

TAXONOMIC RE-EVALUATION AND PHYLOGENY OF THE STELLATE PLANKTONIC FORAMINIFERAL GENUS *HASTIGERINOIDES* BRÖNNIMANN, 1952

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ABSTRACT

The Late Cretaceous (Coniacian-Santonian) planktonic foraminiferal genus *Hastigerinoides* is emended. A new species, *H. atlanticus* nov. sp., is proposed for the tests with one or rarely two last-formed chambers that are strongly radially elongate and distally tapering in the final whorl. *Hastigerinoides* consists of three phylogenetically related species: *H. clavata* (Brönnimann, 1952), *H. atlanticus* nov. sp., and *H. alexanderi* (Cushman, 1931). This genus evolved from *Globigerinelloides escheri*, a Coniacian-middle Campanian, globular- to suglobular-chambered species.

INTRODUCTION

The first Late Cretaceous planktonic foraminifera with a stellate shape resulting from elongated chambers in the final whorl were described by Cushman (1931) from the Eagleford Formation (*Hastigerinella moremani*) and Austin Chalk (*H. alexanderi* and *H. watersi*). These taxa were not subsequently reviewed for more than two decades. Brönnimann (1952, p. 52) proposed the genus *Hastigerinoides* to accommodate the taxa with strongly elongate, distally tapering chambers. This separation between *Hastigerinoides* and *Hastigerinella* was based entirely on the morphology of the chambers' distal terminations, which are tapering in the former and clubbed in the latter genus.

Bolli and others (1957, p. 24) recognized *Hastigerinoides* as valid based on features other than the presence of distally tapering, strongly elongate chambers, namely the planispiral coiling, the primary aperture in an equatorial position, and the presence of relict apertures in the umbilicus. These authors claimed the existence of specimens having both distally tapering and clubbed distal terminations, therefore conferring little taxonomic significance to this feature. Nonetheless, they did not figure such a specimen, nor did any other authors, before their study or afterwards. Such specimens were not observed during re-examination of their original material, which is deposited in the Cushman Collection and the Loeblich and Tappan Topotype Collection at the National Museum of Natural History, Washington, D.C.

A distinct genus, *Eohastigerinella*, was proposed by Morozova (1957, p. 1112) to accommodate tests with club-shaped distal edges on the last-formed chambers of the test, with *E. watersi* (Cushman, 1931) as the type species. This genus was considered invalid by Pessagno (1967), Masters (1977) and Caron (1985). *Eohastigerinella* regained prominence in Loeblich and Tappan's (1987) "Foraminiferal

Genera and Their Classification," where it was defined based on the presence of one to two clavate chambers in the last chambers of the final whorl. *Hastigerinoides* and *Eohastigerinella* were included within the Subfamily Eohastigerinellinae by Loeblich and Tappan (1984).

Careful re-examination of *Hastigerinoides alexanderi* showed that all specimens present strongly elongate chambers that taper distally. The coiling mode is more variable than that previously known, ranging from planispiral to very low trochospiral. A continuous series of phylogenetically related species is recognized, demonstrating that there is a phylogenetic relationship between the genera *Globigerinelloides* as ancestor and *Hastigerinoides* as descendant (Fig. 1), as suggested earlier by Pessagno (1967) and Masters (1977). Accordingly, the genus *Hastigerinoides* is emended to accommodate this lineage, which records the gradual transition between tests with chambers that are clavate and strongly elongate, and those that are distally tapering. The coiling is dominantly planispiral, with *H. alexanderi* being the only species in which some specimens have a very low trochospiral coil.

The geographic distributions of *Globigerinelloides escheri* and *Hastigerinoides* overlap in the Caribbean region, with occurrences on the Trinidad and Yucatan shelves (Fig. 2). All occurrences of the three species of *Hastigerinoides* (i.e., *H. clavata*, *H. atlanticus* and *H. alexanderi*) are restricted in the Western Hemisphere. The occurrences of *Hastigerinoides* from the United States Western Interior by Frerichs and others (1977), Frerichs (1979) and Frerichs and Dring (1981) should be referred to *Eohastigerinella* due to the presence of bulbous projections at the edge of the radially elongate chambers.

MATERIAL STUDIED

The holotype of *Hastigerinoides alexanderi* (Cushman, 1931) was examined in the Cushman Collection at the National Museum of Natural History (NMNH), Washington, D.C. (USNM 309309). Very well preserved topotypes, collected by A. R. Loeblich, Jr. from the Austin Chalk at Howe, Grayson County, Texas, were examined from the Loeblich and Tappan Topotype Collection (NMNH, USNM 473240). These specimens were compared with the holotype and topotypes of *Eohastigerinella watersi* (Cushman, 1931) deposited in the same collections of the NMNH (USNM 309326 and USNM 473243, respectively). Very well preserved hypotypes of *Globigerinelloides escheri* and *Hastigerinoides clavata* were examined from the Van Morkhoven Collection (NMNH).

Additional material was examined from the Santonian sediments of three DSDP sites, namely DSDP Sites 95 (Caribbean, Yucatan Shelf), 356 (western South Atlantic, São Paulo Plateau) and 357 (western South Atlantic, Rio Grande Rise). The samples examined are deposited in the

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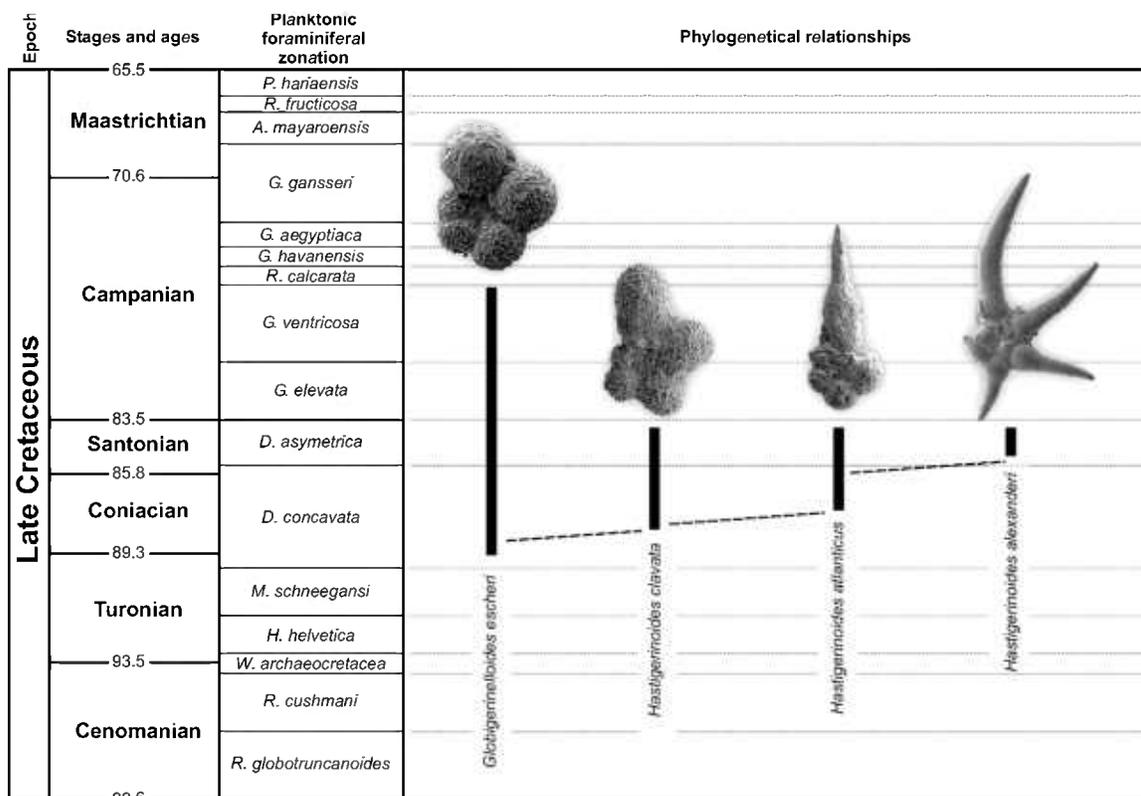


FIGURE 1. Stratigraphic distribution and phylogenetic relationships of the species of *Hastigerinoides* and their ancestor *Globigerinelloides escheri*. Planktonic foraminiferal zonation after Robaszynski and Caron (1995). Ages in Ma after Gradstein and others (2004).

Micropaleontological Reference Center Collection at the NMNH.

SYSTEMATIC DESCRIPTIONS

The classification of higher categories follows that of Loeblich and Tappan (1987). The genus *Globigerinelloides* Cushman and ten Dam, 1948 is not presented in detail, as it is included only to describe and figure *Globigerinelloides escheri*, the ancestor of the genus *Hastigerinoides*.

Order FORAMINIFERIDA Eichwald, 1830
Suborder GLOBIGERININA Delage and Hérouard, 1896
Superfamily PLANOMALINACEA Bolli, Loeblich and Tappan, 1957
Family GLOBIGERINELLOIDIDAE Longoria, 1974

Genus *Hastigerinoides* Brönnimann, 1952 emended
Type species: *Hastigerinella alexanderi* Cushman, 1931, p. 87.

Hastigerinella (*Hastigerinoides*) Brönnimann in Brönnimann, 1952, p. 52.

Hastigerinoides Brönnimann, emended in Bolli, Loeblich and Tappan, 1957, p. 24.

Hastigerinoides Brönnimann in Caron, 1985, p. 23.

Hastigerinoides Brönnimann in Loeblich and Tappan, 1987, p. 460.

Original description. "Test stellate, planispiral in the adult, possibly trochospiral in young stages. Chambers of adult subglobular to subglobular-elongate, broadly rounded at the base, gradually tapering into pointed outer ends. Aperture at base of end chamber, in equatorial plane" (Brönnimann, 1952, p. 52).

Emended description. Test planispiral to low trochospiral, biumbilicate. Chambers globular in the earlier stage and clavate to strongly

radially elongate, tapering distally in the adult portion of the test. Sutures are depressed, straight to slightly curved, radial. Aperture is equatorial, extending into the umbilical areas, and is in the shape of a medium-high to high arch. Relict apertures may be present in the umbilical areas. The aperture is bordered by a well-developed, thin lip. Scattered pustules are often present on the earlier chambers of the test. Test is calcitic, hyaline, finely perforate, rarely microperforate.

Remarks. *Hastigerinoides* differs from *Eohastigerinella* in (i) lacking bulbous projections at the chamber distal edge and (ii) being planispirally coiled except for some tests of the most evolved species of the genus, namely *H. alexanderi*. In contrast, the low trochospiral tests of *Eohastigerinella* indicate that it has a hedbergellid ancestor. Re-examination of topotype material from the Loeblich and Tappan Topotype Collection (NMNH) showed that many tests of *Eohastigerinella watersi* (Cushman, 1931) present a very low trochospiral coil. This is in contradiction with the definition of *Eohastigerinella* by Loeblich and Tappan (1987, p. 460), where this monospecific genus was described as planispiral. *Hastigerinoides* differs from *Globigerinelloides* in presenting radially elongate chambers, which can be clavate or tapering distally.

Species included.
Hastigerinoides alexanderi (Cushman), 1931, p. 87;
Hastigerinoides atlanticus nov. sp.;
Hastigerinoides clavata (Brönnimann), 1952, p. 49.

Stratigraphic range. Coniacian-Santonian (from the *Dicarinella concavata* Biozone throughout the *D. asymetrica* Biozone).

Geographic distribution. Western South Atlantic (Rio Grande Rise and São Paulo Plateau), United States (Texas, Wyoming) and Caribbean (Trinidad, Yucatan Shelf).

Hastigerinoides alexanderi (Cushman, 1931)
Pl. 1, figs. 1–4

Hastigerinella alexanderi Cushman in Cushman 1931, p. 87, pl. 11, figs. 6–9 (Upper Cretaceous, Austin Chalk, Texas, United States).

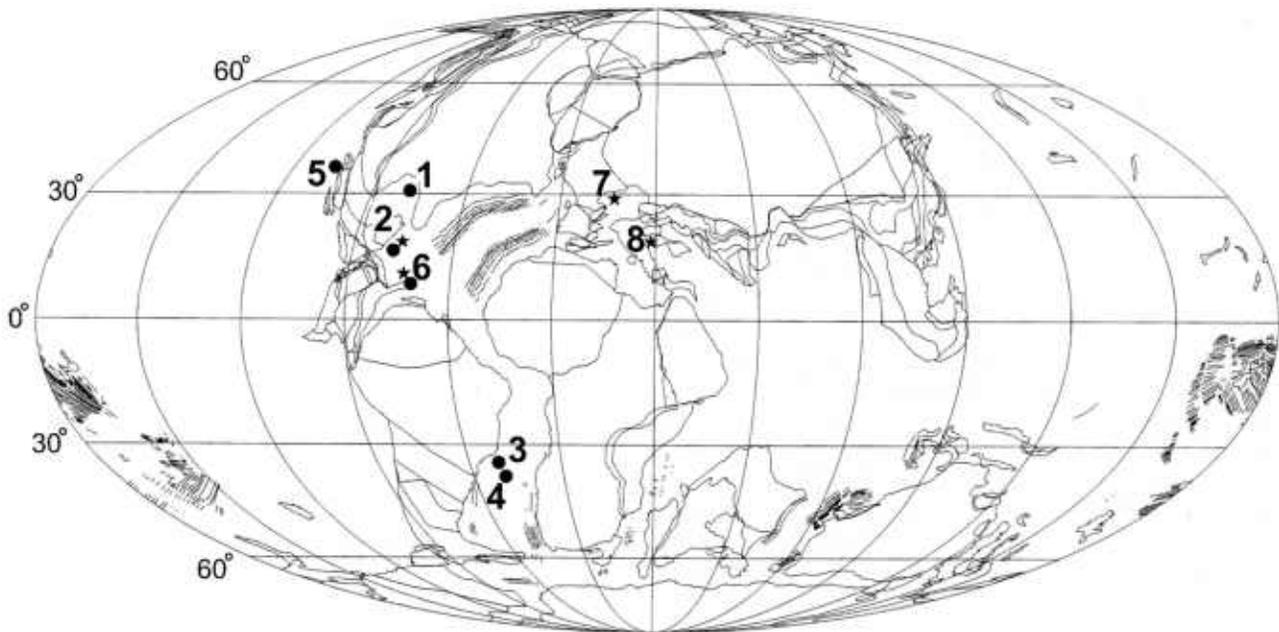


FIGURE 2. Geographic distribution of *Globigerinelloides escheri* (stars) and *Hastigerinoides* (circles): 1 Texas, 2 Yucatan Shelf, 3 São Paulo Plateau, 4 Rio Grande Rise, 5 northern California, 6 Trinidad, 7 Switzerland, and 8 Black Sea offshore. Note that *Hastigerinoides* occurs only in the Western Hemisphere. Base map at 100 Ma after Hay and others (1999).

Hastigerinella alexanderi Cushman in Cushman, 1946, p. 148, pl. 61, figs. 4–7 (Upper Cretaceous, Gulf Coastal Plain, United States).

Hastigerinella (Hastigerinoides) alexanderi Cushman in Brönnimann, 1952, p. 53, text fig. 28:a–m (Turonian–Senonian, Trinidad, Caribbean).

Hastigerinoides alexanderi (Cushman) in Bolli and others, 1957, pl. 1, figs. 7–10 (Austin Chalk, Texas, United States).

Hastigerinoides alexanderi (Cushman) in Pessagno, 1967, p. 273, pl. 60, fig. 6 (Lower Santonian, Gulf Coastal Plain, United States).

Hastigerinoides alexanderi (Cushman) in Masters, 1977, p. 416, pl. 12, figs. 6–7 only (Upper Cretaceous, Austin Chalk, Texas, United States).

Hastigerinoides alexanderi (Cushman) in Caron, 1985, p. 57, fig. 35:14–15 (Upper Cretaceous, Austin Chalk, Texas, United States).

Emended description. Test planispiral or, more rarely, very low trochospiral. Earlier chambers are globular, the last three to five are radially very elongate, tapering, resembling tubulospines; five to six chambers in the last whorl. Sutures are distinct, depressed, straight or slightly curved and radial on both sides of the test. Main aperture is equatorial to sub-equatorial in position, extending into the umbilicus, in the shape of a medium-high to high arch and bordered by a wide lip. Relict apertures can be present in the umbilical areas. Pustules are present only on the earlier chambers of the last whorl; the last-formed chambers are smooth. Test wall calcitic, hyaline, finely perforate; pore diameter in adult specimens is between 1.6 and 1.8 μm .

Remarks. The original description of Cushman (1931, p. 87) is herein emended to accommodate the test ultrastructure and porosity features. *Hastigerinoides alexanderi* differs from *Eohastigerinella watersi* mainly in (i) having a dominantly planispiral coil and (ii) lacking bulbous projections at the top of the radially elongate chambers. This species differs from *H. atlanticus* in having much more elongate chambers in the last whorl (three to five) rather than one, maximum two, and occasionally presenting a low trochospiral coil.

Stratigraphic range. Upper Santonian (*Dicarinella asymetrica* Biozone).

Geographic distribution. Species restricted (Fig. 2) to the western South Atlantic (Rio Grande Rise and São Paulo Plateau), southern United States (Texas) and Caribbean (Trinidad).

Hastigerinoides atlanticus nov. sp.

Pl. 1, figs. 5–7; Pl. 2, figs. 1–3

Hastigerinoides alexanderi (Cushman) in Douglas, 1969, p. 162, pl. 6, fig. 6 (Funks Formation, northern California, western United States).

Holotype. Specimen deposited at the NMNH (USNM 584399).

Dimensions of the holotype. Maximum test diameter: $D_{\text{max}} = 0.359$ mm; maximum diameter of the globular-chambered portion: $D_{\text{maxPL}} = 0.145$ mm; thickness: $T = 0.076$ mm; $D_{\text{maxPL}} / D_{\text{max}} = 0.401$; $T / D_{\text{max}} = 0.212$.

Type location. DSDP Leg 39, Site 356 (São Paulo Plateau); coordinates $28^{\circ}17.220'$ S and $41^{\circ}5.280'$ W.

Type level. Upper Santonian (*Dicarinella asymetrica* Biozone), DSDP Sample 39-356-37-5, 102–106 cm.

Paratypes. Five specimens deposited at the NMNH (USNM 584400).

Etymology. The name of the species comes from that of the Atlantic Ocean where the type locality is situated.

Material. Over one hundred specimens.

Diagnosis. Planispiral throughout with the last-formed one or two chambers radially elongate and tapering distally; planispirally coiled throughout ontogeny.

Description. Test planispiral, biumbilicate, with strongly lobate to stellate outline. Chambers globular to subglobular in the earlier portion of the test; the ultimate chamber or, rarely, the ultimate and penultimate chambers are conical and radially elongate, $4\frac{1}{2}$ to $5\frac{1}{2}$ chambers in the final whorl, increasing slowly in size in the earlier part of the test and at a high rate with the development of the radially elongate ones. Sutures are straight, depressed and radial on both sides of the test. The primary aperture is a medium-high arch that is equatorial in position, symmetrically extending into the umbilicus and bordered by a lip. Relict apertures can be present in the umbilical areas. Scattered pustules are present on the earlier chambers of the test; the radially elongate chambers are commonly smooth. Test wall calcitic, hyaline, finely perforate; pore diameter is in the range of 1.0 to 1.8 μm .

Remarks. *Hastigerinoides atlanticus* nov. sp. differs from *H. clavata* in having well-developed conical, radially elongate last-formed chambers. See also remarks under *Hastigerinoides alexanderi*.

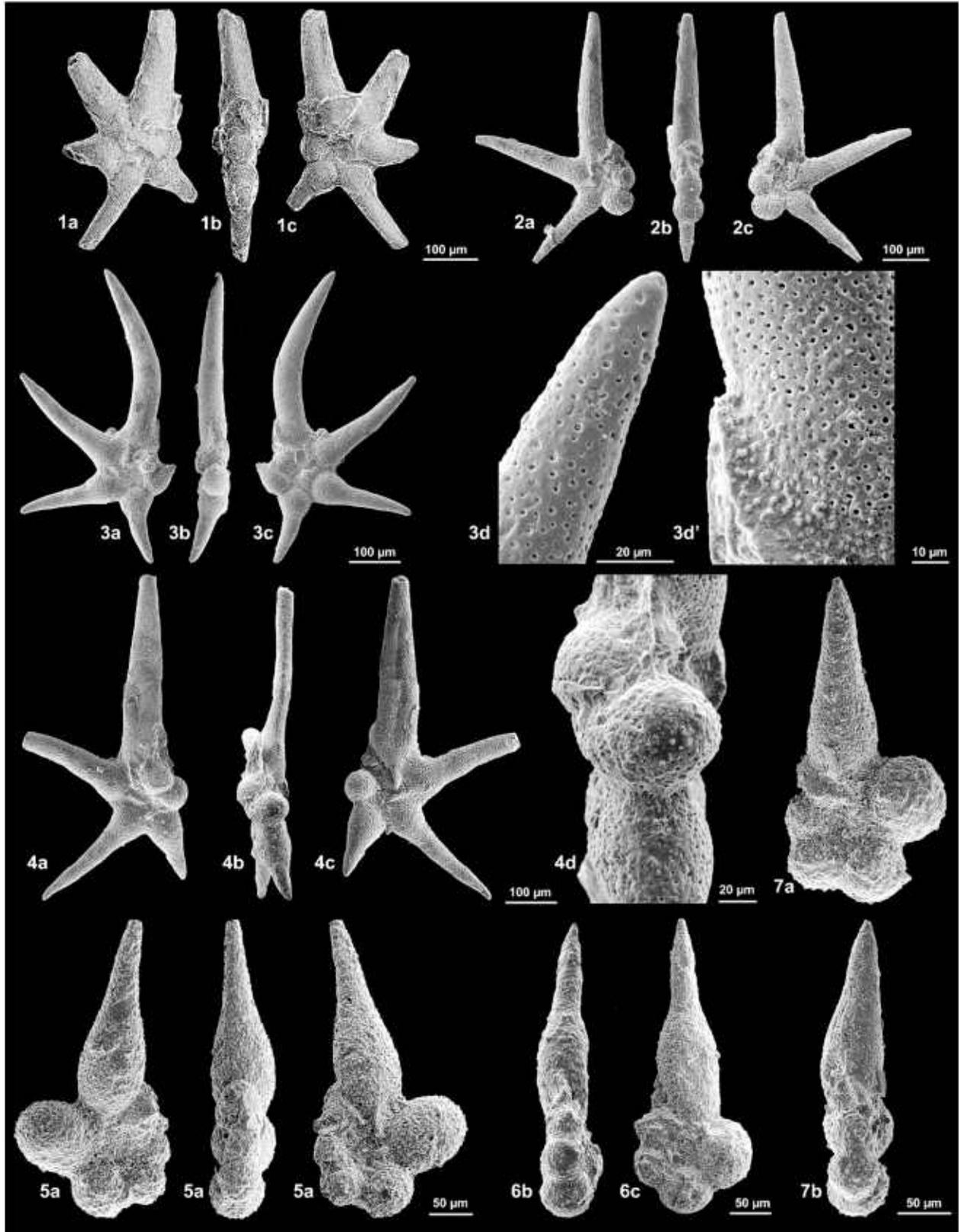


PLATE 1

1 Scanning electron micrographs of the holotype of *Hastigerinoides alexanderi* originally figured by Cushman (1931, pl. 11, fig. 6); specimen from the Austin Chalk (Santonian) of Howe, Grayson County, Texas (USNM 309309). 2–4 Topotypes of *Hastigerinoides alexanderi* from the Lower Austin Chalk, Howe, Grayson County, Texas. Specimens from the Loeblich and Tappan Topotype Collection (USNM 473240). Note the very low trochospiral coiling of the specimen in figures 4a–d. 5–7 *Hastigerinoides atlanticus* nov. sp. from the Santonian of DSDP Leg 39, Site 356 (Sao Paulo Plateau); 5 specimen from Sample 39-356-39-5, 94–108 cm (*Dicarinella concavata* Biozone); 6a–c holotype (USNM 584389), specimen from Sample 39-356-37-5, 102–106 cm (*Dicarinella asymetrica* Biozone); 7 specimen from Sample 39-356-37-5, 15–29 cm (*Dicarinella asymetrica* Biozone).

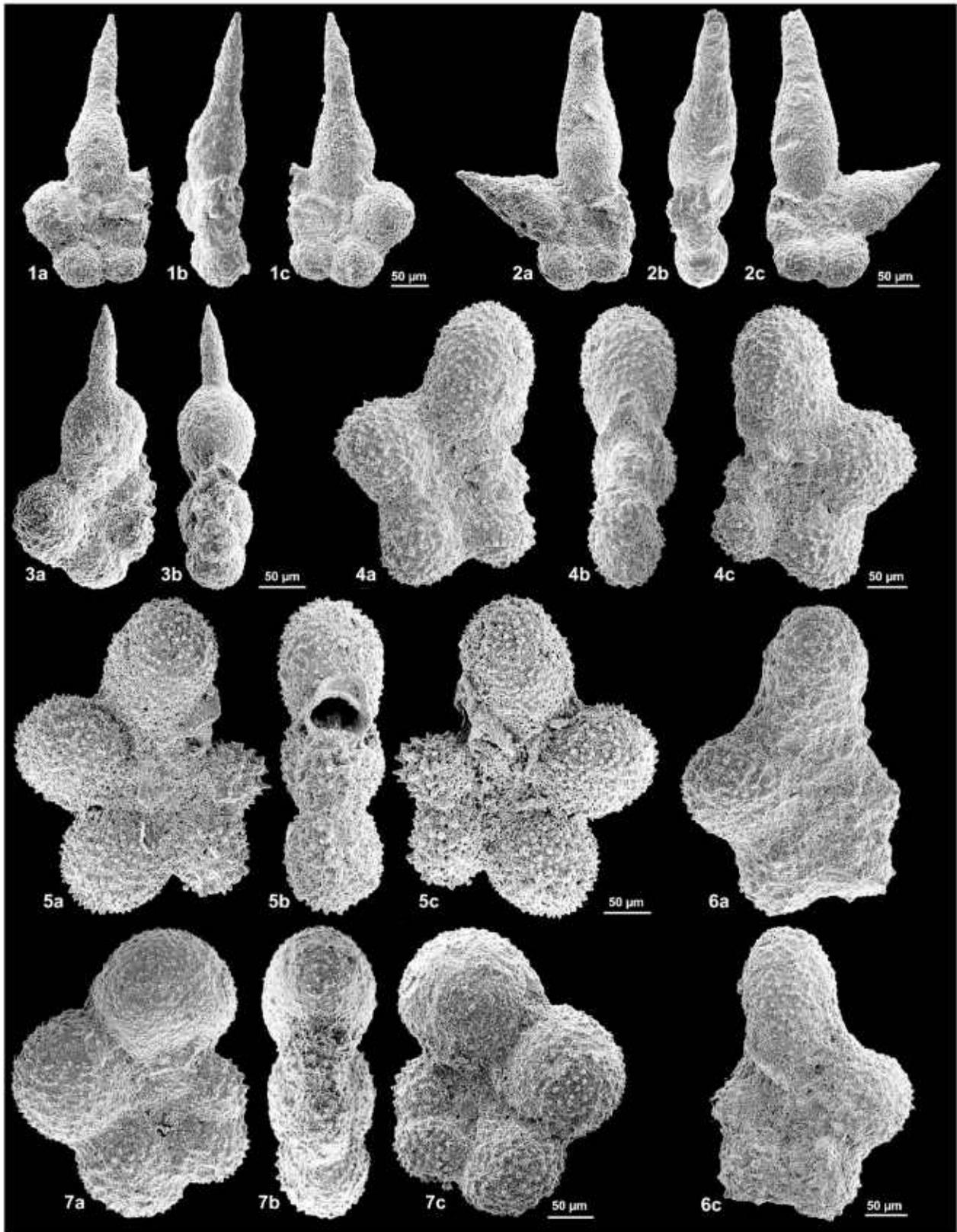


PLATE 2

1–3 *Hastigerinoides atlanticus* nov. sp. from the Santonian (*Dicarinella asymetrica* Biozone) from DSDP Leg 39, Site 356 (Sao Paolo Plateau): 1a–c paratype (USNM 584390); 1, 3 specimens from Sample 39-356-37-5, 102–106 cm; 2 specimen from Sample 39-356-37-1, 82–96 cm. 4–6 *Hastigerinoides clavata* (Brönnimann, 1952); 4, 6 hypotypes from the lower Santonian (*Dicarinella concavata* Biozone) of DSDP Leg 39, Site 356 (Sao Paolo Plateau), Sample 39-356-39-5, 94–108 cm; 5 hypotype from the upper Santonian (*Dicarinella asymetrica* Biozone) of the Gulf of Mexico from a well for which no precise location was given (Van Morkhoven Collection, NMNH, Washington, D.C.). 7 *Globigerinelloides escheri* (Kaufmann, 1865) from the upper Santonian (*Dicarinella asymetrica* Biozone) of DSDP Leg 39, Site 356 (Sao Paolo Plateau), Sample 39-356-37-5, 102–106 cm.

Stratigraphic range. Santonian (from the upper part of the *Dicarinella concavata* Biozone to the *Dicarinella asymetrica* Biozone).

Geographic distribution. Western Atlantic (São Paulo Plateau, Rio Grande Rise) and western United States (northern California).

Hastigerinoides clavata (Brönnimann, 1952)

Pl. 2, figs. 4–6

Globigerinella escheri clavata Brönnimann in Brönnimann 1952, p. 49, pl. 1, figs. 12–13, text-figs. 24a–f, 25a–o, 26a–b (Turonian-Senonian, Trinidad, Caribbean).

Hastigerinoides subdigitata (Carman) in Caron, 1985, p. 57, fig. 35:19 only (early Santonian, Texas, United States).

Description. Test completely planispiral, biumbilicate. Chambers increase moderately in size as added, 4 ½ to 5 ½ chambers in the final whorl, earlier chambers globular and last-formed one to three chambers clavate. Sutures are straight, depressed and radial. Periphery broadly rounded without peripheral structures. Primary aperture is a medium-high to high arch that is equatorial in position and extends into the umbilici, and bordered by a lip. Relict apertures can be present in the umbilical areas. Scattered pustules commonly present on all the chambers of the test, more numerous on the earlier ones due to the successive addition of calcite layers. Test wall calcitic, hyaline, finely perforate; pore diameter ranges between 0.9 and 1.5 µm.

Remarks. *Hastigerinoides clavata* differs from its ancestor, *Globigerinelloides escheri* (Kaufmann, 1865) by (i) the clavate shape of the last-formed one to three chambers and (ii) medium-high to high arched, rather than low arched, primary aperture. This species differs from other species of *Hastigerinoides* in not having distally tapering, last-formed chambers. Development of clavate chambers, increase in aperture height and increase in pore size initiate the *Hastigerinoides* lineage.

Stratigraphic range. Coniacian-Santonian (from the *Dicarinella concavata* Biozone to the *Dicarinella asymetrica* Biozone).

Geographic distribution. Western Atlantic (São Paulo Plateau, Rio Grande Rise), United States (Texas, Wyoming) and Caribbean (Trinidad, Yucatan Shelf).

Genus *Globigerinelloides* Cushman and ten Dam, 1948

Type species: *Globigerinelloides algeriana* Cushman and ten Dam, 1948, p. 43.

Globigerinelloides escheri (Kaufmann, 1865)

Pl. 2, fig. 7

Nonionina escheri Kaufmann in Heer, 1865, p. 198, text-fig. 1102 (Upper Cretaceous, Switzerland).

Globigerinella escheri escheri (Kaufmann) in Brönnimann, 1952, text-figs. 22a–q, 23a–r (Upper Cretaceous, Trinidad).

Globigerinelloides escheri (Kaufmann) in Georgescu, 1996, p. 309, pl. 1, fig. 3 (late Santonian-Campanian, western Black Sea offshore).

Description. Test planispirally coiled, biumbilicate, with 4 ½ to 6 globular to subglobular chambers in the final whorl; chambers increase slowly in size as added. Sutures are straight, depressed and radial. Periphery broadly rounded, without peripheral structures. Primary aperture is a low arch, equatorial in position, extending into the umbilical areas. Relict apertures may be present in the umbilici. Scattered pustules are present on all the chambers of the test. Test wall calcitic, hyaline, microporulate to finely perforate; pore diameters are in the range of 0.8 to 1.3 µm.

Remarks. *Globigerinelloides escheri* differs from *Hastigerinoides clavata* in having globular to subglobular chambers throughout, low-arched rather than a medium- to high-arched primary aperture, and smaller pore size.

Stratigraphic range. Coniacian-middle Campanian (from the *Dicarinella concavata* Biozone throughout the *Globotruncana ventricosa* Biozone).

Geographic distribution. Tethyan Realm (Switzerland, western Black Sea offshore), western Atlantic (São Paulo Plateau, Rio Grande Rise) and Caribbean (Trinidad).

CONCLUSIONS

The Late Cretaceous (Coniacian-Santonian) planktonic foraminiferal genus *Hastigerinoides* (Brönnimann, 1952) is revised. This genus is emended to accommodate a lineage consisting of three species: *H. clavata* (Brönnimann, 1952), *H. atlanticus* nov. sp. and *H. alexanderi* (Cushman, 1931). Although all of these species present radially elongate chambers, the chamber shapes vary significantly. The radially elongate chambers are clavate in *H. clavata* but distally tapering (resembling tubulospines) in *H. atlanticus* and *H. alexanderi*. Test coiling is planispiral in most of the lineage, but *H. alexanderi* may have a very low trochospiral test.

Globigerinelloides escheri (Kaufmann, 1865) of the Coniacian-middle Campanian appears to be the ancestor of *Hastigerinoides*. The former has a regional distribution in both Europe and the Caribbean, whereas *Hastigerinoides* is restricted to the Western Hemisphere.

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