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PARACOSTELLAGERINA NOV. GEN., A MERIDIONALLY COSTELLATE PLANKTONIC FORAMINIFERAL GENUS OF THE MIDDLE CRETACEOUS (LATEST ALBIAN-EARLIEST CENOMANIAN)

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ABSTRACT

A new genus is proposed to accommodate strongly ornamented hedbergellids of the latest Albian-earliest Cenomanian. *Paracostellagerina* nov. gen. is characterized by asymmetrical test ornamentation, rugosities, and costellae that are meridionally arranged on the umbilical side and parallel to the periphery on the spiral side. This genus has a global distribution within tropical-subtropical latitudes and, because of its short stratigraphic range, it is a valuable biomarker for correlation of uppermost Albian-lowermost Cenomanian sequences.

INTRODUCTION

Meridional ornamentation is a feature encountered in a number of Cretaceous planktonic foraminiferal genera. It independently developed in four Cretaceous lineages within the late Albian-Maastrichtian stratigraphic interval. The expression and pattern of meridional ornamentation is quite variable. It is fully developed on both sides of the test in genera such as *Costellagerina* (*Whiteinella-Costellagerina* lineage) and *Rugoglobigerina* (*Archaeoglobigerina-Rugoglobigerina* lineage). Sometimes it is developed on the umbilical side only in genera such as *Abathomphalus* (*Whiteinella-Globotruncanella-Abathomphalus* lineage) and partly in *Rugotruncana* (e.g., *R. circumnodifer*).

The first tests presenting this ornamentation pattern are recorded in the latest Albian-earliest Cenomanian, in a distinct lineage originating from *Hedbergella delrioensis*. Detailed scanning electron microscope (SEM) observation shows that the test ornamentation presents an asymmetrical pattern, being meridional on the umbilical side and parallel to the periphery on the spiral side. A similar asymmetry occurs in three other distantly related species of the latest Cretaceous (Maastrichtian), namely *Abathomphalus intermedius*, *A. mayaroensis* and *Rugotruncana circumnodifer*.

The only species of the latest Albian-earliest Cenomanian stratigraphic interval that presents asymmetrical test ornamentation is *Hedbergella libyca* Barr, originally described from northern Libya and later reported from the Mediterranean region and sites drilled in the subtropical Atlantic Ocean. For a time, this species has been assigned to the genus *Costellagerina*, which bears a meridional ornamentation pattern on both sides of the test and includes *Costellagerina pilula* (Belford, 1960) from the Santonian of Western Australia as its type species (Petters and others, 1983). Assignment of *Hedbergella libyca* to *Costellagerina*, however, is inappropriate for the following reasons: 1) because of its asymmetrically developed ornamentation and 2) an ~13 m.y. stratigraphic gap separating its extinction from the oldest occurrence of *Costellagerina bulbosa* with no known meridionally costellate species in between. A new species with intermediate test morphology between *Hedbergella delrioensis* Carsey (1926) and *H. libyca* Barr, designated as *Hedbergella praelibyca* by Petrizzo and Huber (2006), further documents the existence of a distinct lineage in the latest Albian-earliest Cenomanian that is unrelated to the development of *Costellagerina* (namely the *Whiteinella-Costellagerina* lineage) of the Santonian-early Campanian (Fig. 1). For this reason, the holotype of *Hedbergella libyca* Barr is now included in the new genus *Paracostellagerina* nov. gen.

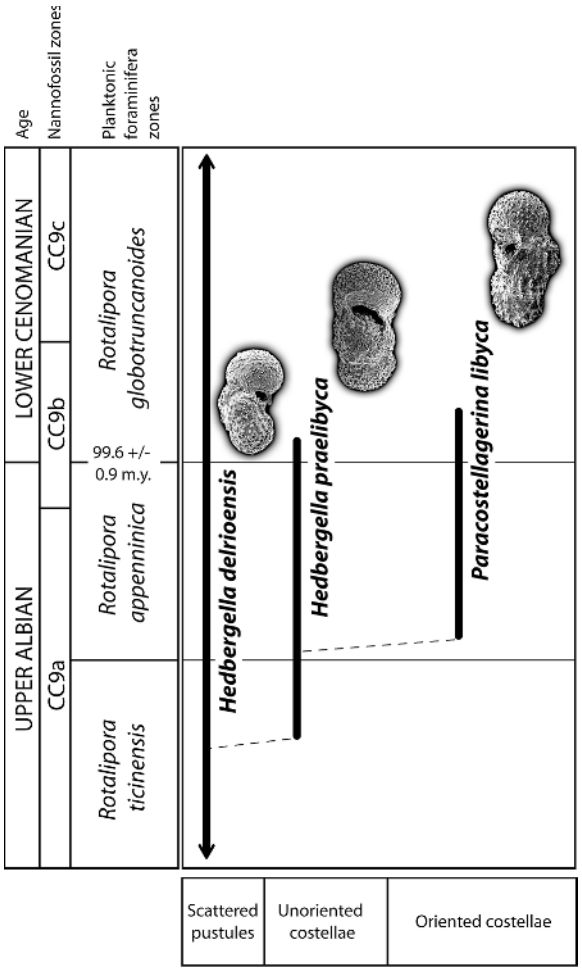

FIGURE 1. Stratigraphic distribution and phyletic relationships of *Paracostellagerina* gen. nov. Absolute ages after Gradstein and others (2004). Planktonic foraminiferal zonation after Petrizzo and Huber (2006). Nannofossil zonation after Watkins and Bergen (2003).

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A HISTORY OF THE TAXONOMIC ROLE OF TEST ORNAMENTATION IN CRETACEOUS PLANKTONIC FORAMINIFERA

The importance of wall texture as a primary criterion for classification of Cenozoic planktonic foraminifera has been emphasized since the phylogenetically based classification of Steineck and Fleisher (1978). However, wall texture has been inconsistently applied to the classification of Cretaceous planktonic foraminifera. One exception is Carsey's (1926) recognition of a polygonal network of fused costellae that distinguishes *Globigerina washitensis* from other Cretaceous taxa. Another important contribution came soon after that of Carsey with the description of the meridionally costellate species *Globigerina rugosa* from the Late Cretaceous of Texas by Plummer (1927).

Later studies that designated test ornamentation as one of the most important features in planktonic foraminiferal morphology were carried out by Brönnimann (1952) and Brönnimann and Brown (1956) on taxa of Campanian-Maastrichtian age. Three genera were proposed by Brönnimann (1952) for taxa presenting ornamentation elements arranged in a meridional pattern: *Plummerita*, *Rugoglobigerina*, and *Trinitella* for taxa with spinose, rounded and non-spinose, and truncated peripheral margins, respectively. A second phase of these studies was made when Brönnimann and Brown (1956) proposed the genera *Kuglerina*, *Bucherina*, and *Rugotruncana* to include forms with a coarse, dense ornamentation on the test surface but absence of a meridional pattern.

Subsequent morphological studies showed that meridional ornamentation can be symmetrically developed on both sides of the test (e.g., *Rugoglobigerina*, *Trinitella*, *Plummerita*), or this test ornamentation can present different patterns on either of the two sides (Berggren, 1962; Pessagno, 1967; Douglas, 1969; Caron, 1981; Robaszynski and others, 1984). The Subfamily Rugoglobigerininae was proposed by Subbotina (1959) to accommodate genera bearing a meridional ornamentation pattern. This group was raised to family level by Loeblich and Tappan (1984, 1988) and represents one of two families within the superfamily Globotruncanacea. The stratigraphic range of the family Rugoglobigerinidae was stated as upper Santonian-Maastrichtian by Loeblich and Tappan (1988). A subdivision within this family was recently proposed by Georgescu (2005), who recognized two subfamilies, namely Rugoglobigerininae and Archaeoglobigerininae, based on the presence or absence of the meridional test ornamentation.

Additional studies revealed that the meridional ornamentation pattern is not peculiar to the representatives of the family Rugoglobigerinidae. The genus *Costellagerina* was proposed for taxa bearing meridionally-arranged ornamentation, a broadly rounded periphery lacking peripheral structures, an umbilical-extraumbilical primary aperture, and a primary aperture bordered by a narrow lip or porticus. In their original definition, Petters and others (1983) noted that the meridional ornamentation pattern is the main feature that distinguishes *Costellagerina* from *Hedbergella*, and further noted that the Rugoglobigerinidae (middle Campanian-Maastrichtian) represents a separate lineage. Originally, the genus *Costellagerina* was considered to range from the late Santonian through Campanian, but Loeblich and Tappan (1988) extended the range to the Cenomanian, presumably to accommodate middle Cretaceous meridionally costellate forms. However, no detailed discussion of the pre-Santonian occurrences was made by these authors.

An attempt to unite all the Cretaceous forms (late Albian and Maastrichtian) bearing meridional ornamentation in the Superfamily Rugoglobigerinacea was recently made by El-Nakhal (2002). By using the meridional ornamentation as a primary taxonomic criterion, this author neglected the iterative evolutionary pattern, which occurs in distant taxonomic groups (e.g., Hedbergellidae and Rugoglobigerinidae), as has been shown by Georgescu (2005). He also ignored asymmetry in the expression of the test ornamentation. Therefore, we suggest that the Superfamily Rugoglobigerinacea lacks any taxonomic and evolutionary meaning, and should be considered a nomen nudum.

ALBIAN-CENOMANIAN MERIDIONALLY COSTELLATE HEDBERGELLID TAXA

Pre-Santonian occurrences of meridionally costellate species have been documented from the late Albian and middle Cenomanian. The first report of meridionally costellate forms from the late Albian-early Cenomanian was presented in Barr's (1972) biostratigraphic study of Cretaceous planktonic foraminifera from Libya. Although no ornamentation pattern was mentioned in his original description of *Hedbergella libyca* (Barr, 1972, p. 14), the figured holotype shows costellate ornamentation on both the spiral and umbilical sides (Fig. 2).

A second species bearing meridional ornamentation was reported from the middle Cenomanian of Lebanon by Saint Marc (1973). *Hedbergella costellata* was considered, since its original report, as having nothing in common with Late Cretaceous rugoglobigerinids despite the similarity in ornamentation, as the position of the primary aperture, periapertural structures, and umbilical system are distinctly different. But test ornamentation was considered as a good discriminator between this species and the other species included in the hedbergellid stock. Scanning electron microscope photographs of the holotype and three paratypes of *H. costellata* (Saint Marc, pl. 1, fig.1–2, pl. 2, figs. 1–3) show significant morphologic variability mainly with

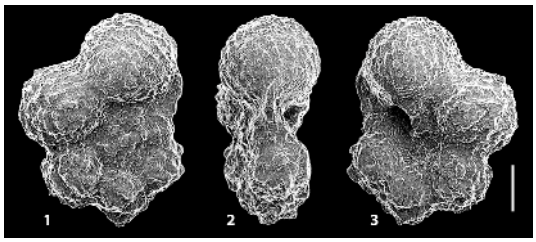

FIGURE 2. SEM micrographs of the holotype of *Hedbergella libyca*, figured by Barr (1972, pl. 10, fig. 5) from the Hilal Shale (lower Cenomanian) of northern Cyrenaica Province, Libya. The specimen is deposited at the United States National Museum of Natural History, USNM 167903. Scale bar = 100 micrometers.

respect to the rate of chamber-size increase in the last whorl, from slow to rapid, and the size of the umbilicus. We consider that *Hedbergella costellata* Saint Marc is a junior synonym of *Hedbergella libyca* Barr. This is based on the similarities between the holotypes of the two species, and range of morphological variability. The middle Cenomanian age of the Lebanon occurrence should be revised, as *Paracostellagerina libyca* (Barr) is not documented in the stratigraphic record above the lowermost part of the *Rotalipora globotruncanoides* Zone (lower Cenomanian; Petrizzo and Huber, 2006).

The first report of the meridionally costate hedbergellids outside the Mediterranean area came from offshore Morocco at DSDP Sites 545 and 547 (Leckie, 1984). *Hedbergella libyca* was documented from the *Planomalina praebuxtorfi-buxtorfi* Zone (latest Albian) throughout the lower part of the *Rotalipora gandolfii* Zone (earliest Cenomanian). Further documented occurrences of this species show a global distribution at tropical and subtropical latitudes (Fig. 3).

SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA Eichwald, 1830
Suborder Globigerinina Delage and Hérouard, 1896
Superfamily Rotaliporacea Sigal, 1958
Family Hedbergellidae Loeblich and Tappan, 1961
Subfamily Hedbergellinae Loeblich and Tappan, 1961
Genus ***Paracostellagerina*** nov.
Type species: *Hedbergella libyca* Barr, 1972, p. 14.

Description. Test low to moderate trochospiral, globular chambers with a broadly rounded periphery, lacking peripheral structures; primary aperture extraumbilical-umbilical, bordered by a narrow, imperforate lip; test ornamentation asymmetrical with respect to the peripheral plane, rugosities and sharp costellae arranged following a meridional pattern on the umbilical side, and parallel to the periphery on the spiral side.

Species included. *Hedbergella libyca* Barr, 1972, p. 14, pl.10, fig.5.

Remarks. The genus *Paracostellagerina* nov. gen. is proposed to accommodate hedbergellid taxa bearing asymmetrical test ornamentation, with meridional costellae on the umbilical side and costellae oriented parallel to the periphery on the spiral side. Test ornamentation is a peculiar feature of the genus, with transitional forms being recently placed in a new species *Hedbergella praelibyca* by Petrizzo and Huber (2006). The asymmetric test ornamentation and extraumbilical-umbilical primary aperture separate *Paracostellagerina* nov. gen. from the early Santonian-early Campanian genus *Costellagerina*. The latter generally has a meridional ornamentation pattern on both sides of the test, although variations in test ornamentation were observed by Huber (1994).

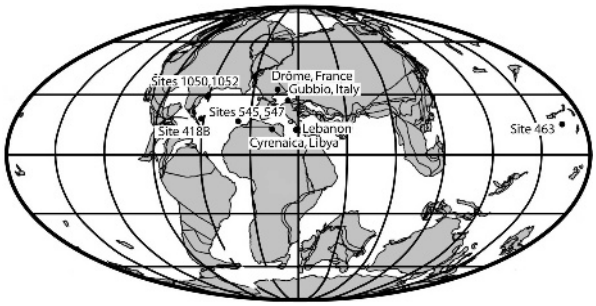

FIGURE 3. Geographic distribution of the occurrences of *Paracostellagerina libyca*, demonstrating its global distribution at tropical and subtropical latitudes.

Differences in test ornamentation, position of the primary aperture, and nature of the periapertural structures provide the impetus to distinguish *Hedbergella libyca* and *Rugoglobigerina pilula* as the type species of the two monospecific genera *Paracostellagerina* nov. gen. and *Costellagerina*. The two species were considered congeneric in the past by Loeblich and Tappan (1988, p. 462) and Premoli Silva and Sliter (1995, pl. 1, fig. 8) under *Costellagerina*, and by El-Nakhal (2002) under his genus *Meridionalla*. *Meridionalla* was based on the figures of the holotype of *Hedbergella murphyi*, which was named by Douglas (1969). Re-examination of the SEM photographs of the *Hedbergella murphyi* holotype by Petrizzo and Premoli Silva (2000) showed that there is no meridional ornamentation as was illustrated in the original figure. Therefore *Meridionalla* lacks taxonomic significance. Separation of *Costellagerina* and *Paracostellagerina* nov. gen. is supported by absence of forms with similar test morphology between the extinction of *Paracostellagerina libyca* and the first occurrence of *Costellagerina pilula*. This stratigraphic interval ranges from the earliest Cenomanian to the earliest Santonian and spans approximately 13 myr.

Phylogeny. *Paracostellagerina* nov.gen. evolved from hedbergellids that bear dense, randomly scattered pustules. *Hedbergella praelibyca* was recently proposed to accommodate a distinct taxon with intermediate morphological features between *Hedbergella delrioensis* and *Paracostellagerina libyca* (Petrizzo and Huber, 2006). Examination of the type material of *Hedbergella praelibyca* from Ocean Drilling Program (ODP) Sites 1050C and 1052E (Blake Nose, subtropical North Atlantic) showed that the surface texture of this species has incipient, randomly arranged, short costellae and scattered pustules. The ornamentation pattern sharply differs from that of the ancestor and descendant species, *Hedbergella delrioensis* and *Paracostellagerina libyca*, respectively. The asymmetrical ornamentation pattern in *Paracostellagerina libyca* is distinct from that of the ancestral species in presenting preferential arrangement of the ornamentation elements. Such complex ornamentation, meridional on the umbilical side and parallel to the periphery on the spiral side, is unique among the early and middle Cretaceous planktonic foraminifera.

Etymology. The Greek prefix '*para*' (= opposed to) is added to the pre-existing planktonic foraminiferal genus name *Costellagerina*.

Stratigraphic range. Latest Albian-earliest Cenomanian (from the upper *Rotalipora appenninica* Zone to the lowermost part of *R. globotruncanoides* Zone).

Paracostellagerina libyca (Barr) 1972
(Pl. 1, figs. 4–6, Fig. 2)

Hedbergella libyca Barr 1972, p. 14, pl. 10, fig. 5 (lower Cenomanian, Cyrenaica province, Libya).

Hedbergella costellata Saint-Marc 1973, p. 11, pl. 1, figs. 1–2, pl. 2, figs. 1–3 (middle Cenomanian, Lebanon).

non *Hedbergella costellata* Saint-Marc. Caron, 1978, p. 658, pl. 4, figs. 1–3, 8–9 (upper Albian, DSDP Leg 40, Sites 363 and 364, Atlantic Ocean, offshore Angola).

Hedbergella libyca Barr. McNulty, 1979, pl. 3, figs. 1–6 (upper Albian, DSDP Leg 43, Site 386, Atlantic Ocean, Bermuda Rise).

Hedbergella libyca Barr, Form 1. McNulty and Barr, 1979, p. 303, pl. 1, figs. 1–5 (upper Albian, DSDP, Leg 43, Site 386, Atlantic Ocean, Bermuda Rise).

Hedbergella libyca Barr. Milles and Orr, 1980, p. 798, pl. 2, figs. 4–5 (lower Cenomanian, DSDP Leg 53, Site 418B, Atlantic Ocean, Bermuda Rise).

Costellagerina libyca (Barr). Petters and others, 1983, p. 248 (no mention about directly studied material).

Hedbergella libyca Barr. Leckie, 1984, p. 598, pl. 11, figs. 5–9 (uppermost Albian-lowermost Cenomanian, DSDP Leg 79, Sites 545 and 547, Atlantic Ocean, offshore Morocco).

Costellagerina libyca (McNulty). Premoli Silva and Sliter, 1995, p. 30, pl. 1, figs. 8, 14, 19 (upper Albian-middle Cenomanian, Gubbio section, northern Italy).

Costellagerina libyca (Barr). Gale and others, 1996, p. 520 (upper Albian, Drôme, southeastern France).

non *Costellagerina libyca* (Barr). Bellier, 1998, p. 338, pl. 1, figs. 4–9 (ODP Leg 159, Site 962, Atlantic Ocean, Gulf of Guinea, offshore Ivory Coast).

Meridionalla costellata (Saint-Marc). El-Nakhal, 1999, p. 85 (no mention of studied material).

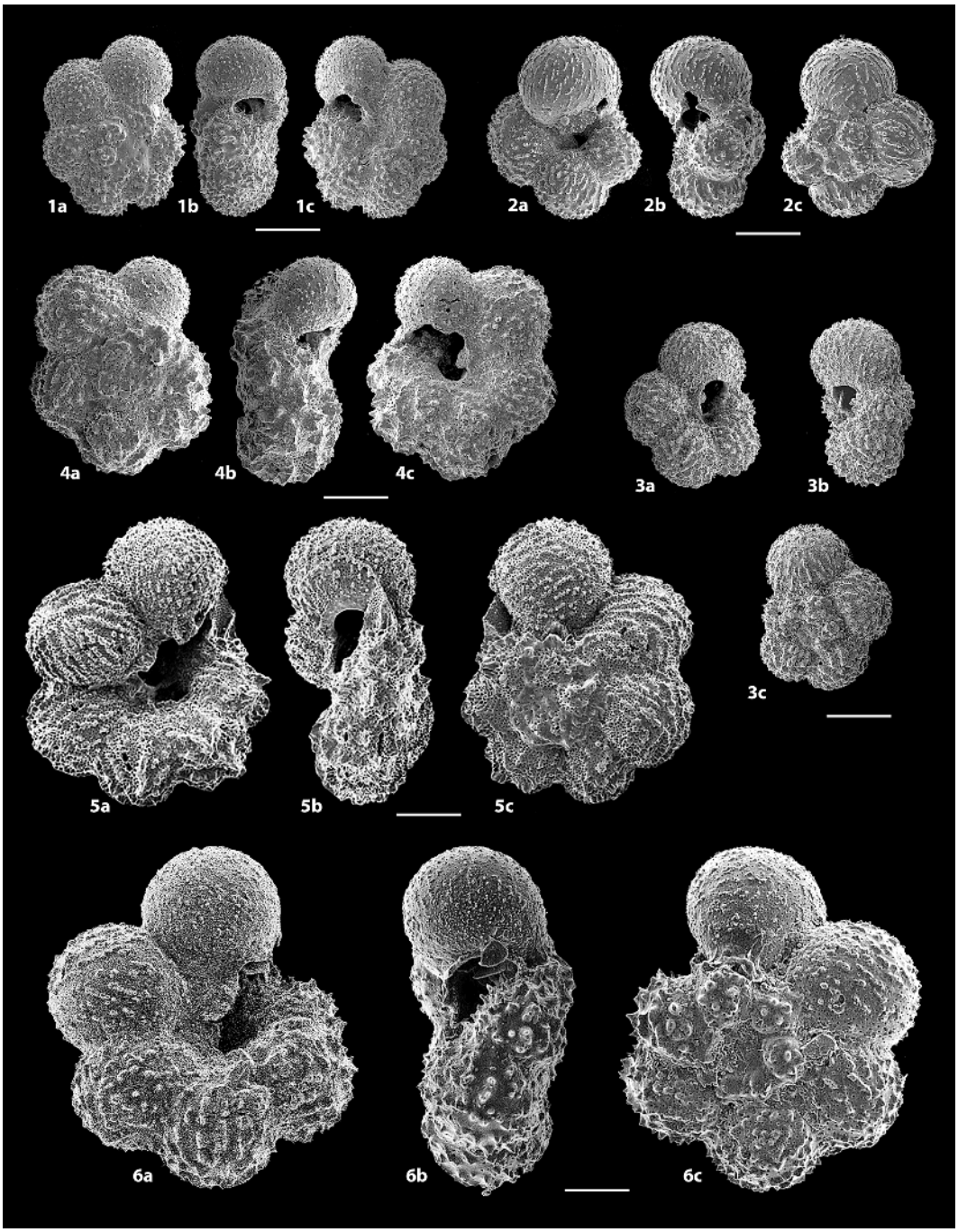

PLATE 1

1a–c. *Hedbergella praeLIBYCA* Petrizzo and Huber. Topotype from the lower Cenomanian (*Rotalipora globotruncanoides* Zone) of ODP Site 1050C-26R-5. 83–86 cm at Blake Nose (western North Atlantic). 2a–c. *Costellagerina pilula* (Belford). Hypotype from the upper Santonian Merchantville Formation (*Globotruncana arca* Zone) of ODP Leg 174AX, 504-17-504.20 m at Bass River site (New Jersey Coastal Plain). 3a–c. *Costellagerina pilula* (Belford). Topotype from the upper Santonian Toolonga Calcilutite of Western Australia (sample Huber). 4a–c. *Paracostellagerina libyca* (Barr). Hypotype from the lower Cenomanian (*Rotalipora globotruncanoides* Zone) of ODP Site 1050C-26R-5. 83–86 cm at Blake Nose (western North Atlantic). 5a–c. *Paracostellagerina libyca* (Barr). Hypotype from the lower Cenomanian (*Rotalipora globotruncanoides* Zone) of ODP Site 1050E-26R-4, 83–86 cm at Blake Nose (western North Atlantic). 6a–c. *Paracostellagerina libyca* (Barr). Hypotype from the late Albian (*Planomalina buxtorfi* Zone) of ODP Site 1052E-41R-2, 104–106 cm from Blake Nose (western North Atlantic).

Costellagerina libyca (Barr). Petrizzo and Huber, 2006, pl. 5, figs. 6a–c (ODP Leg 171B, Sites 1050C and 1052E, Atlantic Ocean, Blake Nose escarpment).

Description. Test low trochospiral, with ten to fourteen globular chambers arranged in 2 to 2 ½ whorls, 4 to 4 ½ chambers in the initial whorl; five to six, rarely seven, chambers in the final whorl with a variable rate of chamber size increase, from fast to slow, but the slower rate is most common; a faster increase in the chamber size is known only in the case of paratype IV of *Hedbergella costellata* figured by Saint-Marc (1973, pl. 2, fig. 3). Dorsal outline varies between lobate to strongly lobate. Sutures are distinct and depressed, straight and

radial on both the spiral and umbilical side. Periphery broadly rounded, without peripheral structures. Umbilicus medium-sized and shallow, its diameter generally comprising between 30 and 40% of the maximum test diameter. Main aperture is interiomarginal, extraumbilical-umbilical, bordered by a thin and narrow lip that extends into the umbilical area. Successive relict apertural lips may occur in the umbilical area as new chambers are added during ontogenetic development. Test ornamented with pustules, rugosities, and costellae arranged in distinct patterns on umbilical and spiral sides, resulting in asymmetric test ornamentation with a meridional arrangement on the umbilical side, and parallel to the periphery on the spiral side. This ornamentation can vary from being either incompletely developed, or completely absent on the earlier chambers.

Remarks. *Paracostellagerina libyca* differs from *Hedbergella praelibyca* in having a fully oriented pattern of the costellae and other ornamentation elements, namely meridional on the umbilical side and parallel to the periphery on the spiral side. By contrast, the latter species lacks orientation of these ornamentation elements (Petrizzo and Huber, 2006), having intermediate morphological features between *Hedbergella delrioensis* and *Paracostellagerina libyca*. *Paracostellagerina libyca* differs from *Rugoglobigerina rugosa* in the nature of periapertural and umbilical structures, which are very simple in the former (imperforate lip), and extremely complex in the latter (perforate tegillum), and in the different ornamentation orientation on the spiral side, which is parallel to the periphery. *Costellagerina pilula*, which ranges from the early Santonian-early Campanian, has meridional ornamentation that extends across both spiral and umbilical sides, in contrast to the asymmetrical pattern as known in *Paracostellagerina libyca*. The periapertural structures differ significantly in the two taxa, with an imperforate lip in *Paracostellagerina libyca* and a more or less developed porticus in *Costellagerina pilula*. Growth patterns in the earlier part of the test significantly differ between the two taxa, with 4.75 to 6 (average 5.32) chambers in the initial whorl of *Costellagerina pilula* (e.g., see Huber, 1994) and 4 to 4 ½ chambers in the initial whorl of *Paracostellagerina libyca*.

Isotopic Paleobiology. Oxygen and carbon isotope analyses of *P. libyca* indicate that it lived predominantly in the surface mixed layer of the open ocean (Huber and others, 2002).

Geographic distribution. Reported in tropical and subtropical sites in the Atlantic, Pacific, and Tethys Ocean.

Stratigraphic range. Latest Albian-earliest Cenomanian, from the upper *Rotalipora appenninica* Zone to the lowermost part of *R. globotruncanoides* Zone. Petrizzo and Huber (2006) record its first appearance datum (FAD) after the FADs of *Planomalina buxtorfi* and *Praeglobotruncana delrioensis*, and its last appearance datum after the LADs of *P. buxtorfi* and *Rotalipora globotruncanoides* at ODP Sites 1050C and 1052E. A similar range was reported by Leckie (1984).

CONCLUSIONS

Paracostellagerina nov. gen. is proposed for a hedbergellid species of latest Albian-earliest Cenomanian age with test ornamentation that is meridional on the umbilical side and parallel to the periphery on the spiral side. This genus is monospecific, including only *Paracostellagerina libyca* (Barr), 1972. It is the first taxon of the Cretaceous in which this asymmetric test ornamentation is developed, as the other three, namely *Abathomphalus intermedius*, *A. mayaroensis*, and *Rugotruncana circumnodifer*, occur only in Maastrichtian sediments. *Costellagerina* of the early Santonian-early Campanian, to which "*Hedbergella*" *libyca* has been assigned, presents fully-developed meridional test ornamentation on both sides of the test. *Costellagerina* is considered a monospecific genus, including only *Costellagerina pilula* (Belford), 1960. In addition, both taxa are separated stratigraphically with no known evolutionary intermediate forms occurring between the two. Thus, the two taxa are considered phylogenetically and taxonomically distinct.

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REFERENCES

Barr, F. T., 1972, Cretaceous biostratigraphy and planktonic foraminifera of Libya: Micropaleontology, v. 18, p. 1–46.

Belford, D. J., 1960, Upper Cretaceous foraminifera from the Toolonga calcilutite and Gingin chalk, Commonwealth of Australia: Bureau of Mineral Resources, Geology and Geophysics, Bulletin, v. 57, p. 1–198.

Bellier, J. P., 1998, Cretaceous planktonic foraminifers, eastern equatorial Atlantic, *in* Swanson, S. E., and Garman, P. M. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 159, p. 335–345.

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.

Brönnimann, P., 1952, Globigerinidae of the Upper Cretaceous (Cenomanian-Maestrichtian) of Trinidad, B.W.I.: Bulletins of American Paleontology, v. 34, p. 1–70.

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

Caron, M., 1978, Cretaceous planktonic foraminifers from DSDP Leg 40, southeastern Atlantic Ocean, *in* Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), Initial Reports of the Deep Sea Drilling Project, v. 40, p. 651–678.

Carsey, D. O., 1926, Foraminifera of the Cretaceous of Central Texas: University of Texas Bulletin, no. 2612, p. 1–56.

Douglas, R. G., 1969, Upper Cretaceous planktonic foraminifera in northern California Part 1-Systematics: Micropaleontology, v. 15, p. 151–209.

El-Nakhal, H. A., 1999, The relation between the Late Cretaceous foraminiferal genera *Meridionalla* El-Nakhal (1982) and *Costellagerina* Petters and others (1983): Journal of Foraminiferal Research, v. 29, p. 85.

———, 2002, Classification of the meridionally costellate Cretaceous planktonic foraminifera: Journal of Micropaleontology, v. 21, p. 1–8.

Gale, A. S., Kennedy, W. J., Burnett, J. A., Caron, M., and Kidd, B. E., 1996, The Late Albian to Early Cenomanian succession at Mont Risou near Rosans (Drôme, SE France): an integrated study (ammonites, inoceramids, planktonic foraminifera, nannofossils, oxygen and carbon isotopes): Cretaceous Research, v. 17, p. 515–606.

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., Shergold, J., Villeneuve, M., Wardlaw, B. R., Ali, J., Brinkhuis, H., Hilgen, F. J., Hooker, J., Horwath, R. J., Knoll, A. H., Laskar, J., Monechi, S., Plumb, K. A., Powell, J., Raffi, I., Röhl, U., Sadler, P., Sanfilippo, A., Schmitz, B., Shackleton, N. J., Shields, G. A., Strauss, H., Van Dam, J., Van Kolfschoten, T., Veizer, J., and Wilson, D., 2004, A Geologic Time Scale 2004: Cambridge University Press, 589 p.

Huber, B. T., 1994, Ontogenetic morphometrics of some Late Cretaceous trochospiral planktonic foraminifera from the Austral Realm: Smithsonian Contributions to Paleobiology, no. 77, p. 1–85.

———, Norris, R. D., and MacLeod, H. G., 2002, Deep-sea paleotemperature record of extreme warmth during the Cretaceous: Geology, v. 30, p. 123–126.

LECKIE, M. R., 1984, Mid-Cretaceous planktonic foraminiferal biostratigraphy off central Morocco, Deep Sea Drilling Project Leg 79, Sites 545 and 547, *in* Blakeslee, J. H. (ed.), Initial Reports of the Deep Sea Drilling Project, v. 79, p. 579–620.

LOEBLICH, JR., A. R., and TAPPAN, H., 1984, Suprageneric classification of the Foraminiferida (Protozoa): Micropaleontology, v. 30, p. 1–70.

———, and ——— , 1988, Foraminiferal Genera and their Classification: Van Nostrand Reinhold Company, New York, 970 p.

MCNULTY, C. L., 1979, Smaller Cretaceous foraminifers of Leg 43, Deep Sea Drilling Project, *in* Kaneps, A. (ed.), Initial Reports of the Deep Sea Drilling Project, v. 43, p. 487–505.

———, and BARR, F. T., 1979, Meridionally costellate hedbergellid foraminifers from the western Atlantic, Deep Sea Drilling Project, Leg 43, Site 386: Gulf Coast Association of Geological Societies, Transactions, v. 29, p. 302–305.

MILLES, G. A., and ORR, W. N., 1980, Planktonic foraminifers from the Bermuda Rise, Deep Sea Drilling Project Legs 51, 52, and 53, *in* Donelly, T., Francheteau, J., Bryan, W., Robinson, P., Flower, M., Salisbury, M., and others. (eds.), Initial Reports of the Deep Sea Drilling Project, v. 51, 52, and 53, Part 2, p. 791–813.

OLSSON, R. K., HEMLEBEN, C., BERGGREN, W. A., and HUBER, B. T., 1999, Atlas of Paleocene Planktonic Foraminifera: Smithsonian Contributions to Paleobiology, no. 85, p. 1–252.

PETRIZZO, M. R., and PREMOLI SILVA, I., 2000, Upper Cretaceous meridionally costellate hedbergellids; *Meridionalla* El-Nakhal, 1982 vs. the genus *Costellagerina* Petters, El-Nakhal and Cifelli, 1983: Journal of Foraminiferal Research, v. 30, p. 306–309.

———, and HUBER, B. T., 2006, Biostratigraphy and taxonomy of Late Albian planktonic foraminifera from Leg 171B (Western North Atlantic Ocean): Journal of Foraminiferal Research, v. 36, p. 166–190.

PETTERS, S. W., EL-NAKHAL, H. A., and CIFELLI, R., 1983, *Costellagerina*, a new Late Cretaceous globigerine foraminiferal genus: Journal of Foraminiferal Research, v. 13, p. 247–251.

PLUMMER, H. J., 1927, Foraminifera of the Midway Formation in Texas: University of Texas Bulletin, no. 2644, p. 1–206.

PREMOLI SILVA, I., and SLITER, V. W., 1995, Cretaceous planktonic foraminiferal biostratigraphy and evolutionary trends from the Bottaccione section, Gubbio, Italy: Palaeontographia Italica, v. 82, p. 1–89.

SAINT-MARC, P., 1973, Presence of *Hedbergella* à "costellae" dans le Cénomanien moyen du Liban: Journal of Foraminiferal Research, v. 3, p. 7–12.

STEINECK, P. L., and FLEISHER, R. L., 1978, Towards the classical evolutionary reclassification of Cenozoic Globigerinacea (Foraminiferida): Journal of Paleontology, v. 52, p. 618–635.

SUBBOTINA, N. N., 1959, Planktonic foraminifera, *in* Rauzer-Chernousova, D. M., and Fursenko, A. V. (eds.), Principles of Paleontology, Part I, Protozoa: Akademia Nauk SSSR, Moscow, 368 p. [in Russian]

WATKINS, D. K., and BERGEN, J. A., 2003, Late Albian adaptive radiation in the calcareous nannofossil genus *Eiffelithus*: Micropaleontology, v. 49, p. 231–252.

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