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EARLY EVOLUTION OF THE CRETACEOUS SERIAL PLANKTIC FORAMINIFERA (LATE ALBIAN–CENOMANIAN)

MARIUS D. GEORGESCU[1,3] AND BRIAN T. HUBER[2]

ABSTRACT

The classification of the late Albian–Cenomanian biserial planktic foraminiferal family Heterohelicidae Cushman, 1927, is reevaluated. This group underwent a period of relatively slow evolutionary change during the late Albian–early Cenomanian followed by rapid evolution in the middle Cenomanian. Three new heterohelicid genera and species in the late Albian–early Turonian are described: *Protoheterohelix obscura*, *Planoheterohelix postmoremani*, and *Globoheterohelix paraglobulosa*. Two reassigned species are also emended: *Protoheterohelix washitensis* (Tappan) and *Planoheterohelix moremani* (Cushman). Reassessment of the taxonomic significance of morphological features of the heterohelicid test leads to the conclusion that the most important characters in their taxonomy are test architecture, symmetry/asymmetry of the periapertural structures, nature of periapertural structures, relative size difference of the proloculus and second chamber, test ornamentation, and pore size. Most heterohelicid taxa of the late Albian–Cenomanian display microperforate test walls. *Heterohelix* Ehrenberg, 1843, which evolved in the early Turonian, is a distinct lineage.

INTRODUCTION

A detailed systematic study of the biserial planktic foraminifera from the late Albian–early Turonian reveals that the group is more diverse than previously thought. The small sizes of heterohelicid tests in this time interval prevented detailed morphological observations with a stereomicroscope. Accordingly, the scanning electron microscope (SEM) played a crucial role in reevaluating the taxonomic significance of a variety of heterohelicid features. In addition, observation of morphologic changes in stratigraphic context permits recognition of distinct lineages that, in turn, might allow phylogenetic classification at species and genus levels.

It is well established that biserial planktic foraminifera initially evolved during the late Albian and that this group had its first adaptive radiation in the late Albian–Cenomanian (Tappan, 1940; Brown, 1969; Masters, 1977). However, diversification proceeded at varying rates, from relatively slow in the late Albian–early Cenomanian to a first climax in the middle–late Cenomanian. Relatively high rates of diversification also occurred in the Turonian-Maastrichtian.

Phylogenetic relationships inferred from stratophenetic observations provide the most useful ordering principle in late Albian–Cenomanian heterohelicid taxonomy. These are documented by comparing stratigraphically ordered electron micrographs. As a result of this study, six species belonging to four genera are recognized, of which three new species and three new genera are described.

[1] Geoscience, University of Calgary, 2500 University Drive N. W., Calgary, Alberta T2N 1N4, Canada

[2] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave., Washington D.C., 20013-7012, USA

[3] Correspondence author. E-mail: dgeorge@ucalgary.ca

HISTORY OF THE HETEROHELICID GENUS CONCEPT

The first genus of Cretaceous heterohelicids, *Heterohelix*, was described by Ehrenberg (1843, p. 429) as having a test characterized by an early planispiral coil and a biserial adult stage in which the last chambers have lateral projections. *Heterohelix* was originally described for a single species, *Textilaria americana* (Ehrenberg, 1843, p. 366, 398, 429). Ehrenberg confused matters in 1844 by describing a new genus and species from the Cretaceous of Mississippi (USA), *Spiroplecta americana*, which also has an early planispiral coil and a biserial adult stage. His succinct description makes no mention of *Heterohelix*. Ehrenberg's revision of heterohelicid taxonomy in 1854 resulted in even more confusion because he conferred no taxonomic significance to adult chamber shape. Consequently, he grouped under *Spiroplecta americana* specimens with a planispiral stage consisting of proloculus followed by five chambers and biserial globular chambers in the adult stage (Ehrenberg, 1854, pl. 32, group 2, fig. 25), as well as specimens with a planispiral stage consisting of a proloculus and two chambers, and chamber projections at the terminal end of the adult biserial stage (Ehrenberg, 1854, pl. 32, group 1, figs. 13–14). It is obvious from the text and figuration that Ehrenberg considered *Heterohelix* a synonym of *Spiroplecta* and grouped together the tests with early planispiral coil irrespective of the number of chambers and adult biserial stage and irrespective of the shape of the final chamber(s).

The taxonomic framework derived by Ehrenberg (1843, 1844, 1854) was poorly understood by subsequent researchers. For example, Reuss (1845, 1860) continued to use the name *Textilaria* Ehrenberg, 1839 (junior synonym of *Textularia* Defrance, 1824), to which Ehrenberg had assigned the first heterohelicid species. Cushman (1927, 1928) suggested that *Heterohelix* should be used instead of *Spiroplecta* because it was described earlier. The *Heterohelix-Spiroplecta* controversy was temporarily resolved when Cushman (1927, 1928) concluded that *Spiroplecta* is a junior synonym of *Heterohelix* (e.g., Loeblich, 1951; Loeblich and Tappan, 1964; Pessagno, 1967; Brown, 1969; Masters, 1977; and Frerichs and Gaskill, 1978).

Early heterohelicid taxonomy was refined with the description of the genus *Guembelina* Egger, 1902. Egger noted that Ehrenberg's heterohelicid taxonomy is imprecise for those species without an early planispiral coil, so he proposed *Guembelina* (type species *Textilaria globulosa* Ehrenberg, 1840) to accommodate them. Egger did not consider chamber arrangement in the adult stage to be of importance at the genus level and, as a result, *Guembelina* was defined to include both tests that are wholly biserial

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and tests that are biserial with chamber proliferation in the adult stage. He also hypothesized that the presence/absence of the early planispiral coil was the expression of alternating generations. Cushman (1927) emended *Guembelina*, considering that a planispiral coil can be present at least in microspheric tests. *Guembelina* was accepted as a valid genus for more than five decades (Egger, 1902; Albritton, 1937; Cushman, 1927; Moreman, 1927; Carman, 1929; White, 1929; Morrow, 1934; Loetterle, 1937; Tappan, 1940, 1943; Kikoïne, 1948; Loeblich, 1951; Sigal, 1952; Hamilton, 1953; LeRoy, 1953; Said and Kenawy, 1956).

Montanaro Gallitelli (1957, p. 137) considered *Guembelina* a junior synonym of *Heterohelix* by including specimens with and without early coiled stage within the same species (e.g., *G. globulosa*, *G. globocarinata*, *G. carinata*, *G. planata*). The presence/absence of the early planispiral stage in the heterohelicid species was not considered in stratigraphic context by Montanaro Gallitelli. The validity of *Guembelina* was further rejected by Loeblich and Tappan (1961), who showed that the name was preoccupied by *Guembelina* Kuntz, 1895, which had been applied to some chitinous Carboniferous microfossils. As a result, all heterohelicid species with a wholly biserial chamber arrangement with or without a planispiral coil were included in *Heterohelix*. *Heterohelix* was further used to include all Cretaceous species with a biserial chamber arrangement at least in the adult stage, depressed sutures, and globular to subglobular chambers (Olsson, 1960; Pessagno, 1967; Brown, 1969; Masters, 1977; Weiss, 1983; Nederbragt, 1989, 1991; Huber, 1990; Georgescu, 1995, 2000, 2006; Nederbragt and others, 1998; Huber and others, 1999).

Masters (1980) provided a major contribution to the taxonomy of this group when he re-examined Ehrenberg's material at the Humboldt Museum in Berlin and redescribed three of Ehrenberg's species that have biserial chambers arrangement at least in the adult stage. All of them were included in *Heterohelix*, namely *H. americana*, *H. globulosa*, and *H. striata*. *Heterohelix americana* is the only species with an early planispiral coil and lateral tubulospine-like projections, which Masters (1980) described as laterally projecting short spines. Subsequent reports of wholly biserially tests of *H. americana* demonstrated that the early planispiral coil consisting of few chambers (proloculus plus two chambers) occurs only occasionally in this species (Frerichs and Gaskill, 1978; de Klasz and others, 1995; this study).

Four heterohelicid genera other than *Heterohelix* have completely biserial tests and were defined according to a small number of morphological features that were considered taxonomically significant: *Pseudotextularia* Rzehak, 1891 (Turonian–Maastrichtian) consists of species with tests formed by chambers that are deeper than wide, and which rarely show multiserial chamber growth in the adult stage; *Pseudoguembelina* Brönnimann and Brown, 1953 (Turonian–Maastrichtian) includes wholly biserial tests with supplementary apertures on the lateral sides of the test; *Sigalia* Reiss, 1957 (Santonian) includes tests with raised sutures and are completely biserial or have an adult multiserial stage; *Laeviheterohelix* Nederbragt, 1991 (Turonian–Maastrichtian) was defined to include biserial tests with a smooth test surface or with pore mounds (stratigraphic ranges after Loeblich and Tappan, 1987 and Nederbragt, 1991). These genera are considered valid by the vast majority of specialists in the field. They are typological units, defined without taking into consideration the iterative pattern of the evolution process.

The SEM and stratophenetic observations discussed above reveal that some morphological structures are not further developed within a lineage, such as the secondary supplementary apertures in *Braunella brauni* Georgescu, 2007 or chamber extensions that attach to the previous chamber in the row and leave no supplementary apertures, as in *Huberella huberi* Georgescu, 2007. The occurrence of chambers with tubulospine-like lateral projections in heterohelicids indicates the terminal stage of this lineage because it is not found in the earlier stage of any other heterohelicid species. Thus, *Heterohelix americana* is part of a distinct lineage originating from a generalized group of the heterohelicid stock, and the use of the generic name *Heterohelix* should be restricted to this specialized taxon.

Heterohelicid Species Previously Described from the Late Albian and the Cenomanian

Despite the fact that they have been reported for approximately 70 years from upper Albian to Cenomanian sediments, there are few detailed morphological studies of the earliest representatives of the biserial planktic foraminifera. Three heterohelicid species were described from the upper Albian and Cenomanian strata: *Guembelina moremani* Cushman, 1938 from the lower part of the Eagle Ford Shale (Cenomanian) of Texas (USA), *Guembelina washitensis* Tappan, 1940 from the lower Cenomanian part of the Grayson Formation of Texas and Oklahoma (USA), and *Heterohelix olssoni* Georgescu, 2000 from the middle Cenomanian Tomis Formation of the western Black Sea off Romania. Their generic assignments will be discussed in the subsequent sections of this paper.

The validity of *Heterohelix washitensis* was the subject of some debate, as it was considered a junior synonym of *H. moremani* by Pessagno (1967, p. 260). This point of view, however, was not accepted by Brown (1969, p. 35) who considered *H. moremani* and *H. washitensis* to represent distinct taxa. Brown (1969) also postulated the existence of a possible phylogenetic relationship between the two species, with H. washitensis being the ancestor and *H. moremani* its descendant. Nonetheless, the point of view of Pessagno (1967) prevailed (see Masters, 1977, and Nederbragt, 1991). *Heterohelix olssoni* is characterized by a large proloculus and smooth to discretely striate surface. It has not been reported outside the western Black Sea region. Additional data on the Cenomanian heterohelicids of Eastern Europe are necessary in order to clarify the phylogenetic relationships of this species.

New Morphological Structures of the Earlier Heterohelicid Tests

The members of the Family Heterohelicidae Cushman, 1927 were traditionally regarded as having biserially arranged chambers at least in the early stage and displaying symmetrical tests and periapertural structures as seen in

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edge view. This study shows that test and periapertural structure symmetries were achieved during the course of evolution and were not present in the earliest representatives of the group. Such observation accuracy was enabled by SEM examination of the late Albian–Cenomanian heterohelicid tests.

The heterohelicids of the late Albian–early Cenomanian display asymmetrical tests or periapertural structures that Georgescu (2009) considered as vestiges of a benthic ancestry. This group later shows a gradual development of symmetrical tests, as seen in edge view (Fig. 1). This trend is paralleled by changes in the periapertural structures, namely the loss of the original rim and ridge and the development of flanges (Fig. 1: B2–B3, C2–C3). The earliest heterohelicids that display an aperture bordered by flanges also show that these structures are asymmetrically developed (Fig. 1: B2–B3).

Heterohelicid Ornamentation and Porosity and Their Role in Group Taxonomy

Early observations made on the Upper Cretaceous heterohelicids of Texas (USA) led Thomas (1927) and Thomas and Rice (1927) to conclude that the members of the group from the Cenomanian and Turonian display smooth test surface and only those from the higher stratigraphic levels of the Cretaceous have costae. Brown (1969) mentioned the existence of faint costae in the Turonian heterohelicids, noting that they are hardly visible at low magnification when viewed with a stereomicroscope. Differences in ornamentation among certain Cretaceous serial planktic foraminifera were also reported by Glaessner (1936) and Cushman (1946), the latter having used it to recognize the phylogenetic relationship between various species (e.g., *Pseudotextularia plummerae* Loetterle, 1937–*P. carseyae* Plummer, 1931).

Detailed SEM observations revealed transitions between distinct test ornamentation patterns in certain lineages of Cretaceous serial planktic foraminifera. Change in ornamentation pattern in a lineage was demonstrated for *Braunella* Georgescu, 2007 (i.e., from costate to incipiently reticulate) of the late Campanian–Maastrichtian (Georgescu, 2007a), *Hendersonites* Georgescu and Abramovich, 2008 (i.e., increasing costae thickness in the central part) of the late Santonian–Campanian (Georgescu and Abramovich, 2008, 2009), and *Gublerina* Kïkoine, 1948 and *Praegublerina* Georgescu, Saupe and Huber, 2009 (i.e., ornamentation concentration over the chamber and development of an incipiently reticulate network, respectively) of the late Campanian–Maastrichtian (Georgescu and others, 2009). Ornamentation displays little variability in other lineages, such as the Turonian *Huberella* Georgescu, 2007 (see Georgescu, 2007b).

Two types of test surface, smooth and costate, are recognized in late Albian–Cenomanian heterohelicids. However, the taxonomic importance and treatment of test ornamentation varies among workers. Some consider ornamentation as a taxonomically useful feature only if it is consistent within the species (Eicher and Worstell, 1970a, 1970b; Caron and others, 2006). In contrast, smooth and finely costate tests have been included in the same species by others, therefore conferring no taxonomic significance to test ornamentation (Nederbragt, 1991; Nederbragt and others, 1998). Different stratigraphic ranges of the tests with and without ornamentation, however, suggest that the latter approach is unjustified.

The earliest planktics with biserial chamber arrangement are smooth (Fig. 2:1), as were their presumed ancestor in the genus *Praeplanctonia* Georgescu, 2009. The first tests with a costate surface are known from the upper part of the *Rotalipora cushmani* Biozone in the upper Cenomanian. Development of costae was apparently a very successful adaptation, as smooth tests are relatively rare above the Cenomanian/Turonian boundary, whereas costate tests are often abundant.

There are two types of costae in late Cenomanian–early Turonian heterohelicids. One type, herein referred to as granular costae, consists of aligned, rather than fused pustules (Fig. 2:2). Granular costae are known only from the *Thalmanninella reicheli* Biozone to the middle part of the *Dicarinella concavata* Biozone of the middle Cenomanian–Coniacian. The other type, referred to as continuous costae are dominant in the Turonian–Maastrichtian (Fig. 2:3).

Pore diameters and their variation in heterohelicid taxa of the late Albian–Cenomanian are systematically studied for the first time. Qualitative description of the pore types according to their size is that adopted by the Mesozoic Working Group on Planktonic Foraminifera (2006) and refined by Georgescu (2009): nannoperforate (0.1–0.5 μm), microperforate (0.5–1.0 μm), finely perforate (1.0–2.5 μm), and macroperforate (diameters >2.5 μm). Pore size in the late Albian–Cenomanian heterohelicids is mostly microperforate. The most primitive heterohelicid tests are nannoperforate, where the pore diameter is closer to that of the presumed benthic ancestor. The finely perforate test wall developed during the late Cenomanian.

Material Studied

This study is based on detailed observations of museum collection specimens and new material from a number of Deep Sea Drilling Project/Ocean Drilling Program (DSDP/ODP) and Tanzania Drilling Program (TDP) boreholes (Fig. 3). The samples are deposited at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C. The primary types of the species described by Cushman (1938) and Tappan (1940) from the southern United States (Texas) are deposited in the Cushman Collection of the NMNH. Additional material came from the NMNH Loeblich and Tappan Topotype Collection and Van Morkhoven Collection of the same institution.

The specimens were initially studied under a standard optical binocular microscope and approximately 200 of them were subsequently imaged with a Phillips XL–30 ESEM. More than 400 electron micrographs were obtained for the present study. Gross test architecture of 14 specimens was observed from X-ray micrographs, an approach developed by Huber (1994) in his study of Santonian–Maastrichtian globular-chambered planktic foraminifera.

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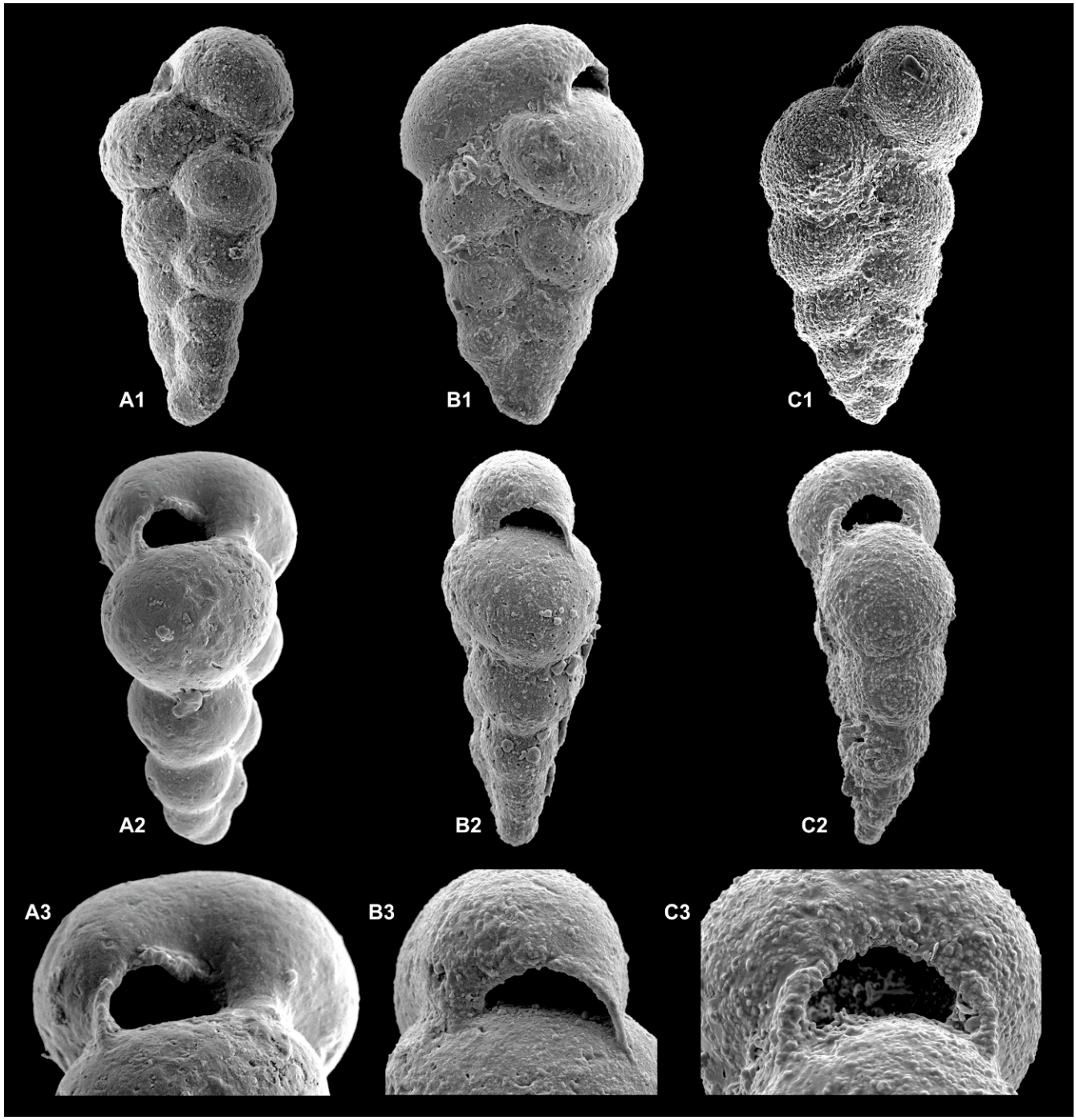


FIGURE 1. Evolution of the test and periapertural structure symmetry/asymmetry in the earliest three species of biserial planktics (lateral views: A1, B1, C1; edge views: A2, B2, C2; apertural views: A3, B3, C3). The tests and periapertural structures, which consist of a rim and a ridge, are asymmetrical in the earliest species of the group (A1–A3), which has the in the late Albian (*Pseudothalmanninella ticinensis* Biozone). Symmetrical tests in edge view and with periapertural structures consisting of unequally developed flanges (B1–B3) first occur in the latest Albian (uppermost part of the *Parathalmanninella appenninica* Biozone). Completely symmetrical tests in edge view (C1–C3) first occur in the middle Cenomanian (*Thalmanninella reicheli* Biozone). Specimen provenance A1: 171B–1050C–26–1, 7–9 cm; A2–A3: 171B–1052E–40–2, 118–121 cm; B1–B3: 171B–1050C–25–2, 70–72 cm; C1–C3: 171B–1050C–21–1, 105–106 cm. No scale implied.

Most of the late Albian–early Turonian specimens are from ODP Holes 1049C, 1050C, and 1052E on Blake Plateau in the western North Atlantic (Table 1). The biostratigraphic framework presented by Petrizzo and Huber (2006) and Ando and Huber (2007) is followed here. Abundant and well-preserved heterohelicid assemblages were collected from upper Albian–Coniacian sediments cored at DSDP Site 463 in the Mid-Pacific Mountains of the equatorial Pacific region. The biostratigraphic framework at this site was provided by Boersma

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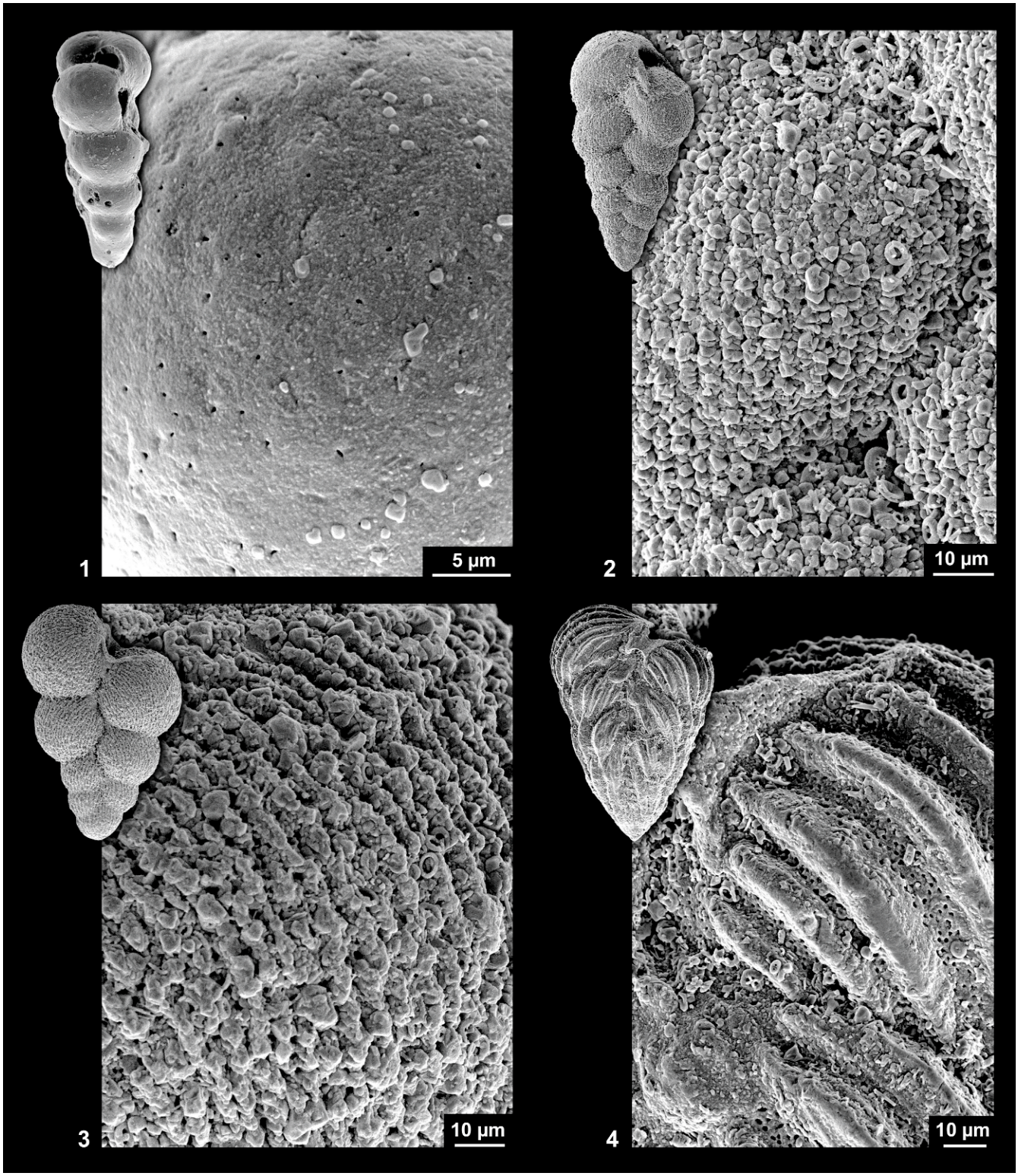


FIGURE 2. Types of ornamentation in the late Albian–Cenomanian heterohelicids. 1–smooth, 2–granular costae, 3–continuous costae, 4–robust costae in the Maastrichtian *Pseudoguembelina excolata* (Cushman, 1926). Specimen provenance: 1: 171B–1052E–40–2, 118–121 cm; 2–3: 62–463–35–1, 17–19 cm; 4: 171B–1050C–15–3, 71–73 cm. Note that the solid costae in Figure 3 can be seen despite the recrystallized test.

(1981), but some improvements are suggested herein for the Turonian–lower Coniacian stratigraphic interval (Table 2) based on recognition of the *H. helvetica* Biozone, which allows good correlation with coeval sediments at the Blake Plateau. The planktic foraminiferal zonation below the Santonian/Campanian boundary at DSDP Site 95 (Yucatan outer shelf) was reviewed. Only the Santonian sediments were documented in the previous zonation by McNeely

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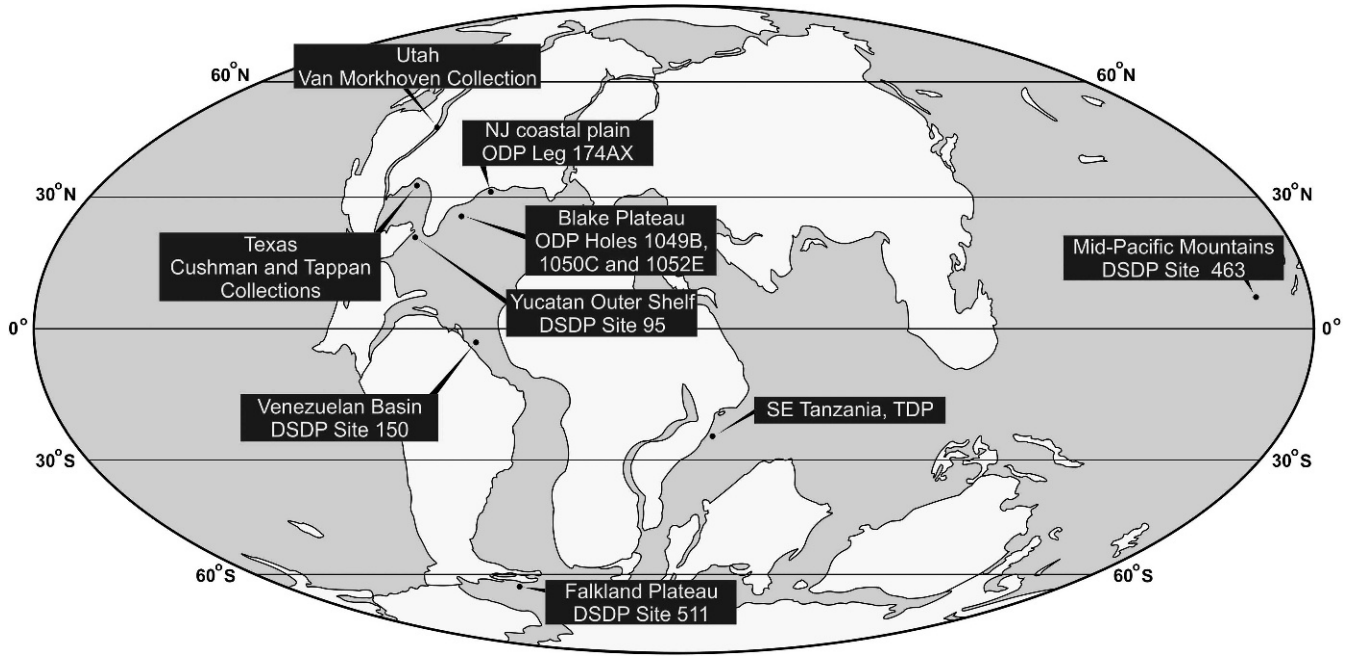


FIGURE 3. Provenance of the studied material. Paleogeographic map after Hay and others (1999) at 100 m.y.

(1973) and Nederbragt (1991), but a complete upper Turonian–Santonian succession is recognized in this study (Table 3). The Yucatan outer-shelf section is particularly important in documenting the last occurrence of a number of species that originated in the late Cenomanian. Additional material came from Turonian–Santonian sediments drilled at DSDP Site 511 in the South Atlantic (Falkland Plateau), Santonian–Campanian sediments from ODP Leg 174AX at the Bass River site on the New Jersey coastal plain, upper Turonian–lowermost Coniacian sediments of DSDP Site 150 in the Venezuelan basin, and lower Turonian sediments from a borehole in southeast Tanzania (Tanzania Drilling Program Sample 22–33–3, 10–30 cm).

SYSTEMATIC CLASSIFICATION

The suprageneric classification outlined below is based on Loeblich and Tappan (1987). The concept of species is discussed in the Appendix.

Order FORAMINIFERIDA Eichwald, 1830
Suborder ROTALIINA Delage and Hérouard, 1896
Superfamily HETEROHELICACEA Cushman, 1927
Family HETEROHELICIDAE Cushman, 1927

Genus *Protoheterohelix* n. gen.
Type species: *Protoheterohelix washitensis* (Tappan), 1940.

Description. Test is biserial throughout, with variable asymmetry as seen in edge view. Earlier species displays twisted tests and periapertural structures; evolved one shows symmetrical tests in edge view and asymmetrical periapertural structures. When compared with the second chamber, the size of the proloculus is variable and generally larger, but in some rarer specimens it is smaller. Chamber shape is globular to reniform. Sutures are distinct, depressed, straight, and oblique to the test axis of growth. Test periphery is rounded. Aperture is a low to medium high arch at the base of the last formed chamber and bordered by asymmetrical periapertural structures. Periapertural structures of the primitive species consist of a subangular ridge on one side and a rim on the opposite side; two asymmetrical flanges border the aperture in the evolved species. A small, relict toothplate can be occasionally present. Chamber surface is smooth. Test wall is calcitic, hyaline, nannoperforate to microperforate.

Remarks. Protoheterohelix is the only Cretaceous heterohelicid planktic foraminiferal genus known with an asymmetrical test or periapertural structures. It includes the earliest biserial planktics and is the only genus of the family Heterohelicidae Cushman, 1927 from the upper Albian–lower Cenomanian stratigraphic interval. Asymmetry of the test and periapertural structures is a vestige of its benthic ancestry (i.e., *Praeplanctonia* Georgescu, 2009). All *Protoheterohelix* descendants display completely symmetrical tests.

Species included. Protoheterohelix washitensis (Tappan), 1940; *P. obscura* n. sp.

Etymology. The Greek prefix "proto-" (= first) is added to *Heterohelix*.

Stratigraphic range. Upper Albian–lower Turonian.

Geographic distribution. USA (Texas), Gulf of Mexico, western North Atlantic Ocean (Blake Plateau) and Europe (Germany, North Sea, and Poland).

Protoheterohelix washitensis (Tappan), 1940, emended
Pl. 1, figs. 1–14; Pl. 2, figs. 1–4; figs. 1: A1–A3, 2: 1

Guembelina washitensis Tappan *in* Tappan, 1940, p. 115, pl. 19, fig. 1 (Grayson Formation, lower Cenomanian, Texas, USA).
Heterohelix washitensis (Tappan) *in* Brown, 1969, p. 34, pl. 1, fig. 7 (upper Albian–Cenomanian, taxonomic reevaluation).
Heterohelix moremani (Cushman) *in* Michael, 1973, p. 208, pl. 6, fig. 12 (upper Albian–Cenomanian, Texas, USA).
Heterohelix moremani (Cushman) *in* North and Caldwell, 1975, pl. 4, fig. 9 (Turonian, Saskatchewan and Manitoba, Canada).

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TABLE 1. Distribution chart and abundances of the upper Albian–lower Turonian biserial planktic foraminifera from Hole 1050C (Blake Plateau, western North Atlantic). Symbols: R = rare (1–5 specimens/sample), C = common (6–10 specimens/sample), F = frequent (11–25 specimens/sample), A = abundant (25 or more specimens/sample). Sample abbreviation: core-section, sampled interval in centimeters. Planktic foraminiferal biozonation after Huber and others (1999), Ando and Huber (2005, 2007) and Petrizzo and Huber (2006). Planktic foraminiferal zones after Robaszynski and Caron (1995).

Sample	Biozone	*Protoheterohelix washitensis*	*Protoheterohelix obscura*	*Planoheterohelix moremani*	*Planoheterohelix postmoremani*	*Globoheterohelix paraglobulosa*	*"Heterohelix" globulosa*
21-1, 0-1				R	R	A	R
21-1, 10-11	*Helveto-globotruncana helvetica*	R		C	R	A	R
21-1 20-21		R		F	R	A	C
21-1 31-34				A	C	A	R
21-1 42-43				R	R	R	R
21-1 47-48		R	R	F	R	C	R
21-1 67-68	*W. archeocr.*						
21-1 68-69		R	R	F	C	C	R
21-1 70-71	*Rotalipora cushmani*			C	R		
21-1 72-73				C	R	R	R
21-1 74-75				F	R		
21-1 82-83		R		R	C		R
21-1 105-106				A	R	C	
21-1 135-136			R	A	R	R	
21-2 99-102				F	R	R	
21-3 56-59			C	A			
21-4 63-66			R	A			
21-4 129-132		R	R	A			
21-6 54-56		R	R	A			
21-7 45-46				C			
21-7 49-50							
21-7 51-52				C			
21-7 53-54				F			
21-7 58-59			R	A			
21-7 105-107				A			
22-1 46-50			C	F			
23-1 4-5	*Rotalipora reicheli*		R	F			
23-1 50-51		R		A			
23-1 126.5-128.5			R	A			
23-2 19-21				R			
23-2 98.5-99.5			R	R			
23-2 109-111			R	R			
23-3 22-24		R	A	A			
23-3 49.5-50.5							
23-3 122-124			R	R			
24-3 127-130			C	C			
24-3 69-71		R	R	C			
25-1 27-30		R	C	R			
25-1 82-85							
25-1 133-136		R	R				
25-2 70-72		R	F	R			
25-2 83-87		R	C	R			
25-2 87-88							
25-2 130-132		R	R	R			
25-3 37-38		R	C				
25-3 60-64	*Rotalipora globotruncanoides*	R	R				
25-3 142-146							
25-4 16-20		R	C				
26-1 7-9		C	C				
26-1 53-56							
26-1 139-141							
26-2 24-26							
26-2 56-59							
26-2 114-116			R				
26-2 115-117							
26-3 33-36							
26-3 73-76							
26-3 120-122			R				
26-4 34-37							
26-4 83-86		R	R				
26-4 140-142			R				
26-5 28-30							
26-5 83-86							

Sample	Biozone	*Protoheterohelix washitensis*	*Protoheterohelix obscura*	*Planoheterohelix moremani*	*Planoheterohelix postmoremani*	*Globoheterohelix paraglobulosa*	*"Heterohelix" globulosa*
26-CC, 9-10	*Rotalipora appenninica*	R					
27-1 5-6			R				
27-1 19-21		C	R?				
27-1 75-76		R					
27-1 125-127		R					
27-2 25-26							
27-2 85-88							
27-2 125-126							
27-3 5-6							
27-3 30-32							
27-3 79-84							
27-3 139-141							
27-4 34-36							
27-4 80-83							
27-4 134-136		R					
27-5 32-34							
27-5 90-94							
27-5 123-125							
27-6 29-31							
27-6 74-78		R					
27-7 20-22		R					
27-CC							
28-1 20-21		R					
28-1 70-73		R					
28-3 60-63	*Rotalipora ticinensis*						
28-4 146-150							
28-5 52-53							
28-6 66-69							
29-1 57-60		C					
29-2 133-135							
29-3 83-86		R					
29-4 80-83							
29-5 72-75		C					
29-6 21-24		R					
29-6 62-65		R					
30-1 102-105							
30-2 72-75		R					
30-1 92-97							
30-3 72-75							
30-4 76-81							
30-5 82-85		R					
30-6 80-84							
31-1 18-85							
31-1 132-134		R					
31-2 80-84		R					
31-2 130-134							
31-3 80-83							
31-4 22-27							
31-4 87-90							
31-5 81-84							
31-6 79-83							
31-6 88-91							
31 CC							

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TABLE 2. Biserial planktic foraminiferal distribution and abundances in the Turonian–lower Coniacian sediments of DSDP Site 463 (Mid-Pacific Mountains, equatorial Pacific). See caption of Table 1 for explanation of symbols. Planktic foraminiferal zones after Robaszynski and Caron (1995).

Sample	Stage	Revised Planktic Foraminiferal Biozonation	*Planoheterohelix moremani*	*Planoheterohelix postmoremani*	*Planoheterohelix planata* plexus	*Globoheterohelix paraglobulosa*	*"Heterohelix globulosa"*	*"Heterohelix" reussi*	*"Heterohelix"* sp. 1	*Huberella praehuberi*	*Huberella huberi*
26-4 52-54	Santonian	*Dicarinella concavata*			F		A		F		
26-5 53-58	Coniacian–lower Santonian				F		R	A	F		
26-6 53-55					R		A	A	A		
27-1 50-52				R	R	C	A	A	R		
27-2 20-22	Turonian					C	A	A	A		C
29-1 50-52		*Marginotruncana sigali*			C	R	A	A	A	R	C
30-1 50-53				R	R	R	F	F	R		
30-2 50-52				R	R	R			R		
31-1 11-13				F		F		A	A	R	
33-1 50-52				C		C		F	R	R	
33-2 52-54		*Helveto-globotruncana helvetica*		A	R	R	R	A			
34-1 50-52				A		A		A		C	
34-2 53-55			R	F		A	C	F	F	R	
34-3 50-53			R	A		A	C		R	R	
35-1 10-12			C	A		A	R			A	

Heterohelix moremani (Cushman) *in* Masters, 1977, p. 346, pl. 2, fig. 1 (middle Albian–Maastrichtian, taxonomic revision).

Heterohelix moremani (Cushman) *in* Hart and others, 1989, p. 346, pl. 7.16, fig. 9 (Cenomanian, North Sea).

Laeviheterohelix sp. *in* Petrizzo and Huber, 2006, pl. 1, fig. 2 (upper Albian, Blake Plateau, western North Atlantic Ocean).

"Heterohelix" washitensis (Tappan) *in* Georgescu, 2009, p. 113, pl. 1, figs. 3–13 (upper Albian–lower Turonian, Blake Plateau, western North Atlantic Ocean).

Emended description. Test is small, loosely twisted, and asymmetrical, and consists of variably overlapping 12–15 biserially arranged globular to subglobular chambers. Proloculus (11.8–15.9 μm) is slightly larger than second chamber in most of the specimens, or, rarely, chambers gradually increase in size throughout ontogeny in others. Sutures are distinct, straight to slightly curved and depressed, oblique to axis of test growth. Test periphery is broadly rounded. Aperture is a medium-high arch at base of last-formed chamber (Pl. 1, figs. 2–3, 5–6, 8, 10, 13, Pl. 2, figs. 2–3); it is bordered by asymmetrical periapertural structures, a rim on one side and a subangular ridge on the opposite side (Pl. 1, figs. 2, 5–6, 8, 10, 13). Test surface is smooth. Test wall is calcitic, hyaline, and nannoperforate to microperforate, with pore diameter ranging 0.4–0.7 μm (Pl. 1, fig. 11, Pl. 2, figs. 3–4).

Remarks. The emendation is proposed to emphasize the test twisting and asymmetry that are key features of the species that were not mentioned in the original description by Tappan (1940). Pessagno (1967) considered *Heterohelix washitensis* as a junior synonym of *H. moremani* and stated that the specimens of the latter were gerontic individuals. This point of view was subsequently adopted by Masters (1977) and Nederbragt (1991), but was disregarded by Brown (1969), who retained *Heterohelix washitensis* as a valid species. Test and periapertural structures asymmetry in *P. washitensis* are primitive features when compared with the other members of the family Heterohelicidae and are shared with its ancestor, *Praeplanctonia globifera* Georgescu, 2009 (Georgescu, 2009).

Stratigraphic range. Upper Albian (171B–1050C–31–2, 81–84 cm) to lower Turonian (171B–1050C–21–1, 0–1 cm), from the *Pseudothalmanninella ticinensis* Biozone throughout the *Helvetoglobotruncana helvetica* Biozone (Table 1).

Geographic distribution. USA (Texas), Canada (Saskatchewan and Manitoba), western North Atlantic Ocean (Blake Plateau) and Europe (North Sea).

Protoheterohelix obscura n. sp.
Pl. 2, figs. 5–11; Pl. 3, figs. 1–12; fig. 1: B1–B3

Heterohelix sp. cf. *H. moremani* (Cushman) *in* Pessagno, 1967, pl. 388, figs. 7–8 (upper Cenomanian–Turonian, Gulf region, southern USA).

Heterohelix moremani (Cushman) *in* Premoli Silva and McNulty, 1983, pl. 2, fig. 10 (upper Albian, DSDP Hole 538A, Gulf of Mexico).

Heterohelix glabrans (Cushman) *in* Weidich, 1984, p. 76, pl. 1, figs. 7, 11 (Turonian–Coniacian, southern Germany).

Heterohelix pulchra Brotzen *in* Weidich, 1984, p. 78, pl. 1, figs. 5, 6, 8, 9, 13 (Turonian–Coniacian, southern Germany).

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TABLE 3. Upper Turonian–Santonian biserial planktic foraminiferal distribution and abundances at DSDP Site 95 (Yucatan Shelf). See caption of Table 1 for explanation of symbols. Planktic foraminiferal zones after Robaszynski and Caron (1995).

Sample	Stage	Revised Planktic Foraminiferal Biozonation	*Planoheterohelix postmoremani*	*Planoheterohelix planata*	*Planoheterohelix papula*	*Globoheterohelix paraglobulosa*	*"Heterohelix globulosa"*	*"Heterohelix" pseudoreussi*	*"Heterohelix" reussi*	*"Heterohelix" sphenoides*	*"Heterohelix" stenopos*	*"Heterohelix" sp. 1*	*Hendersonites carinata*	*Hendersonites hendersoni*	*Laeviheterohelix* sp.	*Pseudotextularia* sp.	*Huberella huberi*	*Ventilabrella eggeri*	*Ventilabrella browni*	*Ventilabrella glabrata*	*Sigalia* div. sp. (biserial)	*Sigalia* div. sp. (multiserial)
13-2 101.5-102.5	Santonian	*Dicarinella asymetrica*					R															R
13-3 100-102				R			A	F		R			R			R		C	C	C		F
13-4 100-101				R			R	R		R										R		F
14-1 102-105							A			F				R		C		F	R		A	A
15-1 97-100				R	R		C			A											R	
15-2 100.5-101.5							A		F	A	C				R	R		R			R	A
15-3 101-102.5							A		C	A	C										F	F
15-4 99.5-100.5							R		F	C	R										F	C
16-1 99.5-101							C		R												C	
16-2 100.5-102.5		*Dicarinella concavata*					A		A						R							
16-3 97.5-99									A			R										
16-4 100.5-101.5	Coniacian								A			R				R						
16-5 100.5-102			R				C		A													
16-6 99-100																						
17-1 99.5-100.5			C			R	F		A													
17-2 101.5-102.5							F		A													
17-3 100-101	upper Turonian					R	C		A			R					R					
17-4 102-103.5		*Marginotruncana sigali*	R			R	F		A			R										
17-5 99.5-100.5			C			C	C		F			C					R					
17-6 100-101						C	A					C										

Heterohelix moremani (Cushman) *in* Nederbragt and others, 1998, pl. 1, fig. 3 only (upper Cenomanian, Tunisia, northern Africa).

Heterohelix sp. *in* Pióro, 2005, pl. 7, fig. 5 (middle–upper Cenomanian, Pieniny Klippen Belt, Carpathians, southern Poland).

Holotype. USNM 534383.

Dimensions of the holotype. L = 0.128 mm; W = 0.076 mm; W/L = 0.593; t = 0.043 mm; t/L= 0.336.

Paratypes. Five specimens, USNM 534384 to 534388.

Type locality. Western North Atlantic (Blake Plateau), ODP Leg 171B, Hole1050C: 30°05.99′N, 76°14.10′W.

Type level. Lower Cenomanian (*T. globotruncanoides* Biozone), ODP Leg 171B, Hole 1050C, Sample 25R-02, 30–32 cm.

Dimensions. L = 0.122–0.167 mm; W = 0.074–0.100 mm; W/L = 0.541–0.635; t = 0.040–0.056 mm; t/L = 0.280–0.386.

Material. Over 200 specimens.

Etymology. From Latin *obscura* (= obscure, difficult to see).

Description. Test is small, consisting of 11–13 biserially arranged chambers throughout. Proloculus is small (9.1–14.3 μm) and followed by a slightly larger second chamber. Earlier chambers are subglobular, those of the adult portion of the test subglobular to reniform and oblique to the test axis of growth (Pl. 2, figs. 5, 10; Pl. 3, figs. 2, 5, 8, 10). Sutures are straight to slightly curved, distinct and depressed and oblique to the test axis of growth. Tests are symmetrical in edge view, with periphery broadly rounded (Pl. 2, figs. 6, 9, 11, Pl. 3, figs. 1, 4, 7, 11). Aperture is an interiomarginal, low- to medium-high arch bordered by two unequally developed periapertural flanges (Pl. 2, figs. 6–7, 9, 11, Pl. 3, figs. 1, 4, 6–7, 9, 11–12). Chamber surface is smooth. Test wall is calcitic, hyaline, and nannoperforate to microperforate; pore diameter ranges 0.4–0.9 μm.

Remarks. Protoheterohelix obscura n. sp. differs from *P. washitensis* in having (1) a symmetrical test in edge view, (2) periapertural structures consisting of unequally developed flanges rather than a rim and a ridge, and (3) reniform chambers in the adult portion of the test.

Stratigraphic range. Upper Albian (171B–1050C–27–1, 5–6 cm)–lower Turonian (171B–1050C–21–1, 47–48 cm) from the upper part of the *Parathalmanninella appenninica* Biozone throughout the *Helvetoglobotruncana helvetica* Biozone (Table 1).

Geographic distribution. USA (Texas), Gulf of Mexico, western North Atlantic Ocean (Blake Plateau) and Europe (Germany and Poland).

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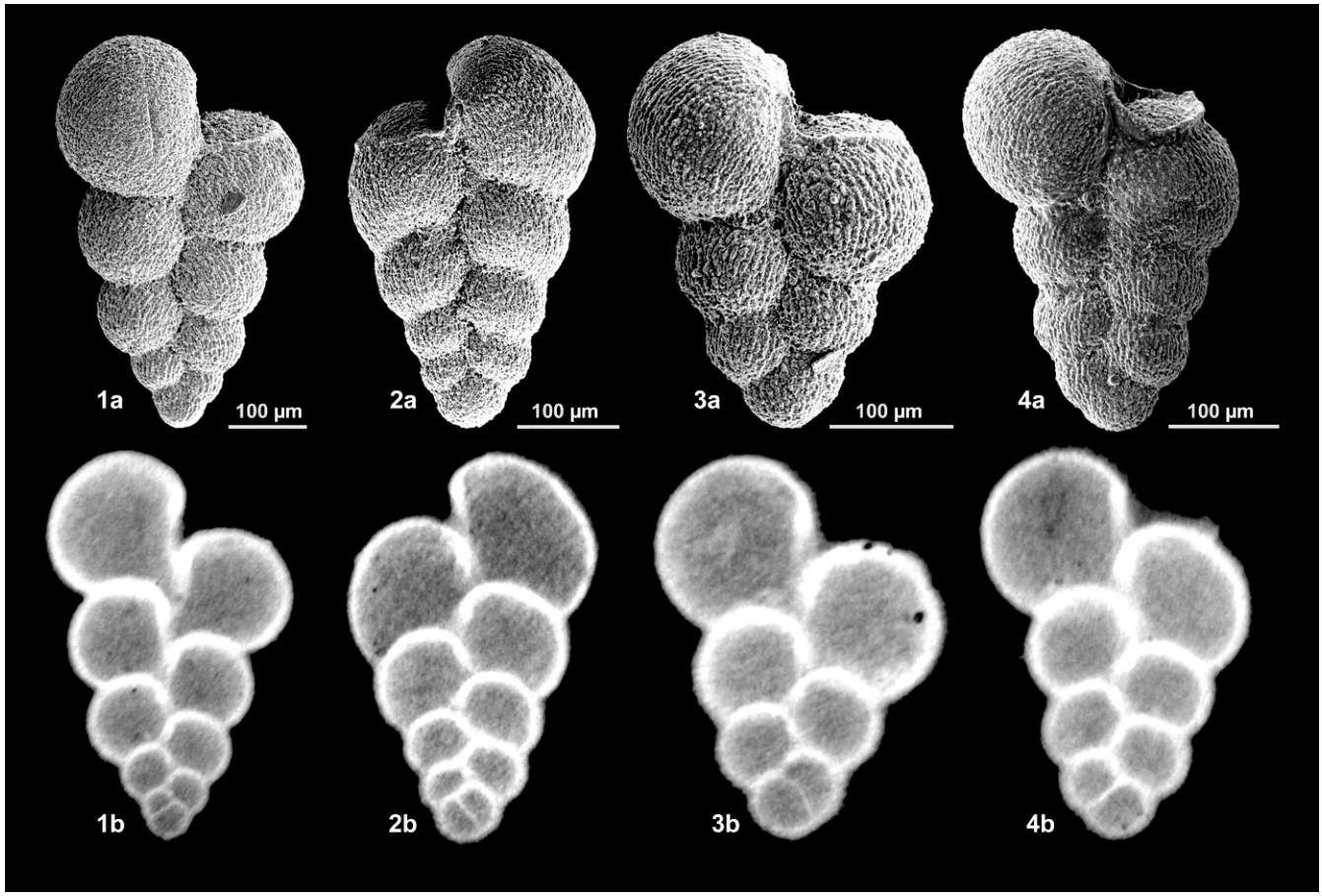


FIGURE 4. Scanning electron microscope photographs and corresponding X-ray micrographs of four specimens of *Globoheterohelix paraglobulosa* n. sp. from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains, DSDP Site 463), Sample 35R–1, 17–19 cm. The four specimens show large-sized proloculus, which is followed by the smaller second chamber (see text for details).

Genus *Planoheterohelix* n. gen.
Type species: *Planoheterohelix postmoremani* n. sp.

Description. Test is biserial throughout. Proloculus is small and followed by larger second chamber. Chambers are subglobular to globular in early portion of test and often reniform in adult. Periphery is broadly rounded. Aperture is a low- to medium-high arch situated at base of last-formed chamber; it is bordered by two symmetrically developed flanges. Chamber surface is smooth or with fine longitudinal costae in earlier species and completely costate in evolved ones. Test wall is calcitic, hyaline, microperforate to finely perforate. Pores are situated in intercostal spaces or they might penetrate and interrupt costae.

Remarks. Planoheterohelix is the first genus of Cretaceous serial planktic foraminifers with completely symmetrical tests as seen in edge view. Test symmetry differentiates *Planoheterohelix* from its ancestor *Protoheterohelix*, which displays asymmetrical tests or periapertural structures. Late Albian–Cenomanian species of *Planoheterohelix* have a microperforate test wall (0.5–0.9 µm); finely perforate species are known only from higher stratigraphic levels (Turonian–lower Maastrichtian).

Species included. Planoheterohelix moremani (Cushman), 1938, p. 10, pl. 2, figs. 1–3; *Planoheterohelix postmoremani* n. sp.; *Planoheterohelix papula* (Belford), 1960, p. 57, pl. 15, figs. 6–8, text-fig. 3:1–6; *Planoheterohelix planata* (Cushman), 1938, p. 12, pl. 2, figs. 13–14; *Planoheterohelix rumseyensis* (Douglas), 1969, p. 159, pl. 11, figs. 9–11. The latter three species occur at higher stratigraphical levels (Coniacian–lower Maastrichtian).

Etymology. The Latin prefix *plano* (= plane) is added to the pre-existing genus name *Heterohelix*.

Stratigraphic range. Middle Cenomanian–lower Maastrichtian.

Geographic distribution. Cosmopolitan.

Planoheterohelix moremani (Cushman), 1938, emended
Pl. 4, figs. 1–13; fig. 1: C1–C3

Guembelina moremani Cushman *in* Cushman, 1938, p. 10, pl. 2, figs. 1–2 only (Eagle Ford Shale, Texas, USA).

Guembelina moremani Cushman *in* Cushman, 1946, p. 103, pl. 44, figs. 15–16 only (Eagle Ford Shale, Texas, USA).

Guembelina moremani Cushman *in* Kikoine, 1948, p. 18, pl. 1, fig. 4a–c (Upper Cretaceous, French Pyrenees).

Guembelina reussi Cushman *in* Said and Barakat, 1957, p. 76, pl. 1, fig. 8 (Cenomanian, Egypt, northern Africa).

Heterohelix moremani (Cushman) *in* Pessagno, 1967, p. 260, only pl. 89, figs.1–2 (Albian–Turonian; Britton Clay, Arcadia Park, Lake Waco, and South Bosque formations of Texas, USA and San Felipe Formation of Mexico).

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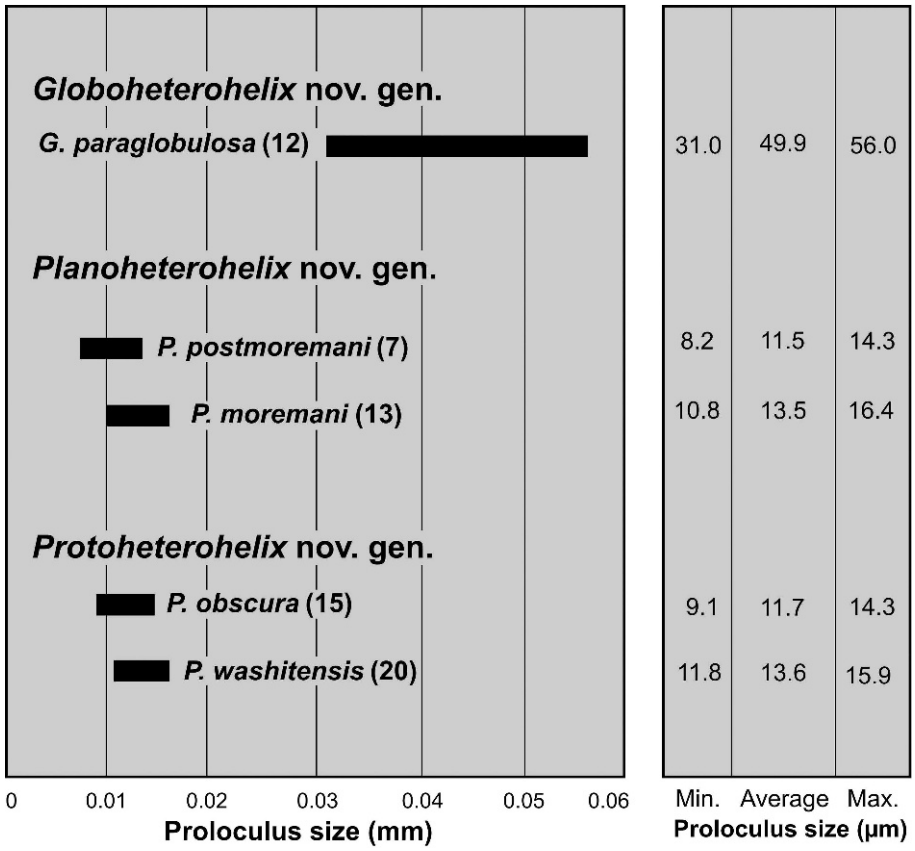


FIGURE 5. Proloculus size in *Globoheterohelix* n. gen., some species of *Planoheterohelix* n. gen. and *Protoheterohelix* n. gen. Measurements were taken from SEM micrographs. The number of measured specimens is given between parentheses. Calibration between the proloculus size measurements on SEM photographs and X-ray micrographs was made on five specimens of each *G. paraglobulosa* and *P. planata* and showed a margin of error of ±2.4% for the former species and ±7.5% for the latter.

(?) *Heterohelix pulchra* (Brotzen) *in* Eicher and Worstell, 1970a, pl. 1, figs. 1–3 (lower Turonian of Colorado, Kansas, South Dakota and Wyoming, USA).

(?) *Heterohelix pulchra* (Brotzen) *in* Eicher and Worstell, 1970b, p. 296, pl. 8, figs. 9–10 (upper Cenomanian–lower Turonian of Colorado, Kansas, South Dakota and Wyoming, USA).

Heterohelix moremani (Cushman) *in* Leckie, 1984, pl. 10, fig. 12 (middle Cenomanian, DSDP Site 547, Mazagan Escarpment, eastern North Atlantic).

Heterohelix moremani (Cushman) *in* Caron, 1985, p. 60, figs. 24:6–7 (Eagle Ford Formation, Dallas County and Texas, USA).

Heterohelix moremani (Cushman) *in* de Klasz, de Klasz and Saint-Marc, 1995, p. 363, pl. 2, fig. 4 (lower Turonian, Senegal, western Africa).

Heterohelix moremani (Cushman) *in* Nederbragt and others, 1998, pl. 1, figs. 4–5 only (middle or upper Cenomanian, Tunisia, northern Africa).

Heterohelix moremani (Cushman) *in* Huber and others, 1999, pl. 1, figs. 1–2 (ODP Hole 1050C, Blake Plateau, western North Atlantic Ocean).

Heterohelix moremani (Cushman) *in* Caron and others, 2006, fig. 7:10 (Cenomanian–Turonian, Tunisia, northern Africa).

Description. Test is slender and symmetrical in edge view. It consists of 14–21 chambers, which are biserially arranged throughout, subglobose in the juvenile portion, and elongate and oblique to the axis of growth in the adult stage. The proloculus (10.8–16.4 μm) is smaller than the second chamber. Sutures are distinct, straight and depressed, and oblique to the test axis of growth. Aperture is a medium-high arch at the base of the last-formed chamber. Two delicate, symmetrically developed periapertural flanges border the aperture (Pl. 4, figs. 2, 5–6, 10, 12). Chamber surface is smooth but aligned pustules and rarer incipient costae can be occasionally observed on the earlier part of the test. Test wall is calcitic, hyaline and microperforate; pore diameter ranges 0.5–0.7 μm.

Remarks. The holotype (USNM 307959), which is deposited in the Cushman Collection, Smithsonian Institution, Washington, D.C., shows 21 chambers (Pl. 4, figs. 1–2). Elsewhere such specimens with numerous chambers and a more elongate appearance are rare, being reported only by Huber and others (1999) from the western North Atlantic (Blake Plateau, ODP Leg 171B). Most of the paratypes (USNM 307960–307962) display tests consisting of 17–19 chambers. *Planoheterohelix moremani* differs from *Protoheterohelix obscura* in having tests consisting of more chambers (16–21 rather than 11–13), lower rate of increase in chamber size and a symmetrical periapertural structures.

Stratigraphic range. Middle Cenomanian (171B–1050C–25–2, 130–132 cm) to lower Turonian (171B–1050C–21–1, 0–1 cm), from the *Thalmannienalla reicheli* Biozone to *Helvetoglobotruncana helvetica* Biozone (Tables 1–2).

Geographic distribution. USA (Texas), Mexico, Africa (Egypt, Senegal, Tunisia), Europe (France) and North Atlantic Ocean (Blake Plateau, Mazagan Plateau).

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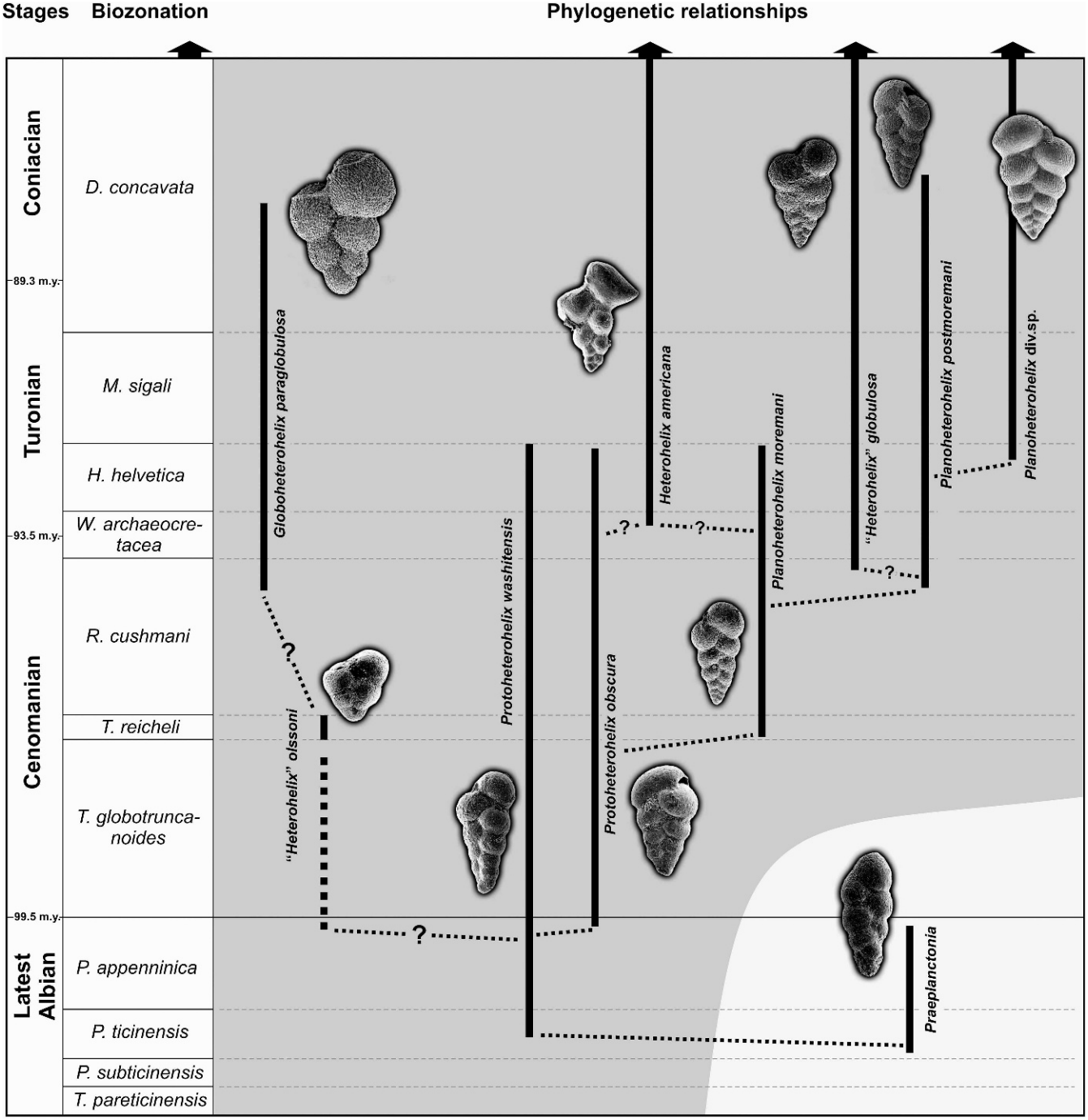


FIGURE 6. Early heterohelicid phylogeny. The group is evolved from the benthic praeplanctonids (light grey); all heterohelicid species are planktic in habitat (dark grey). Ages are after Gradstein and others (2004). Planktic foraminiferal biozonation is after Robaszynski and Caron (1995).

Planoheterohelix postmoremani n. sp.
Pl. 5, figs. 1–11, fig. 2: 2

Heterohelix moremani (Cushman) *in* Nederbragt, 1991, p. 344, pl. 3, fig. 2 only (upper Cenomanian, Tunisia, northern Africa).
Heterohelix moremani (Cushman) *in* Georgescu, 1995, p. 95, pl. 1, fig. 13 only (lower Turonian, western Black Sea, Romanian offshore).
Heterohelix moremani (Cushman) *in* Nederbragt and others, 1998, pl. 1, fig. 6 only (upper Cenomanian, Tunisia, northern Africa).
Heterohelix moremani (Cushman) *in* Wilson and others, 2002, fig. 1:3 (Turonian, Demerara Rise, western North Atlantic Ocean).
Heterohelix moremani (Cushman) *in* Bąk and others, 2005, fig. 5A (upper Cenomanian–lower Turonian, Pieniny Klippen Belt, southern Poland).

Holotype. USNM 534393.

Dimensions of holotype. L = 0.335 mm; W = 0.175 mm; W/L = 0.522; t = 0.103 mm; t/L= 0.307.

Paratypes. Five specimens, USNM 534394 to 534398.

Type locality. DSDP Leg 62, Site 463, equatorial Pacific (Mid-Pacific Mountains). 21°21′N, 174°40′E.

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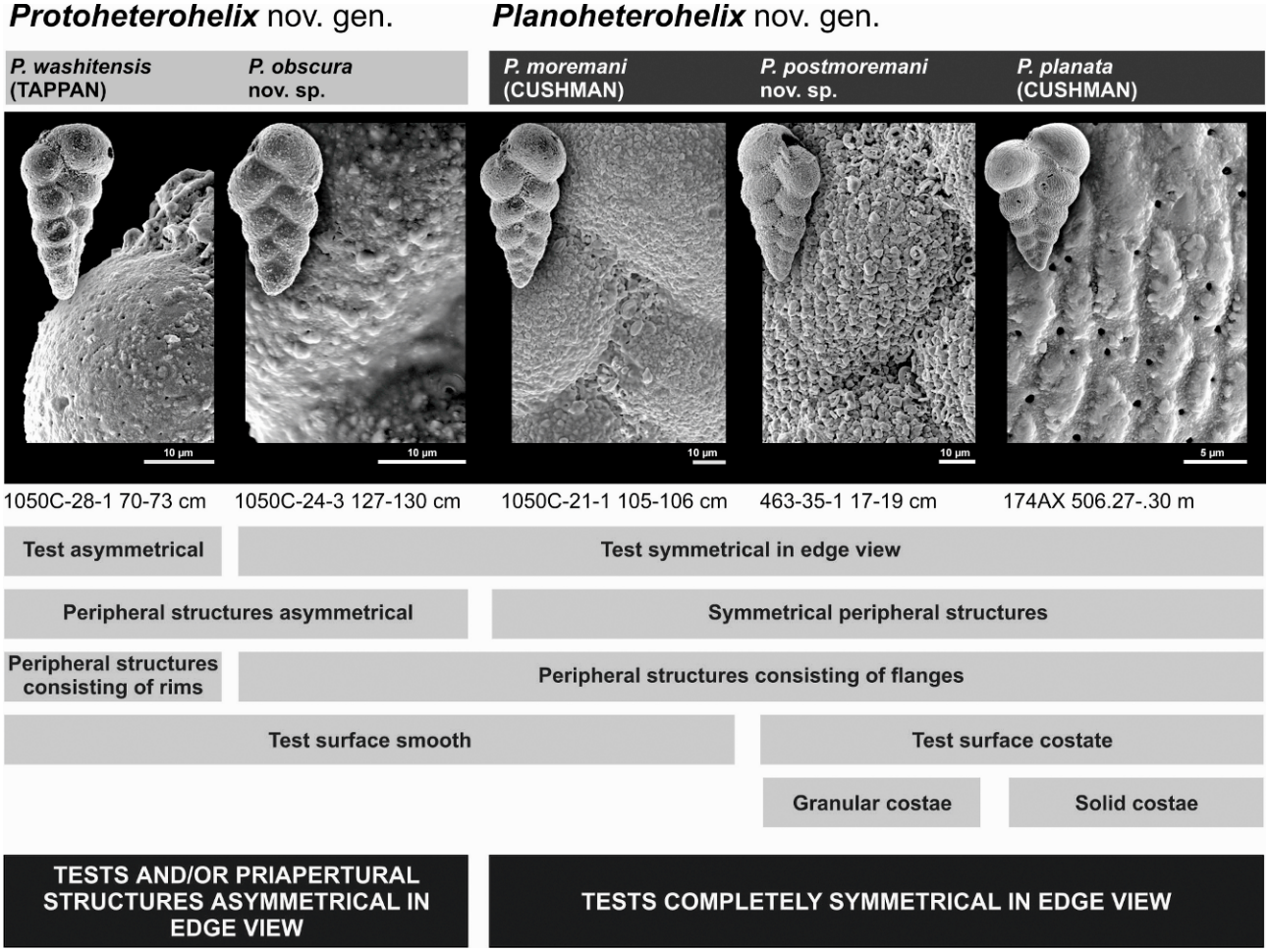


FIGURE 7. Evolution of the major gross test architecture features and ornamentation in the *Protoheterohelix–Planoheterohelix* lineage.

Type level. Lower Turonian (*H. helvetica* Biozone), Sample 62–463–35–1W, 17–19 cm.

Dimensions. L = 0.222–0.351 mm; W = 0.128–0.181 mm; W/L = 0.511–0.577; t = 0.096–0.110 mm; t/L = 0.307–0.432.

Material. Over100 specimens.

Etymology. The Latin prefix *post* (= after) is added to the pre-existing species name *moremani* to emphasize their succession of the two species in the evolutionary sequence.

Description. Test is biserial throughout and consists of 11–15 chambers. Small proloculus (8.2–14.3 µm) is followed by slightly larger second chamber. Chambers increase gradually in size as added. Earlier chambers are subglobular, those of adult stage are reniform and oblique to the test axis of growth (Pl. 5, figs. 1, 4, 9). Sutures are distinct, depressed, and oblique. Tests are symmetrical in edge view, with broadly rounded periphery (Pl. 5, figs. 2, 5, 8). Aperture is medium to high arch at base of last-formed chamber; it is bordered by two symmetrically developed periapertural flanges (Pl. 5, figs. 2, 5, 8, 10). Chamber surface is ornamented with closely spaced costae, each of them consisting of series of aligned pustules, resulting in a granular appearance (Pl. 5, figs. 3, 6). Test wall is calcitic, hyaline, microperforate; pore diameter ranges 0.5–0.9 µm.

Remarks. Planoheterohelix postmoremani differs from its ancestor *P. moremani* by having fine longitudinal costae on the test surface; this primitive ornamentation consists of rows of unmerged pustules, a feature characteristic of costate *Planoheterohelix* species. It differs from *Protoheterohelix obscura* by having symmetrical periapertural structures and a costate surface.

Stratigraphic range. Upper Cenomanian (171B–1050C–21–2, 99–102 cm) to Coniacian (10–95–16–5, 100.5–102 cm), from the upper part of *Rotalipora cushmani* Biozone to *Dicarinella concavata* Biozone (Tables 1–3).

Geographic distribution. Western North Atlantic Ocean (Blake Plateau, Demerara Rise), equatorial Pacific Ocean (Mid-Pacific Mountains), Europe (Poland, Romanian western Black Sea offshore), and northern Africa (Tunisia).

Genus *Heterohelix* Ehrenberg, 1843
Type species: *Textilaria americana* Ehrenberg, 1843

Heterohelix Ehrenberg *in* Ehrenberg, 1843, p. 429.

Description. Tests are symmetrical in edge view, with biserially arranged chambers that gradually increase in size or with incipient, planispirally coiled stage. Earlier chambers are subglobular, then subrectangular to subtriangular, and last formed are subtrapezoidal with peripheral spine or tubulospine-like projections. Test is slightly compressed

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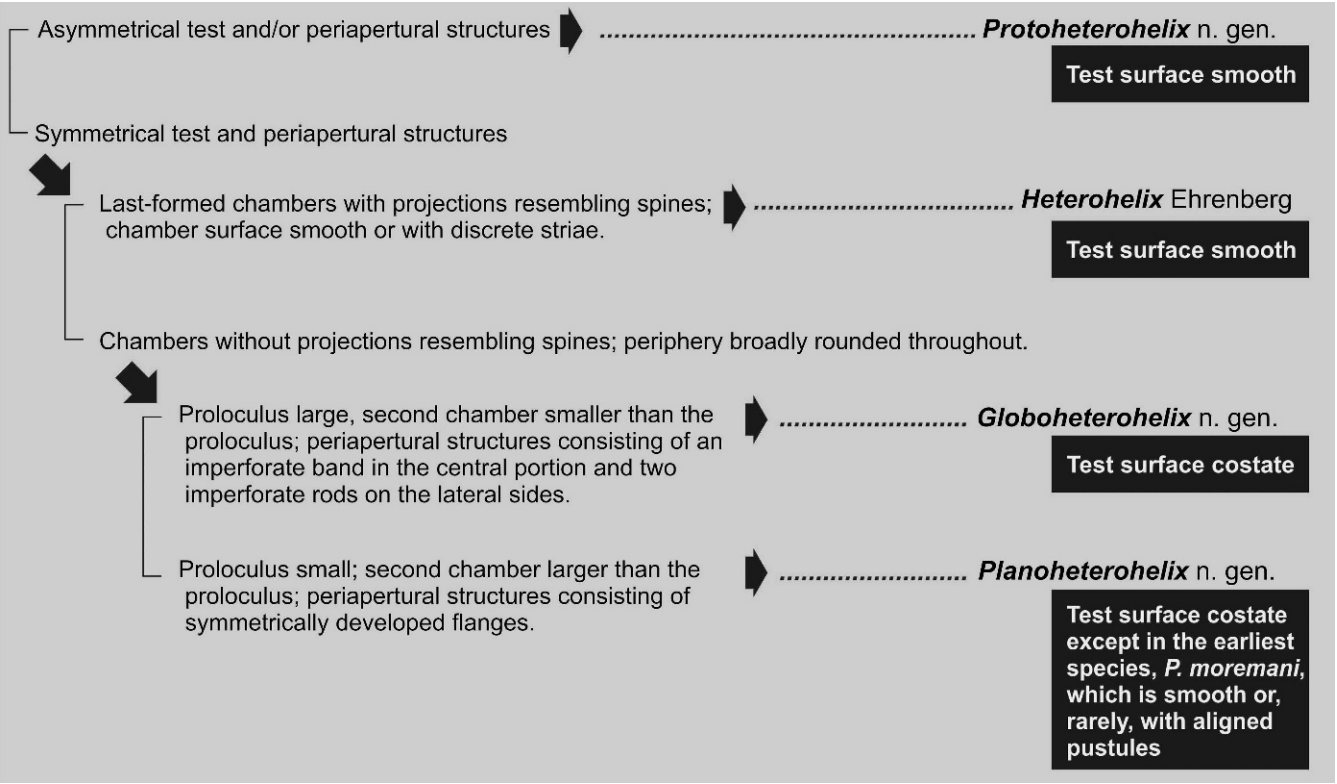


FIGURE 8. Practical dichotomous key for the identification of the late Albian–Cenomanian heterohelicid genera. The genus *Heterohelix* Ehrenberg is added to show that its morphology sharply differs from that of the other three genera.

laterally. Sutures are distinct, depressed, and oblique to the axis of test growth. Aperture is an interiomarginal arch. Test surface is smooth, rarely finely striate in the periphery region. Test wall is calcitic, hyaline, and microperforate.

Remarks. The genus *Heterohelix* appears to be a specialized taxon, as indicated by the tubulospine-like projections in the peripheral region of the last-formed chambers, which are diagnostic at genus level (Eicher and Worstell, 1970a; Loeblich and Tappan, 1987). *Heterohelix* is restricted here to a single species, *H. americana*. Masters (1980, p. 98, figs. 2d, 3d) showed an early planispiral stage both in *Textilaria americana* and its synonym *T. missouriensis* in a refiguration of the original material of Ehrenberg from the Humboldt Museum in Berlin. The planispiral coils in Masters' figures are formed of three chambers (including the proloculus), which is referred to here as the incipient planispiral coil. It sharply differs from the well-developed planispiral coil of *Paraspiroplecta* navarroensis (Loeblich, 1951, p. 107, pl. 12, figs. 1–3), which consists of 4–6 chambers surrounding the proloculus. The specimens described as *Heterohelix americana* (Ehrenberg) and H. sp. from the lower Manville Chalk of the Selma Group by Masters (1980, pl. 2, figs. 1–3; pl. 2, figs. 4–5, respectively) are not congeneric with *Heterohelix americana*, as they are entirely costate and globular-chambered. The earlier stage and test ornamentation have the general appearance of *Planoheterohelix planata* and *''Heterohelix''* striata, respectively. Their taxonomic status needs further investigation. *Lunatriella* Eicher and Worstell, 1970 is a rare genus of the lower Turonian with backward-oriented, tubulospine-like chamber projections.

Species included. Heterohelix americana (Ehrenberg), 1843, p. 366, 398, 429.

Stratigraphic range. Lower Turonian, Santonian.

Geographic distribution. USA (Missouri) and western Africa (Senegal).

Heterohelix americana (Ehrenberg), 1843
Pl. 6, figs. 1–6

Textilaria americana Ehrenberg *in* Ehrenberg, 1843, p. 366, 398, 429 (Cretaceous, Missouri, USA).
Textilaria americana Ehrenberg *in* Ehrenberg, 1854, p. 24, pl. 32, fig. I (4a) (Cretaceous, Missouri, USA).
Textilaria missouriensis Ehrenberg *in* Ehrenberg, 1854, p. 24, pl. 32, fig. I (5) (Cretaceous, Missouri, USA).
Spiroplecta americana Ehrenberg *in* Ehrenberg, 1854, p. 24, pl. 32, figs. I (13–14) (Cretaceous, Missouri, USA).
non *Heterohelix americana* (Ehrenberg) *in* Masters, 1977, p. 338, pl. 1, figs. 1–3 (Upper Cretaceous, Alabama, USA).
Heterohelix americana (Ehrenberg) *in* Frerichs and Gaskill, 1978, p. 144, pl. 1, figs. 1–11 (Santonian, Western Interior, USA).
Heterohelix americana (Ehrenberg) *in* Masters, 1980, p. 97, text–figs. 2–3 (redescription of the type material).
Heterohelix americana (Ehrenberg) *in* de Klasz and others, 1995, p. 361, pl. 5, figs. 5–7, pl. 2, figs. 1–2 (lower Turonian, Senegal, western Africa).

Emended description. Test is biserial throughout, compressed as seen in edge view. Proloculus is small (10–11 μm in lateral view), spherical, and followed by 10–11 biserially arranged chambers that increase gradually in size (Pl. 6, figs. 1, 4). An early incipient planispirally coiled stage might be present (Masters, 1980, figs 2b, 3b). Earlier chambers are subrectangular to subtriangular to rounded in shape, the last one or two are subtrapezoidal and with peripheral

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projections resembling tubulospines (Pl. 6, figs. 1, 4). Sutures are distinct, straight, depressed, and oblique to the test axis of growth. Aperture is arcuate, at the base of the last formed chamber, and bordered by small, rarely preserved flanges (Pl. 6, figs. 2–3). Test surface is smooth or occasionally with fine, discrete striae in the peripheral region (Pl. 6, fig. 4). Test wall is calcitic, hyaline, nannoperforate to microperforate; pore diameter ranges 0.4–0.8 μm (Pl. 6, figs. 3, 6).

Remarks. The emendation of this rare species is proposed to emphasize its compressed tests and smooth-to-striate chamber surface, which sharply differs from that of the type specimens of *Heterohelix americana* that Ehrenberg (1843, 1854) and Masters (1980) illustrate with costae. Unlike *H. americana*, *Textilaria missouriensis* Ehrenberg appears to have smooth test (Ehrenberg, 1854; Masters, 1980). The report of *H. americana* from the United States Western Interior by Frerichs and Gaskill (1978) is from a higher stratigraphic level (Santonian) than that from Senegal (western Africa) by de Klasz and others (1995). The age of the African specimens is reassessed here as uppermost Cenomanian–lowermost Turonian (*W. archaeocretacea* Biozone) based on the absences of rotaliporid species and *H. helvetica*. *Heterohelix americana* is found only in shallow-marine sediments.

Stratigraphic range. Lower Turonian (*Whiteinella archaeocretacea* Biozone), Santonian (equivalent of the *Dicarinella asymetrica* Biozone).

Geographic distribution. USA (Missouri) and western Africa (Senegal).

Genus *Globoheterohelix* n. gen.
Type species: *Globoheterohelix paraglobulosa* n. sp.

Description. Test is biserial throughout, symmetrical in edge view and with globular chambers. Proloculus is large (31–56 μm) and followed by smaller second chamber (fig. 4). Sutures are distinct, straight, and depressed. Aperture is an interiomarginal, low-to-high arch bordered by two symmetrically developed imperforate rims. Test surface is ornamented with continuous and discontinuous costae. Test wall is calcareous, hyaline, and intercostally microperforate to rarely finely perforate.

Remarks. Globoheterohelix differs from *Protoheterohelix* in having (1) a symmetrical test in edge view, (2) symmetrically developed periapertural structures consisting of imperforate rims, (3) globular chambers, (4) a large proloculus (fig. 5), and (5) costae. It differs from *Planoheterohelix* in having (1) a large proloculus that is also larger than the second chamber, (2) globular chambers, and (3) periapertural structures consisting of imperforate rims rather than flanges. *Globoheterohelix* differs from *Heterohelix* mainly in having (1) a large proloculus, (2) costate ornamentation, and (3) globular chambers without tubulospine-like projections.

Species included. Globoheterohelix paraglobulosa n. sp.

Etymology. The Latin prefix *globo* (= globose) is added to the pre-existing genus name *Heterohelix*.

Stratigraphic range. Uppermost Cenomanian–Coniacian.

Geographic distribution. USA (Colorado, Kansas, South Dakota, Wyoming), Gulf of Mexico (Yucatan outer shelf), western North Atlantic (Blake Plateau), Caribbean region (Venezuelan basin), Africa (Egypt, Tanzania) and equatorial Pacific (Mid-Pacific Mountains).

Globoheterohelix paraglobulosa n. sp.
Pl. 6, figs. 7–12; Pl. 7, figs. 1–8; figs. 2: 3, fig. 4

Pseudoguembelina striata (Ehrenberg) *in* Said and Barakat, 1957, p. 77, pl. 1, fig. 17 (Cenomanian, Egypt).

Heterohelix globulosa (Ehrenberg) *in* Eicher and Worstell, 1970b, p. 296, figs. 5, 6 only (late Cenomanian–Turonian of Colorado, Kansas, South Dakota and Wyoming, USA).

Heterohelix globulosa (Ehrenberg) *in* Huber and others, 1999, pl. 1, figs. 1–2 (late Cenomanian, ODP Hole 1050C, Blake Plateau, western North Atlantic Ocean).

Holotype. USNM 534401. L = 0.383 mm; W = 0.250 mm; W/L = 0.652; t = 0.169 mm; t/L = 0.441.

Paratypes. Six specimens, USNM 534402 to 534407.

Type locality. DSDP Site 463, Mid-Pacific Mountains (equatorial Pacific), 21°21′N, 174°40′E.

Type level. Lower Turonian (*H. helvetica* Biozone), Sample 463-35R-1, 17–19 cm.

Dimensions. L = 0.152–0.431 mm; W = 0.101–0.291 mm; W/L = 0.664–0.910; t = 0.066–0.184 mm; t/L = 0.408–0.705. Measurements based on 22 specimens.

Material. Over 400 specimens.

Etymology. The Greek prefix para (= opposed to) is added to the pre-existing species name, globulosa.

Description. Test is biserial throughout. The large proloculus (31–56 μm) is followed by six to eight globular chambers, which increase slowly in size as added. Second chamber is smaller than the proloculus. Sutures are distinct, straight to slightly oblique, depressed. Aperture is an interiomarginal, low- to medium-high symmetrical arch bordered by lateral imperforate rims and an imperforate band in the central part (Pl. 6, figs. 7, 10–11; Pl. 7, figs. 2, 4, 8). Chamber surface displays closely spaced continuous or discontinuous fine (2.5–3.3 μm) costae. Intercostal spaces are commonly narrower than the width of the costae (Pl. 7, figs. 3, 6). Test wall is calcitic, microperforate to finely perforate with pore diameter ranging 0.7–1.1 μm. Pores are intercostal or occasionally penetrate costae.

Remarks. The tests of *Globoheterohelix paraglobulosa* have previously been assigned to *Heterohelix globulosa* (Ehrenberg). After examination of the original material of Ehrenberg, Masters (1980, pl. 1, figs. 6–8) regarded "*Heterohelix*" *globulosa* as having a completely costate test. Entirely smooth specimens of "*H.*" *globulosa* had never been reported, so the redefinition of "*H.*" *globulosa* as a finely costate species is herein accepted. X-ray micrographs through well-preserved specimens of "*H.*" *globulosa* from the Santonian and Campanian show that it has a small-sized proloculus (9–12 μm in diameter) and its chambers gradually increase in size throughout ontogeny. These features suggest that it most likely evolved from a species of *Planoheterohelix*. Accordingly, *Globoheterohelix paraglobulosa* and "*H.*" *globulosa* are retained as non-congeneric species.

Stratigraphic range. Upper Cenomanian (171B–1050C–21–2, 99–102 cm) to Coniacian (10–95–17–1, 99.5–100.5 cm), from the upper part of the *Rotalipora cushmani* Biozone to the middle part of the *Dicarinella concavata* Biozone (Tables 1–3).

Geographic distribution. North America (Colorado, Kansas, South Dakota and Wyoming, USA), Gulf of

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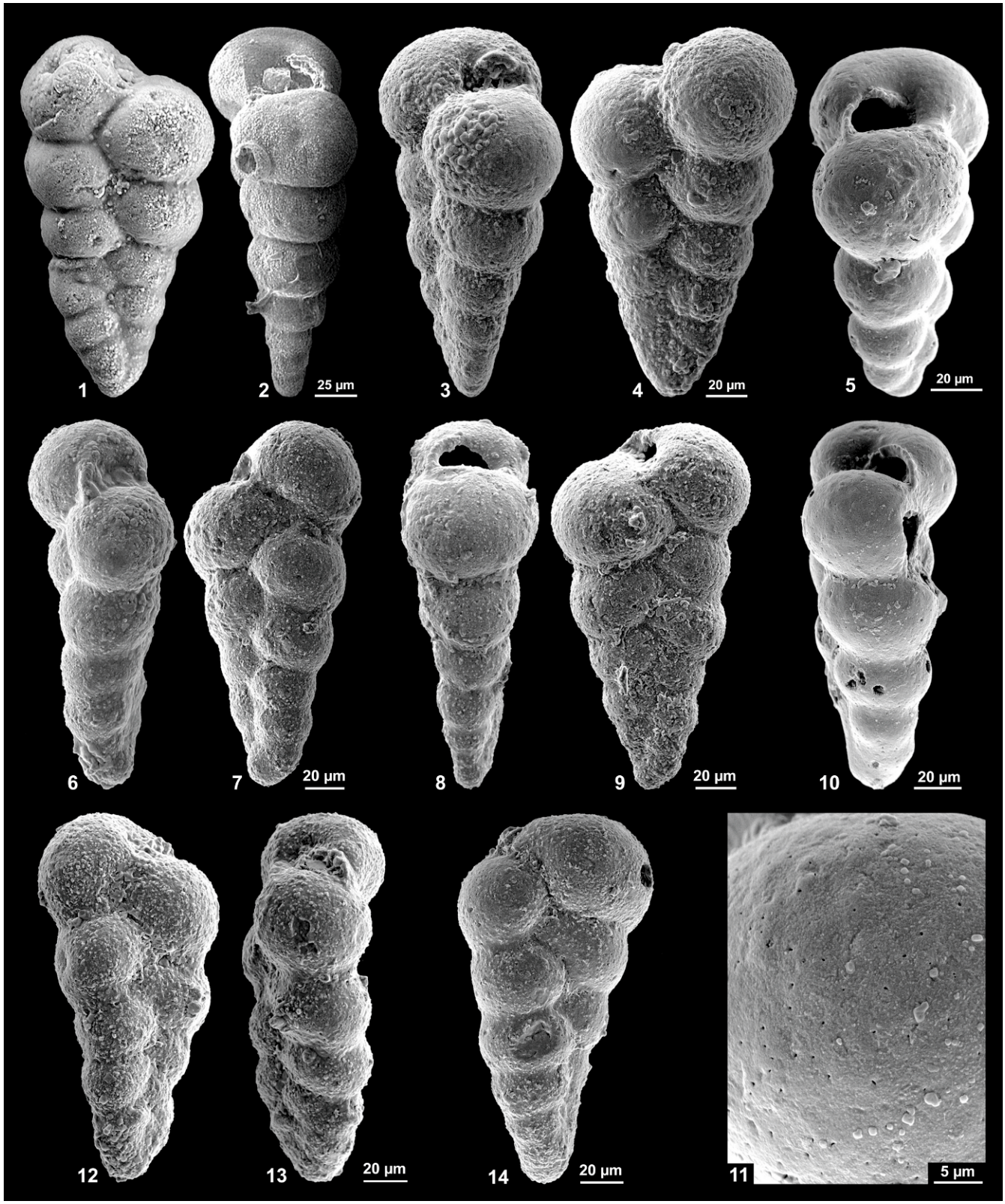


PLATE 1

Protoheterohelix washitensis (Tappan), 1940 from Texas, USA (3–4) and upper Albian of ODP Leg 171B, Blake Plateau, western North Atlantic (5–14). 1 Lateral view of the holotype (USNM 307987) from the Grayson Bluff originally figured by Tappan (1940, pl. 19, figs. 1a–b). 2 Edge view of a paratype (USNM 307988). 3–4 Hypotype from the Del Rio Formation (Austin, Travis County, Texas) deposited in the Loeblich and Tappan Topotype Collection, NMNH (USNM 473118). 5 Hypotype from the upper Albian sediments of ODP Leg 171B, Hole 1052E, Sample 40–2, 118–181 cm (upper part of the *Parathalmanninella appenninica* Biozone). 6–7 Hypotype from the lowermost Cenomanian sediments (lowermost part of

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Mexico (Yucatan shelf), western North Atlantic Ocean (Blake Plateau), northern Africa (Egypt, Tanzania), equatorial Pacific Ocean (Mid-Pacific Mountains).

"*Heterohelix globulosa*" (Ehrenberg), 1840
Pl. 7, figs. 9–12

Heterohelix globuolsa (Ehrenberg) *in* Caron and others, 2006, fig. 7:11 (upper Cenomanian–Turonian, Colorado, USA and Tunisia, northern Africa).

Description. Test is biserial throughout, with small proloculus (10–13 μm) followed by 11–16 globular, and gradually increasing in size chambers. Sutures are depressed and straight to slightly curved. Periphery is broadly rounded (Pl. 7, fig. 9). Aperture is an interiomarginal, low- to medium-high arch.bordered by two small, symmetrically developed flanges (Pl. 7, fig. 10). Chamber surface is ornamented with fine costae (2.2–3.5 μm) (Pl. 7, figs. 9–12). Test wall is calcareous, hyaline, and microperforate; pore diameter ranges 0.5–0.7 μm.

Remarks. "*Heterohelix*" *globulosa* displays globular chambers overlapping at low rates, in contrast with any species of *Planoheterohelix*. This suggests that it is related to "*H.*" *reussi* (Cushman, 1938).

Stratigraphic range. Upper Cenomanian (1050C–21–1, 82–83 cm) to Maastrichtian, from the upper part of the *Rotalipora cushmani* Biozone throughout *Pseudoguembelina hariaensis* Biozone.

Geographic distribution. USA (Colorado), western North Atlantic (Blake Plateau), equatorial Central Pacific (Shatsky Rise), and northern Africa (Tunisia).

CONCLUSIONS

This revision underlines the importance of the following features in heterohelicid classification: (1) symmetry/asymmetry of the test or periapertural structures, (2) nature of periapertural structures (rims, flanges), (3) proloculus dimensions and its size relative to the second chamber, and (4) test ornamentation and pore size. Taxonomic reappraisal of the late Albian–Cenomanian biserial planktic foraminifera (Family Heterohelicidae Cushman, 1927) reveals that the group diversity gradually increases from the late Albian through the Cenomanian at both at genus and species levels.

New heterohelicid genera recognized in the upper Albian–Cenomanian are *Protoheterohelix*, *Planoheterohelix*, and *Globoheterohelix*. A fourth distinct taxon is referred to as "*Heterohelix globulosa*" (Ehrenberg), 1840 pending further study to clarify its affinities. The concept of genus as applied to the heterohelicid group is clarified in the lower Turonian–Santonian genus *Heterohelix* Ehrenberg, 1843.

The earliest heterohelicids are grouped in a distinct new genus, *Protoheterohelix* (type species: *P. washitensis*), which is characterized by asymmetry of its test or periapertural structure. Two species are included in this genus: *P. washitensis* and *P. obscura* n. sp. The former has an asymmetrical test and periapertural structure consisting of a rim on one side and a ridge on the other. The latter is the oldest biserial planktic species with a symmetrical test and periapertural structures consisting unequally developed flanges. *Protoheterohelix* is the only biserial planktic genus in the late Albian–early Cenomanian and it became extinct in the early Turonian (Fig. 6).

Biserial planktic foraminifera with a symmetrical test and periapertural structure first appear in the middle Cenomanian (*Thalmanninella reicheli* Biozone) with the initiation of a lineage formalized as *Planoheterohelix* n. gen. (type species: *P. postmoremani* n. sp.). Its earliest species, *P. moremani*, has a smooth test surface. The costate surface first developed in *P. postmoremani* n. sp., and is a persistent feature of the younger species of the genus. The *Protoheterohelix-Planoheterohelix* phyletic relationship is demonstrated by gradual developments in test and periapertural structure symmetry, flanges, and costae (Fig. 7). *Planoheterohelix postmoremani* has costae formed of aligned pustules (granular costae); whereas younger (Turonian–lower Maastrichtian) *Planoheterohelix* species (e.g., *P. planata*, *P. papula*, and *P. rumseyensis*) display solid costae. *Planoheterohelix* became extinct in the lower Maastrichtian.

Globoheterohelix n. gen. is characterized by a large proloculus (31–56 μm) followed by a smaller second chamber, globular chambers throughout, and chamber surface covered with fine and quasi-continuous costae. *Globoheterohelix paraglobulosa* n. sp. (late Cenomanian–Coniacian) is the only species ascribed to this genus. Major differences between *Globoheterohelix* and *Planoheterohelix* in chamber shape, periapertural structures, and relative size of the proloculus and deuteroloculus prove that they are distinct taxa and not alternating generations of the same species (which has never been documented in Cretaceous or Cenozoic serial planktic foraminifera).

The genus *Heterohelix* Ehrenberg, 1843 (lower Turonian–Santonian) is restudied and presented in the context of the evolutionary classification. The last formed chambers with tubulospine-like lateral projections indicate that it is a specialized genus; therefore, the use of this generic name should be restricted to its lineage. General test architecture, test ornamentation, and porosity suggest that *Heterohelix* evolved from either *Protoheterohelix obscura* or *Planoheterohelix moremani*. A dichotomous key for identifying earlier heterohelicid genera reflects the unique morphology of *Heterohelix* (Fig. 8).

A distinct lineage, here included in "*Heterohelix globulosa*" (Ehrenberg), 1840 initiated in the upper Cenomanian. This species, characterized by small proloculus and globular chambers that increase gradually in size, might have evolved from *Planoheterohelix postmoremani*.

←

the *Thalmanninella globotruncanoides* Biozone) of ODP Hole 1050C, Sample 26–1, 7–9 cm. 8–9 Hypotype from the lowermost Cenomanian sediments (lowermost part of the *Thalmanninella globotruncanoides* Biozone) of ODP Hole 1050C, Sample 26–1, 7–9 cm. 10–11 Hypotype from the upper Albian sediments of ODP Leg 171B, Hole 1052E, Sample 40–2, 118–181 cm (upper part of the *Parathalmanninella appenninica* Biozone). 12–13 Hypotype from the upper Albian sediments of ODP Leg 171B, Hole 1050C, Sample 27–3, 30–32 cm (*Parathalmanninella appenninica* Biozone). 14 Hypotype from the upper Albian sediments of ODP Leg 171B, Hole 1050C, Sample 28–1, 70–73 cm (*Parathalmanninella appenninica* Biozone).

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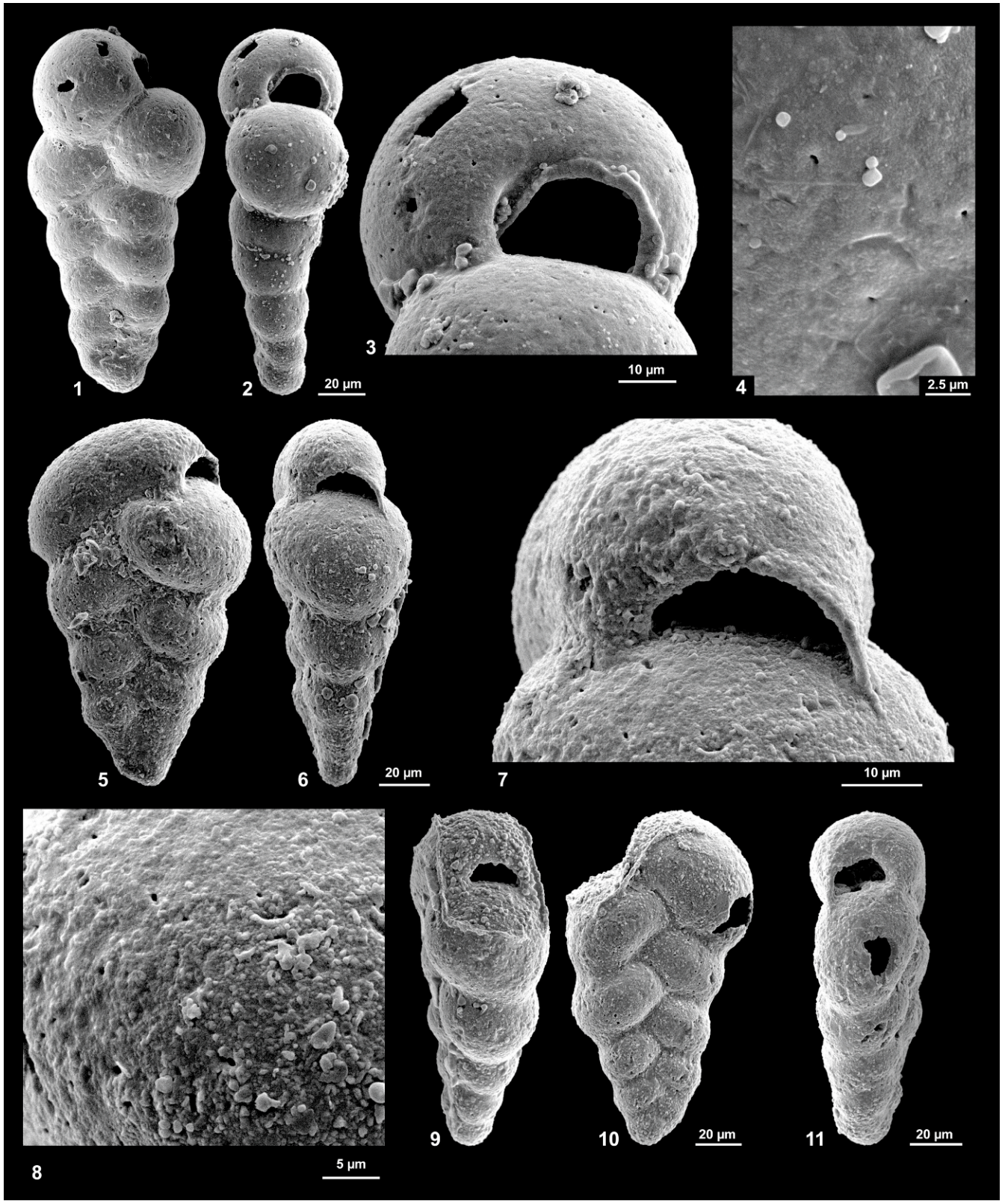


PLATE 2

Protoheterohelix washitensis (Tappan), 1940 (1–4) and *P. obscura* n. gen., n. sp. from the ODP Leg 171B (Blake Plateau, western North Atlantic) (5–11). 1–4 Hypotype of *P. washitensis* from the upper Albian (*Parathalmanninella appenninica* Biozone), Sample 171B–1052E–40–3, 71–75 cm. 5–8 Paratype of *P. obscura* from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534384). 9–10 Paratype of *P. obscura* from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534385). 11 Paratype of *P. obscura* from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534386).

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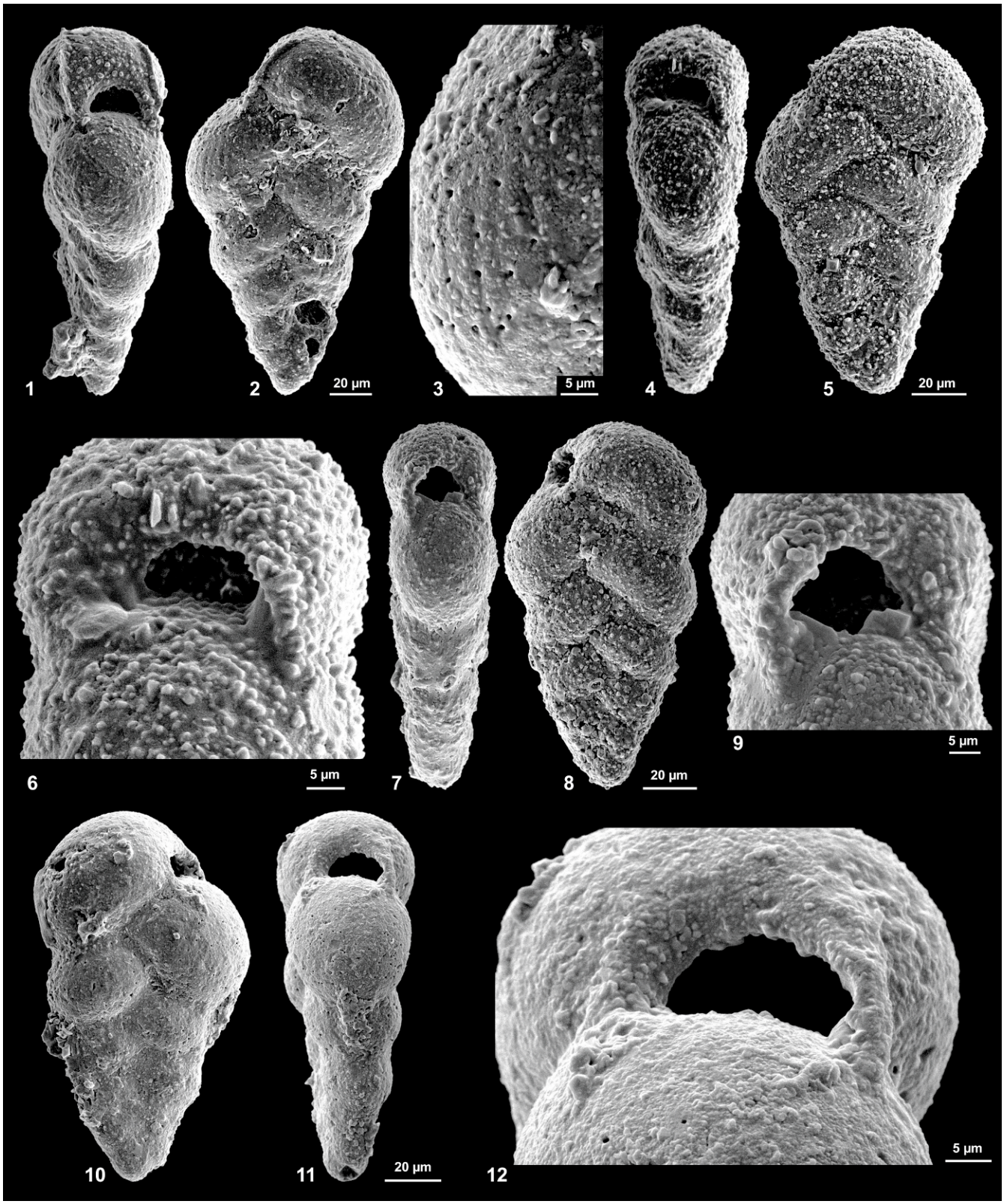


PLATE 3

Specimens of *Protoheterohelix obscura* n. gen., n. sp. from the ODP Leg 171B (Blake Plateau, western North Atlantic). 1–3 Topotype from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25R–02, 83–87 cm. 4–6 Paratype from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534387). 7–9 Paratype from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534388). 10–12 Holotype from the lower Cenomanian (*Thalmanninella globotruncanoides* Biozone), ODP Hole 1050C, Sample 25–02, 70–72 cm (USNM 534383).

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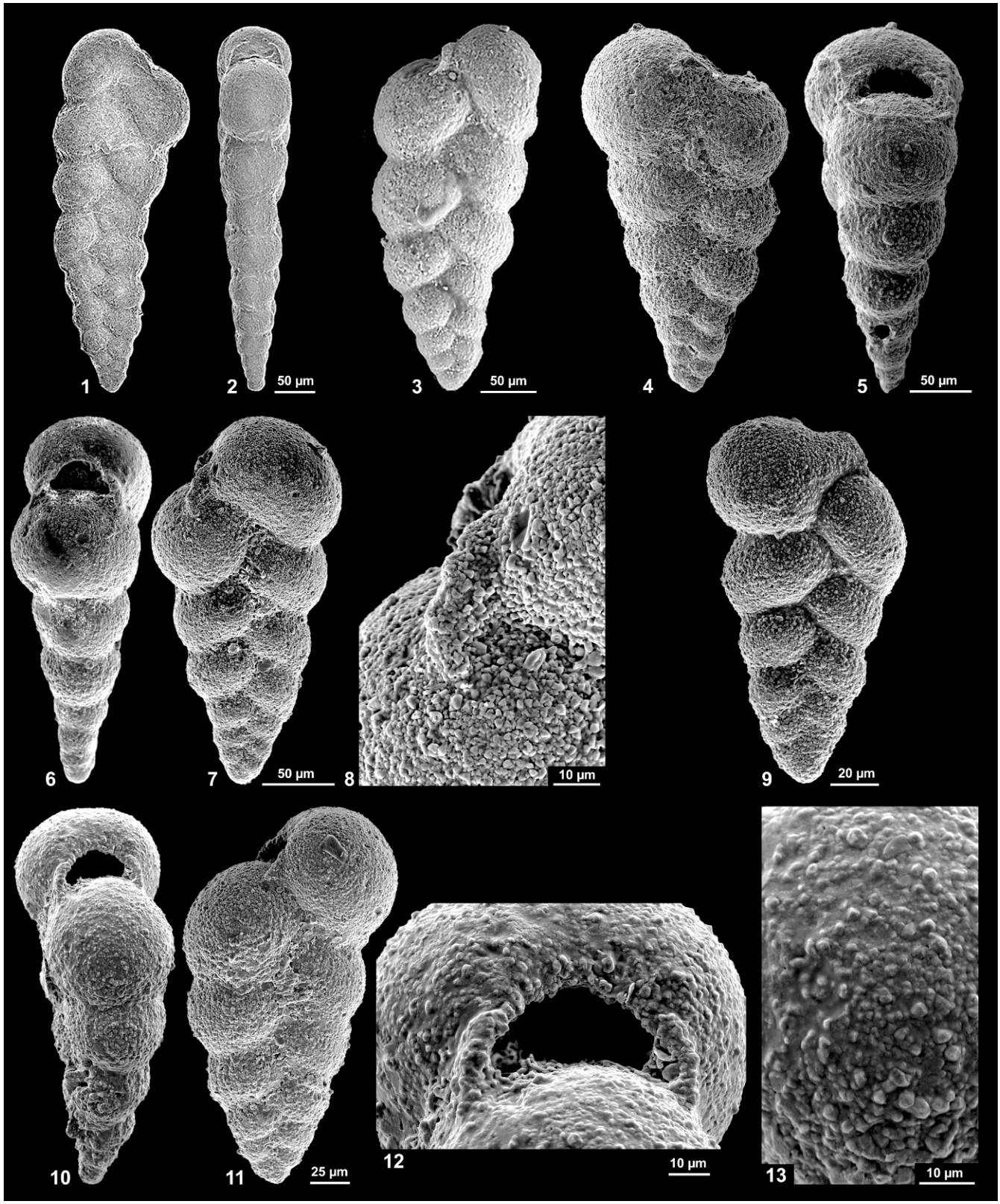


PLATE 4

Specimens of *Planoheterohelix moremani* (Cushman), 1938. 1–2 Holotype (USNM 307959) from the lower part of the Eagle Ford Shale, north of Itasca, Hill County, Texas, USA figured by Cushman (1938, pl. 2, fig. 1). 3 Paratype (USNM 307961). 4–5 Hypotype from the upper Cenomanian (*Rotalipora cushmani* Biozone), ODP Hole 1050C, Sample 21–1, 105–106 cm. 6–8 Hypotype from the upper Cenomanian (*Rotalipora cushmani* Biozone), ODP Hole 1050C, Sample 21–1, 105–106 cm. 9 Hypotype from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone), ODP Hole 1050C, Sample 20–4, 110–111 cm. 10–13 Hypotype from the upper Cenomanian (*Rotalipora cushmani* Biozone), ODP Hole 1050C, Sample 21–1, 105–106 cm.

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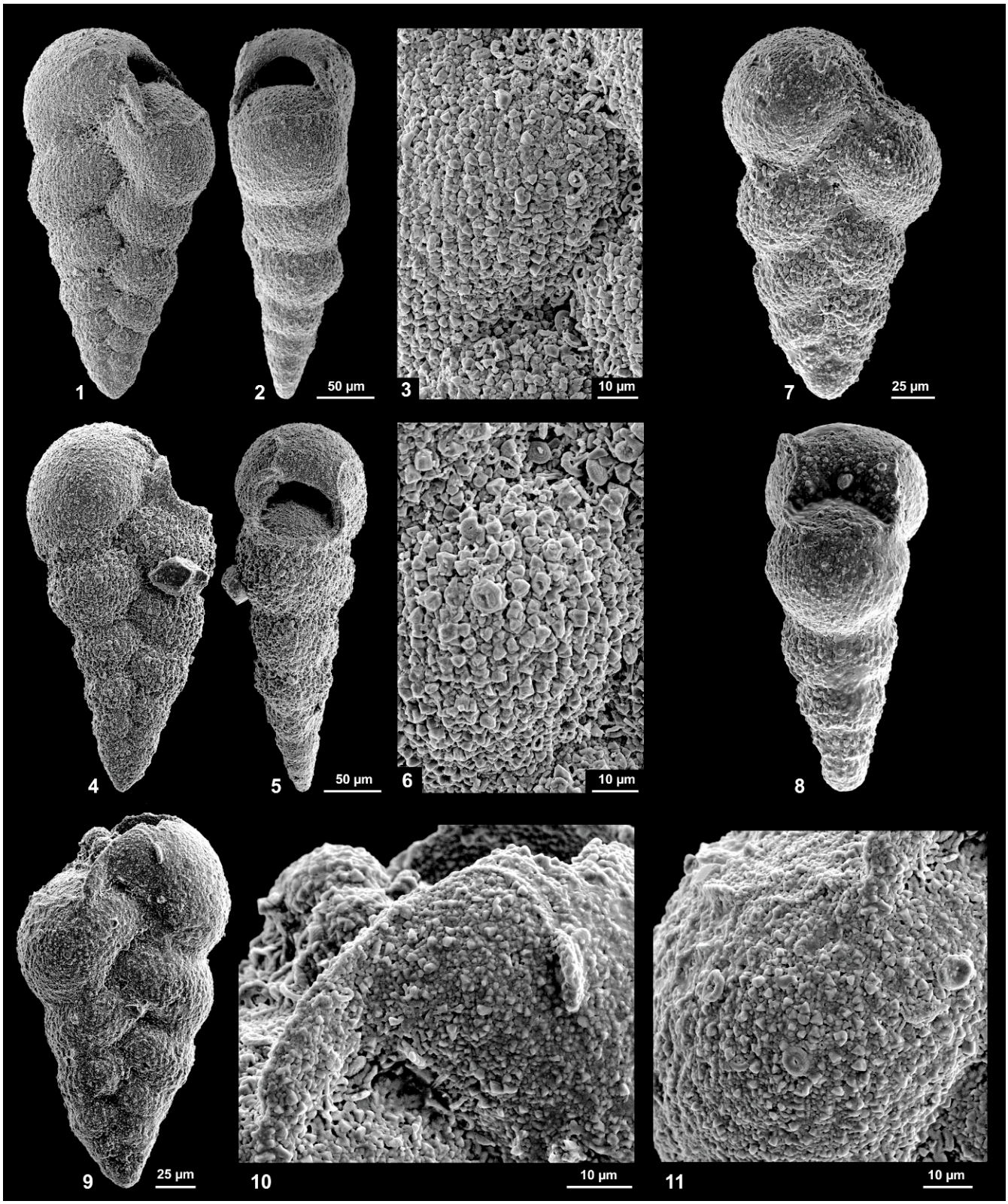


PLATE 5

Specimens of *Planoheterohelix postmoremani* n. gen., n. sp. 1–3 Holotype from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534393). 4–6 Paratype from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534394). 7–8 Hypotype from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone), ODP Hole 1050C, Sample 20–4, 110–111 cm. 9–11 Paratype from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534395).

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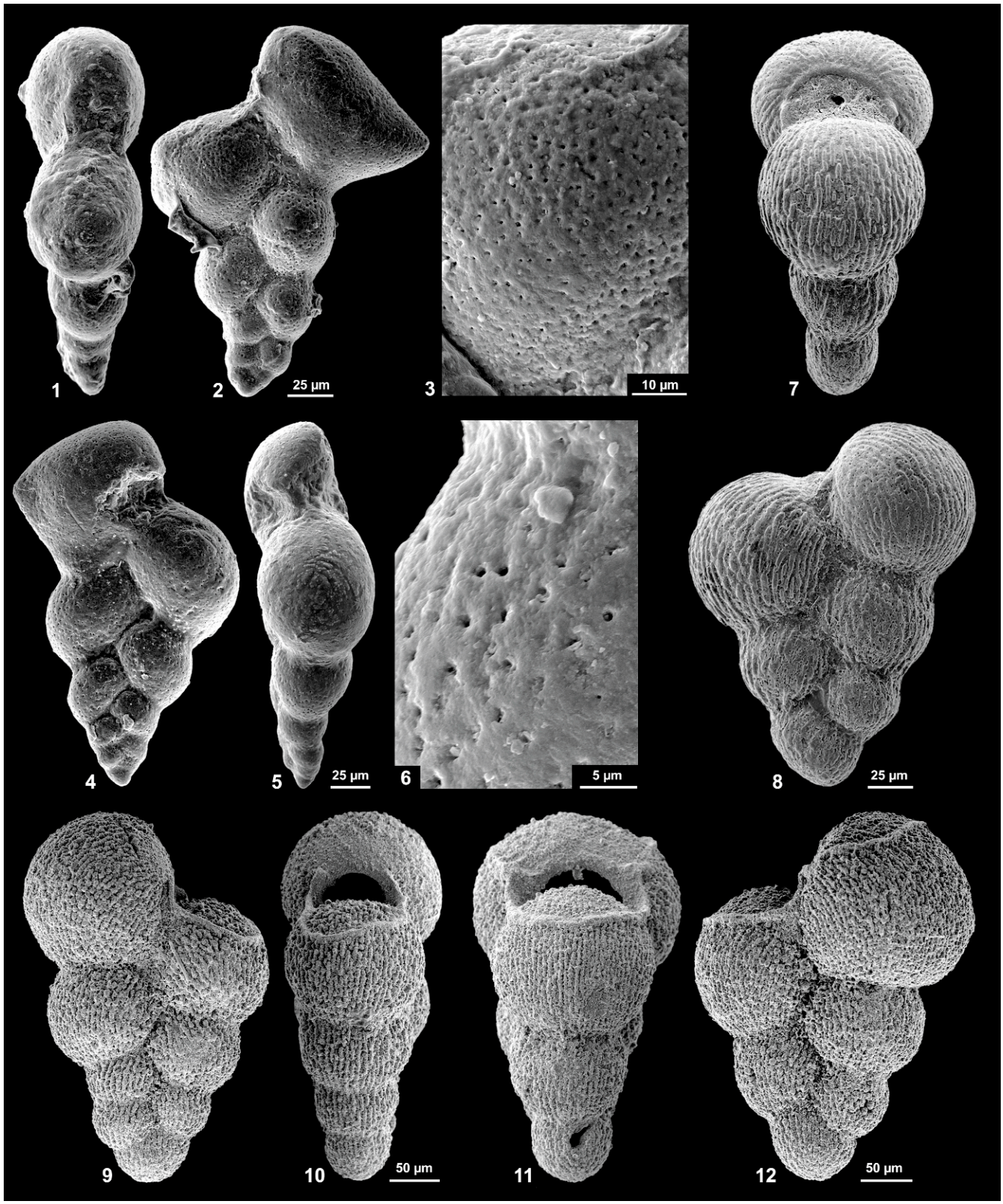


PLATE 6

Specimens of *Heterohelix americana* (Ehrenberg), 1843 (1–6) and *Globoheterohelix paraglobulosa* n. gen., n. sp. (7–12). 1–3 Hypotype of H. americana from the uppermost Cenomanian–lowermost Turonian (*Whiteinella archaeocretacea* Biozone) of western Africa (Senegal), well Rd2, sample depth 1651–1660 m (USNM 473378). 4–6 Hypotype of *H. americana* from the uppermost Cenomanian–lowermost Turonian (*Whiteinella archaeocretacea* Biozone) of western Africa (Senegal), well Rd2, sample depth 1651–1660 m (USNM 473378). 7–8 Hypotype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) of southeast Tanzania (Tanzanian Drilling Program Sample 22–33–3, 22–30 cm) with well preserved periapertural structures consisting of imperforate rims. 9–10 Holotype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534401). 11–12 Paratype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534402).

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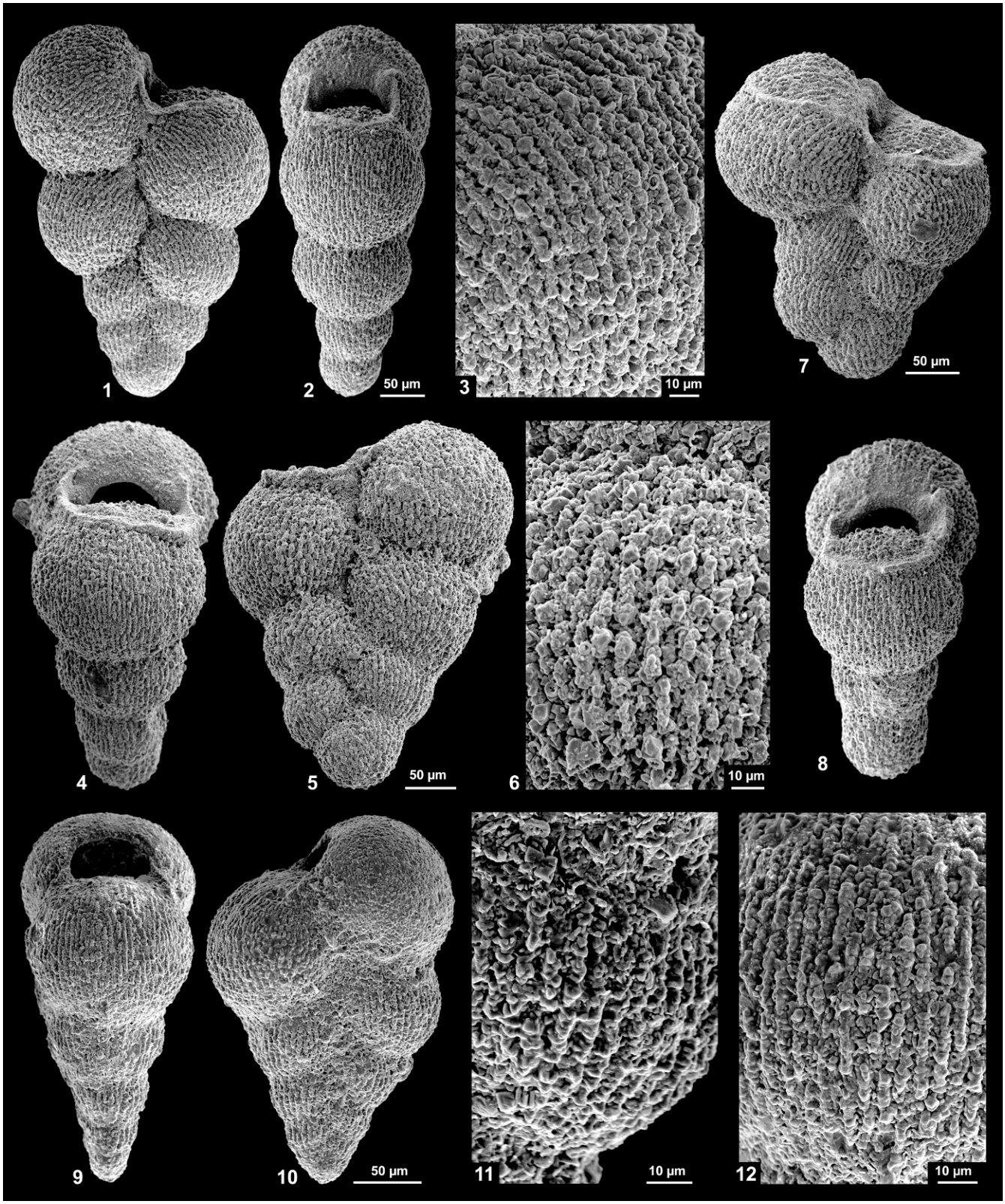


PLATE 7

Specimens of *Globoheterohelix paraglobulosa* n. gen., n. sp. (1–8) and "*Heterohelix globulosa*" Ehrenberg, 1840 (9–12). 1–3 Paratype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534403). 4–6 Paratype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534404). 7–8 Paratype of *G. paraglobulosa* from the lower Turonian (*Helvetoglobotruncana helvetica* Biozone) sediments of the equatorial Pacific (Mid-Pacific Mountains), DSDP Site 463, Sample 35–1, 17–19 cm (USNM 534405). 9–12 Hypotype "*H. globulosa*" from the upper Cenomanian (*Rotalipora cushmani* Biozone) of the western North Atlantic (Blake Plateau), ODP Hole 1050C, Sample 21–01, 72–73 cm.

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APPENDIX 1

Remarks on the concept of species in planktonic foraminifera

A stable species concept is critical to the study of fossil foraminifera because for biostratigraphic frameworks, paleoecologic and paleoceanographic interpretations, and paleobathymetry estimates are entirely or mostly based on species. A taxonomist must take into account all of the possible morphologic features in order to achieve a reliable definition of a foraminiferal species (Sigal, 1966; Reiss, 1971). Despite this, the concept of species received little attention from the taxonomists involved in the study of Cretaceous planktic foraminifera.

In the past, test morphology provided the only set of criteria used for defining Cretaceous planktic foraminiferal species. This approach in studying the fossil record led to the extensive use of the concept of typological species for many decades. However, by using this concept of species, emphasis is placed on similarities between individuals and there is no need for direct reference to the intraspecific variability. This is a major problem to be solved in the case of the fossil planktonic foraminifera, due to the existence of discrete morphological changes in the course of a species evolutionary history and, at least in some cases, significant variability during a peculiar period of their stratigraphic ranges.

Another problem in defining a paleontological species involves species continuity in the stratigraphic record, which must be considered in the context of the iterative pattern of the planktic foraminiferal evolution (Steineck and Fleisher, 1978). The importance of the stratigraphic record in defining species was emphasized by Gingerich (1979), Prothero and Lazarus (1980) and Lazarus and Prothero (1984). In contrast to these advances to understanding the fossil record and how it can be reflected in taxonomy, only the typological species was used in Cretaceous planktic foraminiferal taxonomy for more than two decades (Robaszynski and others, 1984).

The term *concept of well-documented paleontological species* was developed by Georgescu and Huber (2007) to accommodate the substantial advances in understanding species variability and the iterative pattern of the evolutionary process. We propose amending the term as *concept of composite paleontological species*. Georgescu and Huber (2007) first applied the concept to the coarsely ornamented late Campanian–Maastrichtian species *Rugotruncana circumnodifer* (Finlay, 1940). The concept was successfully tested on several heterohelicid lineages (Georgescu, 2007a, 2007b, 2009; Georgescu and Abramovich, 2008; Georgescu and others, 2009) and further proved its usefulness in recognizing the polyphyletic nature of planktonic foraminifera (Georgescu, 2009).

A new term, *concept of composite paleontological species* is proposed herein, in order to replace the older one, namely the well-documented paleontological species. Its definition is an improved version of that of Georgescu and Huber (2007): A composite paleontological species is the basic unit with taxonomic significance in the fossil record, and has the following characteristics: (1) it is monophyletic; (2) it has a distinct range of morphological variability, showing relative stability over a definable period of time and presenting relatively discrete evolutionary changes; (3) it is a morphologically heterogeneous and discontinuous entity, consisting of one or (mostly) more morphological and/or paleoecological varieties; (4) it has its own and continuous developmental history traceable in space and time, which can be directly derived from the fossil record; and (5) 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), as inferred from paleontology and related geological disciplines.

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