H-2, 32-34	93.1	2.0	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				11H-5, 32-34	97.6	2.0	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				12H-2, 29-31	102.8	2.0	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				12H-5, 29-31	107.3	2.0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				13H-2, 29-31	112.4	0.4	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				13H-5, 28-30	117.9	2.0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				14H-2, 30-32	122.0	2.0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				14H-5, 30-32	126.5	1.0	39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
				15H-2, 30-32	131.7	1.0	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
						<i>Bachmannocena apiculata</i>		12H-5, 29-31	107.3	2.0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
						<i>Naviculopsis trispinosa</i>		13H-2, 29-31	112.4	0.4	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
								13H-5, 28-30	117.9	2.0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
								14H-2, 30-32	122.0	2.0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
				14H-5, 30-32	126.5	1.0	39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
				15H-2, 30-32	131.7	1.0	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				

bearing samples below the *pseudofibula* plexus contained only five- and six-sided *Distephanus* and consequently could not be zoned.

**Site 697 (Table 11)**

Silicoflagellates are generally sparse or absent in the upper 250 m of the siliceous muds at Site 697; therefore, these fossils do not provide useful datums for biostratigraphy in Sections 113-697A-1H-1 to 113-697B-11H-3. This paucity of silicoflagellates is probably due to the relatively deep water of this site (3480 m), which would have promoted the dissolution of these fossils. Two diatomaceous intervals from Sections 113-697B-13X-1 to 113-697B-15X-3 and 113-697B-21X-2 to 113-697B-22X-2, however, did contain silicoflagellates in moderate abundance. These intervals indicate enhanced productivity and preservation of biosiliceous material.

Six-sided *Distephanus* was relatively abundant from Sections 113-697B-13X-1 to 113-697B-22X-2. *D. speculum* predominates in the upper part of this interval whereas *D. boliviensis* is most abundant in the lower part; there is no distinct dividing point between these areas of dominance. Silicoflagellates are sparse or absent from Sections 113-697B-25X-1 to 113-697B-32X-3,

except for 113-697B-28X-5 where *D. boliviensis* occurs in modest numbers.

Members of the *pseudofibula* plexus occur in low numbers in the deepest sample shown on the range chart (Table 11) as well as in Sections 113-697B-30X, CC and 113-697B-31X, CC (not on range chart); therefore, these last three cores can be assigned to this interval. The occurrence of the *pseudofibula* plexus coincides closely with the lower portion of the radiolarian Tau Zone (see Lazarus, this volume).

**SILICOFLAGELLATE SKELETAL VARIABILITY AND THE PSEUDOFIBULA PLEXUS**

**Explanatory Note**

One of the most unusual yet consistently present assemblages in the Leg 113 sequences is composed primarily of the group we refer to as the "*pseudofibula* plexus." This consists of the following five forms of *Distephanus speculum speculum*, which have been named formally:

- D. s. s. forma pseudofibula*
- D. s. s. forma varians*

Table 5 (continued).

Silicoflagellates										Ebridians										
<i>D. pentagona</i>																				
<i>D. stapedia</i>																				
<i>Disstephanus boliviensis</i>																				
<i>D. boliviensis major</i>																				
<i>D. crux</i> (s. amph.)																				
<i>D. longispinus</i>																				
<i>D. speculum hemisphaericus</i> (6 sides, 2-4 windows)																				
<i>D. speculum hemisphaericus</i> (6 sides, >4 windows)																				
<i>D. speculum hemisphaericus</i> (7 or more sides)																				
<i>D. speculum minutus</i>																				
<i>D. speculum pentagonus</i>																				
<i>D. speculum pentagonus</i> (cannopliid)																				
<i>D. speculum speculum</i> (6 sides)																				
<i>D. speculum speculum</i> (7 sides)																				
<i>D. speculum speculum</i> (8 or more sides)																				
<i>D. speculum speculum</i> f. <i>notabilis</i>																				
<i>D. speculum speculum</i> f. <i>pseudofibula</i>																				
<i>D. speculum speculum</i> f. <i>varians</i>																				
<i>D. speculum speculum</i> f. <i>pseudocrux</i>																				
<i>D. speculum speculum</i> f. <i>pseudopentagonus</i>																				
<i>Naviculopsis constricta</i>																				
<i>N. eobiapiculata</i>																				
<i>N. ponticola</i>																				
<i>N. ponticola</i> (asperid)																				
<i>N. trispinosa</i>																				
teratoid silicoflagellates																				
<i>Adonnadonna primadonna</i>																				
<i>Ammodochium ampulla</i>																				
<i>Craniopsis octo</i>																				
<i>Ebriopsis antiqua</i>																				
<i>Parathanium tenuipes</i>																				
<i>Triskelion gorgon</i>																				

- D. s. s.* forma *notabilis*
- D. s. s.* forma *pseudocrux*
- D. s. s.* forma *pseudopentagonus*, n. f.

These seemingly distinct and different forms are unusual in that they belong to one subspecies. As such, they demonstrate the considerable morphologic plasticity that can occur within silicoflagellate taxa.

It is well known that silicoflagellates show exceptional variability in modern populations. However, in recent paleontologic literature and especially in silicoflagellate research concerning deep sea drilling, there has been an emphasis on subdividing taxa. Thus the number of silicoflagellate species in the paleontologic literature has increased enormously. This taxonomy may well bear little relation to actual biological relationships. In this section, by way of background information, we review the general silicoflagellate skeletal morphology and its variability. We then discuss the *pseudofibula* plexus found in Leg 113 and elsewhere, as it is an excellent example of silicoflagellate variability in the fossil record.

### Silicoflagellate Skeletal Morphology

The silicoflagellate skeleton is composed of tubular silica elements that are rigidly interconnected to form a three-dimensional framework. This framework consists of a planar polygonal basal ring and an apical structure that forms a dome-like latticework above it. The apical structure usually consists of struts, which attach to the sides of the basal ring at some point between the corners, and an apical bridge or ring. The apical ring, if present, is usually a polygon similar to, and in a parallel plane with, the basal ring. In some forms, including most *Corbisema*, the struts meet at an apex without forming a bridge. Various workers (Mandra and Mandra, 1972; Poelchau, 1974; Bukry, 1976d; Perch-Nielsen, 1985; among others) have previously illustrated the descriptive terminology; the terminology used in this article is shown in Figure 3.

The term "element" is here used to denote a single skeletal rod that makes up a part of the silicoflagellate skeleton. Each skeletal element generally intersects other elements at each end. In all but a few cases, these intersections consist of three ele-







**Table 8. Abundance of silicoflagellates in selected samples from Hole 695A. Species (in alphabetical order) are recorded as total number of specimens found in slides examined.**

Litho- stratigraphic unit	Age	Silicoflagellate zones	Core, section, interval (cm)	Depth (mbsf)	Number of slides examined	Total number of specimens	<i>Dictyochoa</i> <i>pentagona</i>	<i>Distephanus</i> <i>boliviensis</i> (6 sides)	<i>D. boliviensis</i> (7 sides)	<i>D. crux</i>	<i>D. speculum</i> <i>hemisphaericus</i> (2-4 windows)	<i>D. speculum</i> <i>speculum</i> (6 sides)	<i>D. speculum</i> <i>speculum</i> (7 sides)	<i>D. speculum</i> pentagonus	<i>D. speculum</i> pentagonus (cannopliid)	<i>D. speculum</i> <i>speculum</i> f. <i>notabilis</i>	<i>D. speculum</i> <i>speculum</i> f. <i>pseudofibula</i>	<i>D. speculum</i> <i>speculum</i> f. <i>varians</i>	teratoid silicoflagellates		
IA	Pleistocene	<i>Distephanus speculum speculum</i>	1H-2, 30-32	1.8	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
			2H-2, 30-32	4.7	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1B	3H-2, 30-32		14.2	1.0	34	.	.	.	.	.	.	34	.	.	.	.	.	.	.	1	
	4H-2, 30-32		23.8	1.0	300	1	.	.	.	.	.	295	.	2	.	.	.	.	.	31	
1C	Pliocene		5H-2, 30-32	33.4	1.0	16	.	.	.	.	.	16	.	.	.	.	.	.	.	2	
			6H-2, 30-32	43.0	1.0	27	.	.	.	.	.	26	1	.	.	.	.	.	.	.	
1D	Pliocene		7H-2, 31-33	53.6	1.0	41	.	.	.	.	.	34	3	.	.	.	.	.	.	4	
			8H-2, 130-132	63.2	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1E	Pliocene		9H-2, 30-32	71.8	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
			10H-2, 30-32	81.4	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1F	Pliocene		12H-2, 30-32	91.0	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
			13H-2, 30-32	100.6	1.0	22	.	6	2	.	.	11	.	.	.	.	.	.	.	.	3
1G	Pliocene		14H-2, 28-30	110.3	1.0	8	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.
			15H-2, 30-32	120.0	1.0	73	.	65	.	.	.	8	.	.	.	.	.	.	.	.	.
1H	Pliocene		18X-2, 30-32	139.1	1.0	30	.	20	1	.	.	7	.	1	.	.	.	.	.	.	1
			19X-2, 30-32	149.1	1.0	49	.	17	.	.	.	29	1	.	.	.	.	.	.	.	2
1I	Pliocene		20X-2, 31-33	158.8	1.0	86	.	19	1	.	.	58	3	1	.	.	.	.	.	.	4
			21X-2, 30-32	168.6	1.0	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
1J	Pliocene		22X-2, 30-32	178.3	1.0	12	.	12	.	.	.	.	.	.	.	.	.	.	.	.	1
			23X-2, 30-32	188.0	1.0	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
1K	Pliocene		25X-2, 30-32	197.7	1.0	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
			26X-2, 30-32	207.4	1.0	7	.	4	3	.	.	.	.	3	.	.	.	.	.	.	.
1L	Pliocene		27X-2, 130-132	218.1	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
			28X-2, 34-36	226.8	1.0	13	.	6	3	1	.	.	.	3	.	.	.	.	.	.	.
1M	Pliocene	29X-2, 30-32	236.5	1.0	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	
		30X-2, 30-32	246.2	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
II	Pliocene	" <i>pseudofibula</i> <i>plexus</i> "	32X-2, 30-32	255.9	1.0	8	.	.	.	.	.	.	.	.	.	3	.	5	.	.	
			32X-4, 31-33	258.9	0.4	318	.	170	5	6	.	.	88	3	8	.	10	16	12	.	
2A	Pliocene	?	32X-6, 30-32	261.9	1.0	23	.	13	.	.	.	.	2	.	.	.	3	4	1	.	
			33X-2, 32-34	265.6	1.0	8	.	.	.	.	.	1	.	.	.	2	.	2	4	.	.
2B	Pliocene	?	35X-2, 34-36	284.9	1.0	43	.	.	.	.	2	.	.	.	15	.	12	14	.	.	
			35X-3, 40-42	286.5	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2C	Pliocene	?	36X-2, 27-30	294.6	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

ments that meet to form a triple junction (see Poelchau, 1974); the angle between any two elements of this junction is seldom acute. Where two elements meet at an angle, there is usually a spine, which becomes the third member of the triple junction. This is commonly the case at the corners of the basal ring, or on the apical structure (such as on the apex of *Dictyochoa aculeata* or *Naviculopsis trispinosa*). The silicoflagellate skeleton generally has triple junctions at the corners, at the points where the strut attaches to the basal side (here called "strut attachments"), and where the apical end of each strut attaches to the rest of the apical structure (bridge or ring attachment).

Although the skeletal morphology shows remarkable variability, the skeletal morphotypes appear to follow a few simple rules in their design. The number of struts, for example, is equal to the number of basal sides, and there is one strut per side. Similarly, the apical and basal rings have the same number of sides, and the entire skeleton in general has some form of rotational symmetry. In nearly all cases, the apex of the silicoflag-

ellate, or the center of the apical ring, is directly above the center of the basal plane. While exceptions to these rules can be found, they are unusual and generally appear to be aberrant (teratoid) specimens.

The regularly occurring polygonal patterns found in silicoflagellate skeletal morphology are similar in many ways to configurations produced by mathematical optimization of one or more variables. Similar patterns occur among colonial corals or barnacles, the honeycomb structure of the beehive, or the venation of the insect wing (see Thompson, 1942; Smith, 1954; Raup, 1968; Almgren, 1982, for other examples). Some of these, such as the colonial corals, are the result of close packing. This, however, should not apply to silicoflagellates as they are not colonial and the polygons formed by the skeletal elements do not appear to reflect any segmentation within the organism. Instead, the silicoflagellate skeleton appears to be the result of area minimization, as has been previously proposed for some radiolarian skeletons (Thompson, 1942; Almgren, 1982), brach-

**Table 9. Abundance of silicoflagellates in selected samples from Hole 696A. Species (in alphabetical order) are recorded as total number of specimens found in slides examined.**

Litho-stratigraphic unit	Age	Silicoflagellate zones	Core, section, interval (cm)	Depth (mbsf)	Number of slides examined		Total number of specimens								
							<i>Dictyocha fibula</i> (s. amph.)	<i>Distephanus boliviensis</i>	<i>D. boliviensis</i> (7 sides)	<i>D. crux</i> (s. amph.)	<i>D. speculum pentagonus</i>	<i>D. speculum speculum</i> (6 sides)	<i>D. speculum speculum</i> (7 sides)	teratoid silicoflagellates	
IA	Quaternary	<i>Distephanus speculum speculum</i>	1H-2, 30-32	01.8	1.0	6	.	4	.	.	.	.	2	.	.
			2H-2, 30-32	4.3	1.0	0	.	.	.	.	.	.	.	.	.
			3H-1, 37-39	12.4	1.0	6	.	.	.	.	.	.	6	.	.
IB	Pliocene		4H-1, 90-92	22.4	1.0	22	.	.	.	.	.	.	21	1	.
			5H-2, 30-32	33.5	1.0	37	.	2	1	.	1	31	1	1	
			6H-2, 30-32	42.6	1.0	16	1	.	.	2	.	11	.	2	
II			7H-2, 30-32	52.2	1.0	5	.	.	.	.	1	3	.	1	
			8H-2, 30-32	61.8	1.0	20	1	.	.	.	9	9	1	1	
			9H-2, 30-32	71.4	1.0	23	.	12	1	.	10	.	.	.	

**Table 10. Abundance of silicoflagellates in selected samples from Hole 696B. Species (in alphabetical order) are recorded as total number of specimens found in slides examined.**

Litho-stratigraphic unit	Age	Silicoflagellate zones	Core, section, interval (cm)	Depth (mbsf)	Number of slides examined		Total number of specimens										
							<i>Distephanus boliviensis</i> (6 sides)	<i>D. boliviensis</i> (7 sides)	<i>D. crux</i> (s. amph.)	<i>D. speculum speculum</i> (6 sides)	<i>D. speculum speculum</i> (7 sides)	<i>D. speculum speculum</i> (8 or more sides)	<i>D. speculum</i> (7 or more sides)	<i>D. speculum pentagonus</i>	<i>D. speculum speculum f. notabilis</i>	<i>D. speculum speculum f. pseudofibula</i>	<i>D. speculum speculum f. varians</i>
II	Quaternary	<i>Distephanus speculum speculum</i>	2R-1, 74-76	77.4	1.0	3	.	.	1	2	.	.	.	.	.	.	.
			3R-2, 129-131	89.0	1.0	18	.	.	2	15	.	.	.	1	.	.	.
			3R-5, 129-131	93.5	1.0	166	112	10	.	18	2	.	3	21	.	.	.
III	Pliocene	"pseudofibula plexus"	5R-2, 30-32	106.3	1.0	24	.	.	.	.	.	.	.	6	7	11	
			6R-2, 30-32	117.0	1.0	7	.	.	.	.	.	.	.	2	3	2	
			7R-2, 34-36	126.7	1.0	6	.	.	.	.	.	.	.	1	1	3	
			10R-1, 31-33	144.4	1.0	3	.	.	.	.	.	.	.	1	.	2	
VI	Miocene	Unzoned	13R-1, 42-44	173.6	1.0	1	.	.	.	.	1	.	.	.	.	.	
			17R-1, 130-132	213.1	1.0	15	.	.	.	14	.	1	.	.	.	.	
			19R-1, 16-18	221.7	1.0	19	.	.	.	18	.	1	.	.	.	.	
			20R-1, 130-132	232.4	1.0	9	.	.	.	6	.	.	.	3	.	.	
			24R-2, 30-32	271.5	1.0	0	.	.	.	.	.	.	.	.	.	.	
			25R-1, 30-32	279.7	1.0	0	.	.	.	.	.	.	.	.	.	.	
			26R-2, 30-32	290.8	1.0	0	.	.	.	.	.	.	.	.	.	.	
VI			27R-2, 30-32	300.5	1.0	31	25	.	6	.	.	.	.	.	.		
			28R-2, 30-32	310.1	1.0	1	.	.	1	.	.	.	.	.	.		
			32R-2, 30-32	348.8	1.0	5	5	.	.	.	.	.	.	.	.		
			34R-2, 30-32	368.1	1.0	2	2	.	.	.	.	.	.	.	.		

iopods (McGhee, 1980), foraminifers (Brasier, 1982), and is well known in soap bubbles (Almgren and Taylor, 1976; Isenberg, 1976; Fig. 4).

Recent work (McCartney and Loper, 1989) has shown that silicoflagellate skeletal configurations can be produced by a simple mathematical model that minimizes the apical surface area for given basal area and internal volume. A similar model in which the total length of the skeletal elements, and thus the utilization of skeletal material, is the minimizing variable does not

generally produce configurations similar to abundant silicoflagellate morphologies. However, the diversity of known silicoflagellate geometries, and especially the occurrence of relatively simple designs such as *Corbisema* and *Dictyocha*, indicates that factors other than the simple minimization of apical surface area must also be important in skeletal design.

In both the modern and geologic record, relatively more complex silicoflagellate skeletal configurations occur in high latitudes. In the Recent, six-sided *Distephanus* tend to predomi-

**Table 11. Abundance of silicoflagellates in selected samples from Hole 697B. Species (in alphabetical order) are recorded as total number of specimens found in slides examined. \* = Ebridian.**

Litho- stratigraphic unit	Age	Silicoflagellate zones	Core, section, interval (cm)	Depth (mbsf)	Number of slides examined	Total number of specimens									*				
							<i>Distephanus boliviensis</i> (6 sides)	<i>D. boliviensis</i> (7 sides)	<i>D. speculum hemisphaericus</i> (6 sides, 2-4 windows)	<i>D. speculum hemisphaericus</i> (7 or more sides)	<i>D. speculum pentagonus</i>	<i>D. speculum speculum</i> (6 sides)	<i>D. speculum speculum</i> f. <i>notabilis</i>	<i>D. speculum speculum</i> f. <i>pseudofibula</i>		<i>D. speculum speculum</i> f. <i>varians</i>	teratoid silicoflagellates	<i>Ammodoctium ampulla</i>	
IB	Pleistocene	Barren	1H-2, 72-74	20.4	1.0	0	.	.	.	.	.	.	.	.	.	.	.		
			2H-2, 30-32	29.3	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	
			3H-2, 30-32	38.9	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			4H-3, 30-32	50.1	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			6H-2, 30-32	68.0	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			7H-3, 30-32	79.3	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			8H-3, 30-32	89.0	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			9H-2, 140-141	98.3	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	.
			IC	Pliocene	<i>Distephanus speculum speculum</i>	11H-3, 30-32	117.6	1.0	1	.	.	.	.	.	.	.	.	.	.
13X-1, 30-32	128.9	1.0				34	.	.	.	1	.	33	.	.	.	.	.	1	
14X-4, 30-32	143.0	1.0				32	.	.	.	5	.	27	.	.	.	.	.	1	
15X-3, 30-32	171.2	1.0				42	.	.	.	.	1	41	.	.	.	.	.	.	
16X-4, 28-30	162.3	1.0				3	.	.	.	.	.	3	.	.	.	.	.	.	
17X-1, 31-33	168.0	1.0				4	2	.	1	.	1	.	.	.	.	.	1	.	
19X-1, 27-29	186.9	1.0				2	.	.	.	.	.	2	.	.	.	.	.	.	
20X-3, 28-30	199.5	1.0				5	5	.	.	.	.	.	.	.	.	.	.	.	
21X-2, 28-30	207.7	1.0				68	54	.	1	.	1	12	.	.	.	.	.	2	
22X-2, 28-30	218.4	1.0				17	17	.	.	.	.	.	.	.	.	.	1	.	
25X-1, 117-119	245.7	1.0				1	1	.	.	.	.	.	.	.	.	.	.	.	
26X-2, 31-33	256.0	1.0				0	.	.	.	.	.	.	.	.	.	.	.	.	
27X-1, 28-30	264.2	1.0				1	.	.	.	.	.	.	.	.	.	.	.	.	
28X-5, 30-32	279.9	1.0				12	10	1	.	.	1	.	.	.	.	.	.	.	
29X-1, 29-31	283.6	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.				
II		"pseudofibula plexus"	30X-3, 31-33	296.3	1.0	0	.	.	.	.	.	.	.	.	.	.	.		
			31X-2, 28-30	302.5	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	
			32X-3, 28-32	315.5	1.0	0	.	.	.	.	.	.	.	.	.	.	.	.	
			32X-5, 28-30	318.5	1.0	9	.	.	.	.	.	.	2	2	5	1	.	.	

nate in high latitudes while four-sided *Dictyochoa* is dominant in middle and low latitudes. This geographical distribution has led some workers (Yanagisawa, 1943; Poelchau, 1974; Schrader et al., 1986; among others) to propose that the *Distephanus/Dictyochoa* ratio may be useful as a temperature indicator, although Perch-Nielsen (1985) has shown that this may have only regional utility. The dominance of more complex morphologies in high latitudes appears to occur throughout the Cenozoic (McCartney, 1987). For example, the Paleogene high latitudes are dominated by *Dictyochoa* while lower latitudes have a greater abundance of the simpler *Corbisema*. The greater abundance of *Corbisema* has led Bukry (1985) to consider this genus an indicator of very warm water. When more advanced skeletal morphologies first appear in the geologic record, they consistently appear in the high latitudes.

The mathematical modeling of silicoflagellate skeletal morphology indicates that more complex morphologies may occur because of a greater need to minimize apical surface area. McCartney and Loper (1989) speculate that the reason for this is the minimization of surface energy, as is the case with soap bub-

bles (see Almgren and Taylor, 1976). The occurrence of simpler morphologies in lower latitudes might be due to a need to conserve on the utilization of skeletal material or to limit the weight of the organism. In an environment where both minimization of apical surface area and conservation of silica are important, both *Distephanus* and *Dictyochoa* will be efficient, though at a different range of internal volume (volume here is measured as a dimensionless ratio, see McCartney and Loper, 1989).

#### Silicoflagellate Variability

Silicoflagellate skeletons have been especially noteworthy for their simple geometric configurations and for a sometimes remarkable variability. These qualities have provided ample rationale for both "lumpers" and "splitters" among taxonomists. Silicoflagellate biologists (Van Valkenburg, 1970, 1980) generally belong to the first category and believe that a wide variety of silicoflagellate skeletal types can represent a single species. Silicoflagellate paleontologists, on the other hand, tend to subdivide the taxa because of potential biostratigraphic utility. Thus the taxonomy used by biologists often does not cover in detail

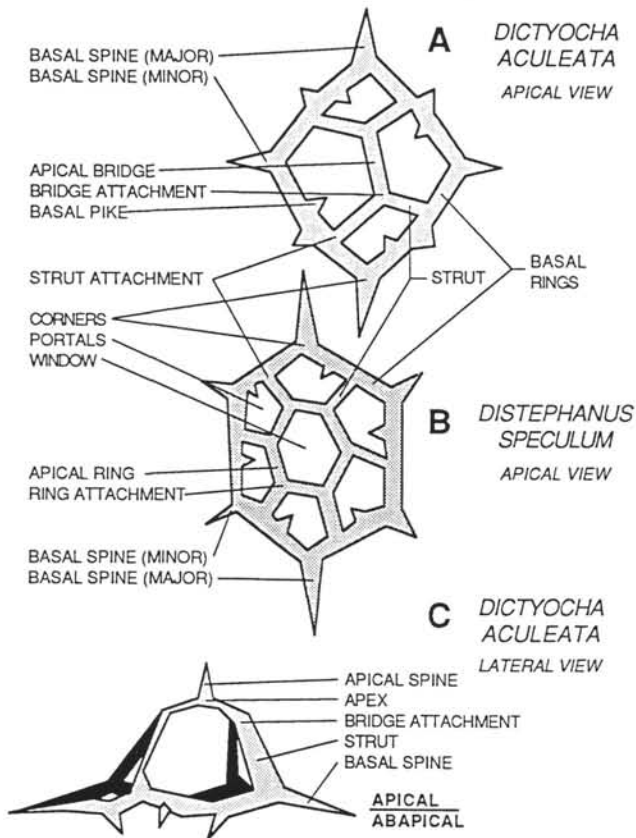


Figure 3. Silicoflagellate descriptive terminology (drawings after Poelchau, 1976). A, C. Apical and lateral views of *Dictyocha aculeata* (equals *D. messanensis* and *D. mandrai* of other workers). B. Apical view of *Distephanus speculum*.

the various skeletal morphotypes, whereas the paleontologic taxonomy covers the relative abundance of the morphotypes in great detail but tends to classify each as a separate taxon.

There is abundant evidence that a silicoflagellate taxonomy based on skeletal design may not show true biological relationships. This evidence consists of multiple skeletal morphologies that are produced by what appears to be a single silicoflagellate species. Six lines of evidence are listed below and then discussed briefly:

1. Cloned cultures of living *Dictyocha fibula*.
2. Variation in modern populations.
3. Variation between members of a paired skeletal set.
4. Teratoid specimens.
5. Intrataxa gradations.
6. Reoccurrence of some morphologies in the geologic record.

Perhaps the most oft-cited example of silicoflagellate variability is the study of Van Valkenburg and Norris (1970). In this study, a single cloned culture of *Dictyocha fibula* produced skeletal morphologies that, if classified by the usual silicoflagellate taxonomy, represent three genera. But although these results give a clear indication that silicoflagellates are capable of extreme variability, it is uncertain how these results should be applied to silicoflagellate taxonomy, as natural populations do not show the variability produced in culture. A large majority of the silicoflagellate skeletons raised by Van Valkenburg are aberrant (e.g., Van Valkenburg and Norris, 1970, fig. 12), and some are

almost unrecognizable as silicoflagellate skeletons (Van Valkenburg, 1980, fig. 1).

While exceptional variability does occur in natural populations (Frenguelli, 1935; Van der Spoel et al., 1973; Shitanaka, 1983), most modern populations, especially in the open sea, exhibit only a limited variability. But variability still occurs; for example, Boney (1973) showed that while 95%–98% of *Distephanus speculum* collected in the Firth of Clyde had hexagonal symmetry, there were also 5-, 7-, and 8-sided specimens. Hovasse (1932c) records a case in which 70%–76% of *Distephanus octonarius* had octagonal symmetry, with the remainder having 6, 7, 9, or 10 sides. Such variability is also found frequently in the fossil record where, for example, a sample with predominantly hexagonal *D. speculum* will have 5- and 7-sided specimens associated with it, or where a sample of 4-sided *Dictyocha* may also have 5-sided or distephanid variants.

Additional evidence of genetic variability comes from the study of double skeletons. These consist of paired silicoflagellate skeletons connected at the abapical face; they apparently represent organisms that have died during vegetative division. Although paired skeletons are usually very similar, variation sometimes can be considerable. Paired skeletons representing two species or even genera by some interpretations of the silicoflagellate taxonomy have been found by Gemeinhardt (1930) and Bukry and Foster (1973). Boney (1976, 1981), however, notes that such pairings are unusual.

Teratoid (aberrant) silicoflagellate skeletons also give some insight into silicoflagellate variability and show that deviations from the regular morphology may not be lethal to the organism. While they usually make up less than 3% of a sample (Martini, 1977), they can at times be exceptionally abundant, and even predominant. Common abnormalities include a disruption in the regular symmetry of the skeleton, failure to close the basal or apical ring, and struts that are forked, fused, or occur two to a basal side. Typical teratoids from recent populations are illustrated in some detail for *Dictyocha messanensis* (Frenguelli, 1935) and *Distephanus speculum* (Frenguelli, 1938; Boney, 1973; Van der Spoel et al., 1973). Unusual numbers of exceptionally grotesque specimens are sometimes found, such as a sample collected off the northern California coast and described by Poelchau (1974). Aberrants appear to be less common in the open sea than in coastal areas (Bukry, 1978c). Explanations for unusual variation include high chlorinity (Shitanaka, 1983), phytoplankton bloom conditions (Mandra, 1968), genetic weaknesses (Van Valkenburg and Norris, 1971) or other abnormal ecologic conditions (Poelchau, 1974). Because the relative abundance of aberrant specimens may be an indicator of environmental stress, a count of aberrant specimens is included in the abundance tabulations in this chapter.

An additional clue to silicoflagellate variability and the biological relationship between taxa is the occasional occurrence of morphologies intermediate between what are described as separate species or genera. These include naviculopsids with a corbisemid apical ring (Perch-Nielsen, 1975c), corbisemids with a naviculopsid or dictyochid morphology (Dumitrica, 1973; Perch-Nielsen, 1975c; Bukry, 1975a, 1976a; Busen and Wise, 1977), strutted naviculopsids (Perch-Nielsen, 1976; Bukry, 1976c) and corbisemids with an apical ring (McCartney and Wise, 1987). It is difficult to derive an explanation for these; they could just be aberrants. But these specimens are not otherwise malformed, and where present they occur in some abundance. They may provide insight into the biologic relationships between separate skeletal morphologies and may indicate that distinct morphologies are closely related.

The last line of evidence cited is the recurrence of certain morphologies in the geologic record, particularly some of those considered here with the upper Miocene-lower Pliocene *pseudo-*

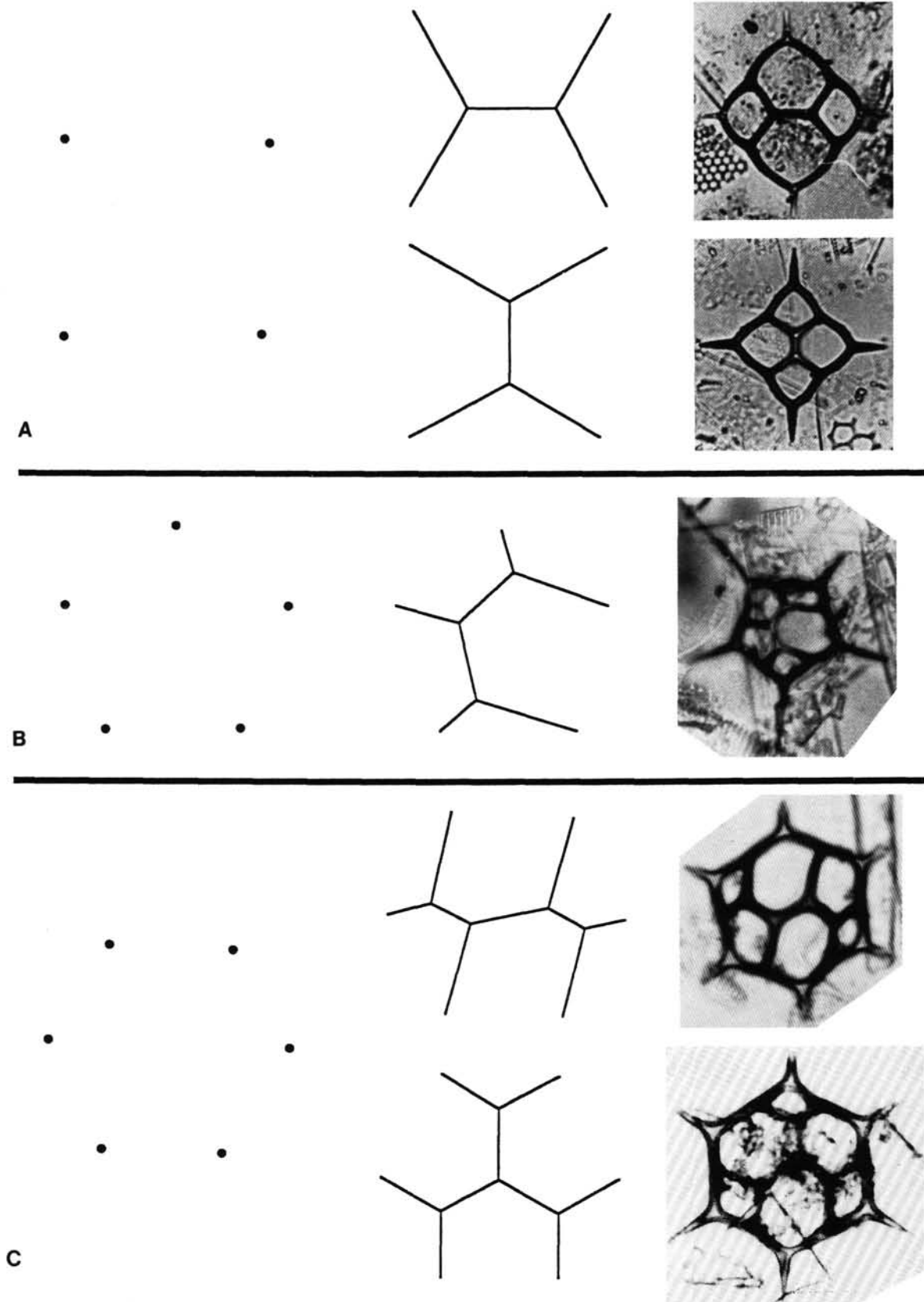


Figure 4. Illustration of optimization and its application to silicoflagellates. The first column shows points positioned at the corners of a square (A), pentagon (B), and hexagon (C) with sides of equal length. The second column shows the minimum-distance configuration that connects all points (from Almgren and Taylor, 1976; Isenberg, 1976). The third column shows dictyochid silicoflagellates with similar apical structures.

*fibula* plexus. As discussed below, some of these morphologies co-occur in narrow intervals of the Paleocene (Shaw and Ciesielski, 1983) and Eocene (Locker and Martini, 1987). As evolution should not repeat itself, serious consideration must be given to environmental adaptations for such occurrences. The seeming contradictions of extreme variability in some circumstances and uniformity in others suggest two alternatives. Unusual morphologies could represent ecophenotypic variation. On the other hand, such variation could be caused by genetic exchange between species, which is quite common in plants (see Burger (1975) and Van Valen (1976) and their discussions on oak).

While silicoflagellates are not known to reproduce sexually, Locker and Martini (1986, 1987) believe, and we concur, that the great stability of the fossil and recent forms, given their known variability, indicates that silicoflagellates possess temporary phases of sexual reproduction. Thus, a more detailed study of silicoflagellate variability and the more unusual morphologies may help answer questions concerning the silicoflagellate species concept and the biological relationship between the skeletal morphologies.

### The Occurrence of the “*pseudofibula* plexus” of *Distephanus speculum*

An exceptionally variable assemblage of six-sided silicoflagellates was found in the upper Miocene/lower Pliocene of most Leg 113 sites. These silicoflagellates generally did not possess an apical ring but instead had a variety of bridge configurations (see Fig. 5). This assemblage, here referred to as the “*pseudofibula* plexus,” apparently represents morphotypes of *Distephanus speculum speculum* that probably developed in response to some type of ecological stress. Members of this group have been illustrated many times in the literature, but their relationships to one another, and to *Distephanus speculum speculum*, have not been discussed in much detail. These relationships are important because they show the considerable skeletal variability of the silicoflagellate species and also illustrate how much the skeletal morphology might be affected by changing ecological conditions.

Members of the *pseudofibula* plexus have been previously reported at high latitudes (Bachmann and Ichikawa, 1962; Ling, 1972; Bukry, 1973, 1975b, 1976a, 1979, 1983; Ciesielski, 1975; Barron, 1976; Shaw and Ciesielski, 1983; Locker and Martini,

1986) but there has been little effort to show the variability and relative abundance of the morphologies. They have been classified under a variety of species, subspecies, or form names including *pseudocrux*, *pseudofibula*, *japonica*, and *varians*, although it is generally obvious from the illustrations that a number of distinct skeletal varieties are lumped into each taxon. The different morphologies do not appear to have contrasting stratigraphic ranges, and in fact appear to occur collectively and in close association with *Distephanus speculum speculum*.

The group is unusual for a number of reasons. To begin with, these silicoflagellates take on what is commonly called a “dictyochid” (apical bridge) morphology, although it appears that they are variants of *Distephanus speculum*, which of course has an apical ring. While the *pseudofibula* plexus discussed here is for the most part restricted to the Neogene, similar morphologies have been found elsewhere in the geologic record (Perch-Nielsen, 1975b; Ling, 1977; Shaw and Ciesielski, 1983) and have been consistently placed taxonomically in *Dictyocha*. The occurrence reported by Shaw and Ciesielski predates the first appearance of *Distephanus*. Thus the general morphologies appear to be polyphyletic.

The *pseudofibula* plexus is both abundant and well-preserved in the lower Pliocene of Leg 113 sites. This assemblage has been used in the Southern Ocean to delineate or help delineate a biostratigraphic zone by Ciesielski (1974, 1975), Bukry (1975c), and Shaw and Ciesielski (1983), and a broad concept of that zone is used in this chapter. As argued below, there is good evidence, however, that it is a group of ecophenotypes, and thus its first and last occurrences should not be viewed as necessarily being time-synchronous. Members of this assemblage have been found within a relatively narrow interval in the uppermost Miocene/lowermost Pliocene of the high southern latitudes (Bukry, 1976a; Ciesielski, 1975; Shaw and Ciesielski, 1983) and confined well within the upper Miocene of low to mid-latitudes elsewhere (Deflandre, 1950; Ling, 1972; Bukry, 1973; Barron, 1976).

Members of the *pseudofibula* plexus are also found in the Recent Bay of Fundy (Gran and Braarud, 1935), coastal Japan (Tsumura, 1963), and within the atrial contents of *Chalina* sponges dredged off coastal Argentina (Frenguelli, 1935). Such occurrences in modern coastal waters may be the result of environmental stress, such as reduced salinity. The unusual morphologies may then represent teratoid *Distephanus speculum*. However, despite their variability, members of this group are relatively consistent in the forms they take, having only three common variants and two others that are less common. The specimens examined from Leg 113 do not have an unusual number of normal silicoflagellate teratologies such as fused or forked spines, two struts connected to a basal side, or distorted basal ring.

Thus it would appear that the unusual assemblage of *Distephanus speculum* morphologies represented by the *pseudofibula* plexus is governed by some adaptive advantage under environmental stress. The adaptive advantage itself is unknown but might be related to salinity, water clarity, or some nutrient abundance.

### Stratigraphy and Paleoenvironmental Relationships of the “*pseudofibula* plexus”

#### Observations

In Figure 6, we plot the occurrence of the *pseudofibula* plexus against lithology at the Leg 113 sites. By this plot we hope to gain some insight into the cause of variation within this group. Included in the figure are the occurrence of dropstones, ice-rafted debris (IRD), and siliceous microfossils as given in the core barrel sheets for each site (Barker, Kennett, et al., 1988). Generally, only dropstones 0.3–0.5 cm were recorded in the

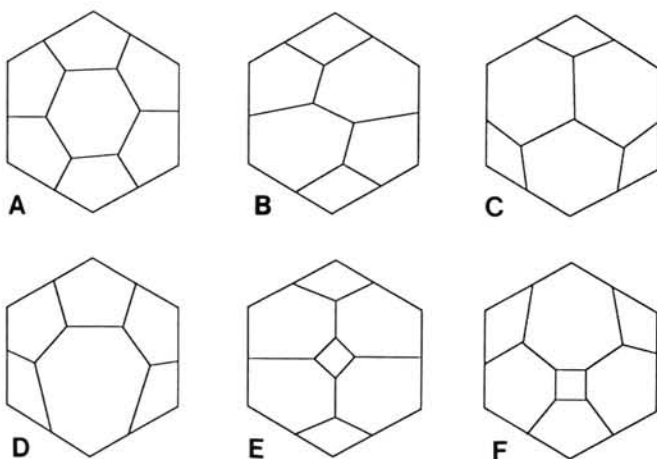


Figure 5. Apical structures of silicoflagellate skeletal morphologies with six basal sides. A. *Distephanus speculum speculum*. B. *f. pseudofibula*. C. *f. varians*. D. *f. notabilis*. E. *f. pseudocrux* (centered ring). F. *f. pseudocrux* (centered ring).

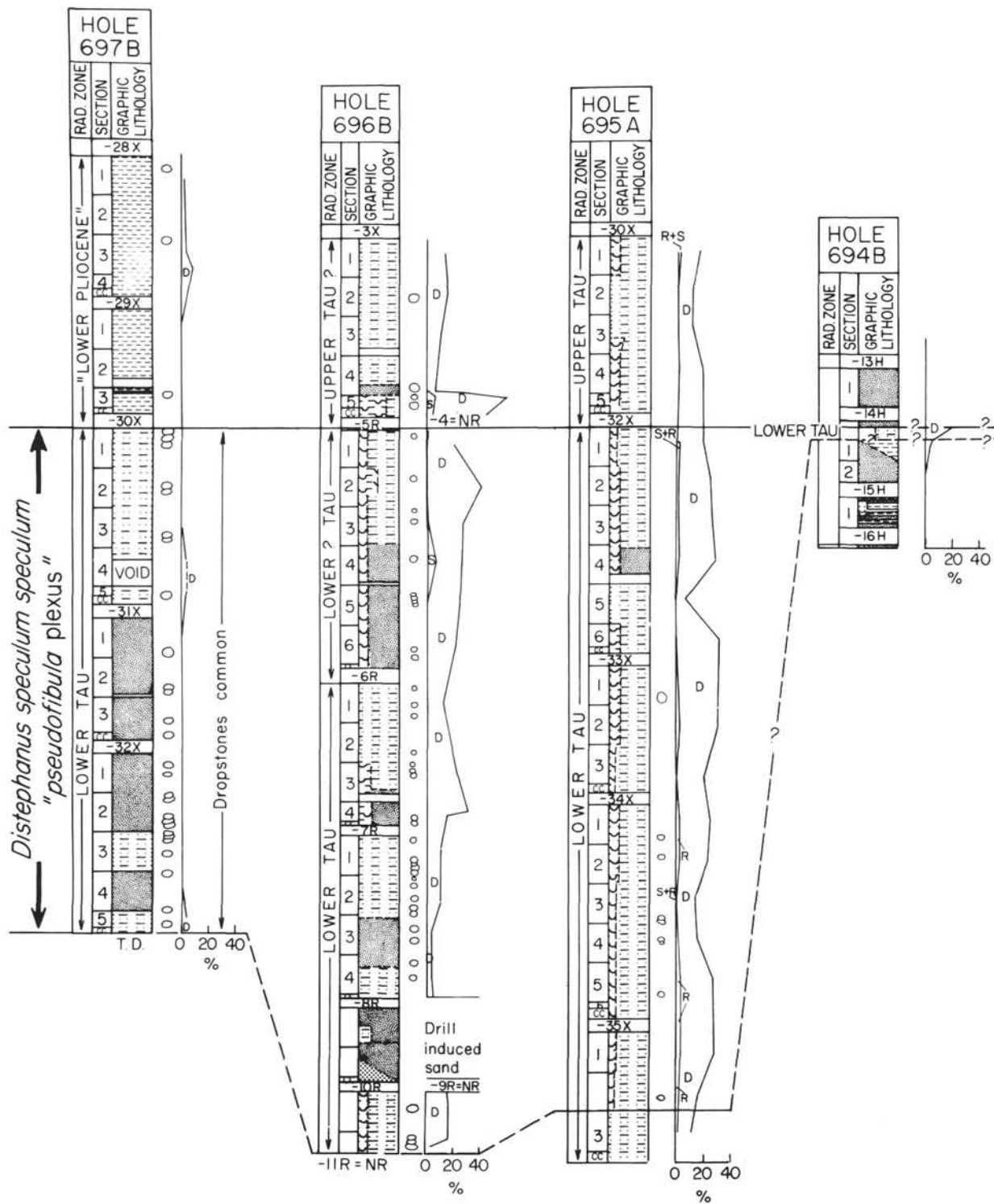


Figure 6. Correlation of the "pseudofibula plexus" among ODP Sites 689-696. Also shown are the occurrences of ice-rafted debris, dropstones larger than 0.3 cm, and siliceous microfossils at each site. Radiolarian zones are from Lazarus (this volume). D = diatoms; S = silicoflagellates; R = radiolarians; irregular circles = dropstones; NR = no recovery; T.D. = total depth; ~ = disconformity.



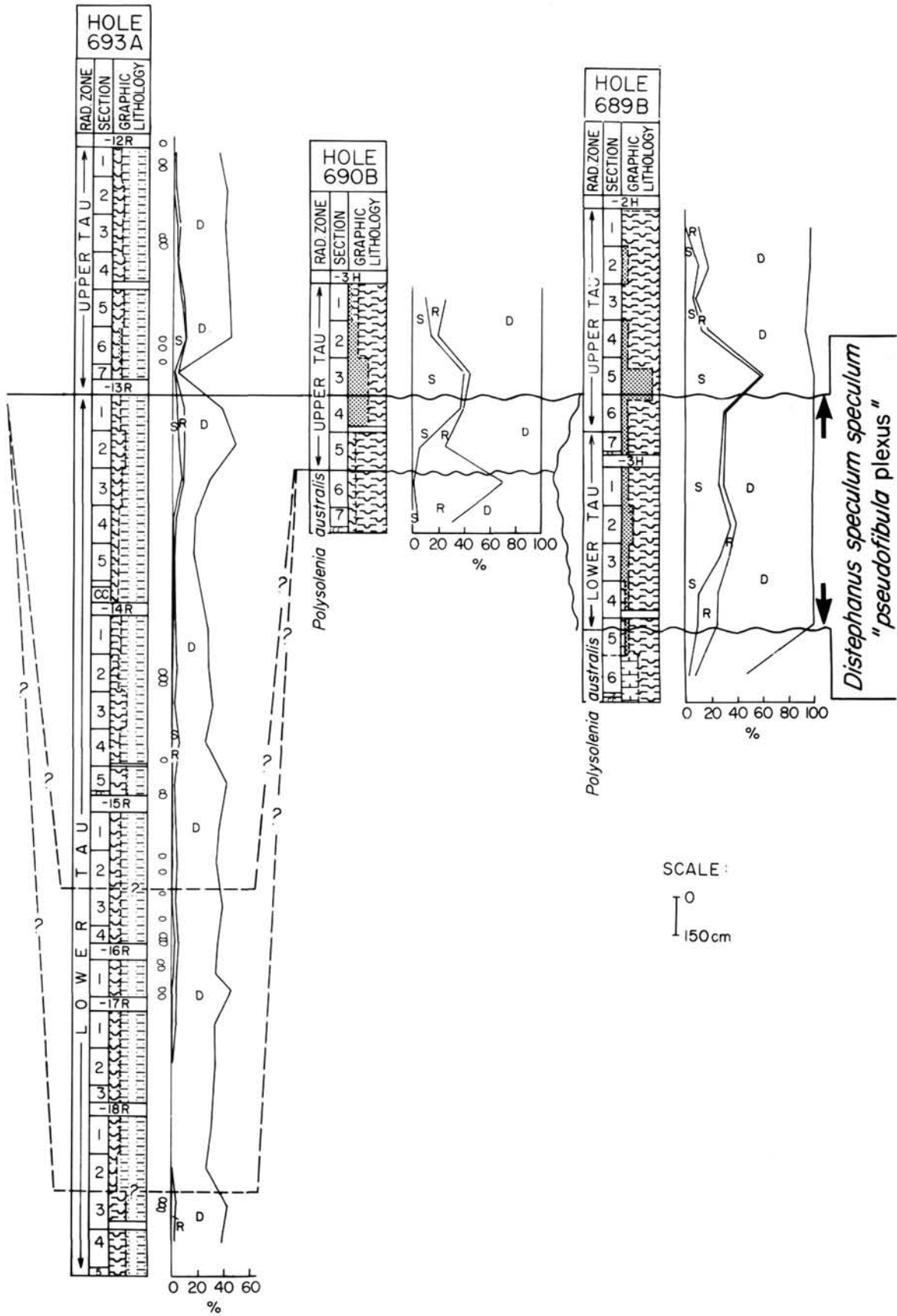


Figure 6 (continued).

barrel sheets. The radiolarian zones determined for these cores are also given according to the barrel sheets or as updated by Lazarus (this volume, chapter 41).

An examination of Figure 6 shows that at these sites the *pseudofibula* plexus occurs within the radiolarian Tau Zone, which is late Miocene to early Pliocene in age (4.4–8.0 Ma) according to Lazarus (this volume), but which may extend into the latest Miocene to about 7.9 Ma, according to the calibration of Gersonde and Burckle (this volume; see discussion by Gersonde et al., this volume). In the western portion of the study area, the occurrence of the *pseudofibula* plexus seems to coincide with the last phases of late Miocene-early Pliocene glaciation, as indicated by the occurrence of dropstones and ice-rafted debris at Sites 694 to 697 (Fig. 6; Barker, Kennett, et al., 1988). This glaciation is considered to have encompassed West as well as East Antarctica, and therefore would have included a glaciated Antarctic Peninsula (e.g., Mercer, 1978). Starting with the northeastern sites in the vicinity of the South Orkney Microcontinent (SOM), there seems to be a strong correlation between the occurrence of dropstones and IRD with the occurrence of the “*pseudofibula* plexus.” At Hole 697B, dropstones and IRD are common in Cores 113-697B-30X to 113-697B-32X, but only sporadic immediately above that level, where the numbers of diatoms increase dramatically. Unfortunately the hole had to be terminated due to time constraints before penetrating completely through the *pseudofibula* plexus.

At Sites 695 and 696 just to the east on the SOM, the same general relationships with IRD and dropstones hold true, but the holes did not penetrate deeper. At both sites, no silicoflagellates were present for several cores below the zone. According to smear slide data given in the barrel sheets, diatoms and other siliceous microfossils drop sharply in number below Core 113-695A-36X. The same seems to be true for Hole 696B, but this is difficult to demonstrate because of poor recovery, a situation which may have been caused or exacerbated by the presence of numerous dropstones in this portion of the section.

Nevertheless, the absence of silicoflagellates and the diminution in the numbers of siliceous fossils in cores immediately below the *pseudofibula* plexus indicate diminished siliceous plankton productivity or dilution of the biogenic component by high siliciclastic input. This could have resulted from increased seasonal ice cover in this area or increased input of glacial-marine sediments, either of which would reflect heightened glacial activity prior to the accumulation of silicoflagellates of the *pseudofibula* plexus.

The only diatom ooze plotted in Figure 6 for these northern sites is in Hole 696B at the base of Core 113-696B-3R, which is the first core recovered above the *pseudofibula* plexus (there was no recovery in Core 113-696B-4R). Although silicoflagellates increase to 4% in Section 113-696B-3R-5, no members of the *pseudofibula* plexus are present, indicating their disappearance once glacial conditions ameliorated and normal siliceous productivity was reestablished.

Site 694, an abyssal site in deep water, characteristically yielded few Pliocene microfossils due to the effects of dissolution at such depths in these latitudes. Recovery in the Pliocene was likewise poor due to the inability to recover poorly consolidated sand turbidites, which constituted most of the lower Pliocene section. Silicoflagellates were recovered only from the lowermost Pliocene. These underlay the bulk of the sand turbidites and belong to the *pseudofibula* plexus.

At Site 693 on the slope off the coast of East Antarctica, dropstones are common throughout the upper Miocene-Pliocene section, but recovery across the Miocene/Pliocene boundary was poor, apparently due to a high number of dropstones which impeded the coring operation. This site differs from previous ones discussed from Figure 6 in that diatoms, and to some

extent silicoflagellates, are more numerous and consistently present throughout the cores. The large number of dropstones would reflect, in part, the proximity of this site to glacial sources and its presence along the coastal iceberg track.

Although truncated by hiatuses, the *pseudofibula* plexus is well developed at Sites 689 and 690 on Maud Rise, but little correlation can be made there with glacial marine sediments because these sites are virtually devoid of IRD and dropstones. These sites were not situated along any prominent iceberg tracks but instead lay in the path of a warm return current of the Weddell Gyre flowing across the rise from the north or northeast, much as today (Fig. 1). Data collected from Leg 113 sites, particularly the sequences from the SOM, indicate that the *pseudofibula* plexus developed in this region during or toward the close of the intense late Miocene-earliest Pliocene “West Antarctic” glaciations. This intense glacial episode affected the entire study area but is more evident in Leg 113 sites that lay in the path of the coastal current and the iceberg tracks through the central and western Weddell Sea (Fig. 1). As glacial conditions began to wane during the earliest Pliocene, the *pseudofibula* plexus disappeared although the general population of siliceous microfossils increased. Accompanying its disappearance was the intense deposition of sand turbidites in the central Weddell Sea, which continued throughout the remainder of the early Pliocene.

### Discussion

The *pseudofibula* plexus in the study area seems to have developed toward the end of or shortly following the late Miocene-early Pliocene Antarctic glaciations, the most intense Cenozoic glaciations known until that time (for reviews, see Kennett, 1978; Wise, 1981; and Wise et al., 1985). This glacial interval was followed immediately during the early Pliocene by an exceptionally strong warming, which may have destabilized and even destroyed much of the accumulated ice sheet (Ciesielski and Weaver, 1974; Wise, 1981; and Wise et al., 1985). These late Miocene-early Pliocene glaciations marked one of the most important transitions in Tertiary Earth history. Although the intense glaciations may have begun as early as Tortonian times (Ciesielski and Weaver, 1983), those of the latest Miocene appear to have coincided with the Messinian salinity crisis. The climate of the Antarctic region during these late Miocene-early Pliocene glacial episodes would have been in a state of flux, experiencing sharp changes in temperature, upwelling, surface water salinity and nutrient supply, and the distributions of water masses, land, and sea ice.

We speculate that the *pseudofibula* plexus developed from the long-ranging *Distephanus speculum speculum* stock as a response to these strong environmental changes. We believe the morphologic variability within the plexus records an ecophenotypic response to any one or a combination of factors such as reduced salinity, change in nutrient supply, upwelling, or rapidly changing temperatures, although it is impossible at this writing to specify what the most important factor(s) would have been. In support of this speculation, we note that the plexus was relatively short-lived in this region, and that several of the variations have been seen at least once previously but at different times in the geologic record of other regions. We see no link between the forms we observed in our Southern Ocean cores and the *pseudofibulids* described from the upper Miocene of the North Pacific. We therefore follow Schulz (1928) and Locker and Martini (1987) in regarding the various morphotypes as forms rather than species or even subspecies.

Of the several possible environmental factors that may have produced the stress or change that led to these variations, we consider a reduction in salinity one of the more likely. Any regional reductions in salinity could have amplified the residual effects of the Messinian salinity crises of the latest Miocene,

which removed a considerable amount of salt from the world's oceans. If interglacial conditions were at all similar to today during the late Miocene-early Pliocene glaciations, then the existence of an equivalent to the present-day Antarctic Surface Water Mass would have produced a photic zone in our study area characterized by very cold temperatures and reduced salinities (see Wise, 1981, fig. 2). Eventual massive melting of the ice sheets (deglaciation) following the glaciations would have done the same. Strongly fluctuating glacial-interglacial conditions leading up to or accompanying such a deglaciation may have also accounted for the extensive sand turbidites seen at Site 694. Although reduced salinities in the Antarctic Surface Water Mass might account for the development of the latest Miocene-early Pliocene *pseudofibula* plexus around Antarctica, this would not necessarily explain the presence of the plexus elsewhere in the world's oceans, such as during the late Miocene in the North Pacific (e.g., Bukry, 1973).

As indicated previously, other factors may have induced the variability seen in the *pseudofibula* plexus. It is possible that the global oceans could have experienced changes in upwelling rates during the late Miocene-early Pliocene glacial episodes. This would have affected the supply of nutrients, both the kind and amount. Silica, for example, is an important and sometimes limiting nutrient. The double-ringed morphology of *Distephanus speculum speculum* does not make minimal use of skeletal material, while the various pseudofibulid morphotypes are more silica efficient (Fig. 4). The latter, then, could be an adaptation to silica-poor nutrient conditions. This is opposed to the normal trend for *Distephanus speculum*, which favors skeletal structures that minimize surface area, as discussed previously in this chapter. Minimal surface area might be more favored by the species in times of exceptionally nutrient-rich upwelling where little surface area is needed to absorb the necessary nutrients and silica is sufficiently plentiful to allow less silica efficient skeletal constructions. If this were the case, the pseudofibulid condition would be favored during deglaciations and long interglacials, whereas the normal *Distephanus speculum speculum* morphology would characterize predominantly glacial times.

Regardless of what induced the pseudofibulid condition, *Distephanus speculum* rather quickly adapted to the predominantly glacial climates that followed the early Pliocene deglaciation. Throughout the remainder of the Pliocene-Pleistocene Epochs, which were predominantly glacial, *D. speculum speculum* and/or the closely allied double-ringed *D. boliviensis* were the overwhelmingly dominant high-latitude silicoflagellate taxa, just as *D. speculum speculum* is in these latitudes today (see range charts).

#### SYSTEMATIC PALEONTOLOGY

The synonymies include only the first description and, if needed, a recent reference that has a more complete taxonomy.

#### Silicoflagellates

Genus *BACHMANNOCENA* Locker, 1974 emend. Bukry, 1987

**Introductory remarks.** The *Mesocena* group is exceptionally diverse and contains a variety of forms that may not be closely related. Some workers (Tappan, 1980; McCartney, 1987) believe that some members of this group are ecophenotypic variants of silicoflagellates that possess apical structures. Other workers (Locker and Martini, 1986) have subdivided this group into a number of different genera. Thus, it is perhaps fortuitous that Bukry (1987) has, on taxonomic grounds, proposed the genus name *Bachmannocena* for all silicoflagellates that have a basal ring without an apical structure. This gives us a new chance to build a useful taxonomy without the ever-more-complex trappings of the old. The authors hope that this new usage will continue until we have a much better understanding of this enigmatic group.

#### *Bachmannocena apiculata* (Schulz) (Plate 2, Figs. 6-10)

*Mesocena oamaruensis apiculata* Schulz, 1928, p. 240, fig. 11.

*Mesocena apiculata* (Schulz) Ling, 1972, p. 173, pl. 28, figs. 2-4.

*Bachmannocena apiculata* (Schulz) Bukry, 1987, p. 403-404.

**Remarks.** *Bachmannocena apiculata* is a relatively large (55  $\mu$ m), three-sided form with short spines. There is wide variation in the shape of the ring, as shown by the illustrated specimens. The basal ring is in some cases equilateral and in others more elongate; the two longer basal sides of elongate morphologies are often curved. This taxon was not subdivided into multiple subspecies (Bukry, 1987) because the various morphologies occurred together and, at least in this study, did not appear to have any biostratigraphic significance.

#### *Bachmannocena circulus* (Ehrenberg)

*Mesocena circulus* (Ehrenberg) Ehrenberg, 1844, p. 65.

*Bachmannocena circulus* (Ehrenberg) Bukry, 1987, p. 404.

**Remarks.** This species was found only in Sample 113-689B-6H-2, 29-31 cm, in which it was dominant.

#### *Bachmannocena diodon* (Ehrenberg)

*Mesocena diodon* Ehrenberg, 1844, p. 71, 84.

*Bachmannocena diodon* (Ehrenberg) Bukry, 1987, p. 404.

**Remarks.** Teratoid forms of this taxon were not found. This contrasts considerably with *Mesocena diodon* discussed in McCartney and Wise (1987).

#### *Bachmannocena occidentalis* (Hanna ex Bukry), n. comb.

*Mesocena oamaruensis* var. *quadrangula* Schulz, 1928 (in part), p. 240, fig. 12.

*Mesocena occidentalis* Hanna, 1931, p. 200, pl. E, fig. 1.

*Mesocena occidentalis* Hanna ex Bukry, 1977, p. 832.

**Remarks.** Four-sided *Bachmannocena occidentalis* were found only in Section 113-689B-13H-2, 29-31 cm.

#### Genus *CORBISEMA* Hanna, 1928

#### *Corbisema apiculata* (Lemmermann)

*Dictyocha triacantha* var. *apiculata* Lemmermann, 1901, p. 259, pl. 10, figs. 19, 20.

*Corbisema apiculata* (Lemmermann) Ling, 1972, p. 153, pl. 24, fig. 1.

**Remarks.** This is a generally middle-sized (40  $\mu$ m) *Corbisema* with relatively robust basal ring and basal spines of moderate length and large sustaining spines. One of the basal sides is usually shorter than the other two, giving the basal ring a slightly elongate shape. Specimens were relatively uncommon in the Oligocene of Hole 689B.

#### *Corbisema hastata* (Lemmermann)

*Corbisema triacantha* var. *hastata* Lemmermann, 1901, p. 259, pl. 10, fig. 16, 17.

*Corbisema hastata* (Lemmermann), Ling, 1972, p. 155, pl. 24, fig. 5.

**Remarks.** The primary characteristic of this species is a basal ring with one side shorter, and often much shorter, than either of the other two sides. This usually gives the basal ring an "arrowhead" shape. This group has considerable variation and some workers (see Bukry, 1976a) have subdivided it into many subspecies. Since the occurrence of *C. hastata* in this study was sporadic and restricted to Site 689, no effort has been made here to subdivide the specimens below the species level.

#### *Corbisema inermis inermis* (Lemmermann)

*Dictyocha triacantha* var. *inermis* Lemmermann, 1901, p. 259, pl. 10, fig. 21.

*Corbisema inermis inermis* (Lemmermann) Bukry, 1976a, p. 892.

**Remarks.** This species has a large basal ring that is relatively fragile in appearance and generally lacks basal spines. The sides are usually close to equilateral. There is much variation in the degree to which the basal sides bow outward, and thus the shape of the corners. The specimens in this study generally have relatively linear sides and sharp cor-

ners, although some specimens have very rounded corners similar to that of *C. geometrica* (but without the apical plate).

*Corbisema triacantha* (Ehrenberg)  
(Plate 1, Fig. 1)

*Dictyocha triacantha* Ehrenberg, 1844, p. 80.

*Corbisema triacantha* (Ehrenberg) Busen and Wise, 1977, p. 713.

**Remarks.** The variation in this taxon was very similar to that found by McCartney and Wise (1987). While several subspecies are recognized (Bukry, 1977, 1978a; Ling, 1972), the specimens observed in this study did not fall into distinct taxa and thus were considered collectively.

Genus *DICTYOCHA* Ehrenberg, 1837  
*Dictyocha aspera* (Lemmermann)  
(Plate 2, Fig. 2)

*Dictyocha fibula* var. *aspera* Lemmermann, 1901, p. 260, pl. 10, figs. 27, 28.

**Remarks.** Any *Dictyocha* in which the apical bridge was parallel to the minor axis were counted in this study as *D. aspera*. This morphology occurred sporadically in Holes 689B and 690B. Asperid specimens generally had a relative short bridge and frequently showed a close similarity to associated *D. fibula*.

*Dictyocha byronalis* Bukry

*Dictyocha byronalis* Bukry in Barron et al., 1984, p. 151, pl. 3, figs. 1-4.

**Remarks.** This taxon has a slightly elongate basal ring and an apical bridge that is rotated sinistrally about 10° (when seen from apical view).

*Dictyocha calida* Poelchau  
(Plate 2, Fig. 4)

*Dictyocha calida* Poelchau, 1976, p. 169, pl. 1, figs. c, d; pl. 3, figs. a-f.

**Remarks.** This species has a basal ring whose corners very nearly delineate a square. Basal spines are usually of equal length. The bridge is generally very short. Poelchau (1976) has shown that this species is commonly found, but is seldom dominant, in the modern North Pacific. In this study it was found only in Section 113-689B-5H-5, where it is relatively abundant.

*Dictyocha deflandrei* Frenguelli ex Glezer  
(Plate 2, Figs. 5A, 5B)

*Dictyocha deflandrei* Frenguelli, 1940 (in part), p. 65, figs. 14a, 14c-f.  
*Dictyocha deflandrei* Frenguelli ex Glezer, Bukry, 1975c, p. 854, pl. 2, figs. 9-13.

**Remarks.** Specimens of *Dictyocha deflandrei* found in Oligocene of Hole 689B were very similar to associate *frenguelli* but lacked apical spines. This taxon can exhibit considerable variability, with some variants having five or seven basal sides (Bukry, 1975c). A number of subspecies have been described (see Glezer, 1966; Bukry, 1978b) but these are not used in this work. For further comment on this interesting group, see the remarks with *frenguelli*.

*Dictyocha fibula* Ehrenberg

*Dictyocha fibula* Ehrenberg, 1839, fide Loeblich et al., 1968, p. 90, pl. 9, figs. 9-12.

*Dictyocha fibula* Ehrenberg, Bukry and Foster, 1973, p. 826-827.

**Remarks.** The authors use a broad interpretation of this species. The taxa occurs sporadically in Holes 689B and 690B.

*Dictyocha frenguelli* Deflandre  
(Plate 2, Fig. 3)

*Dictyocha frenguelli* Deflandre, 1950, p. 194, figs. 188-193.

**Remarks.** *Dictyocha deflandrei* and *D. frenguelli* form a very interesting group of silicoflagellates. Both are generally similar in size and have robust skeletal elements. In addition, both have unusual apical structures that, unlike most other silicoflagellates, appear to make no concession to conserving skeletal material. Skeletons of *D. deflandrei* have struts which arch upwards to support an apical plate; specimens of

*D. frenguelli* have a similar apical structure but with long apical spines. The overlapping ranges found in this study and elsewhere (Bukry, 1975a, 1975c) indicate a close evolutionary relationship, with *D. deflandrei* being the ancestral form. Other unusual silicoflagellates appear also to belong to this group, including the hexagonal or trigonal *D. spinosa* and *D. hexacantha*.

The development of long apical spines in *D. frenguelli* and *D. spinosa*, as well as the additional basal spines that occur on *Dictyocha hexacantha*, is very interesting. In all three cases, the presence of spines appears to violate the rule of triple-junctions (see Poelchau, 1974). In other morphologies where apical spines occur, such as on some *Distephanus speculum*, the apex of *Dictyocha aculeata*, and on *Naviculopsis trispinosa*, the apical spine occurs where two other elements meet at an angle and thus the spine becomes the third member of the junction. On *D. spinosa* and *D. hexacantha*, however, the spine becomes a part of a quadruple junction. On *D. frenguelli* the apical spine does not appear to be located where two elements meet at an angle. The reason why such unusual spines occur, if in fact they do serve a function, is unknown. However, Kitchell (1983) has shown that the effect of silicoflagellate spine length on sinking rate might be considerable and could be a useful indicator of upwelling intensity. Recent experiments with simple models sinking in glycerol of low Reynolds number (Sargeant et al., 1987) indicate that the presence of spines slows the rate of settling, and that settling rate decreases with an increase in spine length. Similar conclusions have been reached with living diatoms (Conway and Trainor, 1972; Walsby and Xypolyta, 1977). The interpretation of this taxon as used by the authors is rather broad and may include specimens of *D. fischeri* (Bukry, 1976a).

*Dictyocha pentagona* (Schulz)  
(Plate 1, Fig. 8)

*Dictyocha fibula* var. *pentagona* Schulz, 1928, p. 255, fig. 41a.

*Dictyocha pentagona* (Schulz) Bukry and Foster, 1973, p. 827, pl. 3, fig. 10.

**Remarks.** All silicoflagellate specimens with five basal sides and an apical bridge, except those that appear to be part of the *pseudofibula* plexus, were counted as *D. pentagona*. While listed here as a separate species, the specimens observed in this study might include variants of both *Dictyocha* and *Distephanus* taxa. One group of five-sided dictyochid forms, however, appeared to be part of the *pseudofibula* plexus and was thus counted as *Distephanus speculum speculum* f. *pseudopentagonus*.

*Dictyocha spinosa* (Deflandre)  
(Plate 2, Fig. 2)

*Corbisema spinosa* Deflandre, 1950, p. 193, figs. 178-182.

*Dictyocha spinosa* (Deflandre) Glezer, 1966, p. 238, pl. 10, figs. 6-8.

**Remarks.** *Dictyocha spinosa* is an unusual species similar to *D. hexacantha*, but has apical spines that are not in the basal plane. Observed specimens of *Dictyocha spinosa* were similar in size and structure to associated *D. frenguelli*.

*Dictyocha stapedia* Haeckel

*Dictyocha stapedia* Haeckel, 1887, p. 1561, pl. 101, figs. 10-12.

**Remarks.** This is a relatively small fibulid form with a long apical bridge that is rotated sinistrally when seen from apical view. It appears to be part of an evolutionary lineage that includes, in more recent strata, *Dictyocha subaculeata* and *D. aculeata*. *Dictyocha aculeata* is larger and has an apical bridge that is further rotated. *Dictyocha stapedia* was occasionally found in the upper Miocene of Hole 689B and 690B.

Genus *DISTEPHANUS* Stohr, 1880  
*Distephanus boliviensis* (Frenguelli)  
(Plate 3, Fig. 4)

**Remarks.** The six-sided *Distephanus* exhibit considerable variability. The group is generally subdivided into two species, but the biologic relationship between these is poorly understood. The first of these, *Distephanus boliviensis*, is a group characterized by a large basal ring and robust skeletal elements whereas morphologies ascribed to *Distephanus speculum* are smaller and have a more fragile appearance. In many samples the two taxa are distinct and easily separated, but in other samples

(e.g., 113-690B-3-2, 30–32 cm) they appear to intergrade (it is for this reason that the *boliviensis* morphologies are not used as a zonal indicator in this study).

Specimens of *D. boliviensis* dealt with in this study generally had long and more-or-less equal spines. However, there is much variation, and some samples were dominated by forms that had two major and four minor spines.

*Distephanus boliviensis major* (Frenguelli)

*Dictyochoa boliviensis* Frenguelli, 1940 (in part), p. 44, figs. 4 b–d.

*Distephanus boliviensis major* (Frenguelli), Bukry, 1978a, p. 817.

**Remarks.** Cannopilid specimens associated with *Distephanus boliviensis* were found in the upper Miocene and late Pliocene of Hole 689B.

*Distephanus crux* (Ehrenberg)

(Plate 3, Figs. 1–2)

*Distephanus crux* Ehrenberg, 1840, p. 207; Ehrenberg, 1854, pl. 18, fig. 56, pl. 33, fig. 9.

**Remarks.** This taxon showed considerable variability, especially in the relative size of the apical ring and the aspect ratio of the basal ring. Specimens with a relatively long major axis were counted as *D. longispinus*, although there appeared to be a close relationship between this form and associated *D. crux*. The forms with a slightly elongated basal ring, however, appear to be useful biostratigraphically.

*Distephanus longispinus* (Schulz)

(Plate 3, Fig. 3)

*Distephanus crux* f. *longispinus* Schulz, p. 256, fig. 44.

*Distephanus longispinus* (Schulz), Bukry and Foster, 1973, p. 828, pl. 4, figs. 7, 8.

**Remarks.** See remarks following *Distephanus crux*.

*Distephanus speculum hemisphaericus* (Ehrenberg)

(Plate 4, Figs. 1A–B, 3A–B, 4A–B, 5A–B, 6, 7)

*Dictyochoa hemisphaerica* Ehrenberg, 1844, pl. 17, fig. 5.

*Distephanus speculum hemisphaericus* (Ehrenberg), Bukry, 1975c, p. 854.

**Remarks.** *Distephanus* with multiple windows occurred sporadically throughout Hole 689B and are especially abundant in Section 113-689B-7H-5. These showed exceptional variability, from forms with two windows to others that were cannopilid in appearance (see Pl. 4). There was similar variability in the number of basal sides. Since the occurrence of these forms together indicates to the authors a close relationship and since there was no obvious criteria for subdividing this complex group, all forms were counted together, although a distinction is made between those that had up to or more than four windows. The abundant cannopilid morphologies found in the Oligocene of Hole 689B appeared to be closely related to co-occurring *Distephanus speculum*, but were sometimes larger in size.

*Distephanus speculum minutus* (Bachmann)

*Dictyochoa speculum* f. *minuta* Bachmann in Ichikawa et al., 1967, p. 161.

*Distephanus speculum pentagonus* Lemmermann

(Plate 3, Figs. 6A–C, 7, 8A–B)

*Distephanus speculum* var. *pentagonus* Lemmermann, 1901, p. 264, pl. 11, fig. 19.

*Distephanus speculum pentagonus* Lemmermann, Bukry, 1976a, p. 895.

**Remarks.** The five-sided *Distephanus* is generally less abundant than associated six-sided forms. However, it occasionally is predominant (Bukry, 1981). In Hole 689B, the pentagonid form is predominant in two widely separated samples. In each case, the association of abundant five-sided *Distephanus* with other unusual silicoflagellates such as *Naviculopsis trispinosa* (Section 113-689B-13H-2) and teratoid specimens (Section 113-689B-5H-5), indicates that the abundant occurrence of this form may be related to some environmental stress.

Two unusual five-sided distephanid forms were found. The first of these (Pl. 3, Fig. 7) has two long basal spines and three smaller ones. The general appearance is of a *Distephanus crux* on one side of the ma-

ior spines and a *D. speculum* on the other; a similar specimen was illustrated by McCartney and Wise, 1987, pl. 2, fig. 9). This form could be a teratoid specimen of either of the above species, or it could indicate that these species are more closely related than is generally believed.

A second unusual five-sided distephanid was represented by four specimens in Sample 113-689B-6H-5. This morphology (Pl. 3, Figs. 6, 8) has a nearly circular basal ring and a relatively large apical ring supported by struts that are almost perpendicular to the basal plane. The apical ring can be as large as the basal ring.

*Distephanus speculum speculum* (Ehrenberg)

(Pl. 3, Fig. 5; Pl. 4, Fig. 2A–B; Pl. 6, Fig. 1)

*Dictyochoa speculum* Ehrenberg, 1840; Ehrenberg, 1854, pl. 18, fig. 57; pl. 19, fig. 41; pl. 21, fig. 44; pl. 22, fig. 47.

**Remarks.** The six-sided distephanids exhibit considerable variability. This variation is most obvious in the size of the basal ring, the relative diameter of the apical ring, and the length of basal spines, but many other morphologic characters vary as well. There also were seven- and more-sided specimens (see Pl. 4, Fig. 2). These were counted separately to show some of the variability within the sample, but were not given subspecies or *forma* rank.

The “*pseudofibula plexus*” of *Distephanus speculum speculum*

**Introductory remarks.** In most sites an upper Miocene/lower Pliocene assemblage of small, six-sided silicoflagellates with an exceptionally variable apical structure was found. This assemblage may represent a group of variants of *Distephanus speculum* that occur because of some type of ecological stress. They have been previously reported at high-latitude sites. They are combined here into one group with three distinct variants that do not have an apical ring and a less common variant that has an apical ring with fewer sides than the basal ring.

Various workers (Bachmann and Ichikawa, 1962; Martini, 1971; Ling, 1972; Bukry, 1973, 1975b, 1976a, 1979, 1983; Ciesielski, 1975; Dzinoridze et al., 1978; Shaw and Ciesielski, 1983; Locker and Martini, 1986) have previously reported unusual six-sided silicoflagellates from upper Miocene or lower Pliocene high latitude sections that have unusual apical structures. These are usually classified under the species or subspecies names *pseudocrux*, *pseudofibula*, *japonica* or *varians*, although it is generally obvious from the illustrations that a number of distinct skeletal varieties are lumped into each taxon. The different skeletal morphologies (shown in Fig. 5 of the text) do not appear to have contrasting stratigraphic ranges, and in fact appear to occur collectively. These unusual skeletal morphologies occur in a relatively short interval from a number of the sites of Leg 113. These are here called *forma pseudofibula*, *varians*, and *notabilis*. Another morphology that is characterized by a four- or five-sided apical ring and referred to here as *pseudocrux* is much less common at Leg 113 sites but appears to be more common elsewhere. The *pseudocrux* morphology is assumed to be a part of the *pseudofibula* plexus, but future work on it is needed; Ling (1972) indicates that the *pseudocrux* morphology may have a slightly different range. A fifth morphotype in this plexus, *Distephanus speculum speculum* f. *pseudopentagonus*, is described below as new. At most Leg 113 sites, the assemblage occurs close to the point in the hole where the deposition of abundant upper Miocene-lower Pliocene ice-rafted material ceased.

*Distephanus speculum speculum* f. *pseudofibula* Schulz

(Pl. 5, Figs. 1–4; Pl. 6, Figs. 2, 3)

*Distephanus speculum* f. *pseudofibula* Schulz, 1928, p. 262, fig. 51a, b.

**Remarks.** The apical structure of this morphology consists of a three-element apical bridge that divides the skeletal morphology into similar halves; the bridge bifurcates at each end and at some place between the bifurcations has two struts that attach to opposite sides of the basal ring. The original description (Schulz, 1928) includes only specimens of this type, but some subsequent workers (for example, Ciesielski, 1975; Locker and Martini, 1986) have used this taxon to cover all the morphologies belonging to what is here referred to as the *pseudofibula* plexus.

*Distephanus speculum speculum* f. *varians* Gran and Braarud

(Pl. 5, Figs. 8–9, 13 [upper]; Pl. 6, Figs. 4, 6)

*Distephanus speculum* f. *varians* Gran and Braarud, 1935, p. 390, fig. 68b (not 68a).

**Remarks.** This morphology has a six-sided basal ring and an apical structure that is triradially symmetric, with a triple-junction directly above the center of the basal plane. Each member of this triple-junction then bifurcates into two struts that attach to adjacent basal sides. Gran and Braarud (1935), in their original description, illustrate both the tri-radiate morphology and the asymmetrical morphology discussed below without specifying one of these as the holotype. Subsequent usage has applied the *varians* term to the triradiate form, and thus we designate figure 68b of Gran and Braarud as the lectotype for the *varians* form.

*Distephanus speculum speculum*  
f. *notabilis*, n. stat.

(Pl. 5, Figs. 5, 10-12, 13 [lower]; Pl. 6, Figs. 5, 7)

*Distephanus speculum* f. *varians* Gran and Braarud, 1935, p. 390, fig. 68a (not 68b).

*Distephanus speculum varians* Gran and Braarud, Bukry, 1976a, pl. 8, fig. 10.

*Distephanus speculum notabilis* f. *notabilis* Locker and Martini, 1987, pl. 5, figs. 40-41.

**Remarks.** The apical structure of this morphology consists of a three-element apical bridge that is asymmetric with respect to any basal axis. The bridge has a curved shape with all struts connected to the outside of the curve. The two struts connected to opposite ends of this apical bridge are attached to adjacent basal sides. The apical structure thus takes the shape of an incomplete and tilted apical ring. Some specimens were found in which the apical ring was complete but not centered above the middle of the basal ring; these were counted as *Distephanus speculum speculum*. The occurrence of these types, as well as normal *Distephanus speculum speculum* of similar size, spine lengths and general construction is evidence that these are varieties of six-sided *Distephanus*. The form name *notabilis* is taken from Locker and Martini (1987), who used this taxon as a subspecies among *Distephanus speculum* morphologies of a much earlier (Eocene) age. The *notabilis* morphologies described by Locker and Martini are similar to those found in the Miocene/Pliocene *pseudofibula* plexus, and their subspecies name is used here as a form name for the general morphology. The Locker and Martini paper is important because it shows that the *pseudofibula* plexus associated with *Distephanus speculum* occurred elsewhere in the geologic record, presumably when the silicoflagellates were again under some environmental stress. To be consistent with our nomenclature for these forms, we transfer this name to form status.

*Distephanus speculum speculum* f. *pseudocrux* (Schulz).  
(Text Figs. 6e, 6f)

*Distephanus speculum* f. *pseudocrux* Schulz, 1928, p. 263, fig. 52a, b.

*Dictyocha japonica* Deflandre, 1950 (in part), pl. 17, fig. 18.

*Distephanus pseudocrux* (Schulz), Ling, 1977, pl. 2, figs. 16-17.

**Remarks.** Much less common than the types discussed above were varieties in which some struts bifurcate so that the apical ring has less skeletal elements than the basal ring. In its best-known forms (Fig. 6 e, f), four struts meet to support a four-sided apical ring. Thus the apical structure has altogether eight struts or, alternatively, six struts, a four-element apical ring and two apical bridges. There are two general morphologies. In one, the apical ring is above the center of the basal ring and the extra struts (or apical bridge elements) attach to opposite corners of the apical ring (see Fig. 6e). The long axis of the apical structure is usually, but not always, parallel to the basal major axis. In a second and apparently less common morphology (Fig. 6f), the apical ring may be centered with the extra struts attaching to adjacent apical corners.

*Distephanus speculum speculum* f. *pseudopentagonus* n. f.  
(Plate 5, Fig. 6)

**Diagnosis.** Five-sided basal ring with an apical structure similar to that of *Distephanus speculum speculum* f. *pseudofibula*.

**Description.** Five short to moderately long spines extend from the corners of the basal ring. The apical structure consists of two central bar segments which bend at their point of intersection, where they are also joined by a strut. At each of their other ends, the segments bifurcate into two struts. These segments and struts subdivide the central area into five portals of varying size. Basal pikes extend into each portal from the basal ring.

**Occurrence.** Lower Pliocene of ODP Sites 689, 690, and 693.

**Size.** Holotype, 45  $\mu\text{m}$ .

**Holotype.** Plate 5, Figure 6.

**Type locality.** ODP Sample 113-689B-2H-2, 33-35 cm.

**Remarks.** Among the variety of five-sided dictyochid forms observed in this study were skeletons that appeared to be part of the *pseudofibula* plexus, and are thus related more closely to *Distephanus speculum speculum* than to any *Dictyocha*. These were tabulated separately on the range charts in order to show the variability within this interesting group. Specimens counted in this group tended to be smaller than those counted as *Distephanus speculum pentagonus*.

Genus *NAVICULOPSIS* Frenguelli, 1940

*Naviculopsis constricta* (Schulz)

(Plate 1, Figs. 6, 7)

*Dictyocha navicula biapiculata constricta* Schulz, 1928, p. 246, fig. 21.

*Naviculopsis constricta* (Schulz), Bukry, 1975c, p. 856.

**Remarks.** This species has a relatively low band with elliptical portals. It was uncommonly found near the bottom of Hole 689B.

*Naviculopsis eobiapiculata* Bukry

(Plate 1, Figs. 2-4)

*Naviculopsis eobiapiculata* Bukry, 1978b, p. 878.

**Remarks.** This taxon has a highly curved band that is of constant width until the band is close to the basal ring. While easily distinguished from *N. constricta* when slightly tilted (see fig. 2 of McCartney and Wise, 1987), identification can be difficult when the specimen lies flat upon its basal ring.

Many of the specimens found in Cores 113-689B-8H to 113-689B-13H have a basal ring similar to *N. biapiculata* but with basal spines that are two-thirds the length of the basal ring. True *N. biapiculata*, according to Bukry (1978b), would have spines that are at least the length of the basal ring. Thus, these specimens appear to be intermediates between *N. eobiapiculata* and *N. biapiculata*. The decision to call these *N. eobiapiculata* was somewhat arbitrary and based upon the range of variation found in these samples.

*Navicula ponticulus* (Ehrenberg)

(Plate 1, Figs. 5, 9)

*Dictyocha ponticulus* Ehrenberg, 1844, p. 258, 267; Bailey, 1845, pl. 4, fig. 21.

*Naviculopsis ponticula* (Ehrenberg), Bukry, 1978a, pl. 8, figs. 9, 10.

**Remarks.** This taxon has a relatively wide basal ring that narrows toward the long-axis end of the basal ring. The termination there is flattened. There is generally, but not always, a very short spine or vestigial swelling. There was considerable variation, especially in the axial-end of the basal ring. Some of the specimens counted here as *Naviculopsis ponticulus* might be counted as *N. navicula* or *N. obtusarca* by other workers (see Bukry, 1978a, 1982).

Two specimens of a strutted variant of this taxon were found in Section 113-689B-8H-2. Strutted naviculopsids are occasionally found in the geologic record (see Perch-Nielsen, 1976; Bukry, 1976c). Other silicoflagellates with a similar morphology are considered as *Dictyocha* (e.g., Ciesielski, 1975, pl. 7) on the basis of association. These variants are important because they give some insight into the relationship between *Naviculopsis* and *Dictyocha*, and to silicoflagellate variability in general. In the late Miocene, a similar group of naviculopsid morphologies appears to have evolved from *Dictyocha brevis* (see Bukry, 1978a; Locker and Martini, 1986).

*Naviculopsis trispinosa* (Schulz)

*Dictyocha navicula trispinosa* Schulz, 1928, p. 246, fig. 23a, b.

*Naviculopsis trispinosa* (Schulz), Bukry, 1975c, p. 857, pl. 7, fig. 5-7.

**Remarks.** This species is very similar to *N. biapiculata* (see Bukry, 1975c) and may be very closely related to it. *Naviculopsis trispinosa*, however, has a large apical spine, and is very distinctive because it usually lies on its side. The abundance of this taxon in samples in which five-sided *Distephanus* are also unusually abundant may indicate that this is an ecophenotype that occurs in high-stress environments.

## Ebridians

Genus ADONNADONNA Gombos, 1982

*Adonnadonna primadonna* Gombos

(Plate 7, Fig. 4)

*Adonnadonna primadonna* Gombos, 1982, p. 446.

**Remarks.** This is an extremely large and unusual ebridian (?) that is probably very closely related to, and in this study co-occurs with, *Triskelion gorgon*. The close relationship between these two taxa is indicated by the many similarities between them, including their enormous size, surface ornamentation, and co-occurrence in Section 113-689B-14H-5. *Adonnadonna primadonna* differs from *Triskelion gorgon* in having a circular inner ring from which skeletal elements radiate outward; the smaller ring is lacking in *Triskelion gorgon*.

Genus AMMODOCHIUM Hovasse, 1932

*Ammodochium rectangulare* (Schulz)

(Pl. 7, Figs. 7, 8)

*Ebria antiqua* var. *rectangularis* Schulz, 1928, p. 274, figs. 72 a-d.*Ammodochium rectangulare* (Schulz), Ling, 1971, p. 694.

**Remarks.** *Ammonochium rectangulare* is readily identified by its rectangular outline although, when positioned on its apical or antapical ring, the outline is triangular (Pl. 7, Fig. 8).

Genus CRANIOPSIS Hovasse ex Frenguelli, 1940

*Craniopsis octo* Hovasse ex Frenguelli, 1940

(Plate 7, Fig. 5)

*Craniopsis octo* Hovasse ex Frenguelli, 1940, p. 95, figs. 31 a, b.

**Remarks.** This taxon was originally found by Hovasse (1932b) in the upper Eocene of New Zealand.

Genus EBRIOPSIS Hovasse, 1932

*Ebriopsis antiqua antiqua* (Schulz)

(Pl. 7, Fig. 6)

*Ebriopsis antiqua* Schulz, 1928 (in part), p. 273, 274, fig. 696.*Ebriopsis antiqua antiqua* (Schulz), Ling, 1977, p. 215, pl. 17, 18.

**Remarks.** *Ebriopsis* specimens with spines or pronounced surface crenulations were not found in this study.

Genus PARATHRANIUM Hovasse, 1932

*Parathranium tenuipes* (Hovasse)*Thranium tenuipes* Hovasse, 1932a, p. 123, fig. 5.*Parathranium tenuipes* (Hovasse), Ling, 1972, p. 198-199.

Genus TRISKELION Gombos, 1982

*Triskelion gorgon* Gombos

(Plate 7, Fig. 1-3)

*Triskelion gorgon* Gombos, 1982, p. 446-447.

**Remarks.** Gombos (1982) found that *Triskelion gorgon* appears to occur over a larger part of the middle Eocene than *Adonnadonna primadonna*.

## ACKNOWLEDGMENTS

We are pleased to acknowledge the able assistance of Kristin Magnusen, who prepared the samples, Walter Thorner, for help and tutelage with computer graphics, and Dennis S. Cassidy, for generous help and use of the laboratories within the Antarctic Research Facility, FSU. Aboard ship, David Lazarus provided screen prints of some taxa that were quite helpful to the study. Support was provided by NSF Grant DPP 84-14268, JOI/USSAC funds, and an equipment grant from the AMOCO Foundation.

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Date of initial receipt: 27 February 1988  
 Date of acceptance: 19 September 1989  
 Ms 113B-142

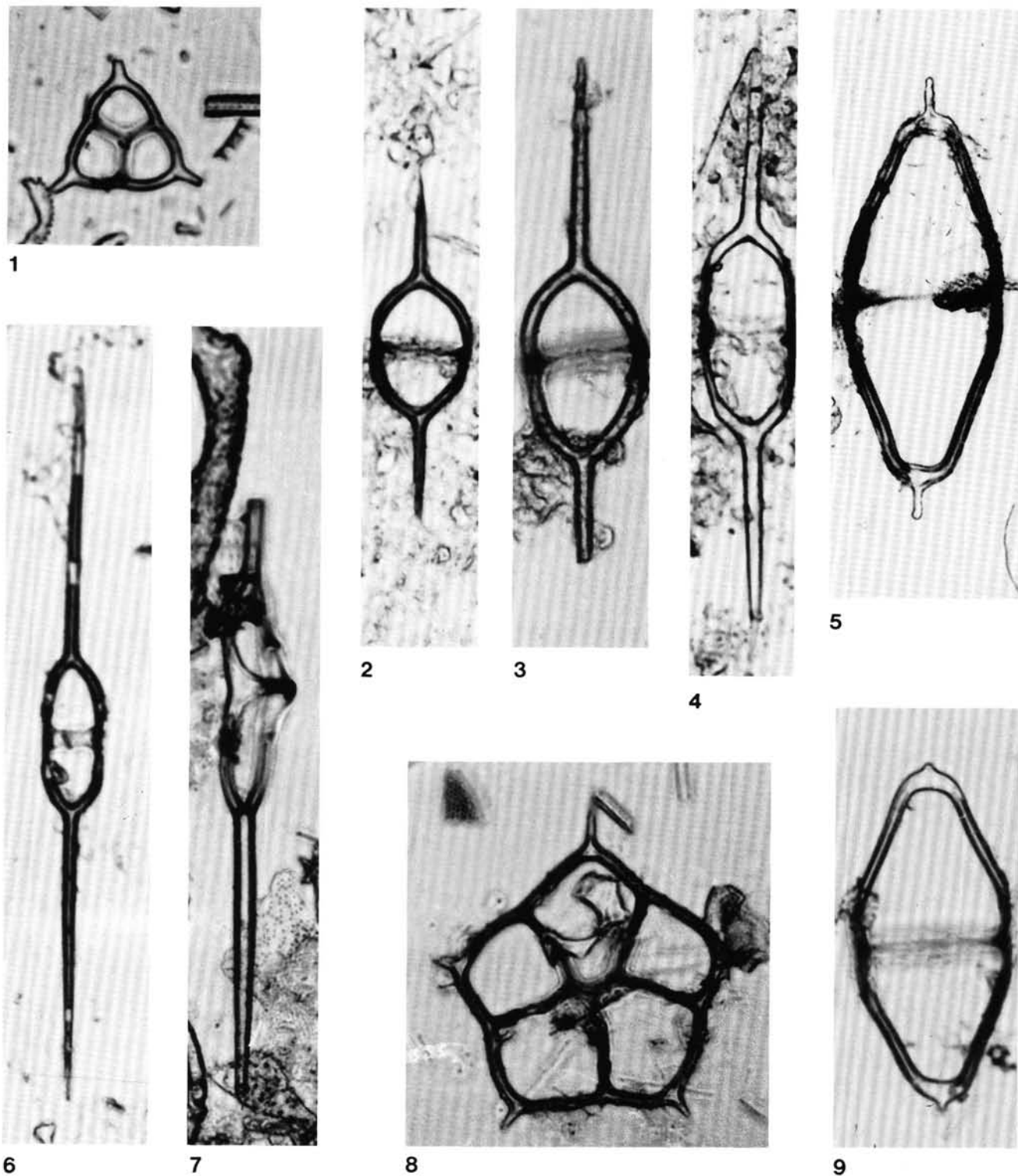


Plate 1. *Corbisema*, *Dictyocha*, and *Naviculopsis* from Hole 689B, ODP Leg 113, 740 $\times$ . 1. *Corbisema triacantha* (Ehrenberg), Sample 113-689B-7H-5, 29-31 cm. 2-4. *Naviculopsis eobiapiculata* Bukry, (2) Sample 113-689B-12H-2, 29-31 cm; (3) Sample 113-689B-9H-2, 29-31 cm; (4) Sample 113-689B-11H-2, 32-34 cm. 5. *Naviculopsis ponticulus* (Ehrenberg), Sample 113-689B-8H-2, 30-32 cm. 6-7. *Naviculopsis constricta* (Schulz), (6) Sample 113-689B-13H-5, 28-30 cm; (7) Sample 113-689B-14H-5, 30-32 cm. 8. *Dictyocha pentagona* (Schulz), Sample 113-689B-2H-2, 33-35 cm. 9. *Naviculopsis ponticulus* (Ehrenberg), Sample 113-689B-8H-2, 30-32 cm.

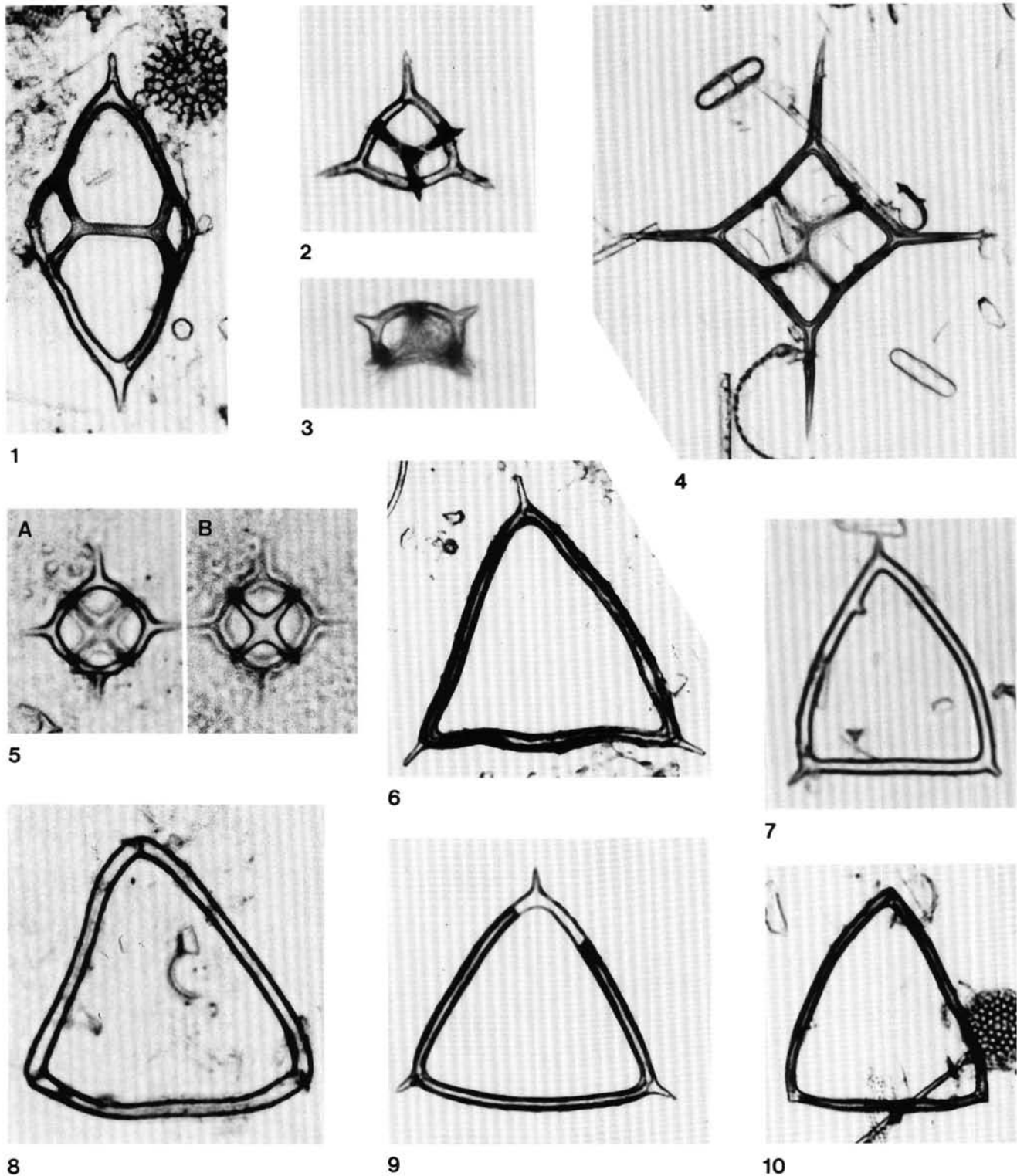


Plate 2. *Dictyocha* and *Bachmannocena* from ODP Leg 113, 740 $\times$ . 1. *Dictyocha aspera*, Sample 113-690B-6H-2, 28–30 cm. 2. *Dictyocha spinosa* (Deflandre), Sample 113-689B-9H-2, 29–31 cm. 3. *Dictyocha frenguelli* Deflandre, lateral view, Sample 113-689B-9H-5, 29–31 cm. 4. *Dictyocha calida* Poelchau, abapical view, Sample 113-689B-5H-5, 29–31 cm. 5. *Dictyocha deflandrei* Frenguelli, Sample 113-689B-10H-5, 30–32 cm. 6–10. *Bachmannocena apiculata* Schulz, showing range of variation, (6) Sample 113-689B-11H-2, 32–34 cm; (7) Sample 113-689B-8H-5, 30–32 cm; (8) Sample 113-689B-8H-2, 30–32 cm; (9) Sample 113-689B-8H-5, 30–32 cm; (10) Sample 113-689B-8H-2, 30–32 cm.

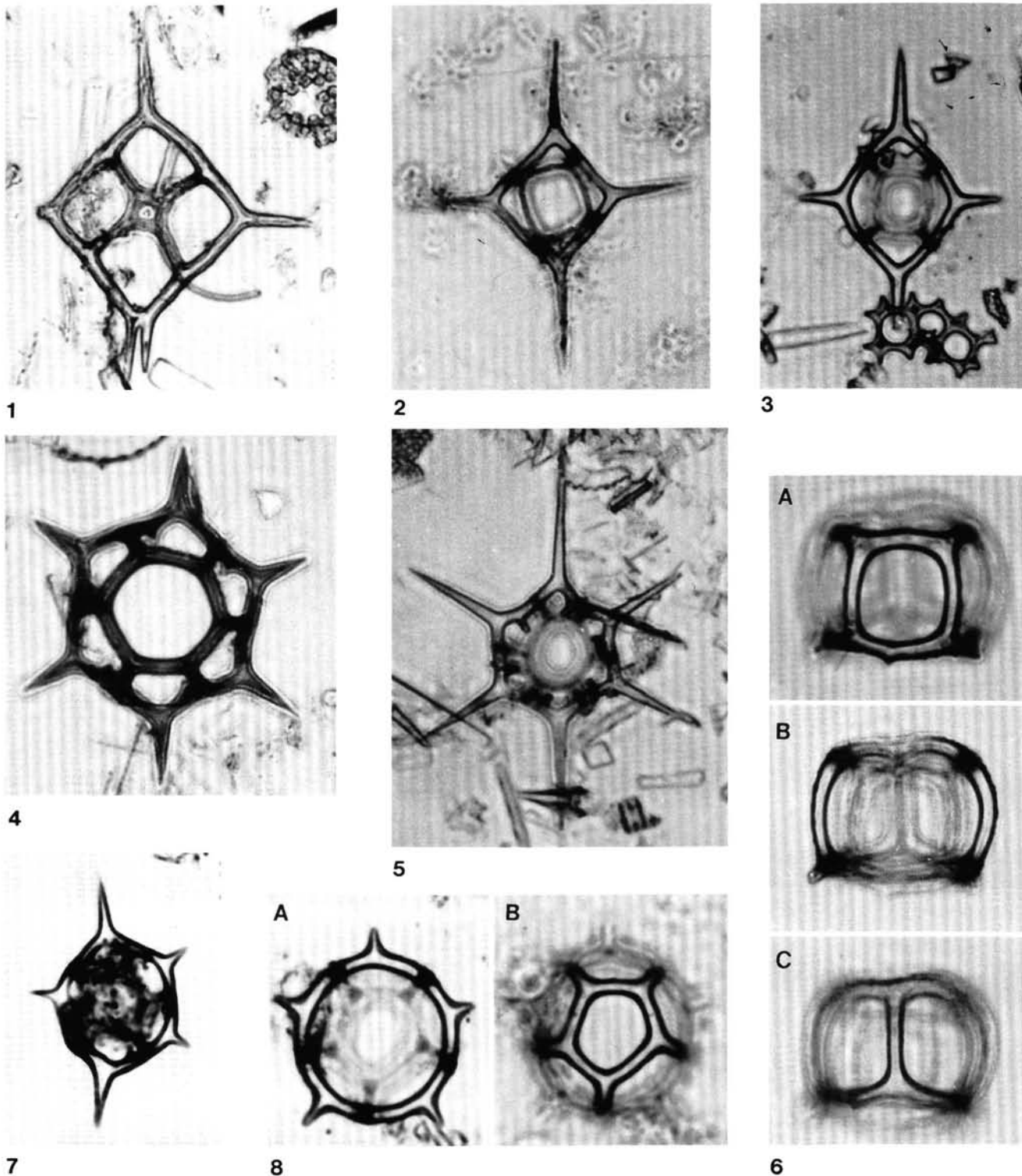


Plate 3. *Distephanus* from Hole 689B, Leg 113, 740 $\times$ . 1-2. *Distephanus crux* (Ehrenberg), (1) Sample 113-689B-6H-5, 29-31 cm; (2) Sample 113-689B-13H-5, 28-30 cm. 3. *Distephanus longispinus*, Sample 113-689B-8H-5, 30-32 cm. 4. *Distephanus boliviensis* (Frenguelli), Sample 113-689B-3H-5, 29-31 cm. 5. *Distephanus speculum speculum* (Ehrenberg), Sample 113-689B-4H-5, 30-32 cm. 6A-C. *Distephanus crux/speculum*, Sample 113-689B-9H-2, 29-31 cm. 7, 8A-B. *Distephanus speculum pentagonus* Lemmermann, Sample 113-689B-6H-5, 29-31 cm.

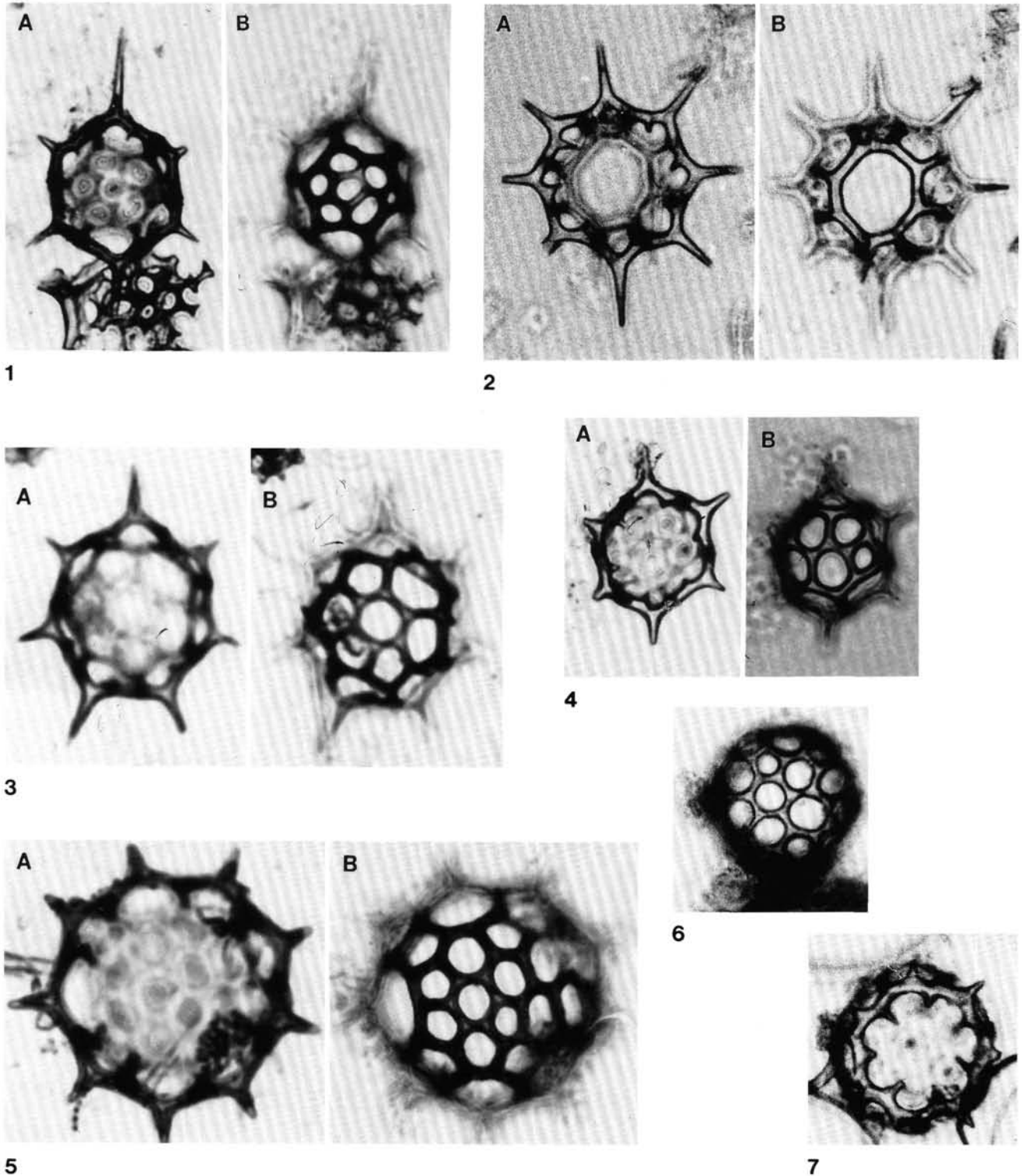


Plate 4. Multiwindowed and many-sided silicoflagellates from ODP Leg 113, 740 $\times$ . 1A-B. *Distephanus speculum hemisphaericus* (high and low focus), Sample 113-689B-8H-5, 30-32 cm. 2A-B. *Distephanus speculum speculum* (eight-sided, high and low focus), Sample 113-690B-2H-1, 30-32 cm. 3-7. *Distephanus speculum hemisphaericus*, (3A-B) (high and low focus), Sample 113-689B-7H-5, 29-31 cm. (4A-B) (high and low focus), 113-689B-10H-5, 29-31 cm. (5A-B) (high and low focus), Sample 113-689B-7H-5, 29-31 cm. (6, 7) (apical and abapical views, different specimens), Sample 113-689B-7H-5, 29-31 cm.

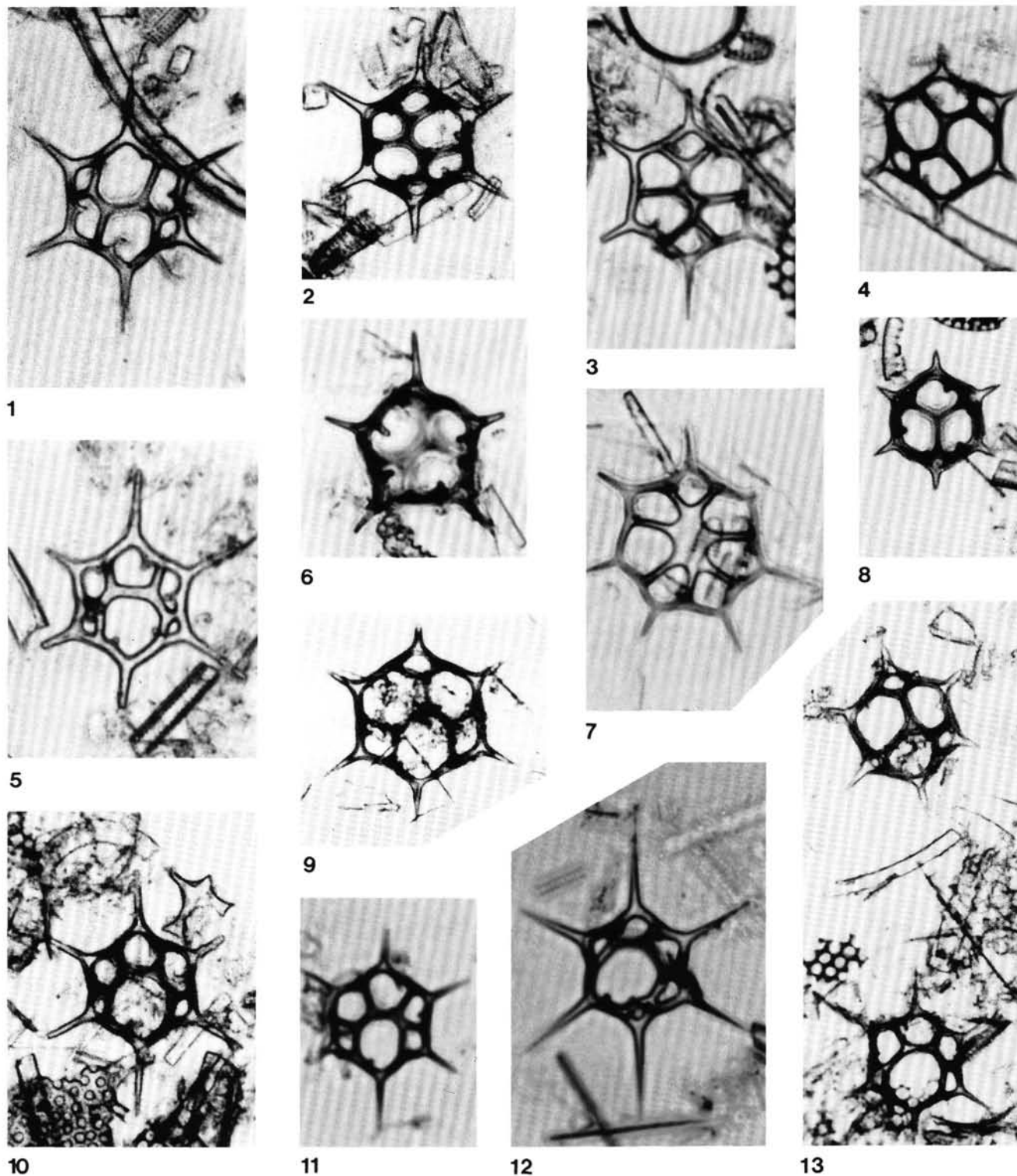


Plate 5. Specimens of the *pseudofibula* plexus of *Distephanus speculum speculum* from ODP Leg 113, 740 $\times$ . 1-4. *Distephanus speculum speculum* f. *pseudofibula*. (1) Sample 113-690B-3H-5, 30-32; (2) Sample 113-689B-3H-5, 29-31 cm; (3) Sample 113-689B-3H-5, 29-31 cm; (4) Sample 113-689B-3H-2, 30-32 cm. 5. *Distephanus speculum speculum* f. *notabilis*, Sample 113-689B-3H-2, 30-32 cm. 6. *Distephanus speculum speculum* f. *pseudopentagonus* n. f., holotype, Sample 113-689B-2H-2, 33-35 cm. 7. Unusual and unnamed morphotype, Sample 113-689B-3H-5, 29-31 cm. 8. *Distephanus speculum speculum* f. *varians*, Sample 693A-13R-2, 30-32 cm. 9. *Distephanus speculum speculum* f. *varians*, Sample 690B-3H-5, 30-32 cm. 10-12. *Distephanus speculum speculum* f. *notabilis*, (10) Sample 113-690B-3H-5, 30-32 cm; (11) Sample 113-689B-2H-5, 29-31 cm; (12) Sample 113-689B-3H-5, 29-31 cm. 13. *Distephanus speculum speculum* f. *varians* (above) and *Distephanus speculum speculum* f. *notabilis* (below), Sample 113-690B-3H-5, 30-32 cm.

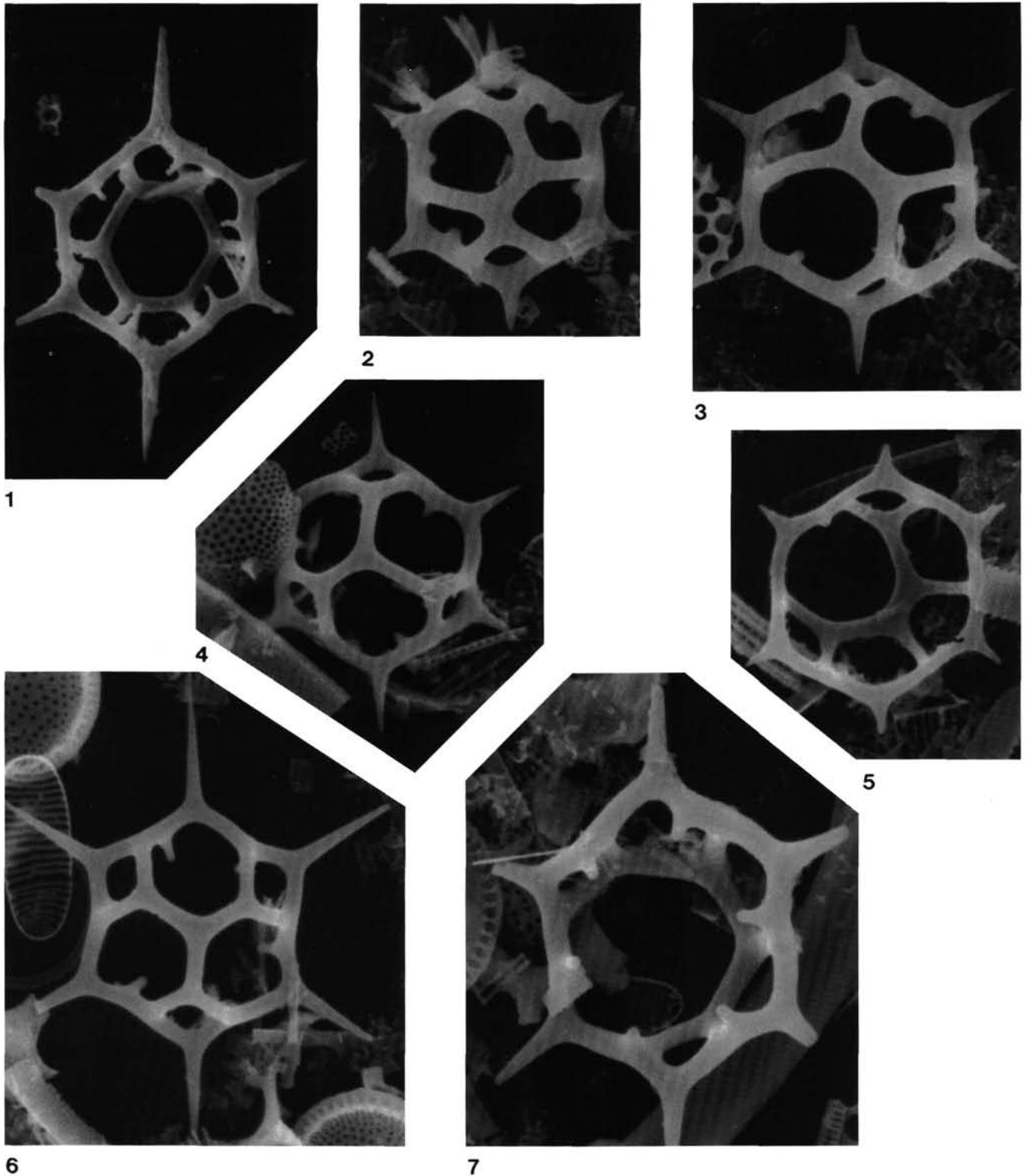
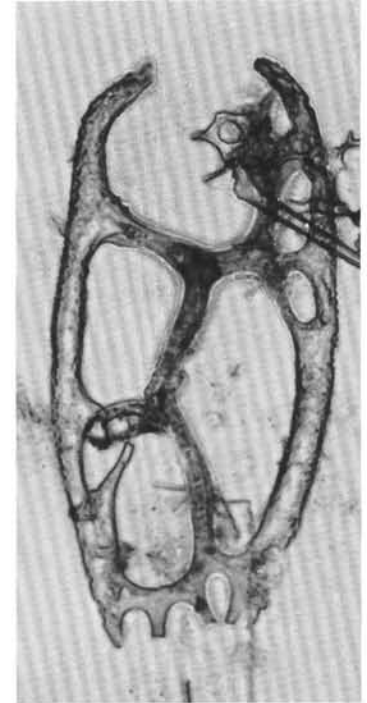


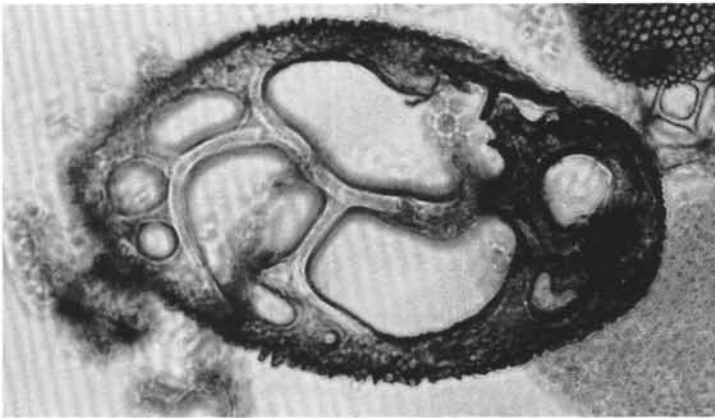
Plate 6. Scanning electron micrographs of specimens of the *pseudofibula* plexus from Leg 113, 100 $\times$ ; all specimens except number 1 are from Sample 113-689B-3H-5, 29-31 cm. 1. *Distephanus speculum speculum* (with apical ring), Sample 113-689B-2H-5, 29-31 cm. 2, 3. *Distephanus speculum speculum* f. *pseudofibula*. 4. *Distephanus speculum speculum* f. *varians*. 5, 7. *Distephanus speculum speculum* f. *notabilis*. 6. *Distephanus speculum speculum* f. *varians*.



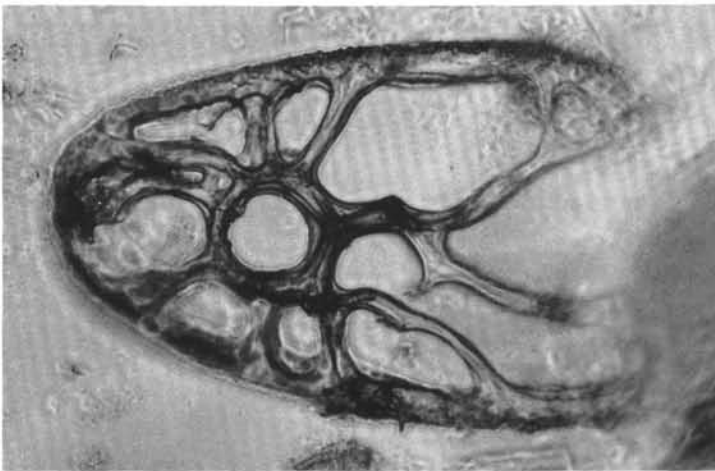
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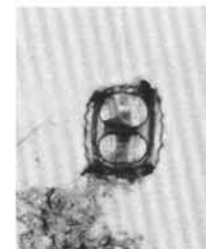
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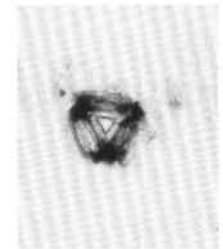
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Plate 7. Ebridian specimens from ODP Leg 113, 435 $\times$ . 1-3 *Triskelion gorgon* Gombos, Sample 113-689B-14H-5, 30-32 cm. 4. *Adonnadonna primadonna* Gombos, Sample 113-689B-14H-5, 30-32 cm. 5. *Craniopsis octo* Hovasse ex Frenguelli, Sample 113-689B-15H-2, 30-32 cm. 6. *Ebriopsis antiqua antiqua* (Schulz), Sample 113-689B-14H-5, 30-32 cm. 7, 8. *Ammodochium rectangulare* (Schulz), (7) Sample 113-689B-14H-5, 30-32 cm; (8) apical view, Sample 689B-15H-2, 30-32 cm.