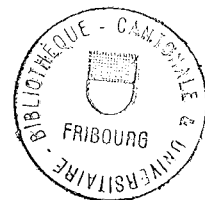


CANDEINA ANTARCTICA, N. SP. AND THE PHYLOGENETIC HISTORY AND DISTRIBUTION OF CANDEINA SPP. IN THE PALEOGENE-EARLY NEOGENE OF THE SOUTHERN OCEAN

R. MARK LECKIE¹ AND PETER-NOEL WEBB²



ABSTRACT

Two poorly known species of *Candeina* from the Southern Hemisphere, *C. cecionii* Cañon and Ernst and *C. zeocenica* Hornibrook and Jenkins, are believed to be part of a lineage that evolved in the temperate Southern Ocean during the Paleogene. *Candeina cecionii* is known from the early Eocene or early middle Eocene of the Magallanes Basin (southern Chile) while *C. zeocenica* has only been found in late middle Eocene to early Oligocene age sediments of New Zealand. Paleoceanographic circulation patterns and widespread hiatuses may be responsible for their present geographic and stratigraphic distribution. This suspected lineage probably gave rise to *Candeina antarctica*, n. sp., described here from the late Oligocene to middle Miocene of the Ross Sea, Antarctica. *Candeina antarctica* was part of a nearly monospecific planktonic foraminiferal assemblage during this period of deteriorating climatic conditions on and around Antarctica and was probably restricted to this region. As glacial conditions intensified during the middle and late Miocene, calcareous plankton were displaced northwards and replaced by siliceous planktonic assemblages. This transition corresponds with the last known occurrence of *C. antarctica*. Other workers have suggested that *Candeina nitida* s.l. evolved from *Globigerina juvenilis* (= *Globigerinita glutinata*) near the base of the late Miocene. An alternative explanation for the origin of *C. nitida* (late Miocene to Recent) is suggested in light of the Paleogene-early Neogene *Candeina* morphoserries proposed here.

INTRODUCTION

The planktonic foraminifer, *Candeina nitida* d'Orbigny has long been recognized as a minor component of tropical and subtropical late Miocene-to-present day pelagic assemblages. *Candeina zeocenica* was described from the Paleogene of New Zealand by Hornibrook and Jenkins (1965). These authors speculated on the possibility of a 'missing link' between *C. zeocenica* and the younger *C. nitida*. Another, apparently older Paleogene species, *C. cecionii*, was described from the Magallanes Basin of southern Chile by Cañon and Ernst (1974). These two Paleogene Southern Hemisphere forms are also minor constituents of their respective planktonic foraminiferal populations. Both

taxa have poorly understood geographic distributions and biostratigraphic ranges. Paleogene species of *Candeina* have never been reported from the Northern Hemisphere.

During the Paleogene to early Neogene the Southern Ocean and its peripheral basins experienced rapidly changing oceanographic conditions. Oceanic circulation responded to southern high-latitude plate movements and waxing and waning of continental scale glaciation on Antarctica. The latest Paleogene-early Neogene also witnessed the appearance and evolution of an important species of the planktonic genus *Candeina* in the Ross Sea region of Antarctica. This taxon is believed to be the direct descendant of the Paleogene *Candeina* stock. The lineage proposed here contributes to biostratigraphic and paleoceanographic control in the marginal areas of the Southern Ocean and Antarctic seaways during this period of dynamic change in Cenozoic climate and oceanography.

SYSTEMATICS

(Superfamily Uncertain)

Family CANDEINIDAE Cushman, 1927

The genus *Candeina* has experienced an uncertain position in classificationary schemes over many years. Authors have recognized that the ontogenetic development of *Candeina nitida* appears to pass through an early globigerine stage and then a globigerinoid stage prior to acquiring its unique adult form (Bolli and others, 1957; Loeblich and Tappan, 1964; Blow, 1969). *Candeina* commonly has been placed in the Family Globigerinidae. Cushman (1940) subdivided this family and recognized a subfamily Candeininae. However, *Candeina* was placed in the subfamily Orbulininae or Family Orbulinidae by other authors (Bolli and others, 1957; Banner and Blow, 1959; Loeblich and Tappan, 1964). A potential problem exists with such a scheme in that orbulinid spheres have been recognized as reproductive stages in several genera and species of globigerinids (Hofker, 1959, 1969; Bandy, 1966; Adshead, 1980). Reiss (1958, 1963) recognized that *Candeina nitida* possesses a monolamellar wall whereas globigerinids are characterized by bilamellar test walls. He rejected the placement of *Candeina* with the Globigerinidae. Recently, Huang (1981) placed *Candeina nitida* with the Family Globorotaliidae on the basis of internal morphocharacters.

Hofker (1954; 1959, p. 2) noted strongly reduced tooth-plates in juvenile stages of *Candeina nitida* and suggested that this represented the "last stage in a reduction series from *Cassidulina* through *Sphaeroidina* to *Candeina*." Hofker (1959) concluded that *Candeina*

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should not be included in the Globigerinidae. This view was supported by Parker (1962). Reiss (1958, 1963) and Jenkins (1971) tentatively placed *Candeina* in the Cassidulinidae, while Hornibrook and Jenkins (1965) suggested that the wall structure is nearer to that of the Buliminidae. It should be noted that Reiss (1958) included such genera as *Cassidulina*, *Ehrenbergina*, *Cassidulinoides* and *Sphaeroidina* in the Cassidulinidae. The first two mentioned genera have granular walls whereas the latter two possess radial calcite wall construction. In a subsequent classification, Loeblich and Tappan (1964) employed wall structure to place the granular-walled *Cassidulina* and *Ehrenbergina* in the Cassidulinacea and *Cassidulinoides* and *Sphaeroidina* in the Buliminacea. Bé (1968, 1977) and Bé and others (1969) concurred with Parker (1967) in suggesting, that because of its unique sutural apertures and extremely low shell porosity, *Candeina* should be placed in a separate family Candeinidae. Loeblich and Tappan (1982) also recognize a Family Candeinidae Cushman, 1927. We adopt this placement here. Its origin, be it planktonic, benthic or even polygenetic (as suggested by Blow, 1969) remains uncertain.

Candeina d'Orbigny in DeLaSagra, 1839

Candeina antarctica, n.sp.

Pl. 1, Figs. 1–17; Pl. 2, Figs. 1–9; Pl. 3., Figs. 3, 6, 8

Description. Test small, free, low trochospiral coil, equatorial periphery lobate, axial periphery rounded; test calcareous, smooth, finely perforate, and very thin; chambers spherical, increasing gradually in size as added, 8–10 most common in adult, arranged in one and one-half to two and one-half whorls; with three and one-half to five chambers in ultimate whorl, four being most common (Pl. 1, Figs. 1–13) and three to three and one-half most typical in penultimate whorl (Pl. 1, Figs. 14–17); sutures depressed, radial to slightly curved on spiral side, radial and pustulose on umbilical side; umbilicus closed; primary aperture interiomarginal-umbilical in early stages (Pl. 1, Fig. 15); adult test with multiple sutural supplementary apertures confined to umbilical side; supplementary apertures generally elongate parallel to the sutures; bar-like partitions may separate sutural apertures but more typically, flat bridge-like structures span suture (Pl. 1, Figs. 1,

12; Pl. 2, Figs. 4, 7); sutural bullae sometimes observed (Pl. 1, Figs. 6, 11; Pl. 2, Figs. 1, 2).

Table 1 lists the dimensions of the holotype, paratypes and other figured specimens.

Discussion. *Candeina antarctica*, n. sp., differs from *C. nitida* d'Orbigny (late Miocene to Recent) in being smaller, having fewer chambers, possessing a low trochospiral form, and well-developed sutural pustulation on the umbilical side. The multiple sutural apertures are restricted to the umbilical side in *C. antarctica*. The sutural apertures of *C. nitida* are discrete, oval-shaped openings surrounded by a thickened rim (Pl. 3, Fig. 13). Such features are not observed in *C. antarctica*.

Candeina antarctica, n. sp., is morphologically similar to *C. cecionii* Cañón and Ernst and *C. zeocenica* Hornibrook and Jenkins. The main distinguishing features of *C. antarctica* are its low, flatter (relative to *C. zeocenica*) quadrilobate form, supplementary sutural apertures confined to the umbilical side, and development of pustules in the umbilicus and along the umbilical sutures.

Stratigraphic range. At present known only from the Ross Sea basins, Antarctica; latest Oligocene-early Miocene of DSDP Site 270 (Leckie and Webb, 1980, 1983), Oligocene-early Miocene of drillhole MSSTS-1 (Webb, 1983), early to middle Miocene of DSDP Site 273 (D'Agostino and Webb, 1980, D'Agostino, 1980) and middle Miocene RISP Site J9 (Webb, 1979a).

Type specimens. The holotype (USNM 385215), figured paratypes (USNM 385216, 385218) and unfigured paratype (USNM 385217) are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC. Some of the other paratypes will be deposited at the New Zealand Geological Survey, Lower Hutt, N.Z. The remaining paratypes will be retained by the authors.

Candeina zeocenica Hornibrook and Jenkins, 1965

Figures 1–3; Pl. 3, Figs. 2, 5, 10, 12

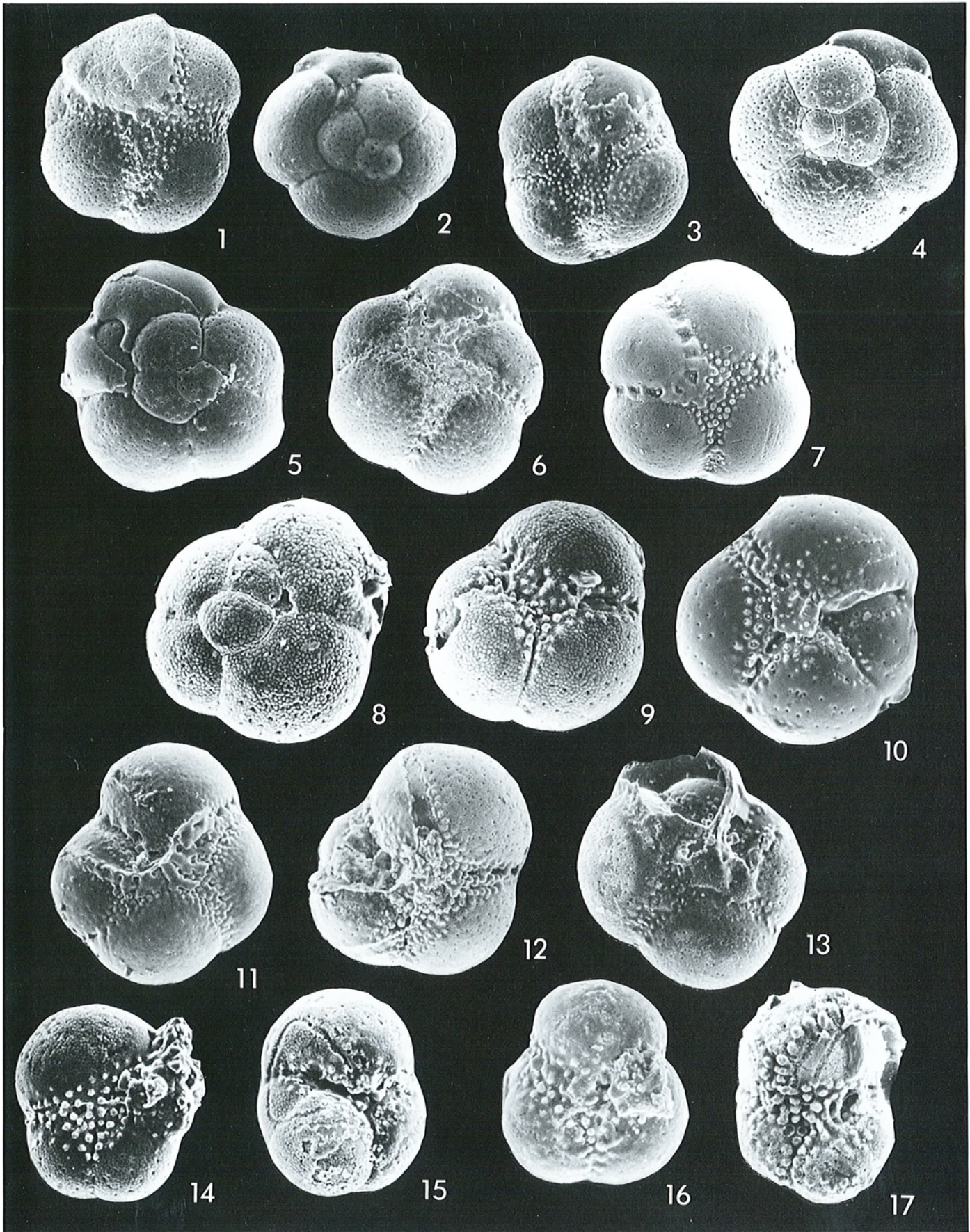
Candeina zeocenica HORNIBROOK and JENKINS, 1965, p. 839–842, text-figs. 1–5. SRINIVASAN, 1968, p. 149, pl. 15, figs. 12, 13. JENKINS, 1971, p. 72, 73, pl. 3, figs. 62–66.

Description. Test small, free, moderate to low trochospiral coil, equatorial periphery lobate, axial periphery rounded; test calcareous, smooth, finely per-

PLATE 1

Candeina antarctica, n. sp.

1, 2 Holotype (USNM 385215); DSDP Site 270, Core 34-3, 28–38 cm. 1. Umbilical side; $\times 178$. 2. Spiral side, same specimen; $\times 156$. 3, 4 Paratype (USNM 385218); DSDP Site 270, Core 35-3, 112–121 cm. 3. Umbilical side; $\times 167$. 4. Spiral side, same specimen; $\times 183$. 5, 6 Paratype; DSDP Site 270, Core 37-4, 133–142 cm (same specimen as Pl. 2, Figs. 2, 6, 9). 5. Spiral side; $\times 161$. 6. Umbilical side, same specimen; $\times 157$. 7 Paratype (USNM 385216); umbilical side; DSDP Site 270, Core 15 CC; $\times 180$. 8, 9 Paratype; DSDP Site 270, Core 33-3, 102–110 cm. 8. Spiral side; $\times 377$. 9. Umbilical side, same specimen; $\times 354$. 10 Paratype; umbilical side; DSDP Site 270, Core 25-2, 50–60 cm; $\times 369$. 11 Paratype; umbilical side; DSDP Site 270, Core 25-2, 50–60 cm; $\times 164$ (same specimen as Pl. 2, Fig. 1). 12 Paratype; umbilical side; DSDP Site 270, Core 21-4, 102–110 cm; $\times 247$. 13 Paratype; umbilical side; DSDP Site 270, Core 13-3, 114–125 cm; $\times 220$ (same specimen as Pl. 2, Figs. 4, 7). 14 Paratype; umbilical side; DSDP Site 270, Core 39-6, 24–36 cm; $\times 354$. 15 Paratype; umbilical side; DSDP Site 270, Core 39-6, 24–36 cm; $\times 364$. 16 Paratype; umbilical side; DSDP Site 270, Core 39-6, 24–36 cm; $\times 360$. 17 Paratype; umbilical side; DSDP Site 270, Core 26-4, 100–114 cm; $\times 382$.



forate; monolamellar; radial wall structure (Hornibrook and Jenkins, 1965); chambers spherical, increasing gradually in size as added, typically nine in adult arranged in one and one-half to two whorls; three and one-half to four chambers in the final whorl; sutures depressed, radial to slightly curved on spiral side, radial on umbilical side; adult test with multiple sutural supplementary apertures on umbilical side and along final whorl on spiral side; each opening separated by small bar-like partition oriented at right angles to suture.

Table 2 lists the dimensions of the holotype, two paratypes (Figs. 1–3) illustrated by Hornibrook and Jenkins (1965) and two previously unillustrated paratypes (Pl. 3, Figs. 2, 5, 10, 12).

Discussion. *Candeina zeocenica* differs from *C. nitida* d'Orbigny in being smaller, having a lower trochospiral form, possessing bar-like partitions between its sutural apertures, and having sutural apertures elongated normal to rather than along the suture as in *C. nitida* (Pl. 3, Fig. 13). *C. zeocenica* differs from *C. antarctica*, n.sp., and *C. cecionii* Cañón and Ernst in having a greater degree of variability in the height of its spire and in possessing characteristic bar-like partitions between the sutural apertures. In addition, it differs from *C. antarctica* in possessing sutural apertures on the spiral side. These may be restricted to the final chamber only. It also lacks the well-developed pustulation characteristic of the umbilicus and umbilical sutures of *C. antarctica*.

Stratigraphic range. Reported only from New Zealand; Bortonian Stage to Whaingaroan Stage (late middle Eocene to early Oligocene, Figure 5) (Srinivasan, 1968; Jenkins, 1971). Is noteworthy that *C. zeocenica* was not recorded at Leg 29 DSDP sites south of New Zealand (Jenkins, 1975) (Figure 9).

***Candeina cecionii* Cañón and Ernst, 1974**
Figure 4; Pl. 3, Figs. 1, 4, 7, 9, 11

Candeina cecionii CAÑÓN and ERNST, 1974, p. 83, 84, pl. 4, fig. 6a–c.

Description. Test small, free, low trochospiral coil, equatorial periphery lobate, axial periphery rounded. Test calcareous, smooth, finely perforate. Chambers spherical, increasing gradually in size as added, eight to ten most common in adult, arranged in two to two and one-half whorls; four chambers in the final whorl. Sutures depressed radial to slightly curved on spiral side, radial on umbilical side. Adult test has supple-

mentary sutural apertures along the umbilical sutures and along the dorso-ventrally directed intercameral sutures of the final whorl. Possesses thickened partitions between the sutural apertures, oriented at right angles to the suture. Table 3 lists the dimensions of the holotype, the previously unillustrated paratype and ten other specimens (two of which are illustrated here).

Discussion. *C. cecionii* is apparently the oldest known *Candeina*. *C. cecionii* is morphologically similar to *C. antarctica*, n.sp., and *C. zeocenica* Hornibrook and Jenkins. Because of the less-than-perfect preservation of primary type material, the authors have considered the possibility that *C. cecionii* may actually be synonymous with *C. zeocenica*. It is retained as a separate taxon in the present study. *C. cecionii* lacks the well-developed bar-like partitions which separate the sutural apertures in *C. zeocenica* and appears to have a consistently low trochospiral form. *C. cecionii* lacks the umbilical pustulation of *C. antarctica*.

Stratigraphic range. At present known only from the Magallanes Basin of southern Chile; Manzanian Stage (early Eocene to early middle Eocene) (Figure 5). This range has been modified from the original age assignment (Cañón and Ernst, 1974) of Miradorian and Gaviotian Stages (Upper Oligocene-Miocene) (Cañón, written communication, 1981). Uncertainty in the stratigraphic position of this taxon was caused by use of well cuttings in the original study. Subsequent clarification of the stratigraphic distribution by Cañón (personal communication) has an important bearing on the discussions presented below.

STRATIGRAPHIC POSITION OF
CANDEINA CECIONII

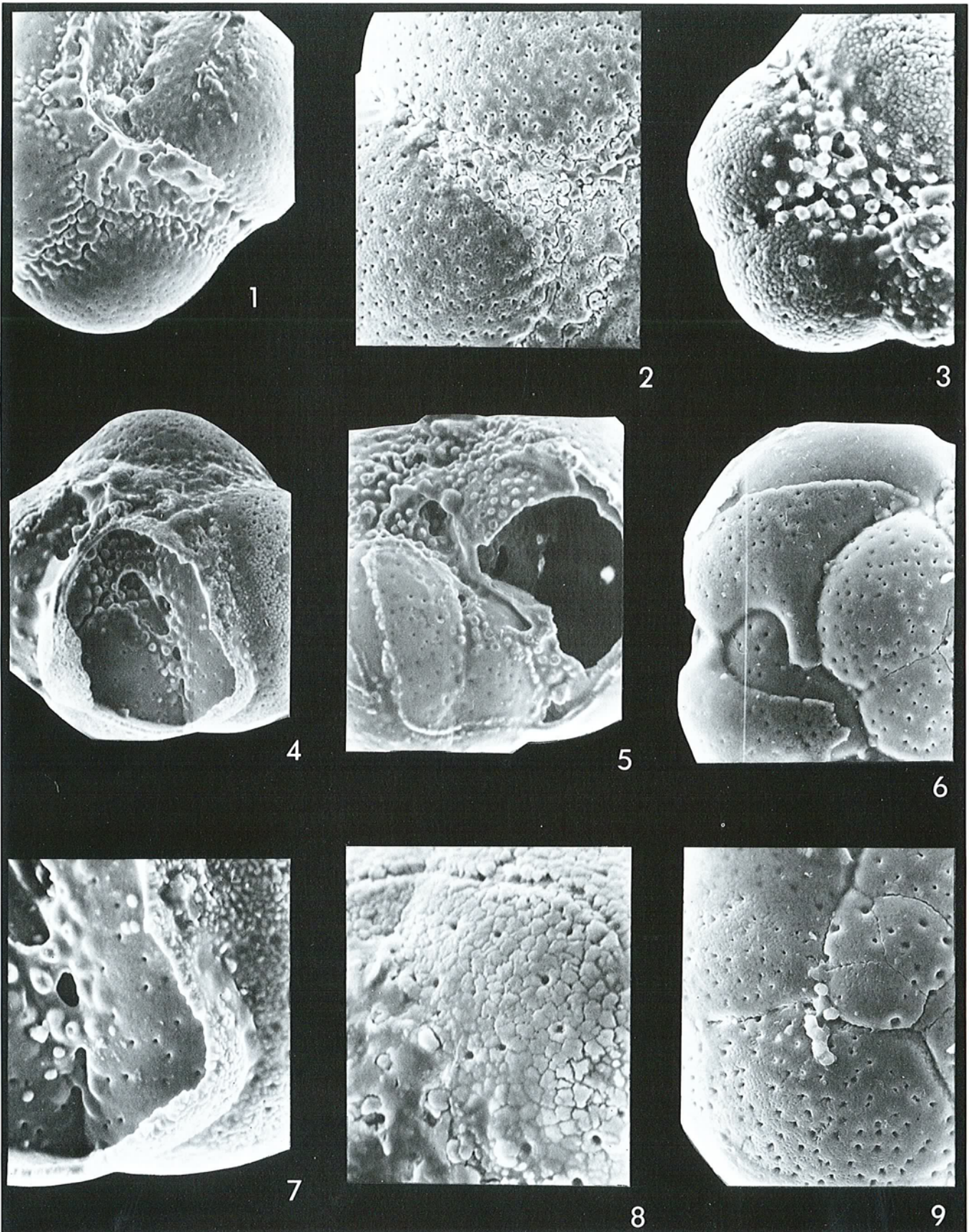
Cañón (personal communication) reported that *Candeina cecionii* Cañón and Ernst is restricted to marine rocks of Manzanian age (early to middle Eocene) in the Magallanes Basin, Chile. A more precise age assessment for the occurrence of *C. cecionii* is necessary in order to delineate possible phylogenetic relationships with the New Zealand taxon, *C. zeocenica* Hornibrook and Jenkins. Age refinement and correlation beyond the type area is difficult due to the low diversity planktonic assemblages that characterize the Paleogene strata of southernmost Chile and Tierra Del Fuego (Magallanes Basin).

Todd and Kniker (1952) described the foraminiferal fauna of the Agua Fresca Formation of southernmost

PLATE 2

Candeina antarctica, n. sp.

1 Paratype; supplementary sutural apertures; DSDP Site 270, Core 25-2, 50–60 cm; × 267 (same specimen as Pl. 1, Fig. 11). 2, 6, 9 Paratype; DSDP Site 270, Core 37-4, 133–142 cm (same specimen as Pl. 1, Figs. 5, 6). 2. Sutural apertures; × 397. 6. Spiral sutures; × 377. 9. Proloculus and early part of coil; × 470. 3 Paratype; umbilicus; DSDP Site 270, Core 39-6, 24–36 cm; × 673. 4, 7 Paratype; DSDP Site 270, Core 13-3, 114–125 cm (same specimen as Pl. 1, Fig. 13). 4. × 540. 7. Sutural apertures; × 1410. 5 Paratype; DSDP Site 270, Core 21-5, 102–112 cm; × 1000? 8 Paratype; slightly etched surface; DSDP Site 270, Core 27-4, 108–118 cm; × 1400?



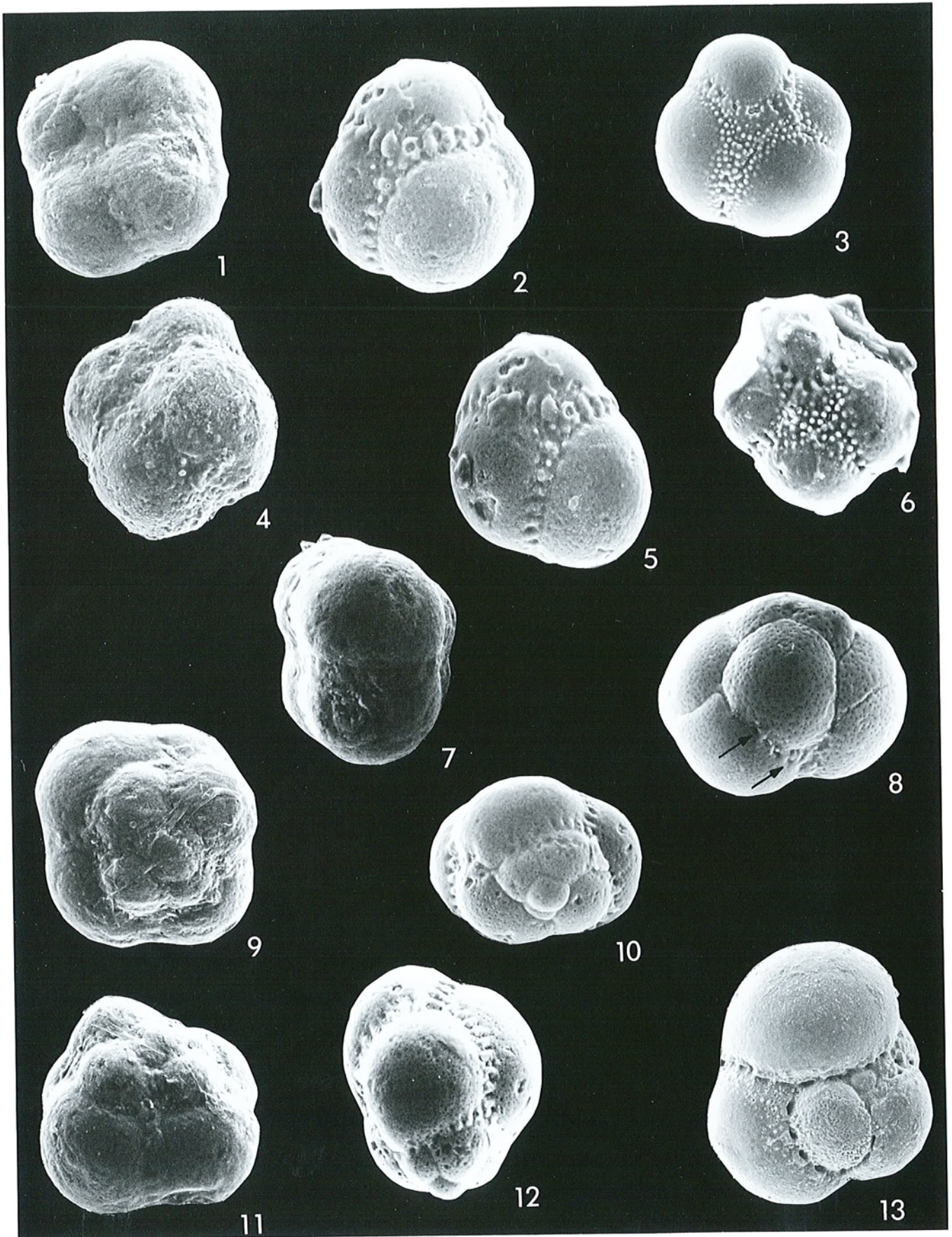


TABLE 1. Dimensions of the holotype and figured paratypes of *Candeina antarctica*, n.sp. All specimens, with the exception of the last two, are from the late Oligocene–early Miocene (Unit 2) of DSDP Site 270. The latter two are middle Miocene in age and derived from sediments at Station J9 of the Ross Ice Shelf Project.

Locality	Maximum diameter	Breadth	Illustrated here as:
270-34-3, 28–38 cm	0.23 mm*	0.17 mm	Pl. 1, Figs. 1–2 (USNM 385215)
270-15, CC	0.25 mm	0.19 mm	Pl. 1, Fig. 7 (USNM 385216)
270-34-3, 28–38	0.23 mm	0.16 mm	Unfigured (USNM 385217)
270-35-3, 112–121	0.24 mm	0.16 mm	Pl. 1, Figs. 3–4 (USNM 385218)
270-37-4, 133–142	0.28 mm	0.19 mm	Pl. 1, Figs. 5–6 Pl. 2, Figs. 2, 6, 9
270-33-3, 102–110	0.13 mm	0.07 mm	Pl. 1, Figs. 8–9
270-21-5, 102–112	0.14 mm	—	Pl. 2, Fig. 5
270-25-2, 50–60	0.13 mm	0.10 mm	Pl. 1, Fig. 10
270-25-2, 50–60	0.28 mm	0.21 mm	Pl. 1, Fig. 11 Pl. 2, Fig. 1
270-21-5, 102–112	0.19 mm	0.14 mm	Pl. 1, Fig. 12
270-13-3, 114–125	0.21 mm	—	Pl. 1, Fig. 13 Pl. 2, Figs. 4, 7
270-39-6, 24–36	0.20 mm	0.13 mm	Pl. 3, Fig. 6
RISP J9	0.29 mm	0.23 mm	Pl. 3, Fig. 8
RISP J9	0.23 mm	0.17 mm	Pl. 3, Fig. 3

* Holotype.

Chile. Natland and others (1974) regarded this formation as a partial temporal equivalent of their Manzanian Stage. Only three planktonic species were noted in the Agua Fresca Formation: *Globigerina patagonica* Todd and Kniker, *Pseudohastigerina wilcoxensis* (Cushman and Ponton), and *Globorotalia* cf. *G. compressa* Plummer. Jenkins (1974a) presented a discussion of the worldwide occurrences of *Globigerina patagonica* and noted that this species is morphologically similar to his *G. boweri* Bolli (= *G. frontosa* Subbotina, after Stainforth and others, 1975) in New Zealand. Jenkins (1974a) reassessed the age of the Agua Fresca Formation, based on its benthic and planktonic foraminifera, and concluded that it is probably equivalent to the early Eocene to early middle Eocene of New Zealand (upper *Globorotalia crater crater* Zone to lower *Globigerinatheka index index* Zone). This corresponds to the New Zealand Mangaorapan to Porangan or Lower Bortonian Stages (Figure 5).

Cañón and Ernst (1974) reported low diversity

TABLE 2. Dimensions of the holotype and figured paratypes of *Candeina zeocenica* from type locality; sample N28/f764, F6398, green-sand from the Ruatungata Sandstone, near Skeleton's Hill, Paparaoa, New Zealand. The largest specimen of *C. zeocenica* was obtained from unillustrated type material and is 0.26 mm in diameter.

Maximum diameter	Breadth	Illustrated here as:
0.25 mm*	0.19 mm	Fig. 1a–c
?	?	Fig. 2
?	?	Fig. 3
0.25 mm	0.20 mm	Pl. 3, Figs. 10, 12
0.20 mm	0.15 mm	Pl. 3, Figs. 2, 5

* Holotype.

planktonic assemblages in the Manzanian and overlying Brunswickian Stages of southern Chile. Associated with *Candeina cecionii* in Manzanian age strata is *Globigerina triloculinoides*. Marking the lower part of the Brunswickian Stage are *Hastigerina iota* (Finlay) (= *Pseudohastigerina micra* (Cole)), *Globorotalia* cf. *G. crassata* (Cushman) var. *aequa* Cushman and Renz, as well as *G. triloculinoides*. Bolli (1957) gave the range for *G. triloculinoides* in Trinidad as *G. trinidadensis* Zone to *G. pusilla pusilla* Zone (Paleocene) and proposed that it evolved into *G. triangularis* White and *G. linaperta* Finlay. However, Loeblich and Tappan (1957) consider *G. triangularis* to be synonymous with *G. triloculinoides*. This interpretation is also adopted by Jenkins (1971) for New Zealand forms thereby extending the range of *G. triloculinoides* s.l. into the early Eocene. Jenkins (1971) further notes that from about the first appearance of *Pseudohastigerina wilcoxensis* (base of the Eocene) specimens of *G. triloculinoides* appear transitional to *G. boweri* (?= *G. patagonica*).

The co-occurrence of *Pseudohastigerina micra* (= *Hastigerina iota*) with *G. triloculinoides* and *G. cf. crassata* var. *aequa* in the lower Brunswickian Stage as reported by Cañón and Ernst (1974) presents a conflict in age. The former species ranges from the middle Eocene to earliest Oligocene (Stainforth and others, 1975) while the latter two forms have a last occurrence in the early Eocene. The illustrated specimen of *P. micra* by Cañón and Ernst (1974, pl. 4, fig. 2a, b) appears to be distinctly trochospiral rather than planispiral and has a subacute rather than subovate peripheral margin. It is suggested that this specimen may be better referred to *Globorotalia chapmani* Parr or

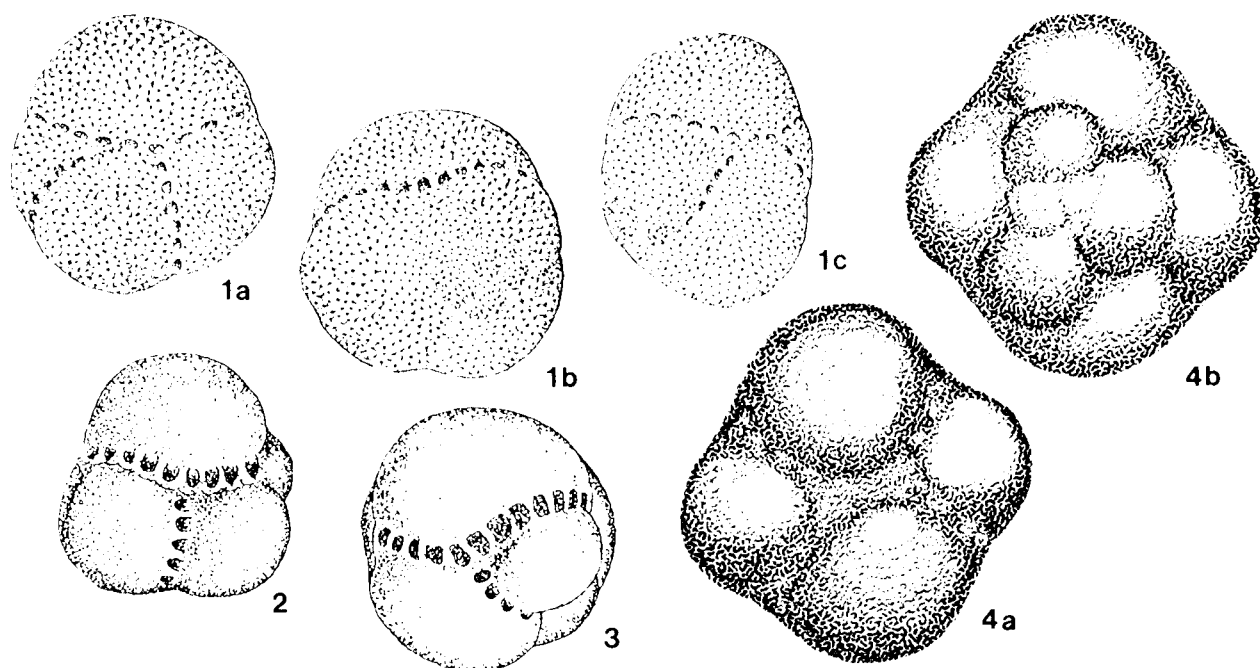
PLATE 3

1, 4, 7, 9, 11 *Candeina cecionii* Cañón and Ernst. 1, 7, 9, 11. Hypotype; Aracelis Well No. 3, 1,588–1,597 m (Magallanes Basin). 1, Umbilical side; ×209. 7, Side view, same specimen; ×194. 9, Spiral side, same specimen; ×218. 11, Oblique spiral side view, same specimen; ×215. 4. Hypotype; oblique umbilical view; Corey Well No. 3, 1,818–1,827 m (Magallanes Basin); ×215.

2, 5, 10, 12 *Candeina zeocenica* Hornibrook and Jenkins. 2, 5. Paratype; Ruatungata Sandstone, New Zealand. 2, Umbilical side, ×220. 5, Side view, same specimen; ×225. 10, 12. Paratype; Ruatungata Sandstone, New Zealand. 10, Spiral side; ×160. 12, Side view, same specimen; ×205.

3, 6, 8 *Candeina antarctica*, n. sp. 3. Paratype; umbilical side; RISP Station J9, 21-A; ×178. 6. Paratype; umbilical side; DSDP Site 270, Core 39-6, 24–36 cm; ×210. 8. Paratype; side view, arrows point to sutural apertures that extend around to the spiral side of the final chamber; RISP Station J9, Webb 14; ×162.

13 *Candeina nitida* d'Orbigny; hypotype; umbilical view; DSDP Leg 9, Site 83 A, Core 14-1 (top); late Miocene; specimen from W. Orr; ×120.



FIGURES 1-4. Type specimens of *Candeina zeocenica* Hornibrook and Jenkins and *C. cecionii* Cañón and Ernst. 1-3 *Candeina zeocenica*. 1a-c. Holotype (New Zealand Geological Survey Reg. No. TF 1494/1). 2. Paratype (TF 1494/3). 3. Paratype (TF 1494/2); all $\times 144$ (from Hornibrook and Jenkins, 1965). 4a, b *Candeina cecionii*, a previously unillustrated paratype (USNM 688437), $\times 220$.

trochospiral variants of *Pseudohastigerina wilcoxensis*, the direct ancestors of *P. micra* (Stainforth and others, 1975). This would point to an early Eocene to early middle Eocene age for the Manzanian and lower Brunswickian Stages (Figure 5).

The stratigraphic distribution of *Candeina cecionii* in the Manzanian Stage of the Magallanes Basin thus appears to be equivalent to the Mangaorapan to Here-taungan/Porangan Stages of New Zealand (Figure 5). This reassessment is based primarily on the known stratigraphic ranges of *Pseudohastigerina wilcoxensis*, *Globigerina patagonica* (?=*G. boweri*, *G. frontosa*), and *G. triloculinoidea* s.l. (?=*G. boweri*) as discussed above, the most common planktonic foraminifera from Manzanian and lower Brunswickian age strata of southern Chile (including the Agua Fresca Formation).

DISTRIBUTION AND PHYLOGENY OF PALEOGENE CANDEINA

Candeina cecionii and *C. zeocenica* appear to be closely related. Proposals for a direct phylogenetic relationship between the two forms are rendered tenuous by the patchiness of their known geographic occurrences; *C. cecionii* is found exclusively in southernmost Chile (Magallanes Basin) (Cañón and Ernst, 1974) while *C. zeocenica* has been reported only from New Zealand (Hornibrook and Jenkins, 1965; Srinivasan, 1968; Jenkins, 1971). If we assume that they are not unrelated homeomorphs and are members of the same lineage, why then have not both species occurred in successive stages of the Magallanes Basin or New Zealand area and why has neither species of *Candeina* been ob-

served in the Australian Paleogene (McGowran, 1978; P. Quilty and N. Ludbrook, written communication) or in any of the southern high latitude DSDP successions? Migration routes controlled by oceanic circulation patterns may provide answers to the known geographic distributions.

The first appearance of *C. cecionii* was in the early Eocene or early middle Eocene. If it is assumed that *C. cecionii* evolved into *C. zeocenica* by the late middle Eocene, migration from the Magallanes Basin to New Zealand should also have occurred by this time. It is likely that surface water circulation was in a direction from New Zealand towards South America due to a major counterclockwise gyre in the South Pacific. The absence of a strong polar high pressure system, as suggested by preliminary late Eocene atmospheric circulation models, would probably enhance the subtropical gyre while suppressing the development of a subpolar, clockwise gyre (E. Barron, personal communication). Therefore, it is unlikely that the *Candeina cecionii-zeocenica* morphoserries migrated from Chile to New Zealand via the South Pacific. A migration route from the Magallanes Basin, clockwise around Antarctica connecting with the southwest Pacific via the narrow marine passage that was developing between Australia and the Wilkes Basin region in the Eocene is possible (Figures 6, 7). The absence of *Candeina* in the Paleogene of southern Australia may reflect the sporadic nature of marginal marine incursions during the early and middle Eocene (McGowran, 1978); or may indicate that *Candeina*-bearing circum-Antarctic waters maintained a high latitude position close to the East Antarctic coastline.

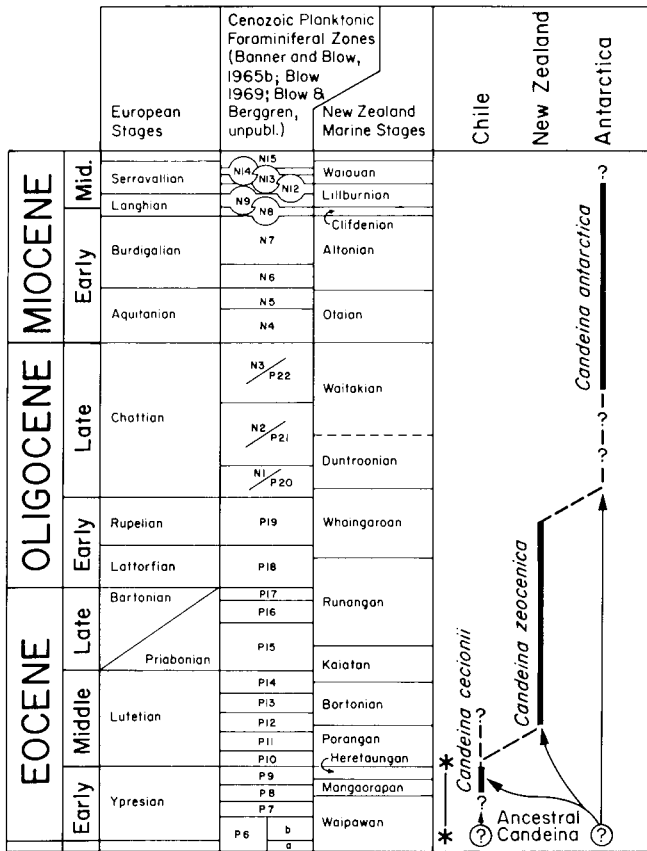


FIGURE 5. Possible phylogenetic relationships for Paleogene-early Neogene species of *Candeiina* in the Southern Ocean. Widespread Oligocene hiatuses in the deep sea and lack of drilled pre-Miocene sediments in the Ross Sea make the first appearance of *C. antarctica*, n.sp., uncertain. It is suspected that it evolved from *C. zeocenica* in the middle or late Oligocene. Time scale and stage correction after Berggren and Van Couvering, 1974. Asterisk and bars indicate approximate time range of Chilean uppermost Oazian, Manzanian and lower Brunswickian stages.

A more direct route was available. Webb (1978, 1979b, 1981), discussed the existence of a Cenozoic Transantarctic Strait connecting the Ross and Weddell regions of Antarctica. More recently Webb and others (1984) also point to the presence of extensive Cenozoic marine deposits in the intracratonic Wilkes and Pensacola Basins (Figure 6). These seaways would have permitted direct communication between the southern Atlantic and Pacific Oceans, allowing ready migration of the Eocene-Oligocene *Candeiina cecionii-zeocenica* group from the Magallanes Basin to the New Zealand region.

Uplift along the Pacific margin of southern South America during the late Cretaceous and earliest Tertiary produced a barrier between the Magallanes Basin and the southeast Pacific (Natland and Gonzales, 1974; Dalziel and others, 1975). Although there may have been a shallow marine connection between southernmost Chile and the tip of the Antarctic Peninsula during the early Cenozoic, the positive expression of the emergent Andes and their eastward curvature (Suarez, 1976; De Wit, 1977) may have 'shielded' the Maga-

TABLE 3. Dimensions of the holotype, paratype and 10 specimens of *Candeiina cecionii*. 1 = Type locality: coast of the Brunswick Peninsula on the south side of Otway Sound, Magallanes Province, southern Chile. 2 = Corey Well No. 3, 1,818-1,827 m (Magallanes Basin). 3 = Aracelis Well No. 3, 1,588-1,597 m (Magallanes Basin). 4 = Manzano Well No. 9, 3,249-3,288 m (Magallanes Basin).

Locality	Maximum diameter	Breadth	Illustrated here as:
1	0.20 mm*	0.16 mm	Unfigured
1	0.21 mm	0.16 mm	Fig. 4a, b
2	0.23 mm	0.17 mm	Pl. 3, Fig. 4
2	0.22 mm	0.15 mm	Unfigured
2	0.22 mm	0.16 mm	Unfigured
2	0.20 mm	0.13 mm	Unfigured
3	0.22 mm	0.16 mm	Pl. 3, Figs. 1, 7, 9, 11
3	0.21 mm	0.14 mm	Unfigured
4	0.21 mm	0.15 mm	Unfigured
4	0.20 mm	0.14 mm	Unfigured
4	0.22 mm	0.13 mm	Unfigured
4	0.21 mm	0.14 mm	Unfigured

* Holotype.

llanes Basin from direct contact with South Pacific oceanic circulation from the west and may explain why the New Zealand *Candeiina zeocenica* has not been found in late Eocene-early Oligocene sediments of the Atlantic Magallanes Basin of Chile. It is still uncertain why this taxon is absent in deep-sea sediments of the South Atlantic (DSDP Legs 36 and 71) (Barker, Dalziel, and others, 1976; Ludwig, Krasheninnikov, and others, 1983). Absence might be ascribed to dissolution or ecologic preference to shallower marginal basins.

The absence of *Candeiina* spp. in Austral Paleogene DSDP sequences limits our ability to better define its distribution and phylogenetic development. There are at least thirty-seven DSDP sites which may have been in a geographic position to receive *Candeiina*-bearing sediments (Figure 8). These are Sites 206-208 (Leg 21), Sites 264-284 (Legs 28, 29), and Sites 322-325 (Leg 35), Sites 326-330 (Leg 36), and Sites 511-514 (Leg 71). Sediments of Sites 265-268 and 280-282 contain no *Candeiina* spp. perhaps because this region was not exposed to open marine circulation until the Late Eocene (Burns, 1977) at which time an eastward flowing shallow marine connection across the South Tasman Rise would have prohibited the westward migration of *C. zeocenica* from the New Zealand area towards Australia and Tasmania. Although Site 264 penetrated marine sediments of early to middle Eocene age there is no reported occurrence of *C. cecionii* (Webb, in Hayes and others, 1975; McGowran, 1977). The same is true of other southern Australian Paleogene sequences. Of the Leg 35 drill sites, only Site 323 penetrated sediments older than early Miocene and this succession contains a late Paleocene-(?Oligocene) early Miocene hiatus (Weaver and others, 1976). The South Atlantic sites (Legs 36 and 71) do not contain any reported Paleogene species of *Candeiina*. Of the remaining sites only Sites 206-208, 274 and 277 penetrated marine sediments of late Eocene to early Oligocene age. The Site Reports for Sites 206-208 do not give details of the planktonic foraminifera recovered, nor was a spe-

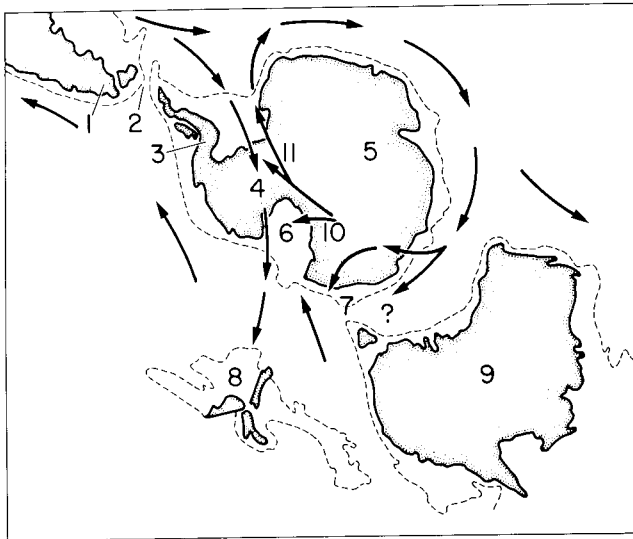


FIGURE 6. Proposed surface water circulation in the middle Eocene, at 45 my ago (New Zealand Bortonian Stage). Reconstruction (1,000 m isobath) after Weissel and others, 1977. 1. Magallanes Basin. 2. Drake Passage. 3. Antarctic Peninsula. 4. Transantarctic Strait. 5. East Antarctica. 6. Ross Sea. 7. South Tasman Rise. 8. New Zealand. 9. Australia. 10. Wilkes Basin. 11. Pensacola Basin.

cial report completed on the Eocene and Oligocene assemblages (Burns, Andrews, and others, 1973). The late Eocene-early Oligocene sediments of Site 274 were barren of planktonic foraminifera (Webb, in Hayes and others, 1975). Site 277 provides a nearly complete Paleogene marine sequence and contains diverse and well-preserved planktonic foraminifera. However, neither species of *Candeina* is present (Jenkins, 1975 and Jenkins, written communication). Although *Candeina* spp. is known to occur in low abundances in marine rocks of New Zealand and Chile, its paucity in the Austral deep-sea record may be a consequence of preservation or as mentioned earlier, the Paleogene species of *Candeina* may have been better adapted to shallower, marginal basins rather than an open-ocean environment. Another explanation for its absence may be the widespread hiatuses created by the production of Antarctic Bottom Water in the latest Eocene-early Oligocene and initiation of the Circum-Antarctic Current with the opening of the Drake Passage in the late Oligocene (Jenkins, 1974b, Kennett, 1977, 1978, 1980; Barker and Burrell, 1977). The deterioration of climate on and near East Antarctica and related paleoceanographic changes brought about major biogeographic shifts during the early to middle Oligocene and a significant decrease in planktonic microfossil diversity worldwide (Kennett, 1978). This time corresponds with the disappearance of *Candeina zeocenica* (in New Zealand) from temperate zone faunas.

EVOLUTION AND DISTRIBUTION OF *CANDEINA ANTARCTICA*, N. SP.

The appearance of *Candeina antarctica*, n.sp. in the Ross Sea basins may be explained in two ways. Evo-

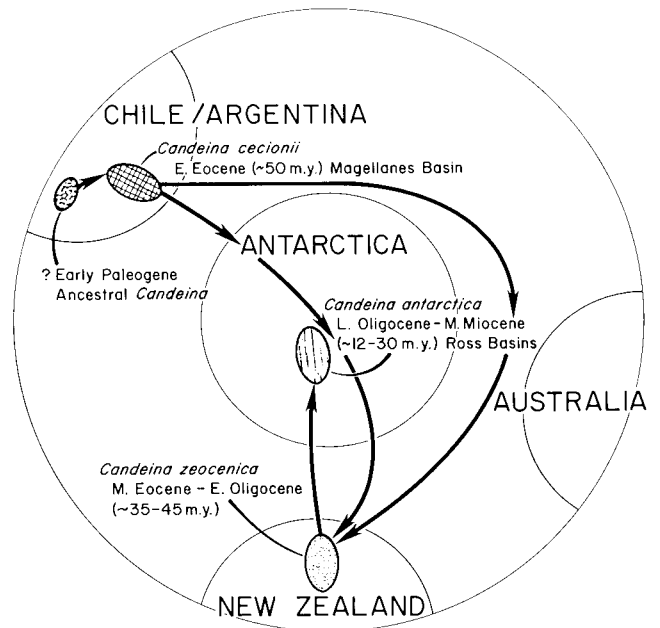


FIGURE 7a. Possible dispersal avenues for the Paleogene *Candeina cecionii-zeocenica* group, assuming an origin in South America and transport between Chile and New Zealand via the transantarctic and/or circum-East Antarctic Seaways. *Candeina antarctica* evolved from *C. zeocenica* during temperate water invasions of Ross basins (from direction of New Zealand).

lution from progenitor *cecionii-zeocenica* stock may have occurred within the intra-Antarctic basins during the Paleogene or early Cenozoic (Figures 6, 7). Neither *C. cecionii* nor *C. zeocenica* has been recovered during preliminary studies of Eocene and Oligocene foraminiferal assemblages (Webb, 1983) but the possibility cannot be dismissed at this time. Cool-temperate waters apparently flowed southward from the Southern Ocean into the Ross Sea during the Oligocene and only sporadically during the early Miocene (Webb, 1981; Leckie and Webb, 1983) and could have carried *C. zeocenica* into the southern high latitudes (Figures 6, 7). It is further speculated that geographic isolation coupled with environmental stress induced evolution from *C. zeocenica* to *C. antarctica*, n.sp., sometime between the Middle and late Oligocene (Figure 5). The gap in time between the last known occurrence of *C. zeocenica* in New Zealand (early Oligocene, Whaingaroan Stage, ~35 m.y.) and the earliest known occurrence of *C. antarctica* in the Ross Sea (late Oligocene, ~30-24 m.y.) (Leckie, 1980; Leckie and Webb, 1983) may well be the consequence of a poor Oligocene sedimentary record in the deep Southern Ocean due to widespread hiatuses (Kennett and others, 1975) and the lack of cored pre-Miocene marine sediments in the Ross Sea. Only DSDP Site 270 and MSSTS-1 (western McMurdo Sound) have been drilled in this area to date.

The sporadic occurrences of temperate pelagic faunas and floras in the Ross Sea early Cenozoic were replaced by monospecific planktonic foraminiferal populations and abundant diatom assemblages during

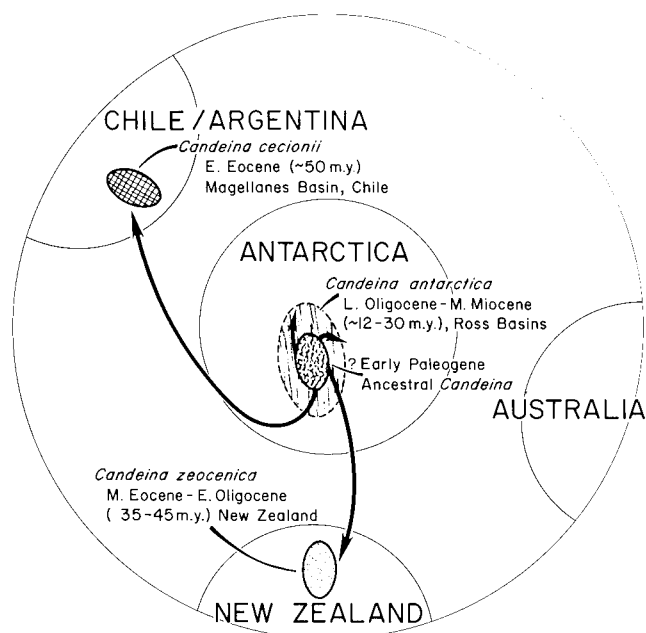


FIGURE 7b. Possible dispersal avenues for *Candeina cecionii-zeocenica-antarctica*, assuming an origin within the antarctic early Paleogene. *Candeina* is as yet unknown in the Paleocene-Eocene of Antarctica.

the early Miocene, as glacial conditions intensified near Antarctica and the Ross Sea evolved towards truly polar conditions (Leckie and Webb, 1983). *Candeina antarctica*, n.sp., was probably confined to the Ross Sea and became the dominant, virtually monospecific planktonic foraminiferal species throughout the Ross Sector during the latest Oligocene through middle Miocene (D'Agostino, 1980; D'Agostino and Webb, 1980; Leckie, 1980; Leckie and Webb, 1983). It appears that *C. antarctica* was more tolerant of the fresher surface waters generated by melting marine ice than stenohaline planktonic species. Its disappearance coincides with the displacement of calcareous plankton northwards and their replacement by siliceous organisms, events associated with the intensified build-up of terrestrial ice during the middle and late Miocene (Kennett, 1977, 1978).

ORIGIN OF *CANDEINA NITIDA*: A DISCUSSION

Blow (1969) proposed the phylogenetic sequence; *Globigerina juvenilis* (= *Globigerinita glutinata*) to *Globigerinoides parkerae* Bermudez to *Candeina nitida praenitida* Blow to *Candeina nitida* d'Orbigny (Figure 9). In this phylogenetic scheme, *Globigerinoides parkerae* developed from *Globigerina juvenilis* within Zone N.14 (?Zone N.13) and ranges to the Recent. *G. parkerae* differs from *G. juvenilis* in possessing slightly more inflated chambers and the possession of dorsal supplementary apertures (Blow, 1969, p. 325). Brönimann and Resig (1971) suggested that *Globigerinoides parkerae* actually belongs to the *Globigerinita glutinata* group and so renamed it *G. glutinata flpar-*

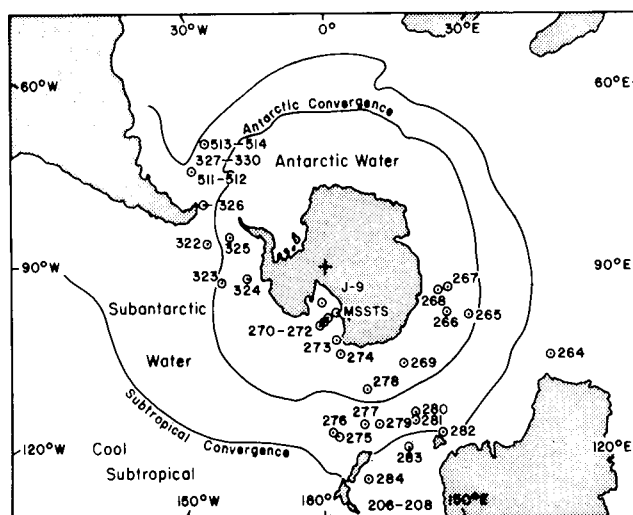


FIGURE 8. Deep Sea Drilling Project sites in the Southern Ocean that might be expected to reveal Paleogene specimens of *Candeina* spp., based on paleo-reconstructions and proposed surface water circulation patterns (modified after Kennett, 1978).

keræ. Within the middle and late part of Zone N.15, Blow recognized specimens intermediate between *G. parkerae* and *Candeina nitida praenitida*. True representatives of *C. nitida praenitida* range from the latest part of Zone N.15 to within Zone N.17. *Candeina nitida praenitida* has also been differentiated in early late Miocene deep sea sequences by various workers (Jenkins and Orr, 1972; Krasheninnikov and Hoskins, 1973; Krasheninnikov and Pflaumann, 1978; Salvadorini and Cita, 1979). According to Blow (1969), *Candeina nitida nitida* developed from *C. nitida praenitida* within the early part of Zone N.17 and ranges to the Recent.

Candeina nitida praenitida is distinguished from *C. nitida nitida* by the presence of intercameral supplementary sutural apertures restricted to the ultimate and penultimate chambers of the final whorl (Blow, 1969). *C. nitida nitida* is recognized when supplementary apertures develop along intercameral sutures of earlier chambers and along the spiral suture (that is, earlier in its ontogeny). Blow (1969, p. 335) further notes that "chambers become much more embracing but the test tends to become more highly trochospiral in younger forms and up to five or six whorls of chambers are sometimes seen in Pliocene to Recent forms." This trend is also observed by Jenkins and Orr (1972). The overall development of late Miocene to Recent *Candeina* is the progressive development of supplementary sutural apertures along the spiral suture, initially being confined to the last two chambers of the final whorl, and with tests becoming more highly trochospiral and variable through time.

AN ALTERNATE HYPOTHESIS FOR THE ORIGIN OF *CANDEINA NITIDA*

The opening of the Drake Passage in the late Oligocene permitted full development of the Circum-Ant-

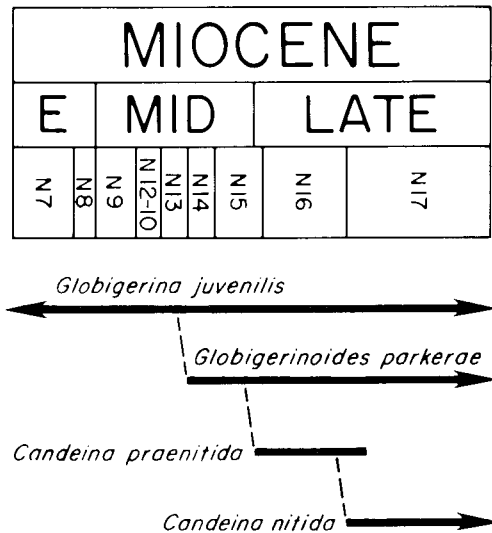


FIGURE 9. Phylogeny of *Candeina nitida* as proposed by Blow (1969). Time scale and planktonic foraminiferal zones after Berggren and Van Couvering, 1974.

arctic Current (Jenkins, 1974b; Barker and Burrell, 1977; Kennett, 1978). This was soon followed by the initiation of significant glaciation in Antarctica and sea-level fluctuations during the latest Oligocene and early Miocene (Hayes, Frakes and others, 1975; Stump and others, 1980; Webb, 1981; Leckie and Webb, 1983). *Candeina antarctica*, n.sp., persisted in low abundances as the dominant planktonic foraminifer in an ecosystem that was directly influenced by the deteriorating climatic conditions around Antarctica (Leckie, 1980; Leckie and Webb, 1980, 1983). The nearly monospecific planktonic populations of *C. antarctica* attest to its being able to adapt to this stressed environment. Glacial conditions intensified during the middle and late Miocene resulting in the development of major terrestrial ice masses (Kennett, 1977, 1978).

As the climate deteriorated in the middle Miocene, calcareous plankton of the seas peripheral to Antarctica were displaced northwards and replaced by siliceous biofacies (Weaver and others, 1976; Kennett, 1978). This period also corresponds with the last recorded occurrence of *C. antarctica* (D'Agostino, 1980; D'Agostino and Webb, 1980). *Candeina antarctica* either became extinct sometime in the middle Miocene, or, it too was displaced northwards with the other calcareous plankton. If the latter scenario is true, the *Candeina* stock (morphotype) was moved back into the warmer latitudes (temperate to subtropical) dominated at that time by other forms of planktonic foraminifer. *Candeina* may have been cast into refugia, being replaced in the higher latitudes by *Neogloboquadrina pachyderma* at the base of the late Miocene (Figure 10). In a study of living planktonic foraminifers in surface waters, Bé and Tolderlund (1971) found that *Candeina nitida* is restricted to tropical or subtropical zones and is one of the rarest species, seldom constituting more than five percent of the foraminiferal populations.

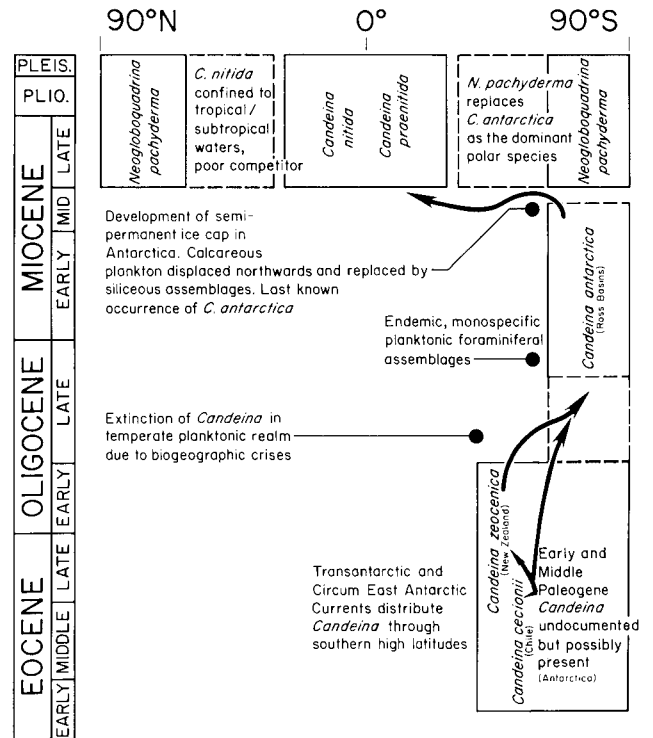


FIGURE 10. Summary diagram of the proposed Paleogene-early Neogene *Candeina* morphoserries and the oceanographic and ecologic factors that account for its past distribution. An alternate hypothesis for the origin of *Candeina nitida* s.l. and its ecologic tolerances is also suggested.

The major differences between *Candeina nitida* and *C. antarctica* are the former's larger size, higher spire and development of sutural apertures on the spiral side. The authors have observed that rare, larger specimens of middle Miocene *C. antarctica* do indeed possess sutural apertures that extend around to the spiral side of the final chamber (Pl. 3, Fig. 8). This is suggestive of morphologic affinity with *C. nitida praenitida*! To date, there are too few specimens to state any definite conclusions but the implications of such variation being present in middle Miocene populations of *C. antarctica* support the argument for a *Candeina* lineage throughout the Cenozoic leading finally to *C. nitida*.

The evolutionary lineage of *Candeina* spp. may provide important insight into the development of oceanic circulation in the Southern Ocean during the Paleogene and early Neogene. We hope that the ideas developed here will encourage re-examination of southern high latitude marginal marine and deep-sea successions specifically for the rare, small planktonic species of *Candeina*.

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