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TAXONOMIC REVISION OF THE LATE CAMPANIAN-MAASTRICHTIAN (LATE CRETACEOUS) PLANKTONIC FORAMINIFERAL GENUS *RUGOTRUNCANA* BRÖNNIMANN AND BROWN, 1956, AND A NEW PALEONTOLOGICAL SPECIES CONCEPT FOR PLANKTONIC FORAMINIFERA

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ABSTRACT

The Late Cretaceous (late Campanian-Maastrichtian) planktonic foraminiferal genus *Rugotruncana* Brönnimann and Brown, 1956 is thoroughly revised. The genus is monospecific, with *Rugotruncana circumnodifer* (Finlay, 1940) being the only species included within it. Taxonomic revision of the genus was made by examination of type specimens of all species assigned to *Rugotruncana* in the past. The genus is characterized by the presence of an imperforate band and a weakly to strongly developed double keel along the test periphery. In addition, detailed scanning electron microscope observations reveal that the test ornamentation is asymmetrical, with variably developed rugae and costellae being parallel to the periphery on the spiral side and meridional on the umbilical side. These features serve to distinguish *Rugotruncana* from *Rugoglobigerina* and *Globotruncana*. Based on the morphological features revealed by the detailed test ultrastructure and ornamentation observations, *Rugotruncana* is included within Family Rugoglobigerinidae. A new paleontological species concept is proposed to accommodate *Rugotruncana circumnodifer* and other species of Cretaceous planktonic foraminifera.

INTRODUCTION

Cretaceous planktonic foraminiferal taxonomy significantly advanced in the early 1950's when Brönnimann (1952) and then Brönnimann and Brown (1956) proposed a number of genera based on combined gross test morphology and ornamentation, introducing test ornamentation as a major feature at the genus level. The presence of meridional test ornamentation was initially taken into consideration by Brönnimann (1952) when three genera presenting this feature were proposed, namely *Plummerita, Rugoglobigerina* and *Trinitella*. Along with the meridionally arranged ornamentation, the presence of a spinose periphery, the unaltered globigeriniform appearance, and truncated last-formed chambers were used to characterize the three genera, respectively. The three genera have received wide recognition among the micropaleontological community.

The use of test ornamentation as a taxonomic criterion was further broadened by Brönnimann and Brown (1956) and applied to other Campanian and Maastrichtian planktonic foraminiferal taxa. Three new genera were proposed by these authors based on both gross test morphology and ornamentation patterns. The genus *Kuglerina* can be largely characterized by high trochospiral tests with a papillose surface and a broadly rounded periphery lacking peripheral structures. *Bucherina* was proposed to accommodate tests with a papillose surface and a truncated periphery presenting one keel on most or all of the chambers of the final whorl. The third genus proposed by Brönnimann and Brown (1956) was *Rugotruncana*, which included a variety of species that are currently placed in the Globotruncanidae and Rugoglobigerinidae. The original definition of *Rugotruncana* comprises a wide range of variability of test shape, presence or absence and expression of peripheral structures, position of the primary aperture, and size and depth of the umbilical system, in contrast to the other five, more narrowly defined genera erected by Brönnimann (1952) and Brönnimann and Brown (1956).

The status of *Rugotruncana* was questioned throughout the following decade, and Pessagno (1967) proposed its emendation. This latter change in taxonomic principles formalized the correlation between test ornamentation and other gross test morphological features. Only two species were retained in *Rugotruncana*, in contrast to the nine proposed by Brönnimann and Brown (1956), namely *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 and *Globotruncana (Rugoglobigerina) pennyi subpennyi* Gandolfi, 1955. Successive reconsiderations of the genus and its type species *Rugotruncana tilevi* Brönnimann and Brown resulted in significant confusion of the taxonomic concepts. Because the type material had not been re-evaluated since the genus was proposed, even the key features of the type species were misunderstood in the opposite sense to that proposed by its authors. This became apparent in the discussion of *R. tilevi* by Loeblich and Tappan (1987, p. 470), who, in contradiction to the original species description, considered it as not having meridional ornamentation.

In order to clear up these ambiguities, re-examination of the type specimens of the various species previously assigned to *Rugotruncana* was necessary. Notably, the genus is now considered monospecific. *Rugotruncana circumnodifer* (Finlay) has proved to be an excellent biostratigraphic marker in the Late Cretaceous of the Austral Realm. Our revision is focused on both the genus and species levels.

A HISTORY OF CONCEPTS

Presentation of the various ways in which *Rugotruncana* was defined in the past is both informative and necessary in

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TABLE 1. Overview of the taxonomic history of species previously assigned to the genus *Rugotruncana*.

Species and author (original description)	Genus (original assignment)	Assigned to *Rugotruncana*	Removed from *Rugotruncana*	Current status (this article)
calcarata Cushman, 1927	*Globotruncana*	Brönnimann and Brown, 1956	Reiss, 1957	Type species of ***Radotruncana*** EL-NAGGAR, 1971
havanensis Voorwijk, 1937	*Globotruncana*	Brönnimann and Brown, 1956	Reiss, 1957	Type species of ***Globotruncanella*** REISS, 1957
circumnodifer Finlay, 1940	*Globigerina*	Webb, 1973	N/A	Type species of ***Rugotruncana*** BRÖNNIMANN and BROWN, 1956
gansseri Bolli, 1951	*Globotruncana*	Brönnimann and Brown, 1956	Bolli, 1957	Type species of ***Gansserina*** CARON, GONZALEZ DONOSO, ROBASZYNSKI and WONDERS, 1984
intermedia Bolli, 1951	*Globotruncana*	Brönnimann and Brown, 1956	Bolli, 1957	Species assigned to ***Abathomphalus*** PESSAGNO, 1967
mayaroensis Bolli, 1951	*Globotruncana*	Brönnimann and Brown, 1956	Bolli, Loeblich and Tappan, 1957	Type species of ***Abathomphalus*** PESSAGNO, 1967
ellisi Brönnimann and Brown, 1956	*Rugotruncana*	Brönnimann and Brown, 1956	N/A	Junior synonym of ***Rugotruncana circumnodifer*** (Finlay), 1940
nothi Brönnimann and Brown, 1956	*Rugotruncana*	Brönnimann and Brown, 1956	Olsson, 1964	Species assigned to ***Globotruncana*** CUSHMAN, 1927
skewesae Brönnimann and Brown, 1956	*Rugotruncana*	Brönnimann and Brown, 1956	This article	Junior synonym of ***Globotruncana aegyptiaca*** Nakkady, 1950
tilevi Brönnimann and Brown, 1956	*Rugotruncana* **(type species)**	Brönnimann and Brown, 1956	N/A	Junior synonym of ***Rugotruncana circumnodifer*** (Finlay), 1940
circumnodifer subcircumnodifer Gandolfi, 1957	*Globotruncana* (*Rugoglobigerina*)	Pessagno, 1967	This article	Species tentatively assigned to ***Globotruncana*** CUSHMAN, 1927
pennyi subpennyi Gandolfi, 1957	*Globotruncana* (*Rugoglobigerina*)	Pessagno, 1967	N/A	Junior synonym of ***Rugotruncana circumnodifer*** (Finlay), 1940
rugosa subrugosa Gandolfi, 1957	*Globotruncana* (*Rugoglobigerina*)	N/A	N/A	Junior synonym of ***Rugotruncana circumnodifer*** (Finlay), 1940
asteroidalis Salaj, 1983	*Abathomphalus*	N/A	N/A	Junior synonym of ***Rugotruncana circumnodifer*** (Finlay), 1940

understanding the taxonomic status of this genus and its included species. Such a diversity of interpretations makes it clear that only examination of the type material of all of the species (both valid and invalid) assigned to the genus will enable accurate re-definition of the taxonomic units both at the genus and species levels.

The genus *Rugotruncana* was erected by Brönnimann and Brown (1956) to accommodate a number of trochospirally coiled species presenting a strongly ornamented chamber surface and a keeled periphery. Chamber ornamentation was considered a highly variable feature as indicated in the original diagnosis: "early chambers are smooth walled, but some or all later chambers exhibit fine discontinuous costellae or traces of costellae" (Brönnimann and Brown, 1956, p. 546). Notably, ornamentation patterns were not considered significant at the genus level, as species with or without meridional ornamentation were initially included within *Rugotruncana*. This contrasts strongly with Brönnimann's (1952) previous study, in which meridional ornamentation was conferred a distinct taxonomic importance at the genus level, and included *Rugoglobigerina*, the first Cretaceous planktonic foraminiferal genus identified mainly on the basis of test ornamentation. No less than nine species were initially included within *Rugotruncana* (Table 1). *Rugotruncana tilevi* was designated the type species of the genus. Inaccessibility of the type location had resulted in increased difficulty in evaluating the validity of the genus. As a result, no specimens other than the holotype figured by Brönnimann and Brown (1956, pl. 22, figs. 1–3) have been illustrated from the type locality.

The validity of *Rugotruncana* was contested by Bolli and others (1957), who considered it a junior synonym of *Globotruncana*. Other genera previously erected by Brönnimann (1952) and Brönnimann and Brown (1956) were also considered junior synonyms of either *Rugoglobigerina* (e.g., *Plummerita, Trinitella* and *Kuglerina*) or *Globotruncana* (e.g., *Bucherina* and *Rugotruncana*). No arguments were provided to support these changes in status. In contrast, *Rugotruncana* was regarded as a subgenus within *Globotruncana* by Berggren (1962). This author synonymized *Rugotruncana tilevi* Brönnimann and Brown, 1956 and *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 and accepted that this species presents distinct ornamentation patterns on the spiral and umbilical sides: "spiral surface relatively smooth with irregular development of pustules and discontinuous costellae; umbilical side distinctly rugose as a result of combined development of dense, discontinuous, meridionally arranged costellae and irregularly spaced pustules (nodes) . . . ." (Berggren, 1962, p. 66). Such asymmetrical test ornamentation is obvious in Berggren's (1962, pl. 10, fig. 4) figured specimen. Synonymization of *Rugotruncana tilevi* Brönnimann and Brown, 1956 under *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gan-

dolfi, 1955 was accepted by Olsson (1964), who also considered *Rugotruncana* as an invalid genus due to the lack of a distinct ornament orientation in specimens from outcrops in the New Jersey Coastal Plain. Such a diversity of ideas concerning the validity of the taxonomic status of *Rugotruncana* required a thorough taxonomic revision of this genus and its species. This revision was made by Pessagno (1967), and it resulted in a widely accepted emendation of *Rugotruncana*, which brought stability at the species level for nearly four decades.

Pessagno's (1967) revision of *Rugotruncana* brought significant changes in the understanding of this genus. Two important aspects of the emended diagnosis are mentioned here: "test trochospiral, planoconvex to spiroconvex with periphery truncated by double keel . . . . Coarse rugosities or costellae, *always* arranged in a distinctive meridorial [*sic*] pattern, present on the surface of the test." Another important feature of the *Rugotruncana* tests is given in the "Remarks" section (Pessagno, 1967, p. 368): "(3) have rugoglobigerine early stages." Pessagno (1967, p. 368) considered the double-keeled periphery as a distinctive feature of *Rugotruncana*, as both genera, *Rugoglobigerina* and *Rugotruncana*, in his opinion, present meridionally arranged ornamentation. Two species were included within the emended genus: *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 and *Globotruncana (Rugoglobigerina) pennyi subpennyi* Gandolfi, 1955. Both the genus emendation and species included in it were widely accepted among the scientific community. It is noteworthy that Caron (1985) included these two species in *Rugotruncana*, but the hypotypes figured by Caron (1985, fig. 34, 12-*Rugotruncana subcircumnodifer*, and 14-*R. subpennyi*) don't show the diagnostic meridional ornamentation pattern.

The genus *Rugotruncana* was not recognized in the European Working Group on Planktonic Foraminifera Atlas of Late Cretaceous Globotruncanids (Robaszynski and others, 1984). Instead, these authors placed meridionally costellate specimens bearing an imperforate keel band and paired discontinuous peripheral keels in *Rugoglobigerina hexacamerata*.

Synonymization of *Rugotruncana tilevi* Brönnimann and Brown, 1956 under *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 was not considered valid by Loeblich and Tappan (1987). After examining topotypes of *Rugotruncana tilevi* provided by N. K. Brown, Loeblich and Tappan (1987, p. 470) concluded that the new examined specimens do not present meridionally arranged ornamentation elements and, therefore, can not be considered congeneric to *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955, which, in their opinion, presents such an ornamentation feature.

Rugotruncana regained prominence in the literature with reports of *R. circumnodifer* from a number of deep-sea sites in the Austral Realm (Webb, 1973; Huber, 1990, 1991a, 1991b; Petrizzo, 2001). The species was originally identified from outcrops in New Zealand by Finlay (1940) and later identified on the Lord Howe Rise by Webb (1973). Examination of the large number of well-preserved southern high-latitude specimens collected from deep sea sites has resulted in a good understanding of the test variability, which is a key feature in characterizing the *Rugotruncana* taxonomic status.

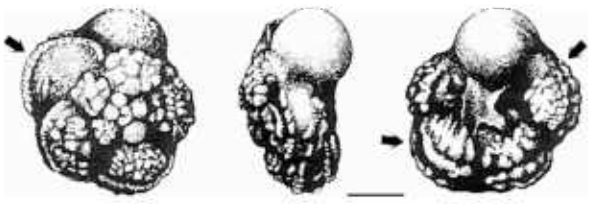

FIGURE 1. Hypotype of *Rugotruncana circumnodifer* figured by Webb (1966, pl. 15, fig. 1a–c) from the Haumurian/Maastrichtian sediments of Hawke Bay. The arrows point to chambers with ornamentation parallel to the periphery on the spiral side and meridional ornamentation on the umbilical side. Scale bar: 100 μm.

STUDIED MATERIAL AND ITS PROVENANCE

The holotype of *Rugotruncana circumnodifer* (TF1223-1) and three paratypes (TF1223-2a, TF1223-2b and TF1223-3) of the original material of Finlay (1940), which are deposited at the Institute of Geological and Nuclear Sciences Limited (New Zealand), were examined and photographed (Pl. 1, figs. 1–4). The type material is poorly preserved, with "the host sediment being a weathered siliceous shale . . ." (P. N. Webb, written communication, 2006). Better-preserved material from New Zealand (Hawke Bay) figured by Webb (1966) shows asymmetrical ornamentation (Fig. 1).

Primary types from the Smithsonian Institution's United States National Museum (USNM, Washington, D.C.) and the Paleontological Research Institute's (PRI, Ithaca, New York) collections were observed using a low kilovoltage setting on a Leica scanning electron microscope (SEM). Types from the USNM examined include holotypes of *Rugotruncana tilevi, R. ellisi, R. nothi* and *R. skewesae*, which were erected by Brönnimann and Brown (1956), and a paratype of *Globigerina circumnodifer* Finlay. Types from the PRI include holotypes of Gandolfi's (1955) subspecies *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer, Globotruncana (Rugoglobigerina) rugosa subrugosa* and *Globotruncana (Rugoglobigerina) pennyi subpennyi*.

Additional examined hypotypes were collected from Maastrichtian intervals at various Ocean Drilling Program (ODP) sites, namely Leg 113 Holes 689B and 690C (Maud Rise; Weddell Sea), Leg 114 Sites 698 and 700 (northeast Georgia Rise, southern South Atlantic Ocean), and Leg 119 Site 738 (Kerguelen Plateau, southern Indian Ocean). Assemblages from these sites were previously studied and reported by Huber (1990, 1991a, 1991b). Other occurrences studied are from the ODP Holes 761B and 762C (Exmouth Plateau, northwestern Australia, Indian Ocean). This is the first report of *Rugotruncana circumnodifer* from the ODP drillholes at the Exmouth Plateau; notably, it was not reported in the previous studies of these ODP holes by Wonders (1992) and Zapeda (1998).

SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA Eichwald, 1830
Suborder GLOBIGERININA Delage and Hérouard, 1896
Superfamily GLOBOTRUNCANACEA Brotzen, 1942
Family RUGOGLOBIGERINIDAE Subbotina, 1959
Subfamily RUGOGLOBIGERININAE Subbotina, 1959
Genus *Rugotruncana* Brönnimann and Brown, 1956 new emendation

Type species. *Rugotruncana tilevi* Brönnimann and Brown, 1956 = junior synonym of *Globigerina circumnodifer* Finlay, 1940.

Rugotruncana Brönnimann and Brown *in* Brönniman and Brown, 1956, p. 546.
Rugotruncana Brönnimann and Brown *in* Pessagno, 1967, p. 368, emended.
Rugotruncana Brönnimann and Brown *in* Caron, 1985, p. 25.
Rugotruncana Brönnimann and Brown *in* Loeblich and Tappan, 1987, p. 470.

Emended description. Test is trochospiral. Chambers are globular, the earliest ones lacking peripheral structures. Sutures are distinct, depressed, straight and radial on both sides. Umbilicus is wide. Periphery is broadly rounded. A wide peripheral imperforate band is present throughout the final whorl and is bordered by two variably developed peripheral keels, which are generally continuous on the earlier chambers of the final whorl and may be discontinuous or weakly developed on the later chambers. Primary aperture is umbilical in position and bordered by a wide tegillum, with successive tegilla almost entirely covering the umbilical area. The test is strongly ornamented, the ornamentation differing on the spiral and umbilical sides. On the umbilical side a meridional pattern dominates, but random orientation of the ornamentation elements can be seen mainly on the last-formed chambers of the test. The spiral side ornamentation pattern ranges from meridional to (mostly) parallel to the periphery. Further variability of the test ornamentation is produced by the successive addition of calcite layers mostly on the earlier parts of the test, often resulting in a complete loss of any ornamentation pattern.

Remarks. The emendation by Pessagno (1967, p. 368) is only partly accepted. Additional material from the Austral Realm showed that the meridional ornamentation is only well developed on the umbilical side, and is rarely present on the spiral side of the test. In most of the tests, the pustules, rugosities, and costellae are distinctly aligned parallel or subparallel to the periphery on the spiral side. This asymmetrical ornamentation is similar to that previously reported for *Paracostellagerina libyca* (Barr), *Abathomphalus intermedia* (Bolli), *A. mayaroensis* (Bolli) and *Globotruncanella citae* (Bolli); the latter species is considered a junior synonym of *Globotruncanalla pschadae* (Keller) by some authors, such as Robaszynski and others (1984) and Caron (1985). *Rugotruncana* differs from *Rugoglobigerina* by the presence of two equal, variably developed peripheral keels on the earlier chambers of the final whorl and asymmetrical ornamentation that is meridional on the umbilical side and parallel to the periphery on the spiral side. Specimens of *Rugotruncana circumnodifer* with meridional ornamentation on both sides of the test that resemble that of the *Rugoglobigerina* ancestor, are also known. These specimens are considered conspecific due to the presence of peripheral structures, which are absent in any *Rugoglobigerina* species. Two other species erected by Brönnimann and Brown (1956) should be included within the genus *Globotruncana*. Re-evaluation of other species previously assigned *Rugotruncana* showed that *Rugotruncana skewesae* Brönnimann and Brown, 1956 is a junior synonym of *Globotruncana aegyptiaca* Nakkady; *Rugotruncana nothi* Brönnimann and Brown, 1956 requires additional study and material because the holotype is poorly preserved; and *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 lacks the test-ornamentation characteristics of *Rugotruncana*, so instead is placed in *Globotruncana*.

Rugotruncana was considered a member of the Family Globotruncanidae by Loeblich and Tappan (1987) and Huber (1994) due to the absence of the preferentially oriented ornamentation. Recently, Georgescu (2005) removed this genus from Family Globotruncanidae and included it within Family Rugoglobigerinidae, Subfamily Archaeoglobigerininae based on the general consistency in test morphology and in the test ornamentation, which was considered as lacking any preferential distribution pattern. Re-examination of the type material of several species previously included within the genus *Rugotruncana* showed that it has asymmetrical ornamentation that is parallel to the periphery on the spiral side and meridional on the umbilical side. Based on these new observations, *Rugotruncana* is now included within the Family Rugoglobigerinidae, Subfamily Rugoglobigerininae. The *Globotruncanella-Abathomphalus* lineage also has asymmetrical test ornamentation and is placed within the Family Globotruncanidae.

Species included. *Rugotruncana circumnodifer* (Finlay, 1940).

Stratigraphic range. From the late Campanian (*Rugotruncana circumnodifer* Biozone) to late Maastrichtian (upper part of *Abathomphalus mayaroensis* Biozone, *Pseudotextularia elegans* Subzone) based on the planktonic foraminiferal zonation for the Austral Realm (Huber, 1992).

Geographical distribution. Cosmopolitan, although most of the occurrences are known from the Austral Realm.

Rugotruncana circumnodifer (Finlay), 1940
Pl. I, figs. 1–4; Pl. 2, figs. 1–5; Pl. 3, figs. 1–5

Globigerina circumnodifer Finlay *in* Finlay, 1940, p. 469, pl. 65, figs. 150–151 (Santonian, New Zealand).
Globotruncana (Rugoglobigerina) pennyi subpennyi Gandolfi *in* Gandolfi, 1955, p. 73, pl. 7, fig. 7 (Colon Shale, Campanian-lower Maastrichtian, Colombia).
Globotruncana (Rugoglobigerina) rugosa subrugosa Gandolfi *in* Gandolfi, 1955, p. 72, pl. 7, fig. 5 (Colon Shale, Campanian-lower Maastrichtian, Colombia).
Rugotruncana tilevi Brönniman and Brown *in* Brönnimann and Brown, 1956, p. 547, pl. 23, figs. 1–3 (upper Maastrichtian, Cuba).
Rugotruncana ellisi Brönnimann and Brown *in* Brönnimann and Brown, 1956, p. 547, pl. 22, figs. 7–9 (Corsicana Marl, lower Maastrichtian, Texas, United States).
Globotruncana (Rugotruncana) subcircumnodifer (Gandolfi) *in* Berggren, 1962, p. 67, pl. 10, fig. 4 (Maastrichtian, southern Scandinavia).
Globotruncana (Rugotruncana) tilevi Brönnimann and Brown *in* Pessagno, 1960, pl. 5, fig. 10 (Rio Yauco Formation, Maastrichtian, Puerto Rico).
Globotruncana (Rugotruncana) tilevi Brönnimann and Brown *in* Pessagno, 1962, p. 364, pl. 4, figs. 1–3 (Rio Yauco Formation, Maastrichtian, Puerto Rico).
Rugotruncana subcircumnodifer (Gandolfi) *in* Pessagno, 1967, p. 369, pl. 62, figs. 14–16 only, not pl. 74, figs. 1–3 (Maastrichtian, United States Gulf Coastal Plain).
Rugotruncana subpennyi (Gandolfi) *in* Pessagno, 1967, p. 370, pl. 76, figs. 12–14, pl. 91, figs. 8–15 (Maastrichtian, United States Gulf Coastal Plain).
Globotruncana (Rugotruncana) circumnodifer (Finlay) *in* Webb, 1973, p. 552, pl. 4, figs. 1–4 (Maastrichtian, DSDP Site 208, Lord Howe Rise, Tasman Sea).
Abathomphalus asteroidalis Salaj *in* Salaj, 1983, p. 208, pl. 2, figs. 1–4, pl. 5, figs. 8–9 (upper Maastrichtian, Tunisia, northern Africa).
Rugotruncana? sp. *in* Huber, 1988, p. 208, figs. 30.1–4, 31.5–6, 9–11 (upper Campanian-lower Maastrichtian, James Ross Island region, Antarctic Peninsula).
Rugotruncana circumnodifer (Finlay) *in* Huber, 1990, p. 505, pl. 4, figs. 4–10, pl. 6, fig. 3 (upper lower Maastrichtian-upper Maastrichtian, ODP Leg 113, Holes 689B and 690C, Weddell Sea, southern Atlantic Ocean).
Rugotruncana circumnodifer (Finlay) *in* Huber, 1991a, p. 292, pl. 2, figs. 4–10 (upper lower Maastrichtian-upper Maastrichtian, ODP Sites 689 and 700 (Maud Rise and Northeast Georgia Rise respectively, Weddell Sea, southern Atlantic Ocean).
Rugotruncana circumnodifer (Finlay) *in* Huber, 1991b, p. 461, pl. 1, fig. 18 (upper Maastrichtian, ODP Leg 119, Hole 738C, Kerguelen Plateau, Indian Ocean).

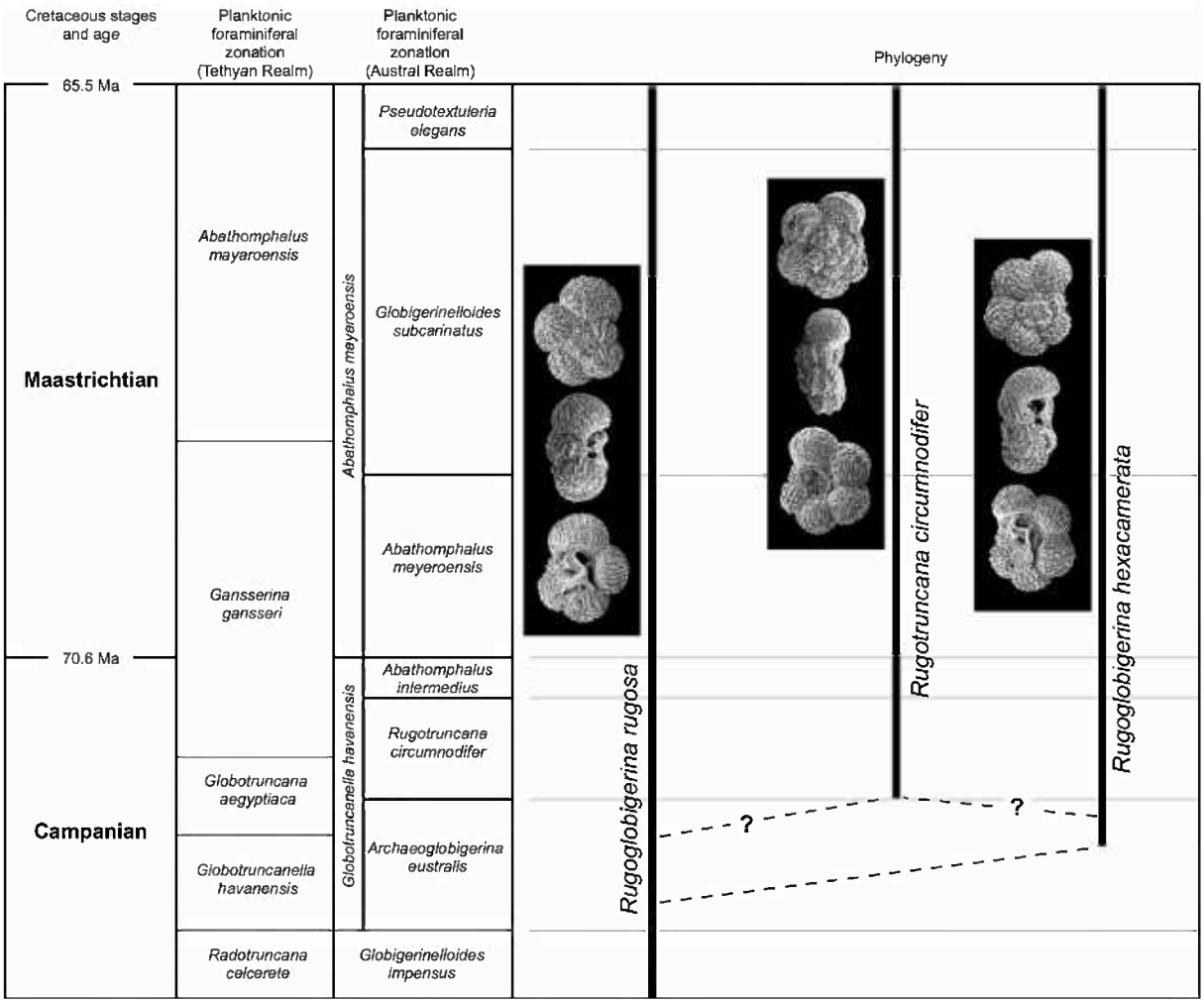

FIGURE 2. Phylogenetic relationships between *Rugotruncana circumnodifer* and selected species of the genus *Rugoglobigerina*. Ages based on Gradstein and others (2004). Tethyan planktonic foraminiferal zonation after Robaszynski and Caron (1995). Austral Realm planktonic foraminiferal zonation after Huber (1992).

Rugotruncana circumnodifer (Finlay) *in* Petrizzo, 2001, p. 852, fig. 9.8 (upper Campanian-Maastrichtian, ODP Leg 183, Hole 1138A Kerguelen Plateau, Indian Ocean).

Rugotruncana subcircumnodifer (Gandolfi) *in* Petrizzo, 2001, p. 852, fig. 9.7 (upper Campanian-Maastrichtian, ODP Leg 183, Hole 1138A Kerguelen Plateau, Indian Ocean).

Emended description. Test low to medium high trochospiral. The test consists of 12 to 14 chambers, which increase slowly to moderately in size as added; 4½ to 6 chambers in the final whorl. Sutures are distinct, depressed, straight and radial on both spiral and umbilical sides. Umbilicus is wide, its diameter representing approximately 30% to 40% of the maximum test diameter. Main aperture is umbilical in position and bordered by a tegillum; successive tegilla can completely cover the umbilical area. Periphery is broadly rounded with two more-or-less developed, quasi-equal keels bordering an imperforate band, which is better developed on the earlier chambers of the final whorl. The two keels can be situated at the equatorial periphery or be slightly offset towards the spiral side. The imperforate peripheral band is pustulose on the earlier chambers; pustules can fuse in some specimens, resulting in the development of an intercarinal ridge, occasionally giving the appearance of a third keel. Ornamentation is highly variable, ranging from meridional on both sides of the test to asymmetrical, meridional on the umbilical side and parallel to the periphery on the spiral side. Ornamentation patterns can be lost on the earlier chambers of the test due to the addition of calcite material during ontogenetic development. The last-formed chambers are less ornamented than the previous ones. The last-formed chambers often show the best development of the asymmetrical ornamentation because they are not obscured by ontogenetic calcite.

Remarks. The poor understanding of the species and its high morphological variability led to the description of a significant number of different morphotypes that were included in *Rugotruncana circumnodifer*. This species is the only one considered valid, and, therefore, the genus *Rugotruncana* is monotypic. *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955 was assigned to *Rugotruncana* by Pessagno (1967). Examination of the holotype (Pl. 2, fig. 8) and well preserved hypotypes from the late Campanian of the New Jersey coastal plain revealed that this species should be included within the genus *Globotruncana*. The following species are considered junior synonyms of *Rugotruncana circumnodifer* (Finlay, 1940): *Rugotruncana tilevi* Brönnimann and Brown, 1956; *Rugotruncana ellisi* Brönnimann and Brown, 1956; *Globotruncana (Rugoglobigerina) pennyi subpennyi* Gandolfi, 1955; *Globotruncana (Rugoglobigerina) rugosa subrugosa* Gandolfi, 1955; and *Abathomphalus asteroidalis* Salaj, 1983.

Phylogenetic relationships. Rugotruncana circumnodifer (Finlay) evolved from either *Rugoglobigerina rugosa* (Plummer) or *R. hexacamerata* Brönnimann (Fig. 2). This evolutionary transition led to the development of an imperforate peripheral band, paralleled by two variably developed keels, and generally asymmetrical test ornamenta-

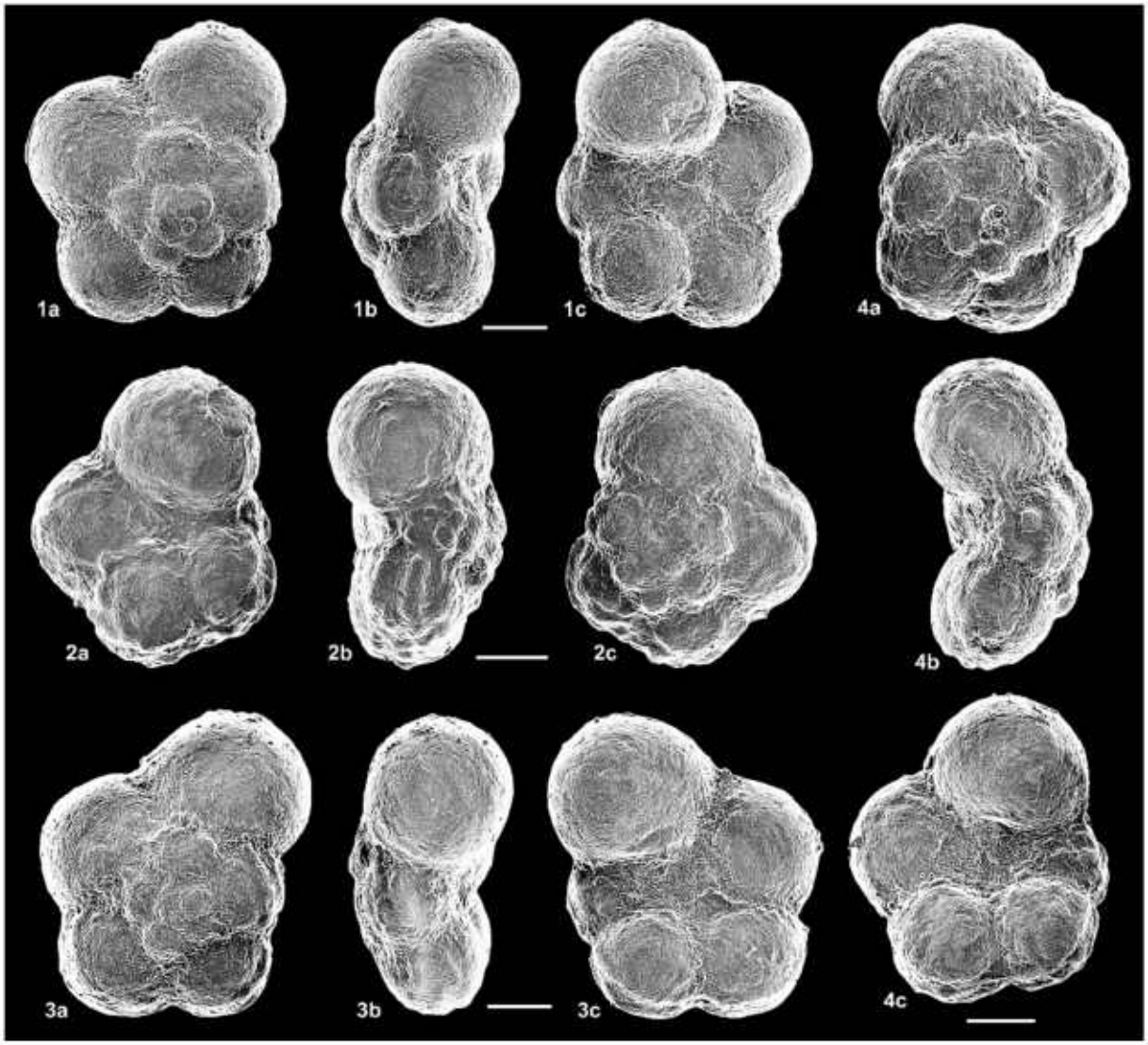

PLATE 1

Rugotruncana circumnodifer type specimens from the Whangara type locality (North Island, New Zealand), and deposited at the Institute for Geological and Nuclear Sciences Limited (New Zealand). Scale bar represents 100 μm. **1** Holotype (TF1223-1). **2** Paratype (TF1223-3). **3** Paratype (TF-I223-2a). **4** Paratype (TF1223-2b).

tion. These diagnostic features of *Rugotruncana circumnodifer* (Finlay) strongly contrast with species of *Rugoglobigerina*, which have a broadly rounded test periphery, lack peripheral structures and have symmetrically distributed meridional costellae.

Stratigraphic range. Upper Campanian through Maastrichtian (lower *Gansserina gansseri* Biozone at low latitudes, upper *Globotruncanella havanensis* Zone at southern high latitudes), within middle Chron C32n, to the uppermost Maastrichtian (uppermost *Abathomphalus mayaroensis* Biozone; Huber, 1990). Using the magnetostratigraphically controlled age model of Huber (1990), calibrated to the Gradstein and others (2004) time scale, the first appearance of this species is estimated as 71.3 Ma for Hole 689B and 72.0 Ma for Hole 690C. A similar stratigraphic distribution was recorded for ODP Holes 698A and 700B of the Georgia Basin in the Southern Atlantic Ocean (Huber, 1991a). In ODP Hole 738C (Kerguelen Plateau, Southern Indian Ocean), *Rugotruncana circumnodifer* was reported only from upper Maastrichtian sediments (Huber, 1991b) and is less abundant when compared to the other southern, high-latitude ODP sites. This species was more recently reported by Coxall (in Shipboard Scientific Party, 2000 a, b) and Petrizzo (2001) from the Maastrichtian sediments of ODP Leg 183 Sites 1135 and 1138, also drilled in the Kerguelen Plateau. The range of *Rugotruncana circumnodifer* was initially considered by Finlay (1940) as Santonian. The age at the type locality was reassigned to the Maastrichtian by Webb (1971).

Geographical distribution. Cosmopolitan. Most of the occurrences are known from the Austral Realm and it has been rarely reported from the Tethyan Realm. It is known from southern Scandinavia (Sweden), the Carribean region (Cuba, Puerto Rico), northern South America (Colombia), northern Africa (Tunisia), Antarctica (James Ross Island region), the Tasman Sea, the southern Atlantic Ocean (Maud Rise and northeast Georgia Rise) and the southern Indian Ocean (Kerguelen Plateau and Exmouth Plateau).

DISCUSSION OF THE SPECIES CONCEPT

The case of *Rugotruncana circumnodifer* (Finlay), the only species of the genus *Rugotruncana*, raises an important

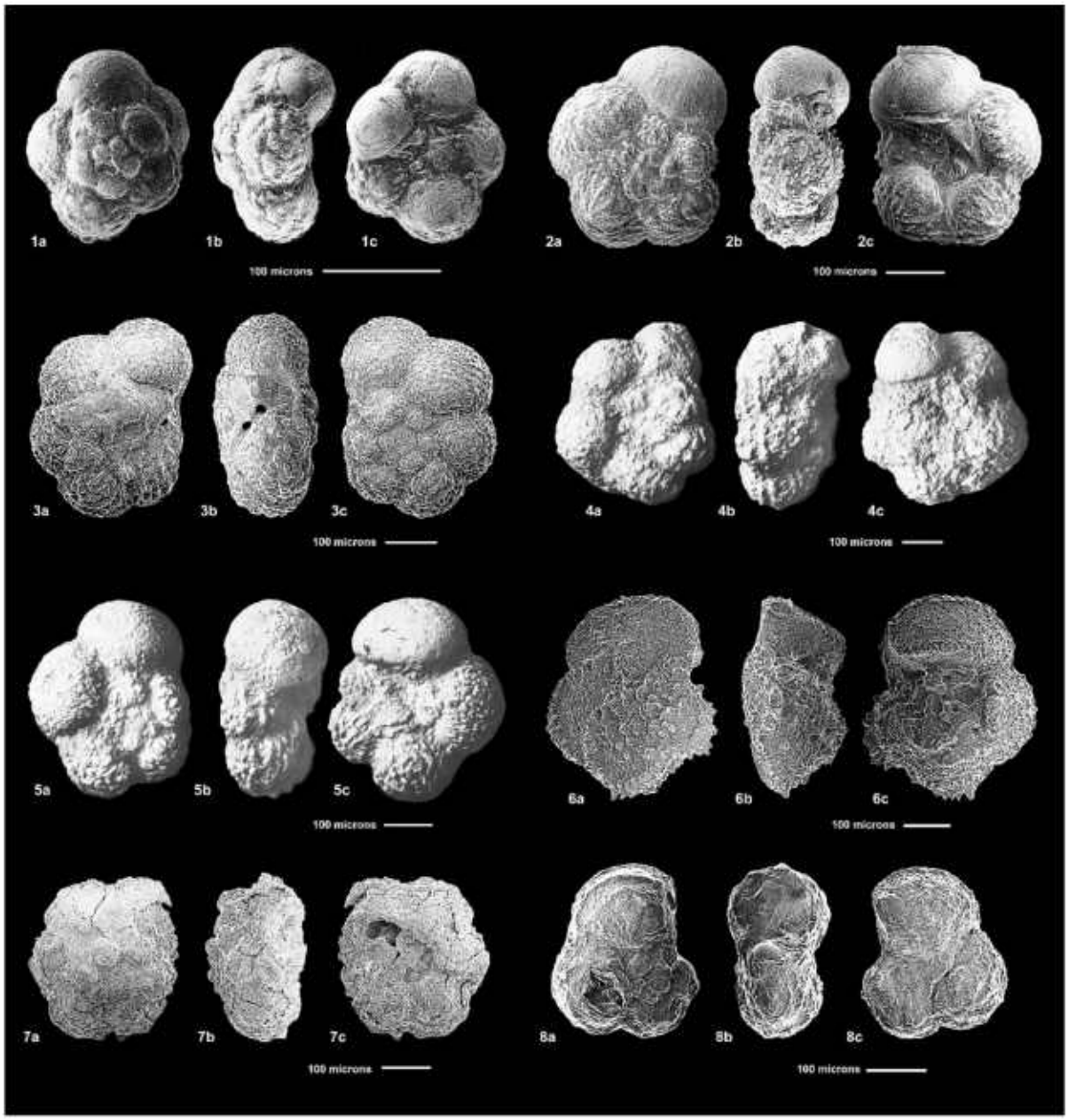

PLATE 2

Primary type specimens of *Rugotruncana circumnodifer* (Finlay) and other species previously assigned to *Rugotruncana*. Scale bar represents 100 μm. **1** *Globigerina circumnodifer* Finlay, 1940. SEM photographs of a paratype from the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 689011. **2** *Rugotruncana tilevi* Brönnimann and Brown, 1956. SEM illustrations of the holotype deposited at the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 628612. Specimen originally figured by Brönnimann and Brown, 1956 (pl. 22, figs. 1–3). Notice that the specimen presents meridional ornamentation on both sides of the test. Such specimens are rare in the assemblages at our disposal, being considered as having intermediary test morphology between the *Rugoglobigerina* ancestor and *Rugotruncana*. **3** *Rugotruncana ellisi* Brönnimann and Brown, 1956. SEM illustrations of the holotype deposited at the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 628611. Specimen originally figured by Brönnimann and Brown, 1956 (pl. 22, figs. 7–9). **4** *Globotruncana (Rugoglobigerina) pennyi subpennyi* Gandolfi, 1955. SEM photographs of the holotype deposited at the Paleontological Research Institute, Ithaca, NY 20864 and photographed at The Natural History Museum (London) courtesy of Dr. John E. Whittaker. Specimen originally figured by Gandolfi (1955, pl. 7, figs. 7a–c). **5** *Globotruncana (Rugoglobigerina) rugosa subrugosa* Gandolfi, 1955. SEM photographs of the holotype deposited at the Paleontological Research Institute, Ithaca, NY 20863 and photographed at The Natural History Museum (London) courtesy of Dr. John E. Whittaker. Specimen originally figured by Gandolfi (1955, pl. 7, figs. 5a–c). **6** *Rugotruncana skewesae* Brönnimann and Brown, 1956. SEM illustrations of the holotype deposited at the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 628613. Specimen originally figured by Brönnimann and Brown, 1956 (pl. 23, figs. 4–6). **7** *Rugotruncana nothi* Brönnimann and Brown, 1956. SEM illustrations of the holotype deposited at the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 628610. Specimen originally figured by Brönnimann and Brown, 1956 (pl. 22, figs. 16–18). **8** *Globotruncana (Rugoglobigerina) circumnodifer subcircumnodifer* Gandolfi, 1955. SEM photographs of the holotype deposited at the Paleontological Research Institute, Ithaca, NY 20837. Specimen originally figured by Gandolfi (1955, pl. 2, figs. 8a–c).

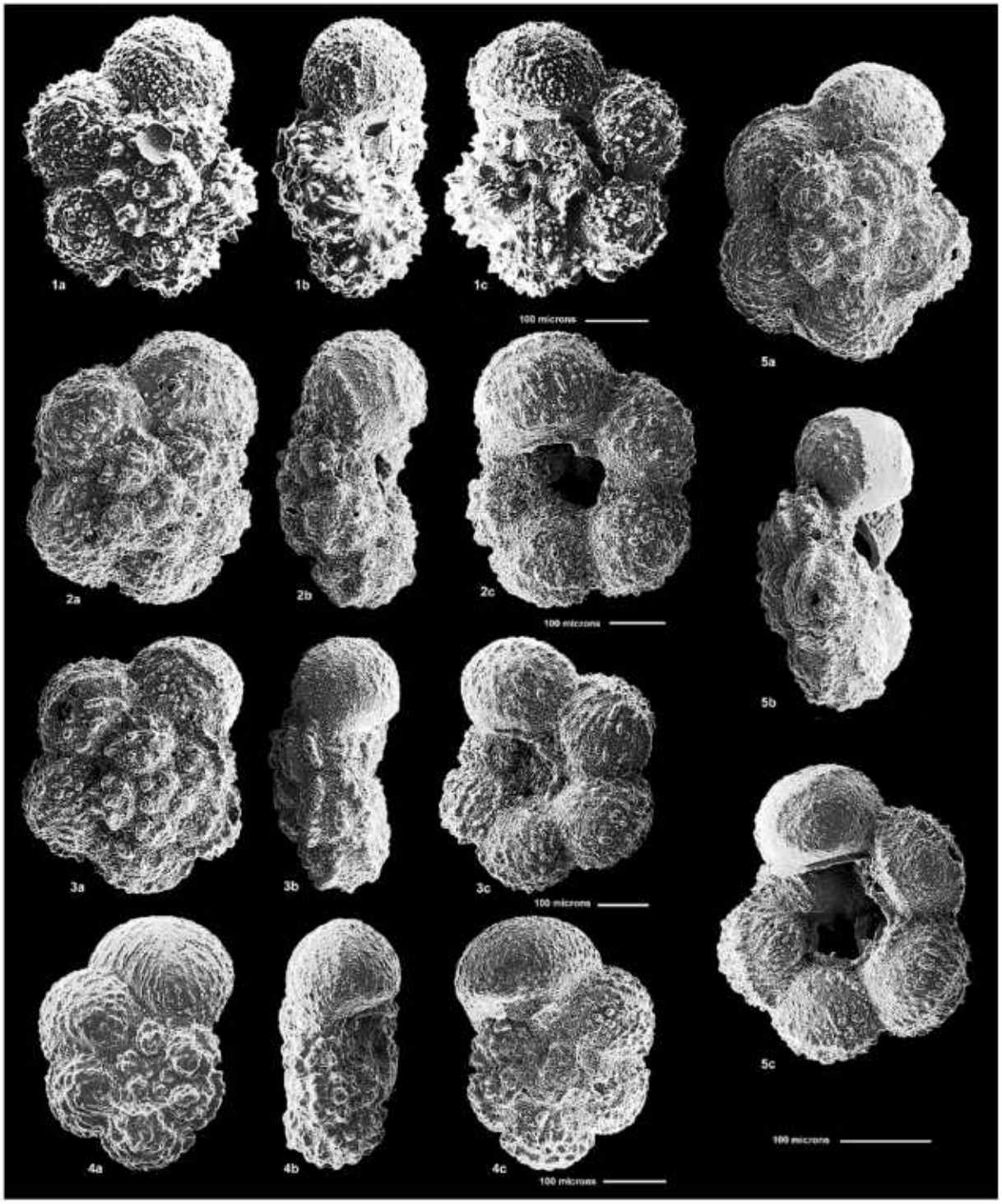

PLATE 3

Five specimens illustrating the high morphological variability of *Rugotruncana circumnodifer* (Finlay). Scale bar represents 100 μm. **1** Hypotype from the upper part of the early Maastrichtian, Leg 113, Hole 690C (Weddell Sea, Maud Rise), previously figured by Huber (1990, pl. 4, figs. 5–7). Sample 113-690C-19X-3, 119–123 cm. **2** Hypotype from the lowermost part of the late Maastrichtian, Leg 113, Hole 690C (Weddell Sea, Maud Rise). Sample 113-690C-17-3, 78–79 cm. **3** Hypotype from the late Maastrichtian, Leg 113, Hole 690C (Weddell Sea, Maud Rise). Sample 113-690C-17-3, 78–79 cm. **4** Topotype of *Rugotruncana tilevi* from the Loeblich and Tappan Collection deposited at the National Museum of Natural History (Smithsonian Institution, Washington D.C.), USNM 478113. The topotype material was offered by N. K. Brown and lead Loeblich and Tappan (1987, p. 470) to the conclusion, "Topotypes of *R. tilevi* . . . do not have the meridional arrangement of costellae shown in the original drawing." Re-examination of this material (approximately fifteen specimens) confirmed the wide range of morphological variability of *Rugotruncana circumnodifer*. **5** Hypotype from the late Maastrichtian, Leg 113, Hole 690C (Weddell Sea, Maud Rise). Sample 113-690C-17-3, 78–79 cm.

question about the species concept applied to a well-documented planktonic foraminiferal species. The major factor that led to the re-evaluation of the *R. circumnodifer* species concept is the species variability. Test variability is significant, with the most variable features being (i) height of the trochospire, (ii) degree of development of the two keels, (iii) presence or absence and, if present, the degree of development of the intercarinal ridge and (iv) test ornamentation, mostly on the spiral side. Individual specimens of *R. circumnodifer* can be recognized on the basis of a combination of these features, although all specimens must display an imperforate band with a weak to strongly developed double keel. It is noteworthy that the two keels are rarely unequally developed (Pl. 3, fig. 1).

Better understanding of the significant test variability unequivocally shows that neither the typological species concept, based on morphological resemblance between individuals, nor the evolutionary or phylogenetic species concepts, based on simple ancestor-descendant relationships and projections of the biological species concept applied to the fossil record, can accommodate well-documented entities such as *Rugotruncana circumnodifer* (Finlay).

In order to increase the accuracy of our interpretation, we consider it necessary to define a new paleontological species concept that can be applied to well-documented Cretaceous planktonic foraminiferal taxa. For this purpose, we propose the following definition. A well-documented paleontological species is the basic unit with taxonomic significance in the fossil record, and has the following characteristics: (i) it is monophyletic; (ii) it has a distinct range of morphological variability, showing relative stability over a definable period of time and presenting relatively discrete evolutionary changes; (iii) it is a morphologically heterogeneous and discontinuous entity, consisting of one or (mostly) more morphological and/or paleoecological varieties; (iv) it has its own developmental history traceable in space and time; and (v) its existence and integrity can be tested not only by comparative morphological distinctiveness, but also by its response to paleoenvironmental and geological factors (e.g., paleoclimatic changes, sea-level fluctuations, etc.), as inferred from paleontology and related geological disciplines.

CONCLUSIONS

The diagnosis of *Rugotruncana* is emended to include globular chambered morphotypes with two keels present, at least on the earlier chambers of the final whorl, and variable but well developed test ornamentation. Test ornamentation varies from symmetrically meridional on all chambers to asymmetrical with meridional costellae on the umbilical side and costellae that are parallel to the periphery on the spiral one. Successive addition of calcite material sometimes obscures the ornamentation pattern, mainly on the earlier formed chambers.

Rugotruncana evolved from the genus *Rugoglobigerina* through the development of two peripheral keels and asymmetrical test ornamentation that is parallel to the periphery on the spiral side and meridional on the umbilical one. The genus *Rugotruncana* is included within the Family Rugoglobigerinidae, Subfamily Rugoglobigerininae.

A new paleontological species concept is formally defined to accommodate taxa with significant test variability, such as *Rugotruncana circumnodifer* (Finlay). This concept is necessary to avoid artificial proliferation of species in the fossil record and should be applied to other species of planktonic foraminifera.

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REFERENCES

BERGGREN, W. A., 1962, Some planktonic foraminifera from the Maestrichtian and type Danian stages of southern Scandinavia: Acta Universitatis Stockholmiensis, Stockholm Contributions to Geology, v. 9, p. 1–106.

BOLLI, H. M., 1951, The genus *Globotruncana* in Trinidad, B.W.I.: Journal of Paleontology, v. 25, p. 187–199.

———, LOEBLICH, A. R., JR., and TAPPAN, H., 1957, Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae, *in* Loeblich, A. R., JR. (ed.), Studies in Foraminifera: United States National Museum Bulletin, no. 215, p. 3–50.

BRÖNNIMANN, P., 1952, Globigerinidae of the Upper Cretaceous (Cenomanian-Maestrichtian) of Trinidad, B.W.I.: Bulletins of American Paleontology, v. 34, no. 140, p. 1–70.

———, and BROWN, N. K., JR., 1956, Taxonomy of the Globotruncanidae: Eclogae Geologicae Helvetiae, v. 48, p. 503–561.

CARON, M., 1985, Cretaceous planktic foraminifera, *in* Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), Plankton Stratigraphy: Cambridge University Press, Cambridge, p. 17–86.

CUSHMAN, J. A., 1927, New and interesting foraminifera from Mexico and Texas: Contributions from the Cushman Foundation for Foraminiferal Research, v. 3, p. 111–119.

EL-NAGGAR, Z. R., 1971, On the classification, evolution and stratigraphical distribution of the Globigerinacea, *in* Farinacci, A. (ed.), Proceedings of the Second International Conference on Planktonic Microfossils, Roma, 1970: Edizioni Tecnoscienza, Rome, v. 1, p. 421–470.

FINLAY, H. J., 1940, New Zealand Foraminifera: Key Species in Stratigraphy-No. 4: Transactions of the Royal Society of New Zealand, v. 69, p. 448–472.

GANDOLFI, R., 1955, The genus *Globotruncana* in northeastern Colombia: Bulletins of American Paleontology, v. 36, no. 155, p. 1–118.

GEORGESCU, M. D., 2005, On the systematics of rugoglobigerinids (planktonic Foraminifera, Late Cretaceous): Studia Geologica Polonica, v. 124, p. 87–97.

GRADSTEIN, F. M., OGG, J. G., SMITH, A. G., AGTERBERG, F. P., BLEEKER, W., COOPER, R. A., DAVYDOV, V., GIBBARD, P., HINNOV, L. A., HOUSE, M. R., LOURENS, L., LUTERBACHER, H. P., MCARTHUR, J., MELCHIN, M. J., ROBB, L. J., SHERGPOLD, J., VILLENEUVE, M., WARDLAW, B. R., ALI, J., BRINKHUIS, H., HILGEN, F. J., HOOKER, J., HOEWATH, R. J., KNOLL, A. H., LASKAR, J., MONECHI, S., PLUMB, K. A., POWELL, J., RAFFI, I., RÖHL, U., SADLER, P., SANFILIPPO, A., SCHMITZ, B., SCHACKELTON, N. J., SHIELDS, G. A., STRAUSS, H., VAN DAM, J., VAN KOLFSCHOTEN, T., and WILSON, D., 2004, A Geologic Time Scale 2004: Cambridge University Press, p. 1–589.

HUBER, B. T., 1988, Upper Campanian-Paleocene foraminifera from the James Ross Island region, Antarctic Peninsula. Geological Society of America, Memoir, no. 169, p. 163–251.

———, 1990, Maestrichtian planktonic foraminifer biostratigraphy of the Maud Rise (Weddell Sea, Antarctica): Leg 113, Holes 689B and 690C, *in* Barker, P. F., Kennett, J. P., and others (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 113: Ocean Drilling Program, College Station, Texas, p. 489–513.

———, 1991a, Planktonic foraminifer biostratigraphy of Campanian-Maestrichtian sediments from Sites 698 and 700, southern South Atlantic, *in* Ciesielski, P. F., Kristoffersen. Y., and others (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 114: Ocean Drilling Program, College Station, Texas, p. 281–297.

———, 1991b, Maastrichtian planktonic foraminifer biostratigraphy and the Cretaceous/Tertiary boundary at ODP Hole 738C (Kerguelen Plateau, southern Indian Ocean), *in* Barron, J. A., Larsen, B. L., and others. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 119: Ocean Drilling Program, College Station, Texas, p. 451–465.

———, 1992, Upper Cretaceous planktonic foraminiferal biozonation for the Austral Realm: Marine Micropaleontology, v. 20, p. 107–128.

———, 1994, Ontogenetic morphometrics of some Late Cretaceous trochospiral planktonic foraminifera from the Austral Realm: Smithsonian Contributions to Paleobiology, v. 77, p. 1–85.

LOEBLICH, A. R., JR., and TAPPAN, H., 1987, Foraminiferal Genera and Their Classification: van Nostrand Reinhold Company, New York, 970 p.

OLSSON, R. K., 1964, Late Cretaceous planktonic foraminifera from New Jersey and Delaware: Micropaleontology, v. 10, p. 157–188.

PESSAGNO, E. A., JR., 1960, Stratigraphy and micropaleontology of the Cretaceous and lower Tertiary of Puerto Rico: Micropaleontology, v. 6, p. 87–110.

———, 1962, The Upper Cretaceous stratigraphy and micropaleontology of south-central Puerto Rico: Micropaleontology, v. 8, p. 349–368.

———, 1967, Upper Cretaceous planktonic foraminifera from the Western Gulf Coastal Plain: Palaeontographica Americana, v. 5, no. 37, p. 245–445.

PETRIZZO, M. R., 2001, Late Cretaceous planktonic foraminifera from Kerguelen Plateau (ODP Leg 183): new data to improve the Southern Ocean biozonation: Cretaceous Research, v. 22, p. 829–855.

ROBASZYNSKI, F., and CARON, M., 1995, Foraminifères planctoniques du Crétacé: commentaire de la zonation Europe-Mèditerranée: Bulletin de la Société Géologique de France, v. 6, p. 681–692.

———, ———, GONZALEZ DONOSO, J. M., WONDERS, A. A. H., THE EUROPEAN WORKING GROUP ON PLANKTONIC FORAMINIFERA, Atlas of late Cretaceous globotruncanids: Revue de Micropaléontologie, v. 26, p. 145–305.

SALAJ, J., 1983, Quelques problèmes taxinomiques concernant les foraminifèrs planctiques et la zonation du Sénonien supérieur d'El Kef: Geologický Zborník-Geologica Carpathica, v. 34, p. 187–212.

SHIPBOARD SCIENTIFIC PARTY, 2000a, Site 1135, *in* Coffin, M. F., Frey, F. A., Wallace, P. J., and others. (eds.) 2000a, Proceedings of the Ocean Drilling Program, Initial Reports, v. 183: Ocean Drilling Program, College Station, Texas, p. I–59.

———, 2000b, Site 1138, *in* Coffin, M. F., Frey, F. A., Wallace, P. J., and others. (eds.) 2000b, Proceedings of the Ocean Drilling Program, Initial Reports, v. 183: Ocean Drilling Program, College Station, Texas, p. 1–205.

VOORWIJK, G. H., 1937, Foraminifera from the Upper Cretaceous of Habana, Cuba: Koninklijke Akademie van Wetenschappen te Amsterdam. Proceedings, v. 40, p. 190–198.

WEBB, P. N., 1966, New Zealand Late Cretaceous Foraminifera and stratigraphy: Unpublished Ph.D. Dissertation, State University of Utrecht, The Netherlands, 320 p.

———, 1971, New Zealand late Cretaceous (Haumurian) foraminifera and stratigraphy. A summary: New Zealand Journal of Geology and Geophysics, v. 14, p. 795–828.

———, 1973, Upper Cretaceous-Paleocene foraminifera from Site 208 (Lord Howe Rise, Tasman Sea), DSDP, Leg 21. *in* Davies, T. A. (ed.), Initial Reports of the Deep Sea Drilling Project, v. 21: U.S. Government Printing Office, Washington, D.C., p. 541–573.

WONDERS, A. A. H., 1992, Cretaceous planktonic foraminiferal biostratigraphy, Leg 122, Exmouth Plateau, Australia, *in* von Rad, U., Haq., and others. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 122: Ocean Drilling Program, College Station, Texas, p. 587–599.

ZAPEDA, M. A., 1998, Planktonic foraminiferal diversity, equitability and biostratigraphy of the uppermost Campanian-Maastrichtian, ODP Leg 122, Hole 762C, Exmouth Plateau, NW Australia, eastern Indian Ocean: Cretaceous Research, v. 19, p. 117–152.

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