

EVOLUTION AND PHYLOGENY OF MID-CRETACEOUS (ALBIAN–CONIACIAN) BISERIAL PLANKTIC FORAMINIFERA

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ABSTRACT

In this paper we critically examine the biostratigraphy and systematics of late Albian–Coniacian biserial planktic foraminifera using measurements and qualitative observations from SEM and X-radiograph images of exquisitely preserved specimens from hemipelagic sediments of southeast Tanzania, augmented by analogous observations of selected Ocean Drilling Program samples and holotypes and paratypes of nearly all species. We document interspecific differences and intraspecific variability, and propose a revised phylogeny for Cretaceous biserial planktic foraminifera placed within a refined biostratigraphic framework. Taxonomic emendations are proposed for the genera *Protoheterohelix* Georgescu & Huber, 2009, and *Planoheterohelix* Georgescu & Huber, 2009, and for the species *Pr. washitensis* (Tappan, 1940), *Pr. obscura* Georgescu & Huber, 2009, *Pl. moremani* (Cushman, 1938), *Pl. reussi* (Cushman, 1938), and *Laeviheterohelix reniformis* (Marie, 1941). In addition, a neotype is designated for *Pl. globulosa* (Ehrenberg, 1840), and *Pl. praenuttalli* n. sp. is described. Biserial speciation events are recognized in the planktic foraminiferal *Rotalipora cushmani* Zone (latest Cenomanian), *Helvetoglobotruncana helvetica* Zone (early Turonian), and at the *Helvetoglobotruncana helvetica*–*Margino-truncana schneegansi* zonal boundary (middle Turonian).

INTRODUCTION

Cretaceous biserial planktic foraminifera (heterohelids) have generally been overlooked in biostratigraphic studies due to their small size and inadequate knowledge of their taxonomy and stratigraphic distribution. In fact, the most important monographs on Cretaceous planktic foraminifera from the 1970s and 1980s either did not discuss biserial taxa (e.g., Postuma, 1971; Robaszynski et al., 1984) or mentioned very few species, most of which were shown with age ranges >10 Myr (e.g., Caron, 1985). Ambiguous and contradictory early descriptions of biserial planktic taxa, loss and/or poor preservation of important biserial type specimens, uncertainties about species-level differences in gross test architecture, and lack of awareness of the importance of test ornamentation for taxonomic classification have contributed to longstanding taxonomic confusion for this fossil group (e.g., Masters, 1980; Georgescu & Huber, 2009).

Nederbragt's (1989, 1991) detailed taxonomic, biostratigraphic, and biogeographic studies of Late Cretaceous bi- and multiserial heterohelids from deep-sea drill holes led to a new appreciation of this group's utility for dating and global correlation. These papers identified four new biserial

species and were the first publications in which wall texture was used to distinguish among different biserial genera. The studies also synonymized a number of the smaller, globular, and weakly ornamented biserial taxa, conclusions justified by the argument that there was a high degree of intraspecific variation in test ornamentation and shell morphology. This taxonomic approach was conservative, and combined with inadequate preservation and incomplete records of pre-Santonian biserial specimens, may have led to the underestimation of biserial species diversity during the Cenomanian (one species) through Coniacian (four species; Nederbragt, 1991). Nonetheless, the Nederbragt heterohelid taxonomy was widely adopted and applied for the ensuing two decades. Recently, Georgescu and collaborators have published a series of taxonomic papers (e.g., Georgescu, 2007a, 2007b, 2009a; 2009b; 2010, 2012, 2013; Georgescu & Abramovich, 2008, 2009; Georgescu et al., 2008, 2011; Georgescu & Huber, 2009) that took a different tack. These papers collectively described 14 new biserial species and 15 new biserial genera (six of which are monospecific), provided numerous taxonomic emendations, and suggested profound changes in the inferred phylogenetic history of Albian–Maastrichtian serial taxa. Morphologic similarities and differences inferred from stratigraphically ordered scanning electron microscope (SEM) images were used to identify ancestor-descendant relationships and taxonomic lineages in this new evolutionary classification. The taxonomic revisions in these papers were intended to improve the biostratigraphic utility of the heterohelids and to provide a natural classification based on monophyletic relationships, but the criteria for distinguishing taxa at the genus and species level were inconsistently applied. Therefore, the practical utility of the new taxonomy has not been rigorously tested.

Recovery of extraordinarily well-preserved Cenomanian–Coniacian foraminifera from southeast coastal Tanzania (Jiménez Berrocoso et al., 2010, 2012, 2015) provides an unusual opportunity to document the early evolution and diversification of the smaller biserial planktic foraminifera. This study utilizes numerous measurements and qualitative observations from X-radiograph (X-ray) images and a large number of SEM images of biserial planktic foraminifera from Tanzanian samples and from well-preserved late Albian–Coniacian deep-sea samples to better establish ancestor-descendant relationships. These observations, along with comparison to SEM and X-ray images and measurements of holotype and paratype specimens, are used to define concise and objective taxonomic concepts at the genus and species level. Results are compared to previous systematic treatments of late Albian–Coniacian biserials. In addition, the observations are used to propose a new phylogenetic framework for the early evolution of the group. Ecology of the taxa is discussed relative to offsets in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures among three Turonian biserial

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species (*Planoheterohelix moremani*, *Pl. globulosa*, and *Pl. paraglobulosa*) from TDP Site 31 and between biserial taxa and other co-occurring planktic species in Tanzania and elsewhere.

MATERIAL

Specimens of biserial planktic foraminifera studied here are from the Tanzania Drilling Project (TDP), Deep Sea Drilling Project (DSDP), and Ocean Drilling Program (ODP) samples. Samples are identified using a standard format with reference to site number, core number, core section, and centimeter interval. A brief overview of the sites and biostratigraphy is presented below. Biserial holotypes and paratypes deposited in the Cushman Collection of Foraminifera at the Smithsonian Institution's National Museum of Natural History (NMNH; Washington, D.C.) were also studied for comparison with the TDP and deep-sea hypotype material. The type specimens are cataloged using USNM (U.S. National Museum) numbers. The online type collection can be searched at <http://collections.nmnh.si.edu/search/paleo/>.

TANZANIA DRILLING PROGRAM SITES

Clay-rich marine siltstones and mudstones in southeastern Tanzania (~30°S paleolatitude; Figs. 1, 2) have yielded some of the best preserved Late Cretaceous foraminifera in the world (Wendler et al., 2011; 2013; MacLeod et al., 2013; Huber & Petrizzo, 2014). The sediments were deposited at an upper-slope to outer-shelf paleodepth ~50–70 km from the coastline (Kent et al., 1971) on a gradually subsiding passive margin during a prolonged period of tectonic stability (Nicholas et al., 2007). Of 19 boreholes drilled during the Cretaceous Tanzania Drilling Project, one (Site 24) recovered up to 50 m of Cenomanian claystones with sandstone intercalations, three (Sites 21, 22, and 31) recovered at least 100 m of Turonian claystones, and one (Site 39) recovered 100 m of Coniacian–Santonian claystones. None of the Cenomanian–Turonian sites recovered a complete boundary interval due to drilling problems and an unconformity or local faulting (Jiménez Berrocoso et al., 2010, 2012, 2015). Presence of a diverse planktic foraminiferal assemblage throughout the Upper Cretaceous enables correlation with standard tropical/subtropical biozonation schemes (e.g., Robaszynski & Caron, 1995).

The distribution of biserial taxa was studied most intensively at TDP Site 31 (Fig. 3, Appendix 1). The site was drilled to 115 meters below the surface (mbs) and, based on the planktic foraminiferal biostratigraphy of Huber & Petrizzo (2014), is biostratigraphically complete from the lower Turonian (lower *Helvetoglobotruncana helvetica* Zone) to the uppermost Turonian (*Dicarinella concavata* Zone). For most Site 31 samples, planktic foraminifera average ~50% of the total foraminiferal assemblage with relative abundance ranging between 40–70% (Huber & Petrizzo, 2014).

Samples from TDP Site 24 include the oldest material recovered in Tanzania and were carefully searched to document biserial first and last occurrences and species diversity (Appendix 2). Recovered cores range from the

upper Albian (*Planomalina buxtorfi* Zone) to the lower Turonian (*Whiteinella archaeocretacea* Zone) with unconformities between the upper Albian (*Pl. buxtorfi* Zone) and lower Cenomanian (lower *Thalmaninella globotruncanoides* Zone), and between the middle Cenomanian (upper *Th. globotruncanoides* Zone) and lower Turonian (*Wh. archaeocretacea* Zone; updated from Jiménez Berrocoso et al., 2010). The hole was drilled to 74 m, and the lithologies recovered are mainly interbedded fine-grained sandstones and dark gray siltstones (Jiménez Berrocoso et al., 2010).

DEEP SEA DRILLING PROGRAM SITE 463

Deep Sea Drilling Program (DSDP) Leg 62, Site 463, was drilled in the equatorial Pacific Ocean (Mid-Pacific Mountains) at 22°S paleolatitude (94 Ma; Hay et al., 1999; Fig. 2), and had a paleowater depth of ~1 km (Winterer & Sager, 1995). Average core recovery in the ~225 m upper Albian–Coniacian sequence of nannofossil chalk was only 18% (Theide et al., 1981). Foraminifer shells in this interval are moderately to strongly recrystallized, but shell interiors and surfaces are devoid of secondary calcite. Washed residues from Cenomanian–Turonian cores 27–39 were used to document the stratigraphic ranges of biserial species (Appendix 3) for comparison with previous observations. Ages assigned to the Cenomanian–Coniacian sediments are based on the strontium isotope chemostratigraphy and planktic foraminifer biostratigraphy of Ando et al. (2009), who determined that this interval is expanded and chronostratigraphically complete.

OCEAN DRILLING PROGRAM HOLE 1050C

An ~200-m thick sequence of upper Albian–Maastrichtian nannofossil claystones and nannofossil chalks was cored in Ocean Drilling Program (ODP) Leg 171B, Hole 1050C, on Blake Nose. The site was at a middle-bathyal paleowater depth at ~25°N paleolatitude during the Late Cretaceous (Norris & Wilson, 1998; Fig. 2). The sequence is chronostratigraphically complete except for a hiatus across the Cenomanian–Turonian boundary interval and several hiatuses and hardgrounds within a condensed Turonian–lower Campanian interval. About 20 samples from Hole 1050C were studied to estimate the stratigraphic distribution and diversity of biserial species in the North Atlantic (Appendix 4).

METHODS

SAMPLE PREPARATION

Samples from the TDP, DSDP, and ODP cores were disaggregated in tap water, washed on a 63- μ m sieve, and dried at 50°C. For TDP Site 31, foraminiferal samples were taken at 0.5–1.0 m intervals. Relative abundances of taxa were calculated from counts on the >125 μ m fraction, which was divided using a microsplitter with the goal of having ≥ 300 benthic specimens per sample. Benthic taxa are being addressed in a separate study (Wendler et al., unpublished data), but the counts were done in parallel, and, because benthics are less abundant than planktics in

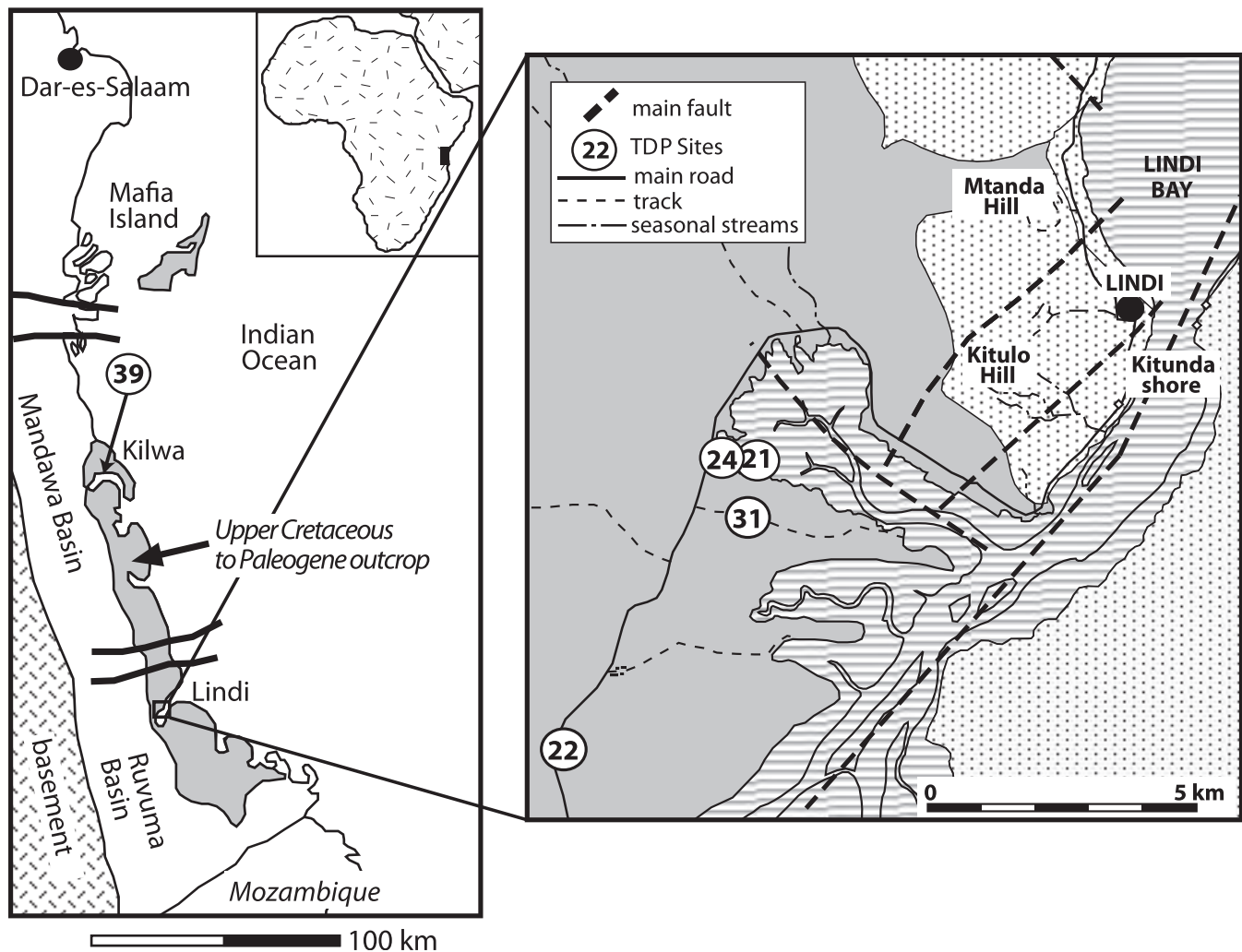


FIGURE 1. Map of TDP sites of interest drilled in Tanzania (gray represents Cretaceous sediments, horizontal patterns represents mangrove swamps). Map from MacLeod et al. (2013), originally figured in Jiménez Berrocoso et al. (2010).

most samples, benthic abundance was the factor that determined the fraction of each sample counted.

BIOMETRIC DATA

Observations and measurements of test features were taken from SEM, X-ray, and reflected light microscopy images and processed using the National Institutes of Health biometric program ImageJ™. Gross test architecture, test ornamentation, and wall pores were largely documented using a Phillips XL-30 Environmental Scanning Electron Microscope. Specimens sputter coated in gold/palladium were imaged under high vacuum and 10 kV accelerating voltage, whereas uncoated primary type specimens were imaged under low vacuum, using 20 kV accelerating voltage and the backscatter detector. X-radiograph (X-ray) images show internal structures and growth patterns. Specimens with no suspected infilling were selected for X-ray images, and mounted in a plastic slide with a grid of aligned holes that was underlain with cellophane tape. A strip of SO 253 High Speed Holographic Kodak film was placed below the slide, and both were

inserted into a Faxitron X-ray machine and exposed for 2.5 minutes at 20 KV. Transmitted light images were obtained using a digital camera mounted on a Leitz Orthoplan microscope.

SYSTEMATIC TAXONOMY

The history of the taxonomic classification of Cretaceous biserial planktic foraminifera was discussed in Georgescu & Huber (2009). They described several new genera and species and proposed fundamental changes to biserial classification and phylogeny based on observations of stratigraphically ordered SEM images primarily from deep-sea sites. The revisions, as well as those presented in Georgescu (2007a), form the basis for the classification adopted herein, albeit with some modifications. In this study ancestor-descendant relationships at the genus level are inferred using stratophenetic observations of changes in the symmetry of apertural and periapertural structures, test breadth:width ratio, wall surface texture (e.g., smooth, pustulose, weakly to coarsely costate, presence or absence of pore mounds), and presence or absence of specialized test

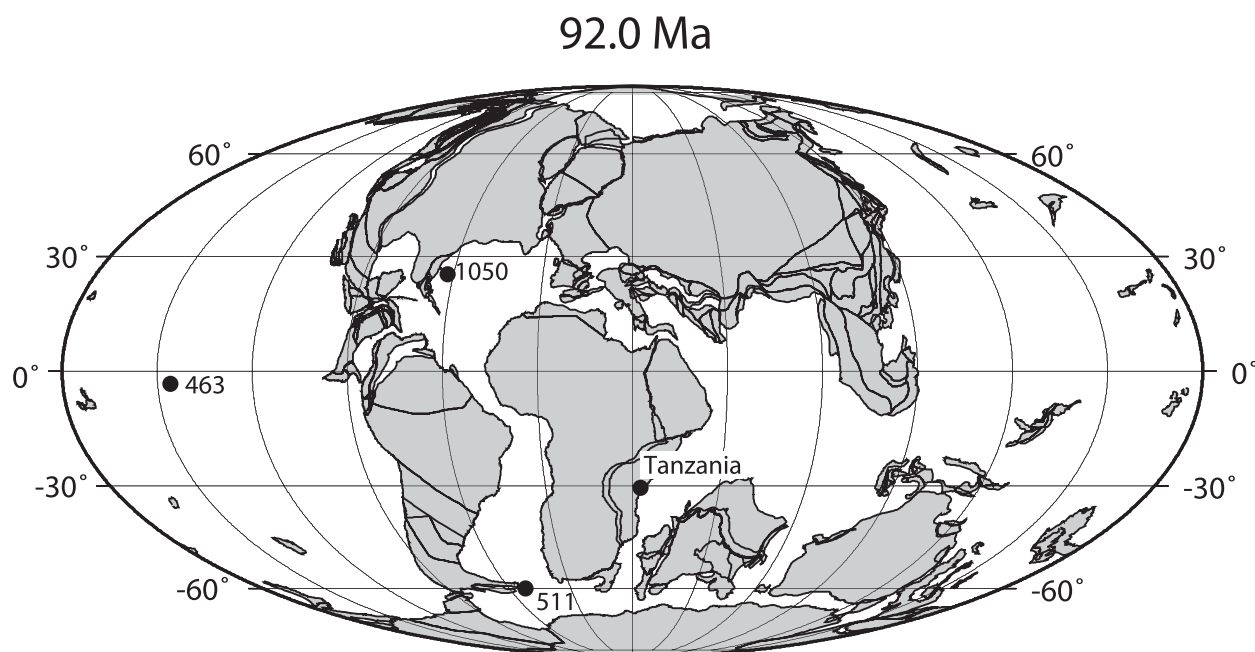


FIGURE 2. Paleogeographic reconstruction for 92 Ma based on Hay et al. (1999), showing locations of sites discussed in this study. Falkland Plateau (DSDP Site 511) is illustrated here but not described in the text, because only three previously unillustrated hypotypes (one each of *Planoheterohelix reussi*, *Laeviheterohelix reniformis*, and *Lv. pulchra*), taken by Brian Huber at the NMNH in Washington D.C., are illustrated here in Figures 18 and 25.

features (e.g., sutural flexure, chamber projections). The presence of clear offsets in proloculus and test size (i.e., length, breadth, cross-sectional area of chambers) among populations is used to discriminate between species. As noted by Georgescu & Huber (2009), the earliest biserial planktic foraminifera are nannoperforate (pore diameter = 0.1–0.5 μm) and Cenomanian–Coniacian biserial taxa are mostly micropore (pore diameter = 0.5–1.0 μm). Tests with finely perforate (1.0–2.5 μm) pores developed during the late Cenomanian and occur in some Turonian–Coniacian forms. Macropore forms (pore diameter > 2.5 μm) do not evolve until the late Turonian. However, pore diameter is variable among the Albian–Coniacian biserial species and is not considered useful for species-level separation.

The systematic taxonomy section that follows is presented in stratigraphic order of first occurrence for the biserial genera and species described. Specimens selected for illustration express the diagnostic features well, and document the range of morphologic variability for each species concept, with an emphasis on forms that most closely resemble the species' holotype.

Supergroup RHIZARIA Cavalier-Smith, 2002
 Class FORAMINIFERA d'Orbigny, 1826
 Order GLOBIGERININA Delage & Hérouard, 1896
 Suborder ROTALIINA Delage & Hérouard, 1896
 Superfamily HETEROHELICACEA Cushman, 1927
 Family HETEROHELICIDAE Cushman, 1927
 Genus *Heterohelix* Ehrenberg, 1843
 Type species: *Textilaria americana* Ehrenberg, 1843

Remarks. The history of *Heterohelix* was discussed in detail by Georgescu & Huber (2009) and is summarized below. The genus was first described by Ehrenberg (1843)

for *Textilaria americana* with the following description (translated by Frerichs & Gaskill, 1978): “*T. americana*, small, more often microscopic, rapidly expanding, smooth, proloculus globular (1/300ths of a unit), chambers ovate, final chambers produced into a spine. In some specimens the early chambers are coiled in a spiral. Such forms, perhaps, should be assigned to a new genus: *Heterohelix*.” The following year Ehrenberg (1844) introduced *Spiroplecta americana* for forms with an early planispiral coil followed by a biserial growth stage comprised of globular chambers (see discussion in Georgescu & Abramovich, 2009). Ehrenberg's two very different descriptions using the same species names assigned to different genera have caused considerable confusion in the taxonomy of the heterohelids during the past 160 years.

Following the designations of *Heterohelix* and *Spiroplecta*, the genus *Guembelina* was created by Egger (1899) to include species that are biserial throughout their ontogeny, with no initial planispiral coil. Cushman (1927) determined that *Spiroplecta* was a junior synonym of *Heterohelix*, because of publication date priority. He placed *Heterohelix* in the Subfamily Heterohelicinae based on the presence of an initial coil and *Guembelina* in the Subfamily Guembelininae based on only biserial growth. *Guembelina* was commonly used for biserial heterohelids until it was placed in synonymy under *Heterohelix* by Loeblich (1951) and Montanaro Gallitelli (1957), who concluded that a coiled early ontogeny was quite common in most biserial species. The genus *Guembelina* was later invalidated by Loeblich & Tappan (1961) because of its prior use for a Carboniferous microfossil that had been named by Kuntze in 1895. Since the synonymization and invalidation of *Guembelina*, *Heterohelix* has been used as the genus for

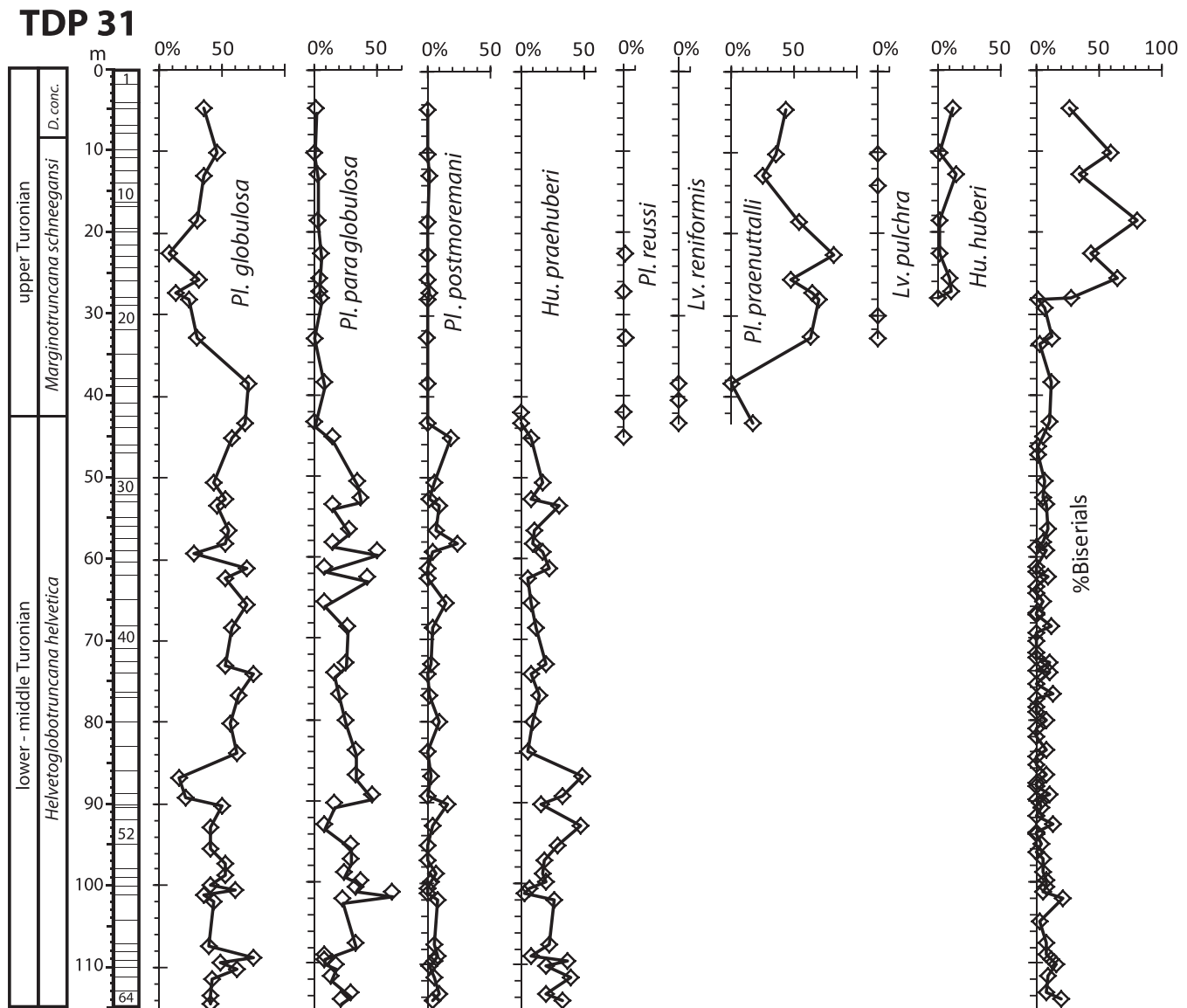


FIGURE 3. Range chart for TDP Site 31, showing distribution of biserial species and the percentage of biserial specimens relative to the total planktic foraminiferal assemblage. Depths are in meters below surface (mbs). Planktic foraminiferal biozonation scheme is based on Huber & Petrizzo (2014).

many biserial species, including *Planoheterohelix moremani* (Cushman, 1938), *Pl. globulosa* (Ehrenberg, 1840), *Pl. reussi* (Cushman, 1938), and *Protoheterohelix washitensis* (Tappan, 1940). Because of the distinct test architecture (i.e., the lateral projections from adult chambers) of the *americana* type specimen first assigned to the genus *Heterohelix*, simple biserial species such as *Pl. globulosa* do not fit the original concept of *Heterohelix* (Georgescu & Abramovich, 2009); therefore, new genera such as *Protoheterohelix*, *Planoheterohelix*, and *Globoheterohelix* have been proposed to accommodate such species (Georgescu & Huber, 2009).

Genus *Protoheterohelix* Georgescu & Huber, 2009
Type species: *Guembelina washitensis* Tappan, 1940

Original description. “Test is biserial throughout, with variable asymmetry as seen in edge view. Earlier species display twisted tests and asymmetrical periapertural struc-

tures; evolved ones show 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 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, nanoporolate to microporolate.”

Remarks. The main features distinguishing species of *Protoheterohelix* from descendant species of *Planohetero-*

helix are the former's small size (generally <200 µm in length), completely smooth test surface, and asymmetry of the aperture and periapertural structures (Figs. 4, 5).

Protoheterohelix washitensis (Tappan, 1940)
Figs. 4.1–4.4

Guembelina washitensis Tappan, 1940, p. 115, pl. 19, fig. 1 [lower Cenomanian, Texas (Grayson Formation)].

Laeviheterohelix sp., Petrizzo & Huber, 2006a, pl. 1, fig. 2 [upper Albian, western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Protoheterohelix washitensis (Tappan). Georgescu & Huber, 2009, p. 340, pl. 1, figs. 3–14 [upper Albian–lower Turonian, Texas, western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Type specimens. Holotype: USNM CC 25096, paratypes: USNM CC 44711 (seven specimens).

Type level. Upper Albian.

Type locality. Grayson Formation, Texas.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test tiny, biserial, tapering gradually; chambers globular, closely appressed; sutures distinct, depressed, more angular toward the base, nearly straight among the later chambers; wall calcareous, finely perforate, surface smooth; aperture low, semilunate, at the base of the last formed chamber. Length of holotype, 0.21 mm; breadth, 0.12 mm; thickness, 0.08 mm.”

Emended description. Test is small, subtriangular in lateral outline, with lengths from 126–211 µm ($n = 10$) and 11–15 ($n = 9$) biserially arranged chambers that have either a straight or twisted arrangement. Chambers are globular and slightly appressed in the axial direction, showing little lateral overlap in side view. Proloculus is small (diameter = 13–24 µm, $n = 7$), and subsequent chambers increase slowly in size, creating a gradually tapering outline. Sutures are straight, moderately depressed and formed at a right to slightly oblique angle relative to the central growth axis. Aperture is an asymmetrical, semicircular arch formed at the base of the final chamber with an imperforate margin, and is generally bordered by apertural flanges that are unequally developed. Test wall is calcitic, nannoperforate (pore diameter = 0.7–0.8 µm, $n = 2$), and completely smooth.

Distinguishing features. *Protoheterohelix washitensis* differs from other heterohelid taxa in having an asymmetrical aperture, a smooth wall texture, and globular chambers throughout its ontogeny.

Remarks. The test size, chamber globularity, and apertural asymmetry of the holotype and paratypes of *Pr. washitensis* are very similar (Figs. 4.1–4.3). The edge view of the holotype and side and edge views of two paratypes are illustrated for the first time in Figures 4.1–4.3. Despite test infilling and wall recrystallization, wall preservation in the primary types is sufficiently good to reveal a completely smooth wall surface devoid of costae or pore mounds (Figs. 4.1–4.3). A very well preserved specimen of this species from the upper Albian of ODP Hole 1050C (Fig. 4.4) also shows a completely smooth test surface.

Protoheterohelix washitensis was originally distinguished from its presumed descendant, *Pr. obscura* Georgescu & Huber, 2009, by having a twisted rather than straight biserial chamber arrangement. Forms currently assigned to

Pr. washitensis commonly have a twisted biserial arrangement, whereas this feature also occurs rarely in *Pr. obscura* (Figs. 4.7b, 4.8b). We use chamber shape and arrangement as additional features to differentiate between species. Both species however, show a similar ontogenetic increase in cross-sectional chamber area (Fig. 7a; Appendix 5).

Similar species. *Protoheterohelix washitensis* differs from *Pr. obscura* in having 1) generally more elongate tests, 2) a greater number of total chambers in adult tests (11–15 rather than 10–13), 3) chambers that do not significantly overlap and that are globular rather than reniform. It differs from *Planoheterohelix moremani* in being smaller and having an asymmetrical aperture and a smooth test with no evidence of costae.

Phylogenetic relationships. Details of wall microstructure and apertural characteristics suggest that the ancestor of *Pr. washitensis* is not the late Albian benthic species *Praplanctonia globifera* Georgescu, 2009b, contrary to the phylogeny suggested by Georgescu & Huber (2009). Determination of whether the direct ancestor of *Pr. washitensis* was planktic or benthic will require detailed study of well-preserved material with identification of transitional forms that show a clear link between *Pr. washitensis* and its proposed benthic ancestor. *Protoheterohelix washitensis* is considered to be the direct ancestor of *Pr. obscura* and *Pl. moremani* (Fig. 8).

Stratigraphic range. The lowest occurrence of *Pr. washitensis*, documented by Georgescu & Huber (2009), is in the upper Albian (*Pseudothalmaninella ticinensis* Zone) and the highest occurrence is in the lower-middle Cenomanian (*Thalmaninella globotruncanoides* Zone; Fig. 8, Appendix 2).

Geographic distribution. United States (Texas), western North Atlantic Ocean (Blake Plateau), Africa (Tanzania).

Stable isotope paleoecology. No data available.

Protoheterohelix obscura Georgescu & Huber, 2009
Figs. 4.6–4.12

Heterohelix moremani (Cushman). Nederbragt et al., 1998, pl. I, fig. 2 [lower Cenomanian, southern North Atlantic (Mazagan Plateau, northwest African Margin, DSDP Leg 79, Hole 547A)].

Protoheterohelix obscura Georgescu & Huber, 2009, p. 342, pl. 2, figs. 5–11 [lower Cenomanian (*Thalmaninella globotruncanoides* Zone), western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)], pl. 3, figs. 1–12 [lower Cenomanian (*Th. globotruncanoides* Zone), western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Type specimens. Holotype: USNM 534383, paratypes: USNM 534384–534388.

Type level. Lower Cenomanian (*Th. globotruncanoides* Zone).

Type locality. Western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C), 30°05.99'N/76°14.10'W.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test is small, consisting of 11–13 biserially arranged chambers throughout. Proloculus is small (9.1–14.3 microns) 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. Sutures are straight to slightly curved, distinct and depressed and oblique to the

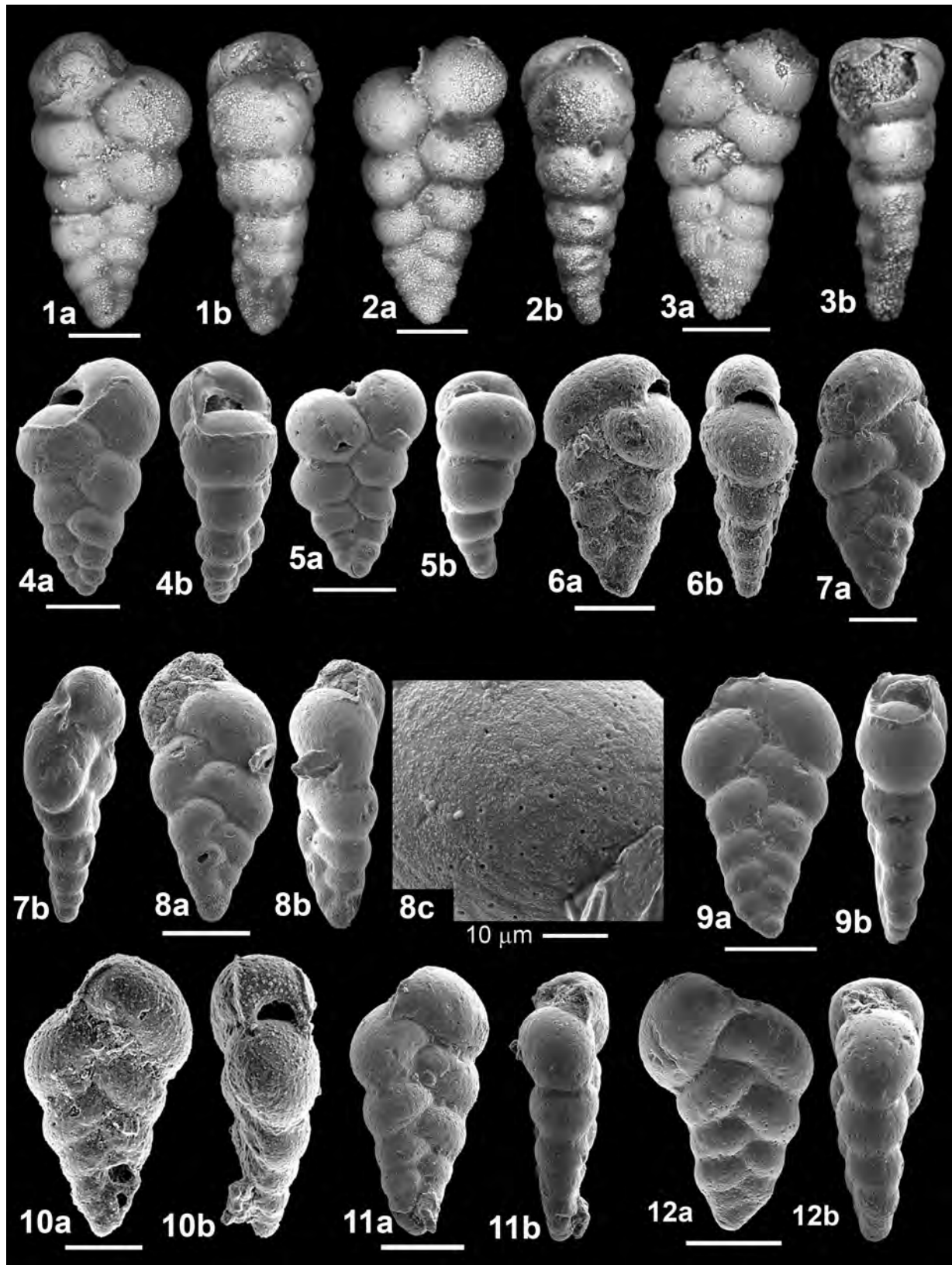


FIGURE 4. *Protoheterohelix washitensis* (Tappan, 1940) and *Pr. obscura* (Georgescu & Huber, 2009). Scale bars = 50 μ m and all SEMs were taken at the National Museum of Natural History, Washington, D.C., unless otherwise noted. 1–5 *Pr. washitensis*; 1–3 from lower Cenomanian, Grayson Bluff, Texas, U.S.A.: 1, Holotype (USNM CC 25096), originally illustrated as a drawing by Tappan (1940, pl. 19, figs. 1a, b), also figured by Georgescu & Huber (2009, p. 350, pl. 1, figs. 1, 2), new SEMs (1a, b) taken at National Museum of Natural History, Washington D.C.; 2, Paratype (USNM CC 44711), previously unillustrated; 3, Paratype (USNM CC 44711), previously unillustrated; 4, lower Cenomanian (*Thalmaninella*

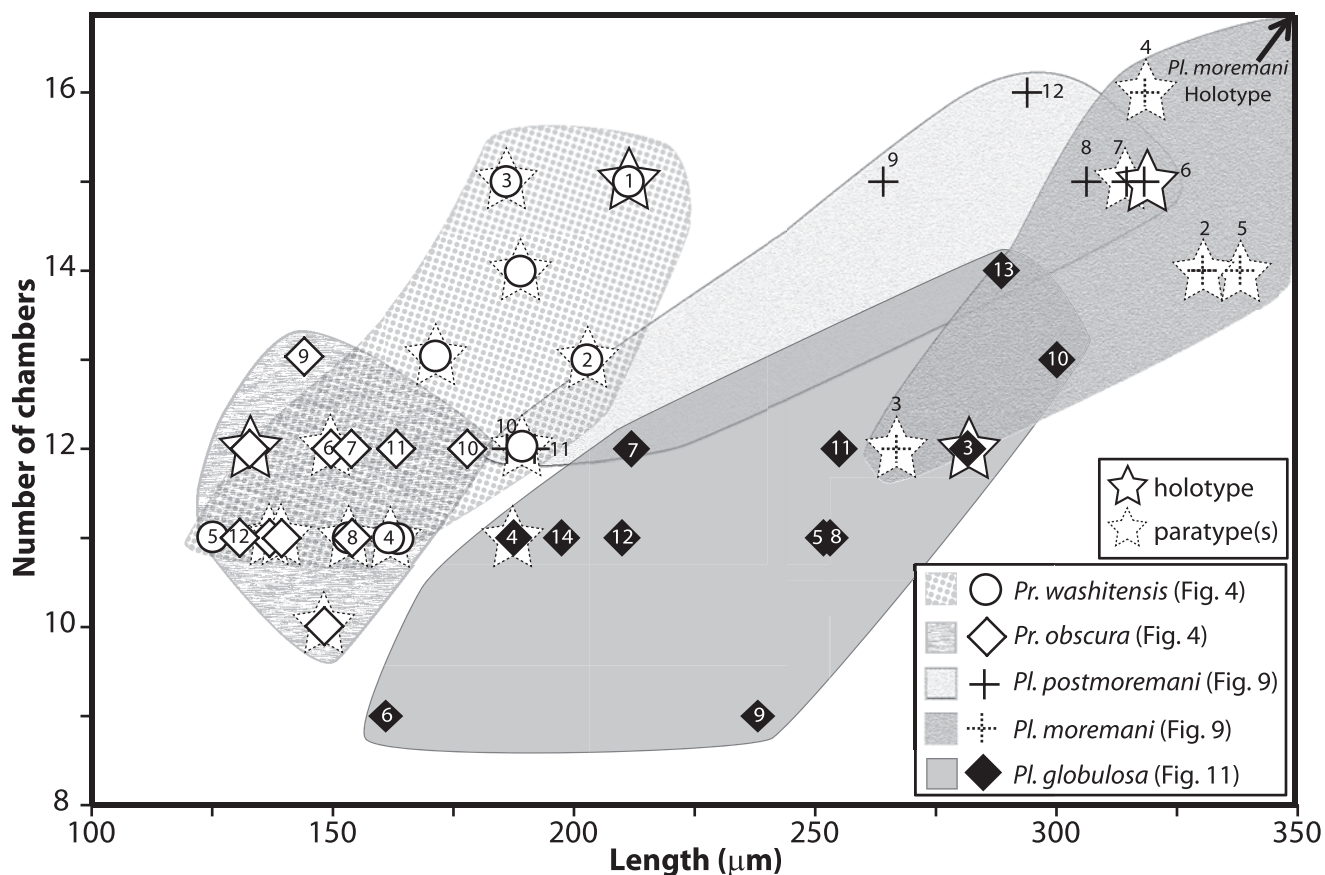


FIGURE 5. Length vs. number of chambers for *Protoheterohelix washitensis*, *Pr. obscura*, *Planoheterohelix moremani*, *Pl. postmoremani*, and *Pl. globulosa*. Marker numbers indicate measured specimen's illustration number on the figure.

test axis of growth. Tests are symmetrical in edge view, with periphery broadly rounded. Aperture is an interiomarginal, low- to medium-high arch bordered by two unequally developed periapertural flanges. Chamber surface is smooth. Test wall is calcitic, hyaline, and nannoperforate to microperforate; pore diameter ranges 0.4–0.9 microns.”

Emended description. Test is small (averaging 147 μm in length, $n = 11$) and consists of 10–13 ($n = 11$) biserially arranged chambers with a straight or twisted orientation. Earliest chambers are globular, but become reniform, and begin to overlap previous chambers by the fourth or fifth chamber. Proloculus is small (12–18 μm in diameter, $n = 9$) and subsequent chambers gradually increase in size resulting in a subtriangular outline in side view. Sutures are moderately depressed and straight to slightly curved, meeting the central axis at an oblique angle, creating a zigzag medial suture. Aperture is an asymmetrical semicircle with a low

arch at the base of the final chamber and is bordered by asymmetrical flanges. Test wall is calcitic, hyaline, and microperforate, with pore diameters ranging from 0.6–0.8 μm ($n = 4$). Surface is usually smooth, but some specimens are ornamented with faint striations and weakly developed, flat-topped pore mounds ~2 μm in diameter ($n = 3$); however, these features are exceptionally rare (Fig. 4.10).

Distinguishing features. *Protoheterohelix obscura* is distinguished from other heterohelicid taxa by having 1) reniform adult chambers, 2) an asymmetrical rather than symmetrical aperture, and 3) a generally smooth test surface.

Remarks. Most SEM images of well-preserved specimens from Tanzania show a characteristic, generally smooth wall texture; however, occasional specimens show evidence of weakly developed costae (Fig. 4.10a) and faint pore mounds (Figs. 4.8a–c), which were previously undocumented. Although the original description of *Pr. obscura* states

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globotruncanoides Zone), Spl. TDP 24-9-2, 38–55 cm; 5, upper Albian (*Parathalmanninella appenninica* Zone), western North Atlantic Ocean (Blake Nose), ODP Hole 1050C, Spl. 27-1, 19–21 cm. 6–12 *Pr. obscura*; specimens come from the (*Th. globotruncanoides* Zone) unless otherwise noted: 6, Paratype (USNM 534384), lower Cenomanian, western North Atlantic Ocean (Blake Nose), ODP Hole 1050C, Spl. 25-02, 70–72 cm, images from Georgescu & Huber (2009, pl. 2, figs. 5, 6); 7, upper Cenomanian, Spl. TDP 24-23-1, 28–38 cm; 8, lower Turonian (*Whiteinella archaeocretacea* Zone), Spl. TDP 24-5-1, 7–24 cm; 9, lower Cenomanian, Spl. TDP 24-16-1, 76–97 cm; 10, Topotype, lower Cenomanian (age based on Ando et al., 2009), western North Atlantic Ocean (Blake Nose), ODP Hole 1050C, Spl. 25-2, 83–87 cm, images from Georgescu & Huber (2009, pl. 3, figs. 1, 2); 11, 12, upper Cenomanian, Spl. TDP 24-23-1, 28–38 cm.

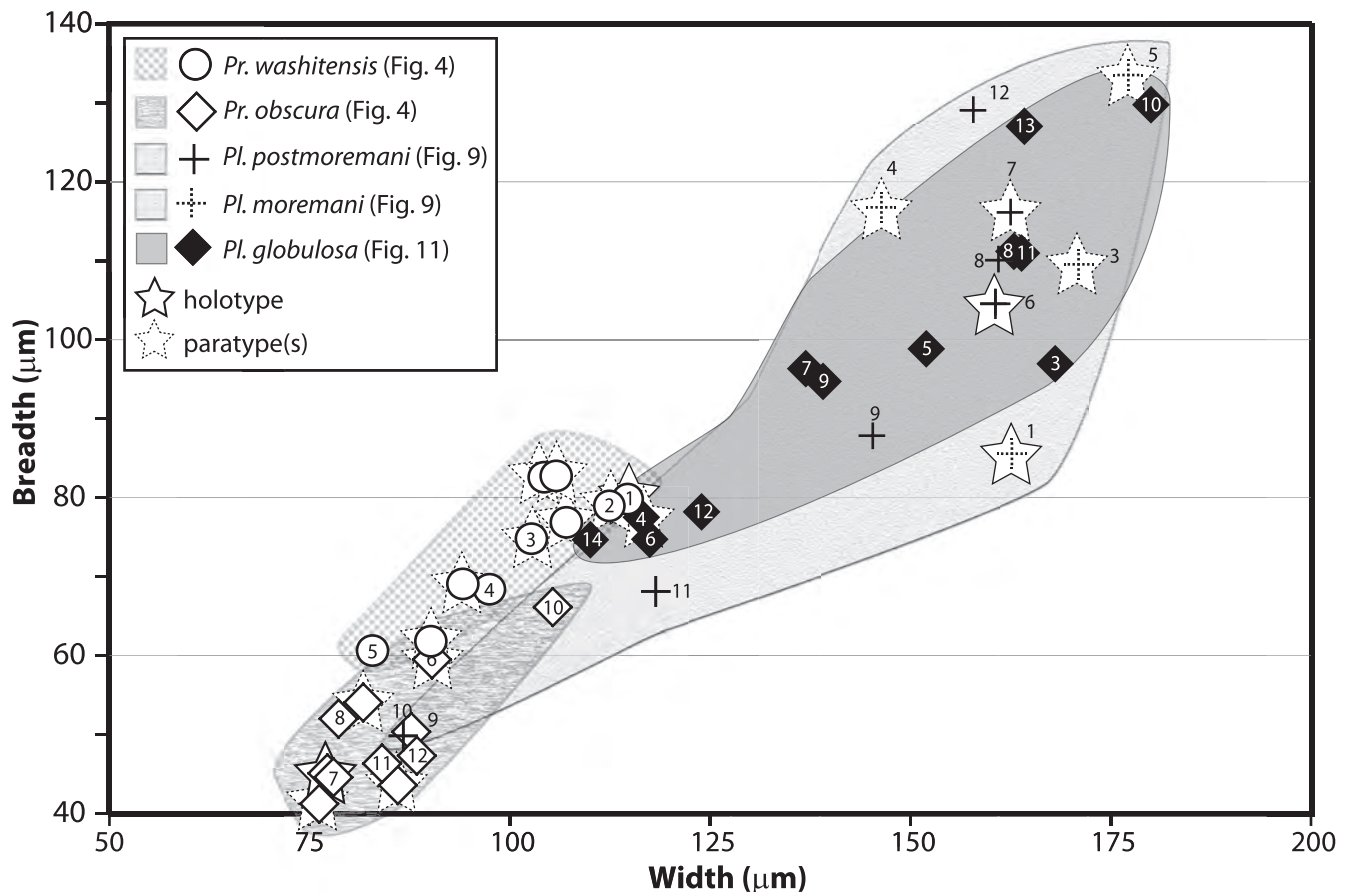


FIGURE 6. Width vs. breadth for *Protoheterohelix washitensis*, *Pr. obscura*, *Planoheterohelix moremani*, *Pl. postmoremani*, and *Pl. globulosa*. Marker numbers indicate measured specimen's location on respective figure.

that the diameter of the proloculus ranges from 9.1–14.1 μm (Georgescu & Huber, 2009), no measurements $<12 \mu\text{m}$ were encountered in the present study (Appendix 5). In addition, the original species description refers to it being nannoperforate to microperforate; each of the four images that had high enough resolution to take precise pore measurements indicates that the species is microperforate (Appendix 5).

The reniform chambers are here considered diagnostic of *Pr. obscura* and are recognizable even in strongly recrystallized specimens (Figs. 4.9a, b). Although the original description of *Pr. obscura* states that it differs from its ancestor *Pr. washitensis* by having a test profile that is symmetrical and straight rather than asymmetrical and twisted, Tanzanian specimens with reniform chambers show both twisted and straight biserial chamber arrangements (Figs. 4.6–4.8).

Measurements comparing test length vs. number of chambers (Fig. 5) and test width vs. breadth (Fig. 6) show that *Pr. obscura* is a small species that largely occupies a distinct morphospace and typically has fewer chambers than the other Cenomanian–Turonian heterohelids. *Protoheterohelix washitensis* and *Pr. obscura* have a slower rate of chamber-size increase than the younger heterohelids (Fig. 7A).

Similar species. It differs from *Planoheterohelix moremani* and *Pl. postmoremani* by 1) having an asymmetric aperture,

2) being smaller in size, and 3) commonly having a smooth, unornamented test. It differs from *Laeviheterohelix pulchra* in having 1) a smaller size, 2) more poorly developed or no true pore mounds, and 3) an asymmetric aperture. See “Similar species” section of *Pr. washitensis* for more comparisons.

Phylogenetic relationships. The species descended from *Pr. washitensis*, probably during the early Cenomanian, and has no known descendants (Fig. 8).

Stratigraphic range. It occurs in the lower Cenomanian (*Thalmaninella globotruncanoides* Zone) to the upper Cenomanian (*Rotalipora cushmani* Zone) at ODP Hole 1050C (Fig. 8; Appendix 4; Georgescu & Huber, 2009). This species was identified in the lowermost *Th. globotruncanoides* Zone at TDP Site 24 (Appendix 2).

Geographic distribution. Africa (Morocco, Tanzania), southern North Atlantic Ocean (Mazagan Plateau), western North Atlantic Ocean (Blake Plateau).

Stable isotope paleoecology. No data available.

Genus *Planoheterohelix* Georgescu & Huber, 2009
Type species: *Planoheterohelix postmoremani* Georgescu & Huber, 2009

Globoheterohelix Georgescu & Huber, 2009.

Original description. “Test is biserial throughout. Proloculus is small and followed by larger second chamber.

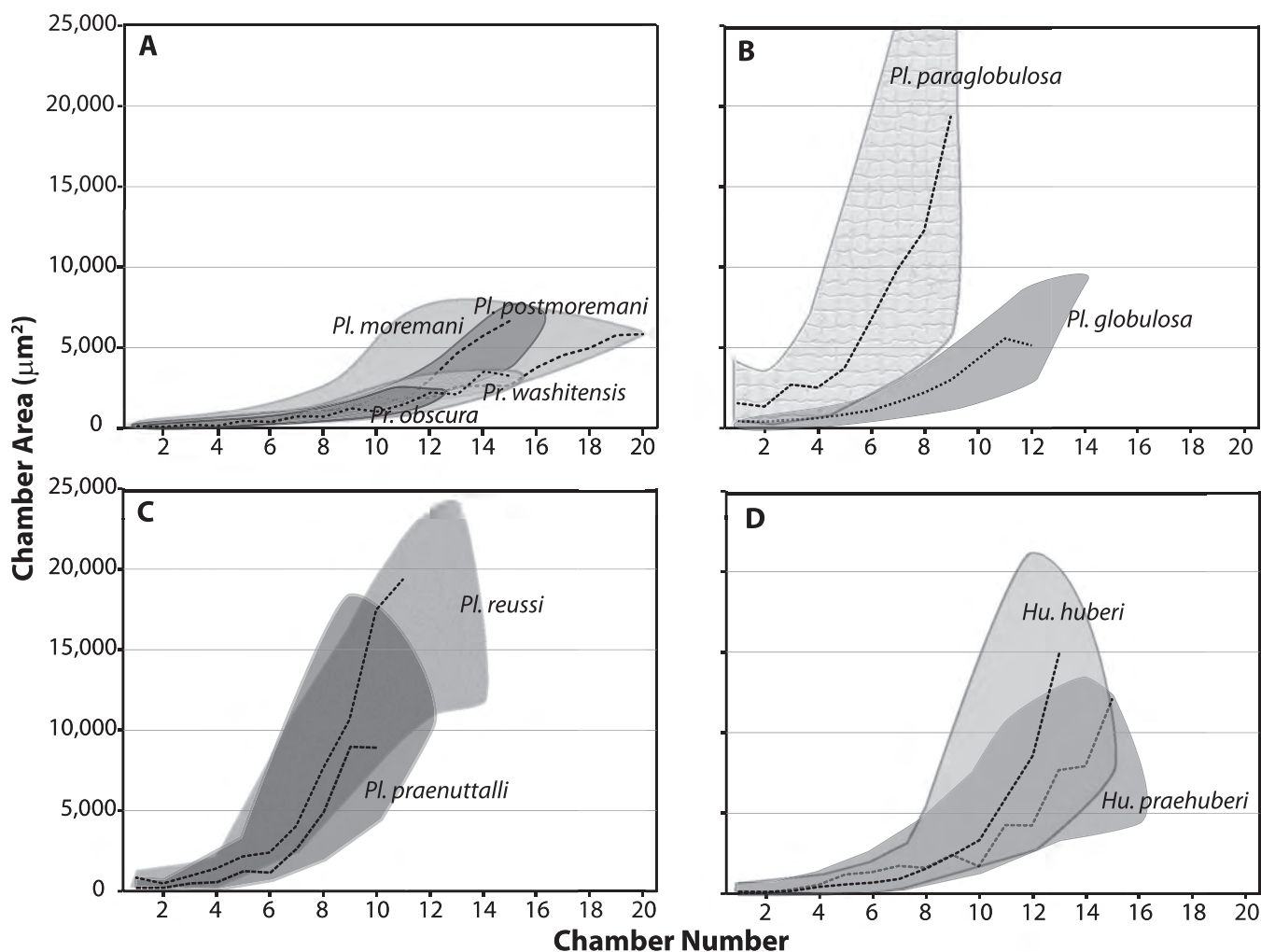


FIGURE 7. Chamber area measurements. Shaded regions represent measured specimens illustrated on figures. Holotype measurements are indicated by dotted lines. **A** *Protoheterohelix washitensis*, *Pr. obscura*, *Planoheterohelix moremani*, and *Pl. postmoremani*. **B** *Pl. globulosa* and *Pl. paraglobulosa*. **C** *Pl. reussi* and *Pl. praenuttalli*. **D** *Huberella praehuberi* and *Hu. huberi*.

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.”

Emended description. Test is moderate in size and has globular to subglobular chambers that are biserially arranged throughout and become reniform in some species. Proloculus diameters range from 12–72 µm and subsequent chambers increase in size at varying rates. Aperture is a symmetrical semicircular arch at the base of the final chamber. Sutures are depressed and form at an oblique angle to the central axis. Apertural structures vary but typically consist of symmetrical flanges or an imperforate apertural lip. Test wall is calcitic, ornamented with fine,

continuous costae and is microperforate to finely perforate (pore diameter = 0.6–3.2 µm).

Remarks. *Planoheterohelix* was erected to accommodate the earliest biserial forms with symmetrical apertures and a test wall surface that is smooth or ornamented with discontinuous costae (= granular costae sensu Georgescu & Huber, 2009). Distinction between forms with granular costae and forms with continuous longitudinal costae is not supported by observations of the type specimens or well-preserved specimens from Tanzania, which all show weakly developed costae (e.g., Fig. 9.8).

Planoheterohelix is here emended to include Cenomanian–Coniacian taxa that are wholly biserial but lack the: 1) asymmetrical aperture that is characteristic of *Protoheterohelix*, 2) sutural inflections and tube-like structures that are used to define *Huberella*, 3) completely smooth chamber surface with well-developed pore mounds that are key to identifying *Laeviheterohelix*, and 4) lateral trapezoidal projections on the final chambers used to define *Heterohelix*. Cenomanian–Coniacian species now assigned to *Planoheterohelix*.

Stages Biozonation

Phylogenetic Relationships

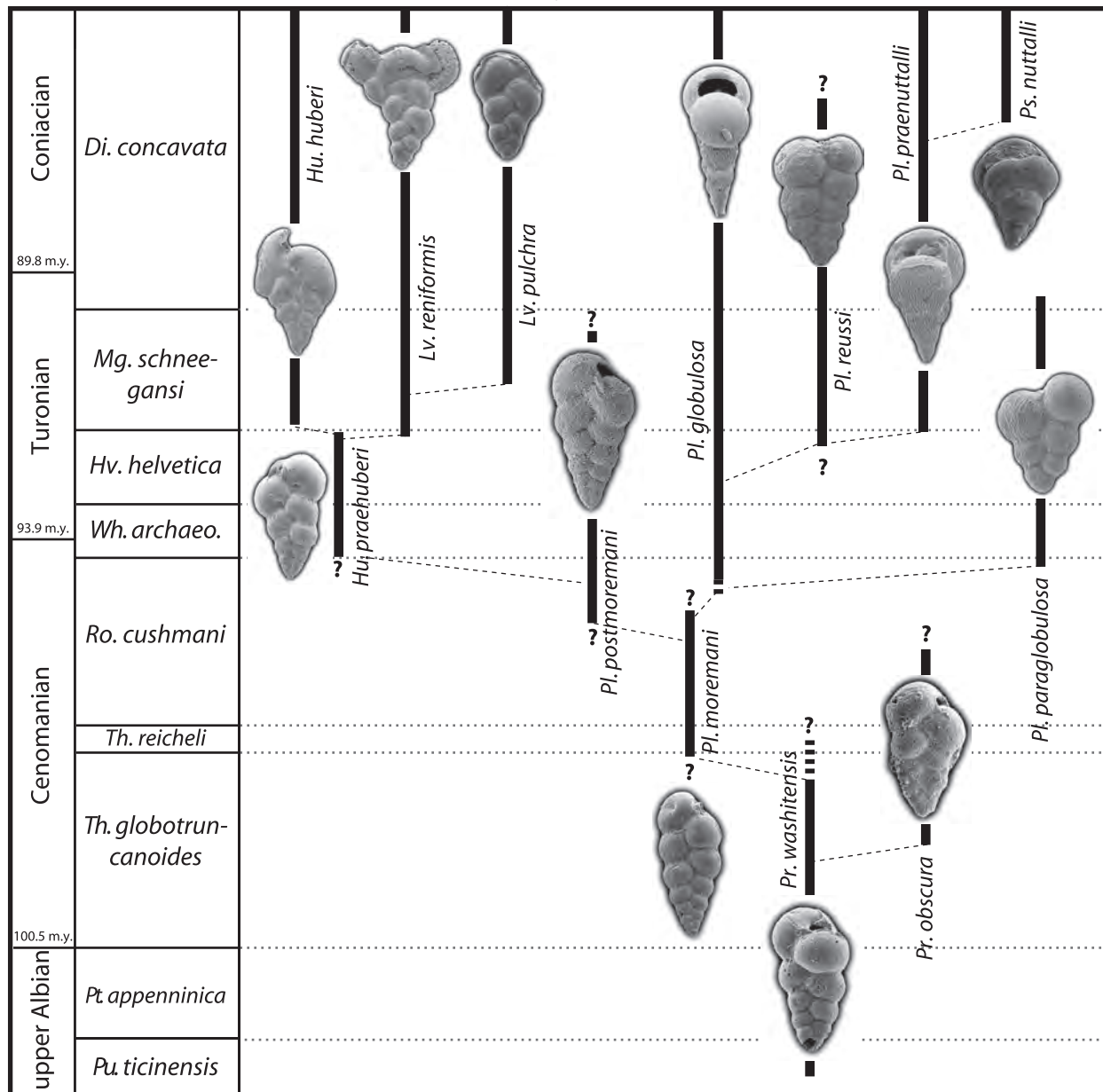


FIGURE 8. Proposed phylogenetic relationships of late Albian–Coniacian biserial planktic foraminifera. Biozonation scheme is originally from Georgescu & Huber, 2009. Generic abbreviations are as follows *Di.* = *Dicarinella*, *Hu.* = *Huberella*, *Hv.* = *Helvetoglobotruncana*, *Lv.* = *Laeviheterohelix*, *Mg.* = *Marginotruncana*, *Pl.* = *Planoheterohelix*, *Pr.* = *Protoheterohelix*, *Ps.* = *Pseudotextularia*, *Pt.* = *Parathalmanninella*, *Pu.* = *Pseudothalmanninella*, *Ro.* = *Rotalipora*, *Th.* = *Thalmanninella*, *Wh.* = *Whiteinella*.

ohelix include *Pl. moremani*, *Pl. postmoremani*, *Pl. globulosa*, *Pl. reussi*, *Pl. praenuttalli* n. sp., *Pl. paraglobulosa*, *Pl. papula* (Belford, 1960), *Pl. planata* (Cushman, 1938), and *Pl. rumseyensis* (Douglas, 1969). The latter three species are not discussed in this paper as they do not occur within the interval studied (Albian–Coniacian).

Georgescu & Huber (2009) defined *Planoheterohelix paraglobulosa* as the type species for the monospecific genus *Globoheterohelix* that was established to accommodate biserial forms with a large proloculus (31–56 μ m). Because proloculus diameter is a highly variable character, we do not consider it to be a useful attribute for genus-level

distinction and, therefore, *Globoheterohelix* is here considered a junior synonym of *Planoheterohelix*.

Planoheterohelix moremani (Cushman, 1938)

Figs. 9.1–9.5

Guembelina moremani Cushman, 1938, p. 10, pl. 2, figs. 1, 2 (Cenomanian, Eagle Ford Shale, Texas, U.S.A.).

Heterohelix moremani (Cushman). Nederbragt et al., 1998, pl. 1, figs. 4–5 [middle or upper Cenomanian, northern Africa (Oued Mellengue, Tunisia)]; Huber et al., 1999, p. 413, pl. 1, figs. 3, 4 [upper Cenomanian (*Rotalipora cushmani* Zone), western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)]; Wilson et al., 2002, fig. 1.3 [Turonian, western North Atlantic

Ocean (Demerara Rise, DSDP Leg 14, Hole 144A)]; Caron et al., 2006, fig. 7:10 [Cenomanian–Turonian, northern Africa (wadi Bahloul, Tunisia)].

Planoheterohelix moremani (Cushman). Georgescu & Huber, 2009, p. 344, pl. 4, figs. 1–13 [Cenomanian (*Ro. cushmani* Zone)–Turonian (*Helvetoglobotruncana helvetica* Zone), Eagle Ford Shale, Hill County, Texas, U.S.A., and western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Type specimens. Holotype: USNM 24370, paratypes: USNM 24371 (2 specimens) and USNM 31316 (6 specimens).

Type level. Cenomanian.

Type locality. South bank of small stream, 100 yards east of highway, 2.1 miles north of Itasca, Hill County, Texas.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Slender test with up to 18 chambers that are subglobular to slightly reniform, or deeper than wide.”

Distinguishing features. *Planoheterohelix moremani* is distinguished from its ancestors in having a symmetrical aperture and from the younger Turonian species in generally being more compressed, having more chambers (>12), and being more weakly striate.

Remarks. New images of the type specimens of *Pl. moremani* include SEMs and X-rays of the holotype (Fig. 9.1b) and paratypes (Figs. 9.2–9.5). The holotype of *Pl. moremani* is morphologically very different from the paratypes as it has 10 biserial pairs of chambers and is nearly parallel sided in edge view, whereas the paratypes have 6–7 pairs of biserial chambers that are more inflated and spherical and are more strongly tapering in edge view. The paratypes are so different from the holotype that their placement in a new species may be warranted.

Planoheterohelix postmoremani was proposed as the direct descendant of *Pl. moremani* and differentiated by having discontinuous costae rather than a smooth test surface (Georgescu & Huber, 2009), but high magnification images of the holotype and a paratype of *Pl. moremani* clearly show discontinuous costae on pre-terminal chambers (Figs. 9.1a, c, d, 9.3a). Although *Pl. moremani* is more weakly costate than *Pl. postmoremani*, distinction of the two species based on test ornament is impractical (Fig. 10). The elongate, 20-chambered holotype of *Pl. moremani* can easily be distinguished from *Pl. postmoremani* and the other biserial species; however, width, breadth, length, chamber-number, and chamber-area measurements of the infilled *Pl. moremani* paratypes reveal no consistent offsets from measurements of *Pl. postmoremani* (Figs. 5–7A), but are differentiated primarily by having globular rather than reniform chambers (Figs. 9, 10).

Similar species. *Planoheterohelix moremani* differs from *Pl. globulosa* by 1) having a more finely costate surface texture (Figs. 9, 11) and 2) generally having more chambers (>12; Fig. 5). It differs from *Pl. postmoremani* in having 1) typically more chambers, 2) costae that are more weakly developed, and 3) globular rather than reniform chambers (Fig. 10). See “*Similar species*” section of *Pr. obscura* for more comparisons.

Phylogenetic relationships. *Planoheterohelix moremani* evolved from *Pr. washitensis* during the early Cenomanian

and is considered the direct ancestor of *Pl. postmoremani* and *Pl. globulosa* (Fig. 8).

Stratigraphic range. *Planoheterohelix moremani* occurs from the middle Cenomanian (*Thalmaninella reicheli* Zone; Fig. 8; Appendix 4) to the upper Cenomanian (*Ro. cushmani* Zone; Fig. 8).

Geographic distribution. United States (Texas), western North Atlantic Ocean (Blake Plateau), equatorial Pacific Ocean (Mid-Pacific Mountains), and Mexico (San Felipe Formation).

Stable isotope paleoecology. No collected data.

Planoheterohelix postmoremani Georgescu & Huber, 2009
Figs. 9.6–9.12

Planoheterohelix postmoremani Georgescu & Huber, 2009, p. 346, pl. 5, figs. 1–11 [Turonian (*Helvetoglobotruncana helvetica* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463), and western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Type specimens. Holotype: USNM 534393, paratypes: USNM 534394 and 534395.

Type level. Turonian (*Hv. helvetica* Zone).

Type locality. Equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463), 21°21'N/174°40'E.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test is biserial throughout and consists of 11 to 15 chambers. Small proloculus (8.2–14.3 microns) 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. Sutures are distinct, depressed, and oblique. Tests are symmetrical in edge view, with broadly rounded periphery. Aperture is medium to high arch at base of last formed chamber; it is bordered by two symmetrically developed periapertural flanges. Chamber surface is ornamented with closely spaced costae, each of them consisting of series of aligned pustules, resulting in a granular appearance. Test wall is calcitic, hyaline, microperforate; pore diameter ranges 0.5–0.9 microns.”

Distinguishing features. This species is unique among Cenomanian forms in having a completely symmetrical aperture, slightly rectangular chambers, and being finely costate. Relative to younger Turonian species, *Pl. postmoremani* has more weakly expressed costae and exhibits a lower rate of chamber-size increase.

Remarks. Holotype and paratype SEM images of *Pl. postmoremani* are reillustrated along with new X-ray images (Figs. 9.6, 9.7). The X-ray images of the types and those from Tanzania illustrate that *Pl. postmoremani* has more reniform chambers than *Pl. moremani* (Figs. 9.6b, 9.7b, 9.8b). In the recrystallized type specimens costae are not apparent (Figs. 9.9–9.11), but well-preserved specimens from TDP Site 31 show that the test is initially smooth and later becomes weakly costate (Figs. 9.8, 9.12).

Biometric comparison between *Pl. postmoremani* and the *Pl. moremani* paratypes demonstrates the difficulty of distinguishing between these species using the measured parameters. Biometric plots show moderate overlap for *Pl. postmoremani* and *Pl. globulosa* particularly in width vs. breadth (Fig. 6). The plot of length vs. number of

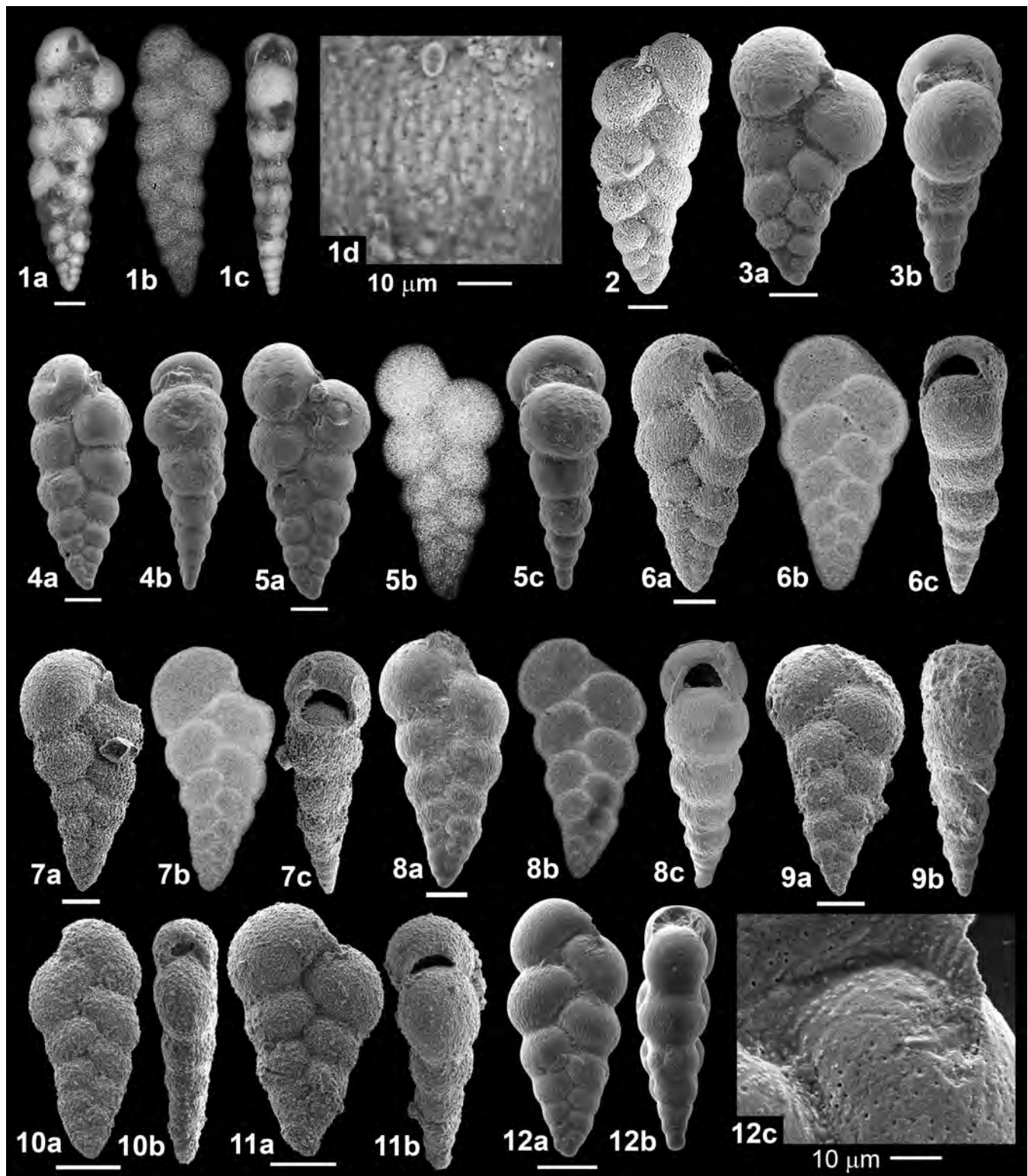


FIGURE 9. *Planoheterohelix moremani* (Cushman, 1938) and *Pl. postmoremani* (Georgescu & Huber, 2009). Scale bars = 50 µm and all SEMs were taken at the National Museum of Natural History, Washington, D.C., unless otherwise noted. 1–5 *Pl. moremani*, all from the lower part of the Eagle Ford Shale, north of Itasca, Hill County, Texas, U.S.A.: 1, Holotype (USNM 24370), originally figured by Cushman (1938, pl. 2, fig. 1), also figured by Georgescu & Huber (2009, pl. 4, figs. 1, 2), new SEMs (1a, c, d) and X-ray (1b) taken at the National Museum of Natural History, Washington, D.C.; 2, Paratype (USNM 24371), originally illustrated as a drawing by Cushman (1938, pl. 2, fig. 2), image from Georgescu & Huber (2009, pl. 4, fig. 3); 3, Paratype (USNM 31316), previously unillustrated; 4, Paratype (USNM 31316), previously unillustrated; 5, Paratype (USNM 24371), previously unillustrated, X-ray (5b) taken at National Museum of Natural History, Washington D.C. 6–12 *Pl. postmoremani*: 6, Holotype (USNM 534393), lower Turonian (*Helvetoglobotruncana helvetica* Zone), equatorial Pacific (Mid-Pacific Mountains), DSDP site 463, Spl. 35-1, 17–19 cm, SEM images (6a, c) from Georgescu & Huber (2009, pl. 5, figs. 1, 2), X-ray (6b) taken at National Museum of Natural History, Washington D.C.; 7,

chambers, however, shows that, relative to *Pl. globulosa*, *Pl. postmoremani* is slightly longer and generally has more chambers (Fig. 5). In addition, the plot of chamber number vs. chamber area shows that cross-sectional chamber areas increase faster in *Pl. globulosa* than in *Pl. postmoremani* (Figs. 7A, B).

Similar species. It differs from *Huberella praehuberi* in the absence of pore mounds and sutural inflections on the surfaces of the adult chambers (Fig. 10), and from *Pl. globulosa* in 1) being more finely costate and 2) generally having more chambers that increase in size at a slower rate. See “*Similar species*” section of *Pl. moremani* for more comparisons.

Phylogenetic relationships. Descended from *Planoheterohelix moremani* and is ancestral to *Hu. praehuberi* (Fig. 8).

Stratigraphic range. The first occurrence of *Pl. postmoremani* was documented in the late Cenomanian *Rotalipora cushmani* Zone (Georgescu & Huber, 2009), and the taxon is present in the lower Turonian in Tanzania. At TDP Site 31 it ranges through the middle Turonian *Marginotruncana schneegansi* Zone (Figs. 3, 8; Appendix 1) but may extend up into the Coniacian (*Dicarinella concavata* Zone) according to Georgescu & Huber (2009).

Geographic distribution. Africa (Tanzania), equatorial Pacific Ocean (Mid-Pacific Mountains), and western North Atlantic Ocean (Blake Plateau).

Stable isotope paleoecology. No data available.

Planoheterohelix globulosa (Ehrenberg, 1840)
Figs. 11.1–11.14

Textularia globulosa Ehrenberg, 1840, p. 135, pl. 4, fig. 2β (Jutland, Denmark), 5β (Muedon, near Paris, France), 7β (“Mokattamgebirge” near Cairo, Egypt), 8β (Thebes in Upper Egypt from the *Nummulites* limestone of the pyramids).

Guembelina globulosa (Ehrenberg). Said & Kenawy, 1956, p. 139, pl. 3, fig. 29 [Maastrichtian, Egypt (Sinai)].

Heterohelix reussi (Cushman). Said & Sabry, 1964, p. 390, pl. 3, fig. 24 [Maastrichtian, Egypt (Esna Shale, Gebel Aweina)].

Heterohelix globulosa (Ehrenberg). Masters, 1980, p. 100, pl. 1, figs. 6, 7 (upper Campanian, Meudon, near Paris, France); Bergstresser & Frerichs, 1982, p. 356, pl. 1, figs. 3, 4 [Wyoming, U.S.A. (Pierre Shale, Red Bird)]; de Klasz, et al., 1995, p. 367, pl. 2, fig. 3 [lower Turonian, western Africa (Senegal)]; Wilson et al., 2002, fig. 1.5 [Turonian, western North Atlantic Ocean (Demerara Rise, DSDP Leg 14, Hole 144A)]; Caron et al., 2006, fig. 7:11 [upper Cenomanian–Turonian, Colorado, U.S.A., and northern Africa (wadi Bahloul, Tunisia)].

“*Heterohelix globulosa*” (Ehrenberg). Georgescu & Huber, 2009, pl. 7, figs. 9–12 [upper Cenomanian, western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)].

Type specimens. Neotype: USNM 264610 (designated herein), topotypes: USNM 264609 and 264611.

Type level. Upper Campanian based on the calcareous nannoplankton biostratigraphy cited in Masters (1980).

Type locality. The illustrated neotype and topotypes are from Meudon near Paris, France.

Repository. National Museum of Natural History, Washington, D.C. Ehrenberg’s (1840) paralectotypes are stored at the Humboldt Museum in Berlin, Germany.

Original description (translated from the Latin). “Shell microscopic, surface smooth, longer than larger in the adult, chambers globular.”

Emended description. Test is moderate in size, ranging from 161–300 μm (n = 11) in length with 9–14 biserially arranged chambers. Proloculus is moderately sized, averaging 22 μm in diameter among the 10 specimens measured, with subsequent globular to subglobular chambers increasing slowly in size. In side view the test is subtriangular in outline and weakly tapered, and in edge view the test is slightly compressed. Sutures are straight to slightly curved, moderately depressed, and meet the central axis at an oblique angle. Aperture is a medium to low-arched, symmetrical semicircular arch formed at the base of the final chamber, and is commonly bordered by either symmetrical flanges or an apertural lip. Test wall is calcitic, hyaline, and ornamented with costae that are expressed variably in terms of continuity and thickness but are generally fine and continuous (average thickness = 2.6 μm, n = 6). Test wall is micropore with an average pore diameter of 0.8 μm (n = 1).

Distinguishing features. Relative to species that evolved in the late Albian–early Cenomanian, *Pl. globulosa* is larger and more rapidly widening. However, compared to forms from the latest Cenomanian–Turonian, the test is more compressed in edge view and the rate of chamber growth is slower.

Remarks. Ehrenberg (1840) illustrated five specimens of *Textularia globulosa*, but Masters (1980) could not find any of the balsam slides containing the illustrated specimens. Pessagno (1967) noted that the original mica slides with the illustrated type specimens may have been lost during the destruction of Berlin at the end of World War II. More recently, Georgescu (communication, 2011) visited the repository in Berlin, Germany, and was also unable to locate slides containing the original material illustrated by Ehrenberg. Two of the original drawings of *Pl. globulosa* by Ehrenberg (1840) are reproduced on Figure 11, including the figure 5β specimen that Pessagno designated as the lectotype for the species (Fig. 11.2).

Masters (1980) published SEM images of topotype specimens removed from a bulk sample of the same outcrop as Pessagno’s lectotype (Meudon, near Paris, France). Because illustrations of the topotypes in Masters (1980) included only one view, new SEM and X-ray images are presented in Figures 11.3 and 11.4 (= Pl. 1, figs. 7 and 8 of Masters, 1980, respectively), including an enlarged view of the costae.

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Paratype (USNM 534394), lower Turonian (*Hv. helvetica* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 35-1, 17–19 cm, SEM images (7a, c) from Georgescu & Huber (2009, pl. 5, figs. 4, 5), X-ray (7b) taken at National Museum of Natural History, Washington D.C.; 8, lower–middle Turonian (*Hv. helvetica* Zone), Spl. TDP 31-46-1, 3–23 cm, X-ray (8b) taken at National Museum of Natural History, Washington D.C.; 9, upper Cenomanian (*Rotalipora cushmani* Zone; age based on Ando et al., 2009), western North Atlantic Ocean (Blake Nose), ODP Hole 1050C, Spl. 21-1, 135–136 cm; 10, upper Cenomanian (*Thalmaninella globotruncanoides* Zone; age based on Georgescu, 2012), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 38-1, 17–20 cm; 11, upper Cenomanian, (*Rotalipora cushmani* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 37-1, 1–6 cm; 12, lower Turonian (*Hv. helvetica* Zone), Spl. TDP 22-39-1, 48–66 cm.

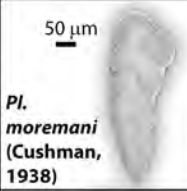
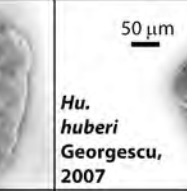
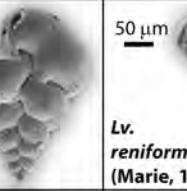
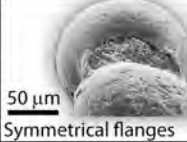
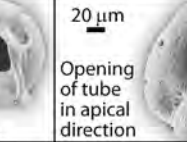
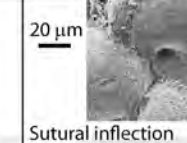
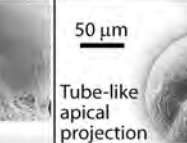
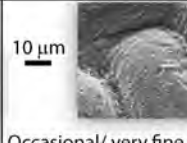
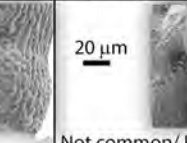
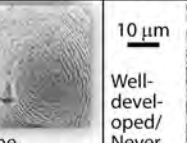
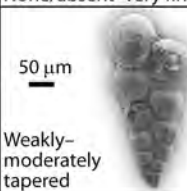
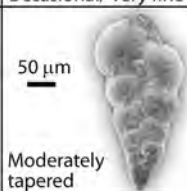
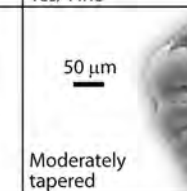
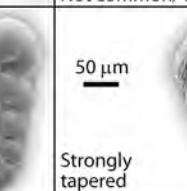
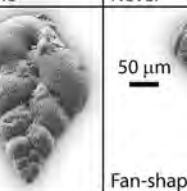
	 <i>Pl. moremani</i> (Cushman, 1938)	 <i>Pl. postmoremani</i> Georgescu & Huber, 2009	 <i>Hu. praeuberi</i> Georgescu, 2007	 <i>Hu. huberi</i> Georgescu, 2007	 <i>Lv. reniformis</i> (Marie, 1941)
Aperture structures	 Symmetrical flanges	 Symmetrical flanges	 Pocket common, symmetrical flanges	 Opening of tube in apical direction	None well-preserved
Adult chamber structures	None	None	 Sutural inflection	 Tube-like apical projection	 Large, flat inter-chamber area
Presence of pore mounds/costae	 None/absent—very fine	 Occasional/very fine	 Yes/Fine	 Not common/Fine	 Well-developed/ Never
Peripheral outline	 Weakly-moderately tapered	 Moderately tapered	 Moderately tapered	 Strongly tapered	 Fan-shaped

FIGURE 10. Key characteristics of *Planoheterohelix moremani*, *Pl. postmoremani*, *Huberella praeuberi*, *Hu. huberi*, and *Laeviheterohelix reniformis*. Figured specimens were selected from both the type series and TDP Sites 22 and 31.

Planoheterohelix globulosa exhibits a large amount of variability within samples and through time; however, the relationship between certain morphological features make this species consistently identifiable among Cenomanian–Turonian heterohelids. *Planoheterohelix globulosa* is characterized by having a finely costate test and globular chambers that increase in size at a slow rate compared to *Pl. reussi*, *Pl. paraglobulosa*, *Pl. praenuttalli* n. sp., and *Pseudotextularia nuttalli* (Fig. 7B) and at a slightly faster rate compared to *Pl. moremani*, *Pl. postmoremani*, *Pr. obscura*, and *Pr. washitensis* (Fig. 7A). Figures illustrating the relationship between length vs. breadth (Fig. 12A), width vs. breadth (Fig. 12B), and test taper (Figs. 13, 14) show that, relative to *Pl. reussi*, *Pl. praenuttalli* n. sp., and *Ps. nuttalli*, *Pl. globulosa* is smaller and less tapering in side and edge views. The species is also shorter than *Pl. reussi* and has a smaller proloculus than *Pl. paraglobulosa* (Fig. 15).

Similar species. It differs from *Pl. paraglobulosa* by having 1) more chambers, 2) a smaller proloculus (<31 µm; Fig. 13; Appendix 5), and 3) a greater degree of test taper in edge view quantified by the breadth/proloculus thickness ratio (Figs. 13, 14), and from *Huberella praeuberi* by having 1) fewer chambers and 2) spherical chambers with no sutural inflections. See “*Similar species*” presented for *Pl. postmoremani* above.

Phylogenetic relationships. We suggest that *Pl. globulosa* evolved from *Pl. moremani* in the late Cenomanian (Fig. 8). Poor stratigraphic recovery of this interval and

poor preservation of Cenomanian specimens from DSDP Site 463 and ODP Hole 1050C make it difficult to reliably determine the first occurrence of *Pl. globulosa* that is considered the ancestor to Turonian and younger heterohelid species (Fig. 8). This is particularly a problem with species that appear at close stratigraphic intervals such as *Pl. globulosa* and *Pl. paraglobulosa*, which both first occur in the *Ro. cushmani* Zone (Appendices 3, 4).

Stratigraphic range. The first occurrence of *Pl. globulosa* is in the uppermost Cenomanian and is documented in an undetermined zone above the *Thalmaninella globotruncanoides* Zone at DSDP Site 463, Sample 37-CC, and in the *Ro. cushmani* Zone at ODP Hole 1050C, Samples 21-2 (Fig. 8; Appendices 3, 4), but it was not identified in the lower-middle Cenomanian sediments in Tanzania. *Planoheterohelix globulosa* is present throughout the entire Turonian section recovered at TDP Site 31 (Fig. 3; Appendix 1) and ranges to the Cretaceous-Paleogene boundary (e.g., Nederbragt, 1991).

Geographic distribution. Cosmopolitan.

Stable isotope paleoecology. *Planoheterohelix globulosa* $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are both lower than values in non-heterohelid planktic foraminifera from TDP Site 31. The range of $\delta^{13}\text{C}$ values includes lower values than seen in two other biserial taxa (*Pl. moremani* and *Pl. paraglobulosa*) from the same samples, but this difference may be an artifact of sample size (Fig. 16).

Planoheterohelix paraglobulosa (Georgescu & Huber, 2009)
Figs. 17.1–17.15

Heterohelix globulosa (Ehrenberg). Nederbragt, 1991, p. 341, pl. 2, fig. 2 [Coniacian (*Dicarinella concavata* Zone), western North Atlantic Ocean (Yucatan Outer Shelf, DSDP Leg 10, Site 95)]; Nederbragt & Koning, 1994, p. 443, pl. 1, figs. 1, 2 [Coniacian (*Di. concavata* Zone), Africa (El Kef, Tunisia)]; Huber et al., 1999, p. 413, pl. 1, figs. 1, 2 [late Cenomanian, western North Atlantic Ocean (Blake Plateau, ODP Leg 171B, Hole 1050C)]; Ando et al., 2009, fig. 4:4 [lower Turonian (*Whiteinella archaeocretacea* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463)].
Globoheterohelix paraglobulosa, Georgescu & Huber, 2009, p. 349, pl. 6, figs. 7, 8 [lower Turonian (*Helvetoglobotruncana helvetica* Zone), southeast Tanzania (TDP Site 22)], figs. 9–12 [lower Turonian (*Hv. helvetica* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463)], pl. 7, figs. 1–8 [lower Turonian (*Hv. helvetica* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463)].

Type specimens. Holotype: USNM 534401, paratypes: USNM 534402–534405.

Type level. Lower Turonian (*Hv. helvetica* Zone).

Type locality. Equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463), 21°21'N/174°40'E.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test is biserial throughout. The large proloculus (31–56 microns) 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. Chamber surface displays closely spaced continuous or discontinuous fine (2.5–3.3 microns) costae. Intercoastal spaces are commonly narrower than the width of the costae. Test wall is calcitic, microperforate to finely perforate with pore diameter ranging 0.7–1.1 microns. Pores are intercostal or occasionally penetrate costae.”

Distinguishing features. *Planoheterohelix paraglobulosa* is distinguished from other Turonian biserials by its unusually large proloculus ($\geq 31 \mu\text{m}$ in diameter; Georgescu & Huber, 2009) and the low tapering angle of the test in edge view.

Remarks. The SEM images of the holotype and paratype (Figs. 17.1, 17.2), reillustrated from Georgescu & Huber (2009), are excellent representations of the abundant forms found throughout TDP Sites 22, 24, and 31 (Figs. 17.3–17.15). The low morphologic variability of the specimens is consistent with the relatively uniform morphology of this taxon in TDP samples.

The key feature used to distinguish this species from closely related forms is its large ($>31 \mu\text{m}$) proloculus (Georgescu & Huber, 2009). The plot of length vs. proloculus diameter (Fig. 15) shows significant variability but is offset from the other taxa. The specimen on Figure 17.15 is likely a transitional or juvenile form of *Pl. paraglobulosa*, as indicated by its small proloculus and straight sutures, and represents its oldest occurrence. Figure 15 also shows that within *Pl. paraglobulosa* there is a positive correlation between length and diameter of proloculus. Although the large proloculus is a key trait of this species, *Pl. reussi*, *Pl. praenuttalli*, and *Pseudotextularia nuttalli* also commonly have proloculi with diameters $\geq 31 \mu\text{m}$ (Fig. 13; Appendix 5), but these species have a

higher test taper in edge view, which is quantified in this paper as the breadth of the adult portion (or broadest portion) of the test over the breadth of the proloculus (Figs. 13, 14; Appendix 5).

Cross-sectional chamber area increases faster during growth in *Pl. paraglobulosa* than in other Albian–Turonian heterohellicids. Albian–early Cenomanian heterohellicids (i.e., *Protoheterohelix washitensis*, *Pr. obscura*, *Pl. moremani*, *Pl. postmoremani*, and *Pl. globulosa*) tend to have very slow growth rates relative to those that evolved in the Turonian (i.e., *Huberella praehuberi*, *Hu. huberi*, *Pl. reussi*, and *Pl. praenuttalli*; Fig. 7).

Similar species. It differs from *Pl. praenuttalli* in having 1) fewer chambers (Fig. 13, Appendix 5), and 2) chambers that increase in size more rapidly (Fig. 7). See “*Similar species*” presented for *Pl. globulosa* above.

Phylogenetic relationships. *Planoheterohelix paraglobulosa* is considered as part of the *Pl. moremani* lineage and likely evolved directly from *Pl. globulosa* in the latest Cenomanian (*Wh. archaeocretacea* Zone), although a continuous record of this transition has not been documented (Fig. 8).

Stratigraphic range. *Planoheterohelix paraglobulosa* ranges from latest Cenomanian (*Wh. archaeocretacea* Zone; Fig. 8)–late Turonian (*Di. concavata* Zone) at the top of TDP Site 31 (Core 1), but the species range may extend above this level (Figs. 3, 8; Appendix 1).

Geographic distribution. United States (Colorado, Kansas, South Dakota, Wyoming), Africa (Egypt, Tanzania), Gulf of Mexico (Yucatan shelf), western North Atlantic Ocean (Blake Plateau), and equatorial Pacific Ocean (Mid-Pacific Mountains).

Stable isotope paleoecology. Like other biserial species at TDP Site 31, *Pl. paraglobulosa* consistently has lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values relative to co-occurring trochospiral planktic species. At TDP Site 31 it exhibits higher $\delta^{18}\text{O}$ values than *Hu. praehuberi* and intermediate $\delta^{13}\text{C}$ values compared to the other taxa analyzed, but differences may be an artifact of small sample size (Fig. 16).

Planoheterohelix reussi (Cushman, 1938)
Figs 18.1–18.9

Guembelina reussi Cushman, 1938, p. 11, pl. 2, figs. 6–9 [Turonian, Sherman, Texas, U.S.A. (Lower Austin Chalk)].

Heterohelix reussi (Cushman). Walaszczyk et al., 2012, figs. 9.8a, b [Turonian–Coniacian, northeast New Mexico, U.S.A. (Springer composite section, sample Spr-3)].

Type specimens. Holotype: USNM 24374, paratypes: USNM 24375 and 24480 (3 figured specimens).

Type level. Turonian.

Type locality. Lower Austin Chalk, ditch west side of Sherman–Dennison highway, 3 miles north of Sherman, Texas.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test about 1.5 times as long as broad, rapidly tapering, greatest breadth formed by the last pair of chambers, periphery of early part usually entire, later distinctly indented; chambers globular, and in the later portion distinctly set apart with a triangular, depressed area between; sutures distinctly depressed throughout; wall smooth, finely perforate, the earliest portion sometimes

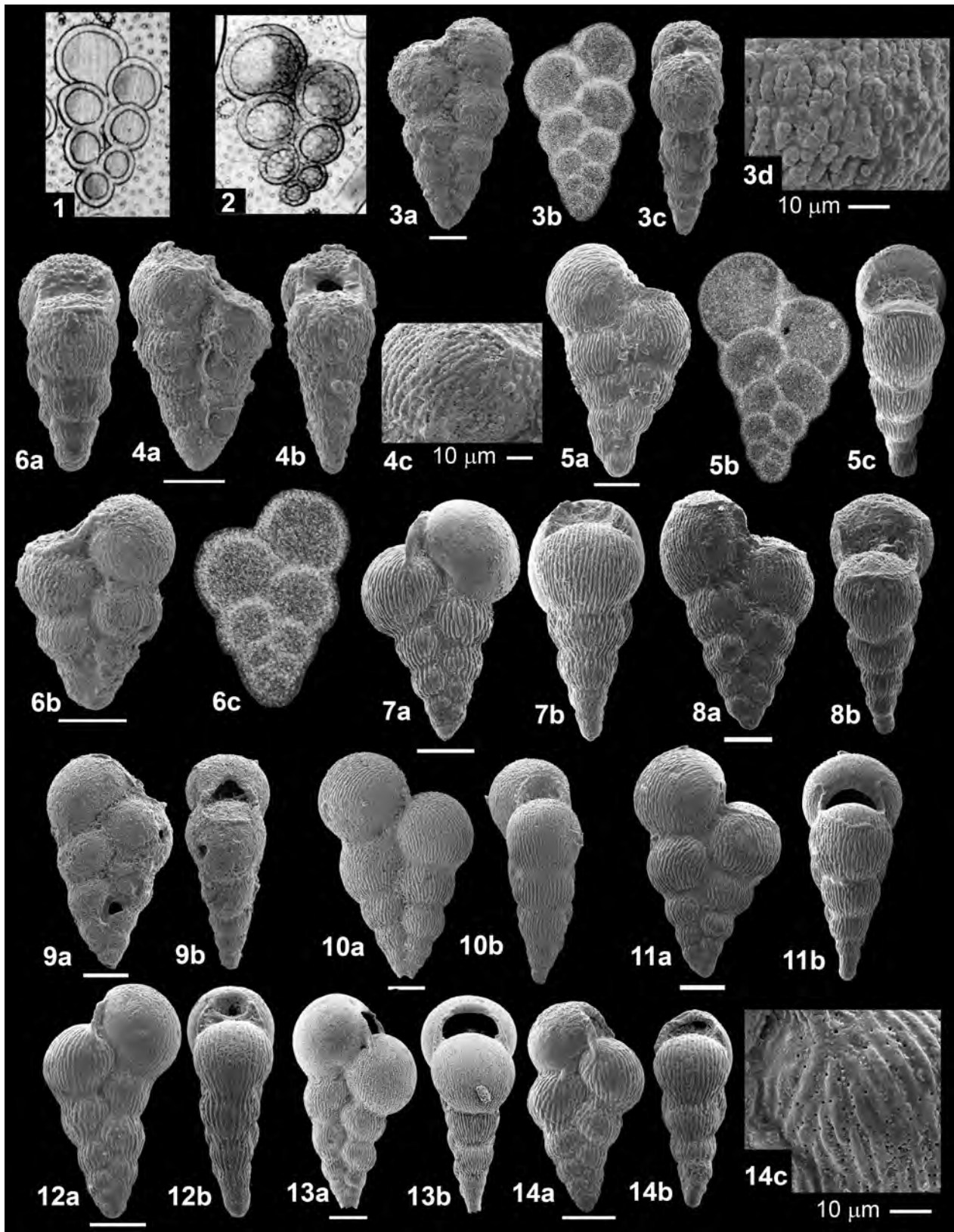


FIGURE 11. 1–14 *Planoheterohelix globulosa* (Ehrenberg, 1840); scale bars = 50 µm and all SEMs were taken at the National Museum of Natural History, Washington, D.C., unless otherwise noted: 1, original drawing by Ehrenberg (1840, pl. 4, fig. 2β), specimen has since been lost, collected from Jutland, Denmark; 2, original drawing by Ehrenberg (1840, pl. 4, fig. 5β) of lectotype (designated by Pessagno, 1967), specimen has since been lost, collected from Meudon, near Paris, France; 3, Neotype (USNM 264610), upper Campanian, Muedon, France, Ehrenberg Spl. 2217, originally figured in Masters (1980, pl. 1, fig. 7), new SEM images (3a, c, d) and X-ray (3b) taken at National Museum of Natural History, Washington D.C.; 4,

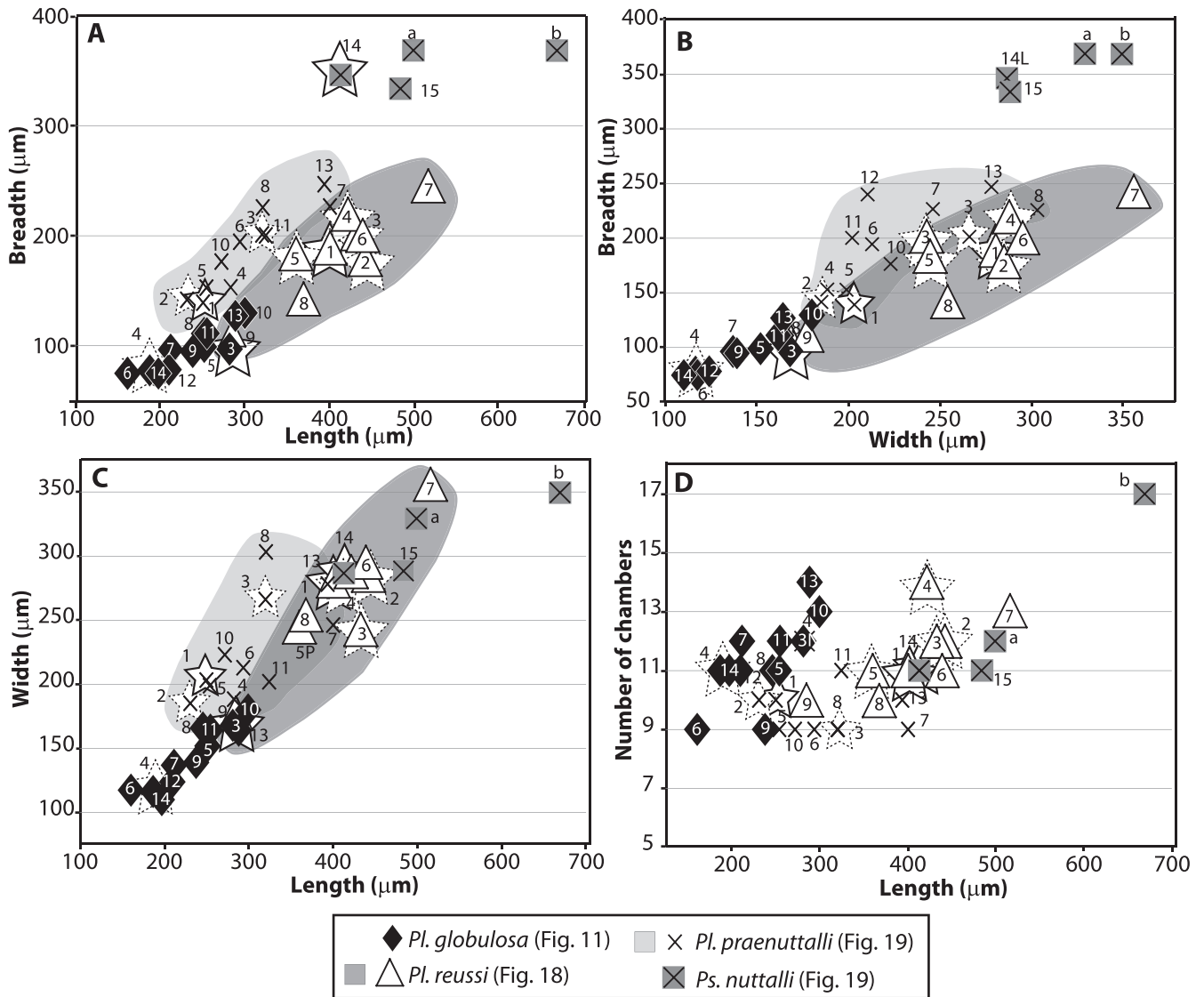


FIGURE 12. **A** Length vs. breadth, **B** width vs. breadth, **C** length vs. width, and **D** length vs. number of chambers for *Planoheterohelix globulosa*, *Pl. reussi*, *Pl. praenuttalli*, and *Pseudotextularia nuttalli*. Point marker numbers represent the location of the specimen on its respective figure. For *Ps. nuttalli* the markers labeled “a” and “b” are not figured, but are hypotypes from Nederbragt (1991 and 1989, respectively).

showing longitudinal rows of perforations; aperture high, semicircular, at the inner border of the chamber.”

Emended description. Test is large (average length = 407 μm, n = 9) and consists of 8–14 (n = 9) biserially arranged chambers. A large proloculus (average diameter = 39 μm, n = 7) is followed by globular chambers that generally increase rapidly in size, creating a widening test

with a subtriangular outline in side view. The point at which the chambers begin to increase quickly in size is variable, because in many forms the first 3–5 chambers increase slowly in size and then become much larger by the sixth or seventh chamber, again increasing in size gradually throughout the remaining ontogeny. Final chamber is occasionally kummerform. Specimens are broad (average

Topotype (USNM 264609), upper Campanian, Muedon, France, Ehrenberg Spl. 2217, originally figured in Masters (1980, pl. 1, fig. 6), new SEMs (4a–c) taken at National Museum of Natural History, Washington D.C.; 5, lower mid-Turonian (*Helvetoglobotruncana helvetica* Zone), Spl. TDP 31-38-1, 29–49 cm, X-ray (5b) taken at National Museum of Natural History, Washington D.C.; 6, Topotype (USNM 264611), upper Campanian, Muedon, France, Ehrenberg Spl. 2217, originally figured in Masters (1980, pl. 1, fig. 8), new SEMs (6a, b) and X-ray (6c) taken at National Museum of Natural History, Washington D.C.; 7, upper Turonian (*Marginotruncana schneegansi* Zone), Spl. TDP 31-25-1, 77–88 cm; 8, upper Turonian (*Mg. schneegansi* Zone), Spl. TDP 31-7-1, 75–90 cm; 9, upper Cenomanian (*Thalmaninella globotruncanoides* Zone; age from Georgescu, 2012), DSDP Site 463, Spl. 42-CC, 0–20 cm, transitional from *Pl. postmoremani*; 10, from the Toolonga Calcilitute, Pillawara Hill, Australia, near the type level of *Pl. papula*, Spl. 7164-0040 collected by D. J. Belford; 11, lower mid-Turonian (*Hv. helvetica* Zone), Spl. TDP 31-47-1, 57–77 cm; 12, upper Turonian (*Mg. schneegansi* Zone), Spl. TDP 31-21-2, 40–50 cm; 13, middle Turonian (*Hv. helvetica* Zone), Spl. TDP 22-5-1, 68–88 cm (no biostratigraphy table provided in Appendix); 14, upper Turonian (*Mg. schneegansi* Zone), Spl. TDP 31-25-1, 77–88 cm.

All metrics in: average/range form	<i>Pl. globulosa</i> (Ehrenberg, 1840)	<i>Pl. reussi</i> (Cushman, 1938)	<i>Pl. praenuttalli</i> n. sp.	<i>Ps. nuttalli</i> (Voorwijk, 1937)	<i>Pl. paraglobulosa</i> (Georgescu & Huber, 2009)
Number of chambers	(n = 11): 12/ 9–14	(n = 9): 11/ 8–14	(n = 12): 10/ 9–12	(n = 4): 13/ 11–17	(n = 18): 7/ 5–9
Length	(n = 11): 236 μ m/161–300 μ m	(n = 9): 407 μ m/278–516 μ m	(n = 11): 304 μ m/ 231–401 μ m	(n = 4): 516 μ m/ 413–669 μ m	(n = 18): 276 μ m/ 204–429 μ m
Maximum proloculus diameter	25 μ m (n = 10): 22 μ m/ 17–27 μ m	25 μ m (n = 7): 39 μ m/ 34–46 μ m	25 μ m (n = 7): 21 μ m/ 15–32 μ m	No good close-ups (n = 3): 39 μ m/ 30–48 μ m	25 μ m (n = 18): 54 μ m/ 32–72 μ m
Brdth/width	(n = 11): 0.7/ 0.6–0.8	(n = 9): 0.7/ 0.6–1.1	(n = 12): 0.8/ 0.7–1.1	(n = 4): 1.2/ 1.1–1.2	(n = 17): 0.7/ 0.5–0.8
Side view taper (width/proloculus diameter)	50 μ m (n = 10): 6.8/ 4.4–9.8	50 μ m (n = 7): 6.4/ 4.3–7.2	50 μ m (n = 7): 10.3/ 6.6–13.2	50 μ m (n = 3): 8.6/ 6.8–11.7	50 μ m (n = 18): 4.0/ 2.3–5.1
Edge view taper (breadth/proloculus breadth)	50 μ m (n = 11): 5.0/ 3.0–8.3	50 μ m (n = 9): 6.9/ 4.3–9.6	50 μ m (n = 10): 8.9/ 7.3–11.7	50 μ m (n = 4): 11.3/ 8.3–14.5	50 μ m (n = 17): 2.4/ 1.4–3.1

FIGURE 13. Key characteristics chart with *Planoheterohelix globulosa*, *Pl. reussi*, *Pl. paraglobulosa*, *Pl. praenuttalli*, and *Pseudotextularia nuttalli*. Measurement notation (n = number of specimens measured): average of values measured/range of measured values [minimum–maximum]. Top-row images were selected from type collections; remaining images are from TDP Site 31 and DSDP Site 511.

breadth = 193 μ m, n = 9), but have a relatively low amount of taper in edge view. Sutures are moderately depressed, straight, and meet the central axis at a right to slightly oblique angle. Aperture is a low-arched semicircle at the base of the final chamber, commonly bordered by an imperforate lip. Test wall is microporolate to finely perforate (average pore diameter = 1.0 μ m, n = 2), ornamented with fine discontinuous costae (thickness = 2.9 μ m, n = 1) and is calcitic and hyaline.

Distinguishing features. *Planoheterohelix reussi* can be distinguished from other Turonian species by its large size, with most specimens being >350- μ m long, finely costate surface ornamentation, and relatively low taper angle in edge view.

Remarks. New high-resolution SEM images of the holotype and paratypes of *Pl. reussi* (Fig. 18) show that all are large with fine costae on all chambers. The peripheral test outline varies from being subtriangular to subrectangular, as opposed to the rapid flaring of *Pl. praenuttalli*, and the edge view is slowly to moderately tapering. All type specimens are infilled and unsuitable for study with X-ray images. *Planoheterohelix reussi* is rare in Tanzania and the three illustrated specimens are infilled (Figs. 18.7–18.9). The traditionally cited “triangular depression” between the last three chambers, with the final chamber being offset from the previous two, that has been used to distinguish *Pl. reussi* from *Pl. globulosa* (e.g.,

Cushman, 1946; Pessagno, 1967) is now not considered useful for discriminating these species.

Similar species. *Planoheterohelix reussi* differs from *Pl. globulosa* in its larger size in all dimensions (length, width, and breadth; Figs. 12, 13; Appendix 5) and from *Pl. praenuttalli* in that *Pl. reussi* is consistently less tapering (Figs. 13, 14).

Phylogenetic relationships. *Planoheterohelix reussi* likely descended from *Pl. globulosa* during the late Turonian and is the proposed ancestor of *Pl. praenuttalli* (Fig. 8).

Stratigraphic range. At TDP Site 31 *Pl. reussi* ranges from middle Turonian (upper *Helvetoglobotruncana helvetica* Zone)–Coniacian (*Dicarinella concavata* Zone; Fig. 3; Appendix 1).

Geographic range. United States (New Mexico, Texas), Africa (Tanzania), and the Caribbean.

Stable isotope paleoecology. No data available.

Planoheterohelix praenuttalli n. sp.
Figs. 19.1–19.13

Pseudotextularia elegans (Rzehak). Smith & Pessagno, 1973, p. 30, pl. 9, figs. 5–11 (Texas, U.S.A.); Nederbragt, 1989, p. 202, pl. 7, fig. 8 [Upper Maastrichtian (*Abathomphalus mayaroensis* Zone), western North Atlantic Ocean (DSDP Leg 93, Site 605)].

Pseudotextularia nuttalli (Voorwijk). Lamolda et al., 2007, fig. 4.N [Coniacian, northern Spain (Olazagutia)].

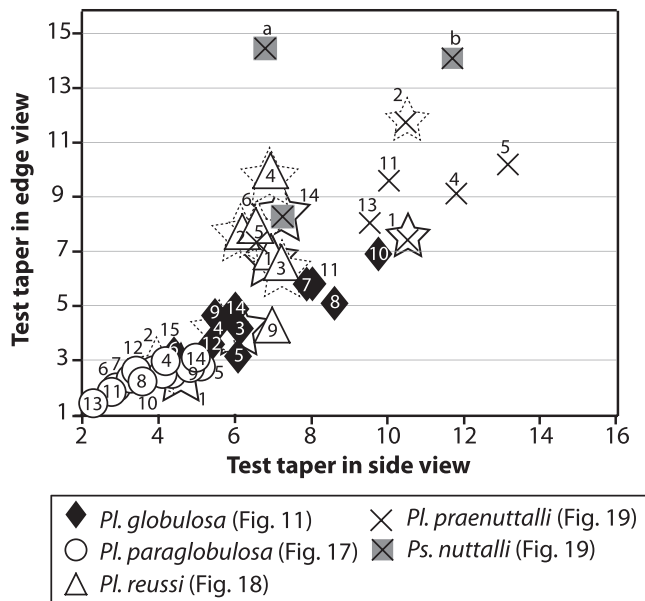


FIGURE 14. Side view vs. edge view taper for *Planoheterohelix reussi*, *Pl. globulosa*, *Pl. praenuttalli*, and *Pseudotextularia nuttalli*. Side view taper is maximum test width/diameter of proloculus. Edge view taper is maximum test breadth of penultimate chamber/breadth of proloculus. Point marker numbers represent the illustration number of the specimen on its respective figure. For *Ps. nuttalli* the markers labeled “a” and “b” are not illustrated on the figure, but are hypotypes from Nederbragt (1991 and 1989, respectively).

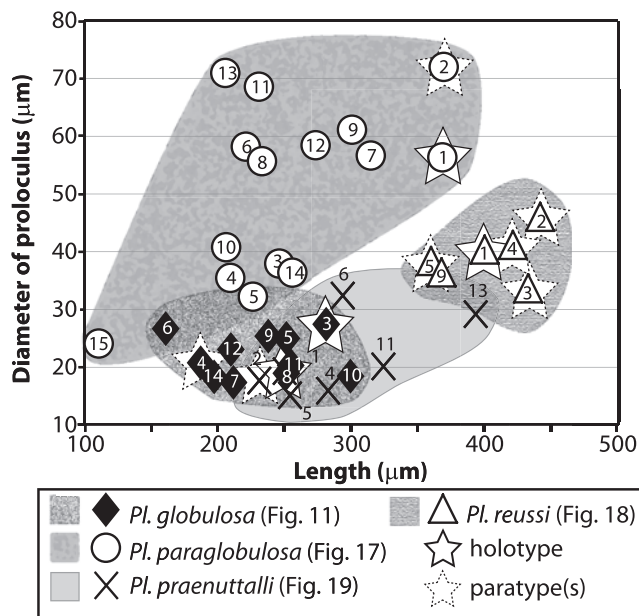


FIGURE 15. Test length vs. maximum diameter of proloculus of *Planoheterohelix paraglobulosa*, *Pl. globulosa*, and *Pl. reussi*. Point marker numbers represent the illustration number of the specimen on its respective figure.

Heterohelix reussi (Cushman). Walaszczyk et al., 2012, figs. 9.5a, b [Turonian-Coniacian, northeast New Mexico, U.S.A. (Springer composite section, sample Spr-3)].

Heterohelix cf. *globulosa* (Ehrenberg). Egger et al., 2013, p. 102, figs. 12.12, 12.13 [Santonian, Morzg, Salzburg, Austria (Gosau Group, northern Alps)].

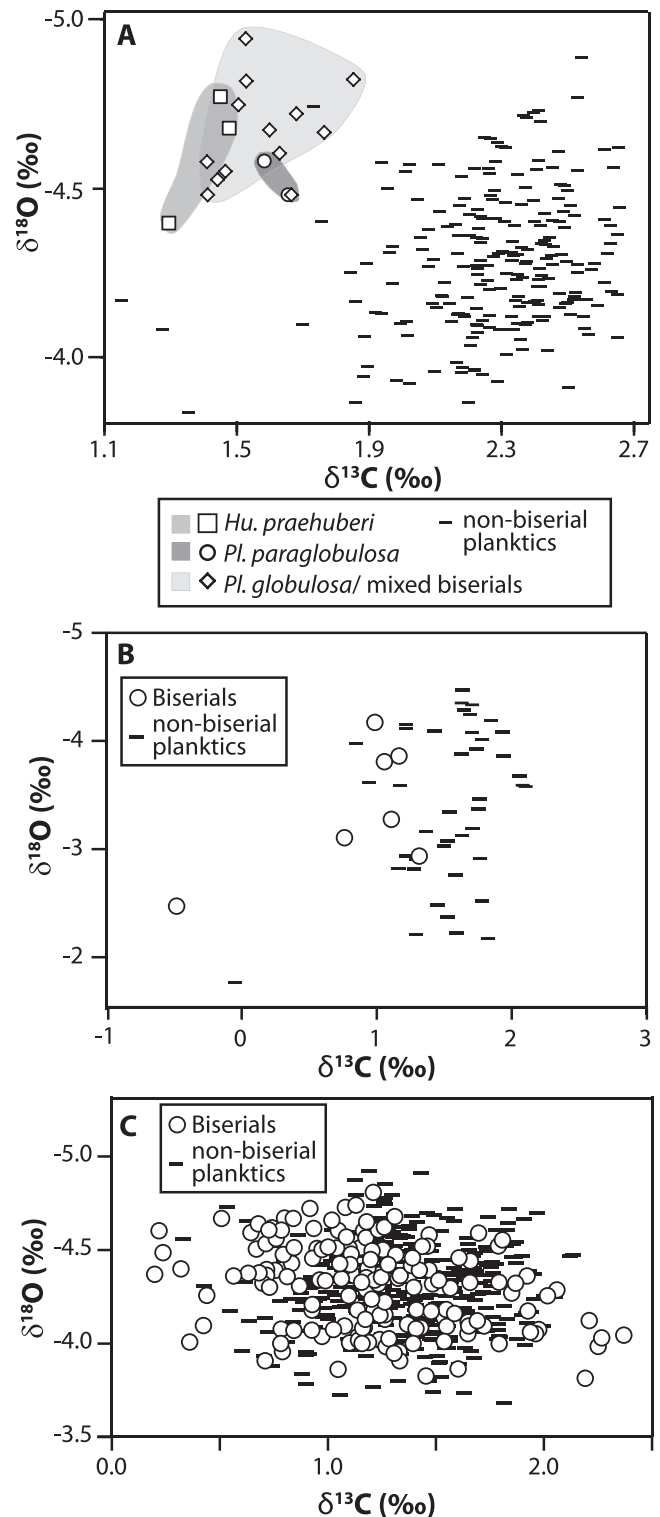


FIGURE 16. Cross plots of $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ for biserial planktic foraminifera relative to non-biserial planktics. **A** TDP Site 31 (data from Wendler et al., 2013); **B** DSDP Site 511 (data from Bice et al., 2003); **C** DSDP Site 1259 (data from Bornemann et al., 2008). *Hu.* = *Huberella*, *Pl.* = *Planoheterohelix*.

Type specimens. Holotype: USNM 560331, paratypes: USNM 560332, 560333, and 606424–606428.

Holotype dimensions. Length: $L = 250\ \mu\text{m}$; width: $W = 203\ \mu\text{m}$; breadth: $B = 139\ \mu\text{m}$; $L/W = 1.2$; $B/W = 0.7$.

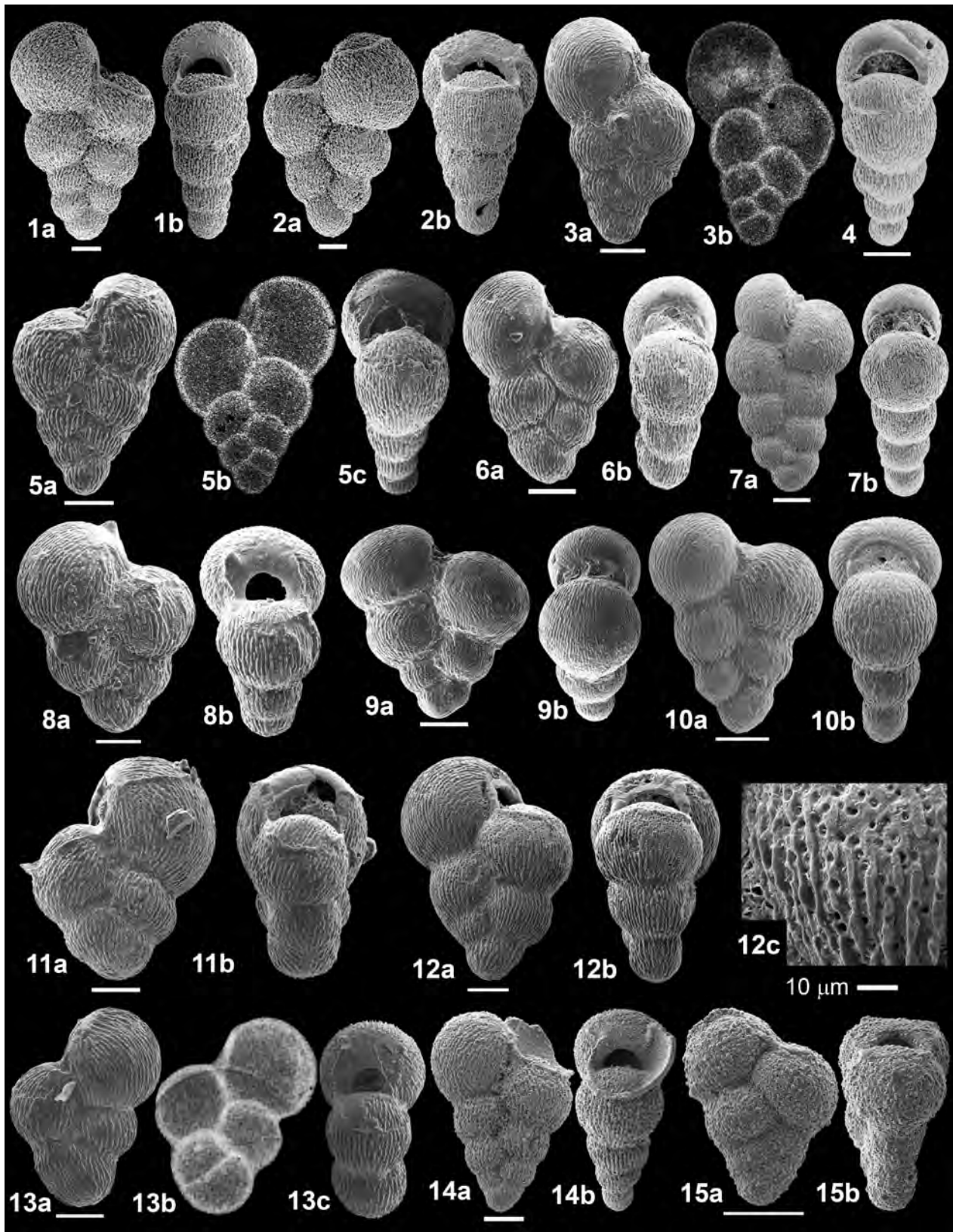


FIGURE 17. 1–15 *Planoheterohelix paraglobulosa* (Georgescu & Huber, 2009); unless otherwise noted, scale bars = 50 μ m, all SEMs were taken at the National Museum of Natural History, Washington, D.C., and specimens come from the lower-middle Turonian (*Helvetoglobotruncana helvetica* Zone): 1, Holotype (USNM 534401), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 35-1, 17–19 cm, images from Georgescu & Huber (2009, pl. 6, figs. 9, 10); 2, Paratype (USNM 534402), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 35-1, 17–19 cm, images from Georgescu & Huber (2009, pl. 6, figs. 11, 12); 3, Spl. TDP 31-38-1, 29–49 cm, X-ray (3b) taken at National Museum of Natural

Average paratype dimensions. L = 276 μm ; W = 226 μm ; B = 171 μm ; L/W = 1.2; B/W = 0.8.

Type level. Middle Turonian (*Marginotruncana schneegansi* Zone).

Type locality. Tanzania Drilling Project Site 31, south-eastern coastal region of Tanzania, Africa. Geographic coordinates: 10°1'49.8"S/39°38'44.0"E.

Repository. National Museum of Natural History, Washington, D.C.

Etymology. From the Latin *prae*, meaning “before,” referring to the species that is directly ancestral to *Pseudotextularia nuttalli* (Voorwijk, 1937).

Description. Test relatively large (typically >300 μm in length, average = 304 μm , n = 11), broadly rounded, consists of 9–12 chambers (n = 12) that are biserially arranged and globular throughout. The diameter of the proloculus is variable (range = 15–32 μm , n = 7) and subsequent chambers rapidly increase in size, resulting in a strongly tapered, subtriangular outline in side and edge views. Sutures are straight, strongly depressed, and generally meet the central axis at a right angle. Aperture is a symmetrical semicircular, low, broad arch at the base of the final chamber, bordered by an imperforate lip. Periapertural flanges are absent. Test wall is calcitic and hyaline. Chamber surface is finely perforate to macro-perforate (pore diameter = 0.9–3.2 μm , n = 2) and is ornamented with costae that vary from almost completely smooth to those with discontinuous costae that are up to 4.3- μm thick.

Distinguishing features. *Planoheterohelix praenuttalli* is generally large, strongly tapering, and almost as broad (in edge view) as it is wide (in side view).

Remarks. The holotype (Fig. 19.1) and first paratype (Fig. 19.2) of *Pl. praenuttalli*, being the best preserved specimens found in TDP Site 31 samples, present the key morphological features of the species, but are smaller than most other specimens included in the species (Figs. 12a–d; Appendix 5). Although another paratype (USNM 560333; Fig. 19.3) has a broken proloculus, it shows the range of variability in chamber ornamentation, with its nearly smooth wall texture (e.g., Fig. 19.10). Additional illustrated paratypes (USNM 606424–606428) and figured specimens from TDP Sites 21, 22, and 31 show the range of morphological variability for the species.

Planoheterohelix praenuttalli accommodates biserial forms that represent evolutionary intermediates between *Pl. globulosa* and *Pseudotextularia nuttalli*. In previous studies these forms have been confused with *Ps. nuttalli* (e.g., Lamolda, 2007) because of the wide test breadth, fine costae, and rapid chamber-size increase (Figs. 12A, B, 13). The key distinction separating *Pl. praenuttalli* from *Ps.*

nuttalli is that the latter species has a test that is “deeper than wide” (Nederbragt, 1989), i.e., the chamber breadth is greater than the chamber width (Fig. 13, Appendix 5), whereas chamber width and chamber breadth are subequal in *Pl. praenuttalli*. The new species is a conspicuous component of planktic assemblages within the lower *Mg. schneegansi* Zone in the TDP boreholes, making it an important biostratigraphic marker in the upper Turonian of Tanzania. Specimens in its lowermost range (e.g., TDP Site 31 Cores 25 through 19) are smaller than those that occur in Core 18 and above. The increase in abundance of these large forms probably accounts for the dramatic increase in the abundance of biserial taxa observed from TDP Site 31, Cores 19 to 18 (Fig. 20).

Planoheterohelix praenuttalli has chambers that increase in size more rapidly than most other Turonian biserial species (Fig. 7A). Comparison of the amount of test taper shows that *Pl. praenuttalli* is generally less strongly tapering in edge view than its descendant *Ps. nuttalli* (Fig. 14) but has a similar taper in side view. Measurements from the penultimate and ultimate chambers (Appendix 5), including penultimate chamber breadth (Z), ultimate chamber breadth (C), penultimate chamber height in edge view (T), penultimate chamber width (X), and ultimate chamber width (H), are used to more clearly discriminate between *Pl. praenuttalli* and its descendant *Ps. nuttalli* that clearly occupies separate morphospace (Fig. 21).

Specimens of *Pl. praenuttalli* exhibit two distinct sizes. The smaller (Figs. 19.2, 19.8, 19.9) has a shorter length and generally consists of fewer chambers than the larger (Figs. 19.11, 19.12). These two forms have the same stratigraphic distribution, but the larger forms tend to be more common in the uppermost Turonian samples and appear to be closer to *Ps. nuttalli*, while the smaller form is most common among the lower–mid-Turonian samples at TDP Site 31 (and may be transitional from *Pl. globulosa*).

Similar species. *Planoheterohelix praenuttalli* differs from *Pl. globulosa* in that it is 1) larger, 2) broader, and 3) more strongly tapering in both side and edge view. See “Remarks” presented for *Pl. praenuttalli* above for comparison to *Ps. nuttalli*.

Phylogenetic relationships. *Planoheterohelix praenuttalli* evolved from *Pl. reussi* and is the direct ancestor of *Ps. nuttalli* (Fig. 8).

Stratigraphic range. Documented in Tanzania at TDP Site 31 from the lower *Mg. schneegansi* Zone through the *Dicarinella concavata* Zone at the top of the borehole (Fig. 3; Appendix 1). This species was recorded in the Coniacian (*Di. concavata* Zone) at TDP Site 39 (Jiménez Berrocoso et al., 2015; M. R. Petrizzo, communication,

History, Washington D.C.; 4, Spl. TDP 22-9-1, 79–96 cm (no biostratigraphy table provided in Appendix); 5, Spl. TDP 31-38-1, 29–49 cm, X-ray (5b) taken at National Museum of Natural History, Washington D.C.; 6, Spl. TDP 31-30-1, 40–60 cm; 7, Spl. TDP 22-5-1, 68–88 cm (no biostratigraphy table provided in Appendix); 8, Spl. TDP 31-63-1, 29–49 cm; 9, Spl. TDP 31-57-3, 65–85 cm; 10, Spl. TDP 22-33-3, 10–30 cm (no biostratigraphy table provided in Appendix); 11, Spl. TDP 22-39-1, 48–66 cm (no biostratigraphy table provided in Appendix); 12, upper Cenomanian–lower Turonian (*Rotalipora cushmani*–*Whiteinella archaeocretacea* zones), Spl. TDP 24-4-1-2, 98–108 cm; 13, Spl. TDP 31-38-1, 29–49 cm, X-ray (13b) taken at National Museum of Natural History, Washington D.C.; 14, upper Cenomanian (*Ro. cushmani* Zone) western North Atlantic Ocean (Blake Nose), ODP Hole 1050C, Spl. 21-2, 99–102 cm; 15, upper Cenomanian (*Ro. cushmani* Zone), equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 37-1, 1–6 cm, transitional from *Pl. globulosa*.

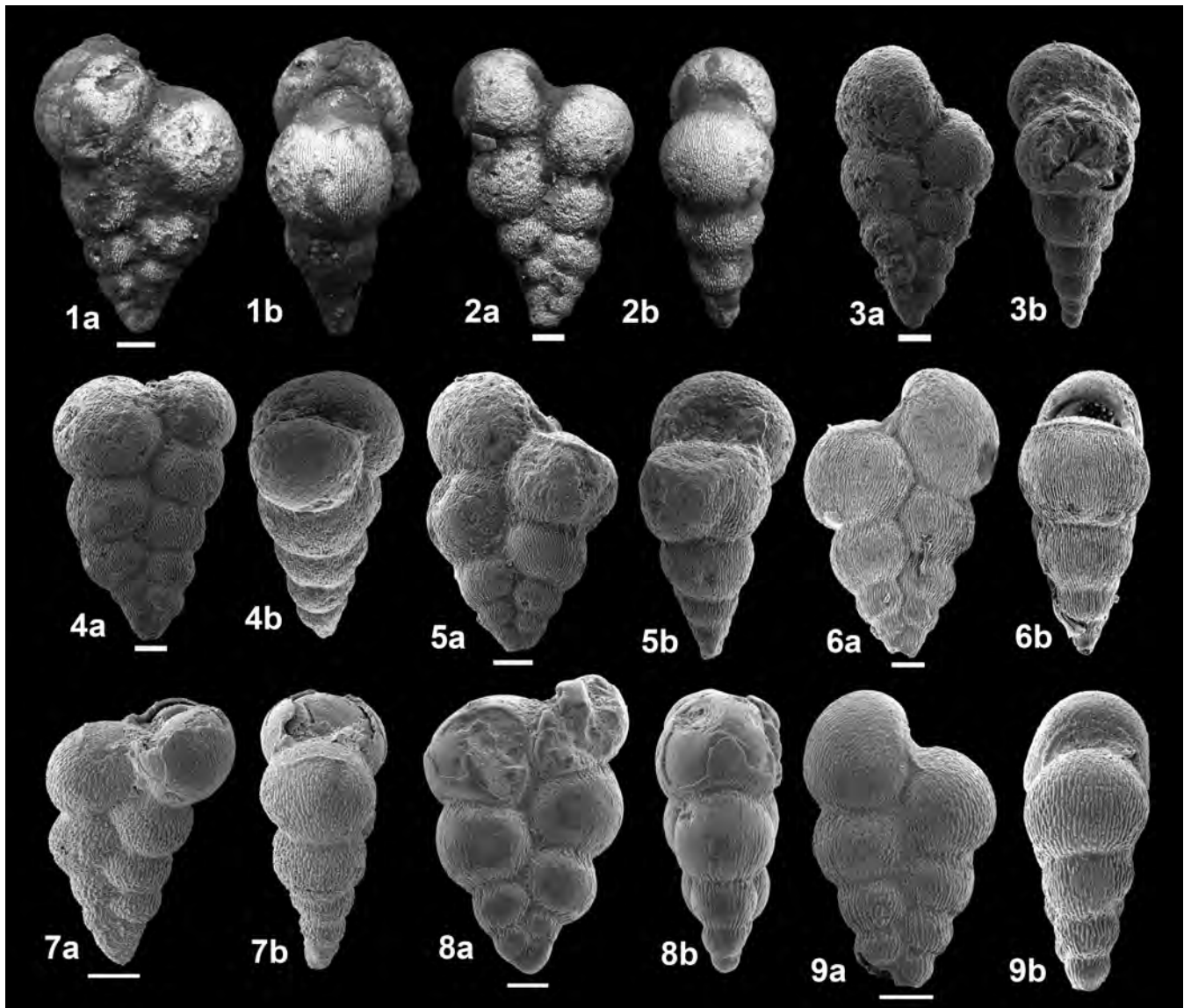


FIGURE 18. 1–9 *Planoheterohelix reussi* (Cushman, 1938); scale bars = 50 μ m and all SEMs were taken at the National Museum of Natural History, Washington, D.C., unless otherwise noted; 1–5 from the Turonian lower Austin Chalk, in ditch on west side of Sherman-Dennison highway, 3 mi. north of Sherman, Texas: 1, Holotype (USNM 24374), originally illustrated in Cushman (1938, pl. 2, fig. 6a, b), new SEMs were taken at the National Museum of Natural History, Washington, D.C.; 2, Paratype (USNM 24375), originally illustrated in Cushman (1938, pl. 2, fig. 7), new SEMs were taken at the National Museum of Natural History, Washington, D.C.; 3, Paratype (USNM 24480), previously unillustrated; 4, Paratype (USNM 24480), previously unillustrated; 5, Paratype (USNM 24480), originally illustrated in Cushman (1938, pl. 2, fig. 8); 6, middle Turonian (*Helvetoglobotruncana helvetica* Zone), South Atlantic Ocean (Falkland Plateau), DSDP Site 511, Spl. 40-1, 21–23 cm; 7, middle Turonian (uppermost *Hv. helvetica* Zone), Spl. TDP 31-27-2, 5–25 cm; 8, upper Turonian (*Marginotruncana schneegansi* Zone), Spl. TDP 31-18-1, 50–52 cm; 9, upper Turonian (*Mg. schneegansi* Zone), Spl. TDP 31-25-1, 77–88 cm.

2013), but additional work will be required to document its upper stratigraphic range.

Geographic distribution. United States (New Mexico, Texas), Africa (Tanzania), northern Spain, and Austria.

Stable isotope paleoecology. No data available.

Genus *Pseudotextularia* Rzehak, 1891

Type species: *Cuneolina elegans* Rzehak, 1891

Emended description (Nederbragt, 1991). “Test biserial throughout, or with an initial spiral coil. Adult chambers notably deeper than wide. Multiserial growth may be present in a terminal stage.”

Pseudotextularia nuttalli (Voorwijk, 1937)

Figs. 19.14, 19.15

Gümbelina nuttalli Voorwijk, 1937, p. 192, pl. 2, figs. 1–9, [Maastrichtian, Cuba (Havana)].

Guembelina plummerae Loetlerle. Said & Kenawy, 1956, p. 139, pl. 3, fig. 33 [Maastrichtian, Egypt (northern Sinai)].

Guembelina reussi Cushman. Said & Kenaway, 1956, p. 149, pl. 3, fig. 32 [Maastrichtian, Egypt (northern Sinai)].

Pseudotextularia nuttalli (Voorwijk). Nederbragt, 1989, p. 204, pl. 8, fig. 2 only [upper Maastrichtian (*Abathomphalus mayaroensis* Zone), western North Atlantic Ocean (New Jersey Margin, DSDP Leg 93, Site 605)] and p. 204, fig. 9 [drawing of lectotype, Maastrichtian, Cuba (Havana)]; Nederbragt, 1991, p. 364, pl. 10, fig. 4 [Maastrichtian (*Ab. mayaroensis* Zone), South Atlantic Ocean

(Rio Grande Rise, DSDP Leg 3, Site 21)], fig. 6 [Santonian (*Dicarinella asymetrica* Zone), northern Africa (El Kef, Tunisia)]. *Pseudotextularia ultimatumida* (White). D'Hondt & Arthur, 1995, fig. 1, top left [Maastrichtian (uppermost *Ab. mayaroensis* Zone), western North Atlantic Ocean (northern rim of Blake Nose Plateau, DSDP Leg 44, Site 390A)].

Pseudotextularia elegans (Rzehak). Abramovich et al., 2003, fig. IV.2 [Maastrichtian (*Pseudogumbelina hariensis* Zone), South Atlantic Ocean (Walvis Ridge, DSDP Leg 74, Hole 525A)].

Type specimen. Lectotype named by Nederbragt (1989); slide label: D12267.

Type level. Maastrichtian.

Type locality. Havana, Cuba.

Repository. Rijksuniversiteit micropaleontological collection, University of Utrecht, The Netherlands.

Original description. "Typical for this species is the flattening of the test in a direction opposite to most forms of this genus, so that the broad side shows one, and the narrow side, two series of chambers. The great change in the ratio of length, breadth and width is remarkable and can be seen on pl. 2, figs. 1–9. The figured specimens are from different localities."

Emended description (Nederbragt, 1989). "Test biserial, bi-concave to bi-convex in edge view. Sutures depressed, chambers clearly deeper than wide. Last pair of chambers of bi-concave specimens ovate to subglobular in edge view. Surface finely costate; aperture a wide, low arc."

Distinguishing features. *Pseudotextularia nuttalli* can be easily distinguished from other Turonian heterohelics as it is broader in edge view than wide in side view.

Remarks. The gradual evolution from *Planoheterohelix praenuttalli* to *Ps. nuttalli* is manifested by an increasingly tapering edge profile (e.g., Figs. 19.11, 19.12), and forms that attain a 1:1 ratio for maximum test breadth/width are assigned to *Ps. nuttalli* (Figs. 19.14, 19.15). The transition is well-documented here in the upper *Marginotruncana schneegansi* Zone of TDP Site 31. In addition to the lectotype (Nederbragt, 1989, p. 204, figs. 9A, B; Fig. 19.14), only one SEM image of an unbroken specimen from TDP Site 39 (Fig. 19.15) was available for accurate measurement. Additional measurements were made using SEM photomicrographs from Nederbragt (1989, 1991; *Ps. nuttalli* point markers labeled "a" and "b" on Figs. 12, 14, 21). Drawings included in Voorwijk's 1937 paper (p. 192, pl. 2, figs. 1–9) were also measured to try to obtain enough size data for comparison with other species; however, these measurements are not included in Figure 19 as the scale bars may have been inaccurately drawn.

Size measurements of *Ps. nuttalli* are significantly different from those obtained from other studied biserial taxa (Figs. 12, 13). The breadth/width measurements (Fig. 12B) show that *Ps. nuttalli* is much broader than all other biserial species measured, but its length is comparable to other large biserial species (i.e., *Pl. praenuttalli* and *Pl. reussi*). *Planoheterohelix praenuttalli*, however, distinctly differs from *Ps. nuttalli* in height, width, and breadth measurements of the ultimate and penultimate chambers (Fig. 21; in-depth discussion of these measurements in previous section).

Similar species. See "Remarks" presented for *Pl. praenuttalli* above.

Phylogenetic relationships. *Pseudotextularia nuttalli* evolved from the large-sized, strongly tapering *Pl. praenuttalli* within the late Coniacian *Di. concavata* Zone (Fig. 8).

Stratigraphic range. The first occurrence of *Ps. nuttalli* s. s., with a breadth/width ratio >1, is in Sample TDP 39-31-1, 1–25 cm (Fig. 19.15) within the *Di. concavata* Zone near the Coniacian-Santonian boundary (Fig. 8). This species ranges into the upper Maastrichtian at a number of locations worldwide.

Geographic distribution. Cosmopolitan.

Stable isotope paleoecology. Thus far, there have been no $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements made for *Ps. nuttalli* at any TDP site. Previous work shows that $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of *Ps. nuttalli* are temporally and geographically variable (D'Hondt & Arthur, 1995, therein referred to as *Ps. ultimatumida*; Abramovich et al., 2003, therein referred to as *Ps. elegans*). In D'Hondt & Arthur (1995) the taxon's $\delta^{18}\text{O}$ values span most of the range exhibited by other planktic taxa, whereas $\delta^{13}\text{C}$ values fell near the midpoint of other planktic species. Abramovich et al. (2003) characterized members of *Pseudotextularia* as occupying deeper portions of the surface mixed layer and showed the genus as having $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values near the median of those exhibited by co-occurring planktic foraminifera.

Genus *Huberella* Georgescu, 2007a

Type species: *Huberella huberi* Georgescu, 2007a

Original description. "Test biserial throughout. Proloculus is smaller than second chamber. Chambers are subglobular to reniform in shape, tilted to the axis of growth at least in the adult portion of the test. Chamber projections attached to the previously formed ones in the row are present in the morphologically advanced tests. Sutures are distinct, depressed, straight to curved, and oblique to the test axis of growth. Periphery broadly rounded, without peripheral structures. Aperture is situated at the base of the last-formed chamber and is bordered by two symmetrical periapertural flanges. No accessory apertures are present along the zigzag suture. Chamber surface is ornamented with fine, closely spaced and often discontinuous costae. Test wall is calcareous, hyaline, microporiferate."

Remarks. Species assigned to *Huberella* have a zigzag medial suture (Georgescu, 2007a; Figs. 22–24), which are easily observable under a light microscope. The extent to which costae are present on species belonging to this genus is variable, as is the wall structure.

Huberella praehuberi Georgescu, 2007a

Figs. 23.1–23.16

Heterohelix pulchra (Brotzen). Eicher & Worstell, 1970a, p. 296, pl. 8, fig. 10 [lower Turonian, southwest Kansas, U.S.A. (Hartland Shale member of the Greenhorn Formation)]; Eicher & Worstell, 1970b, pl. 1, fig. 2 [lower Turonian, southwest Kansas, U.S.A. (Fairport member of the Carlile Shale)].

Heterohelix moremani (Cushman). de Klasz et al., 1995, p. 363, pl. 2, fig. 4 [lower Turonian, western Africa (Senegal)].

Laeviheterohelix pulchra (Brotzen). Caron et al., 2006, fig. 7:9 [lower-middle Turonian (*Helvetoglobotruncana helvetica* Zone), Africa (wadi Bahloul, Tunisia)].

Huberella praehuberi, Georgescu, 2007a, p. 216, pl. 3, figs. 4–8 [lower Turonian (*Hv. helvetica* Zone), equatorial Pacific Ocean (Shatsky Rise [sic], Mid-Pacific Mountains, DSDP Leg 62, Site 463)].

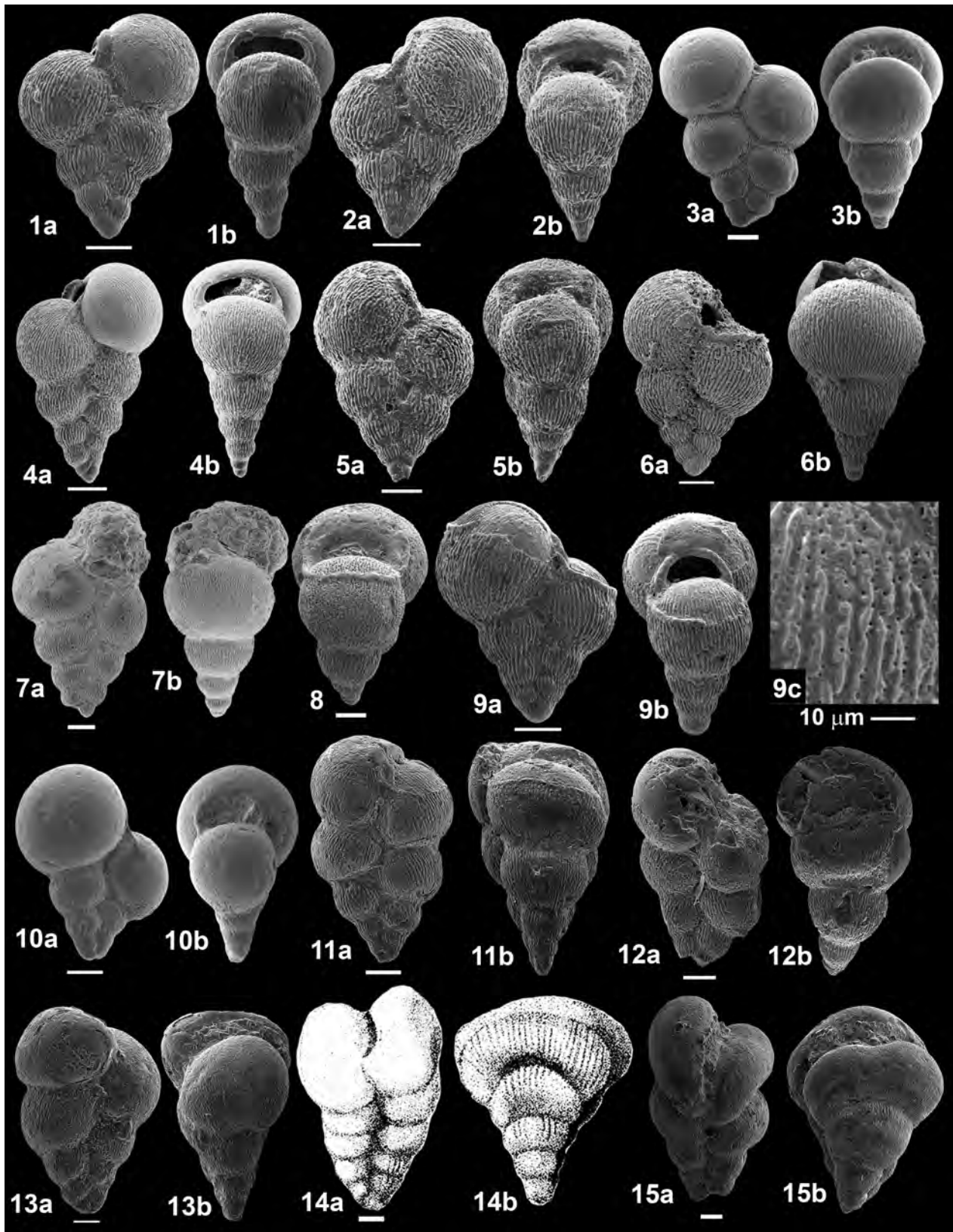


FIGURE 19. Transition from *Planoheterohelix praenuttalli* n. sp. to *Pseudotextularia nuttalli* (Voorwijk, 1937); scale bars = 50 μ m and all SEMs were taken at the National Museum of Natural History, Washington, D.C., unless otherwise noted. 1–13 *Pl. praenuttalli*; specimens come from the upper Turonian (*Marginotruncana schneegansi* Zone) unless otherwise noted: 1, Holotype (USNM 560331), Spl. TDP 31-19-1, 2–20 cm; 2, Paratype (USNM 560332), Spl. TDP 31-7-1, 75–90 cm; 3, Paratype (USNM 560333), Spl. TDP 31-19-1, 30–70 cm; 4, middle Turonian (*Helvetoglobotruncana helvetica* Zone), Spl. TDP 22-9-1, 76–96 cm; 5, Paratype (USNM 606424), Spl. TDP 31-7-1, 75–90 cm; 6, specimen from Toolonga Calcilitite,

Type specimens. Holotype: USNM 534391, paratype: USNM 534392.

Type level. Lower Turonian (*Helvetoglobotruncana helvetica* Zone).

Type locality. Equatorial Pacific Ocean (Mid-Pacific Mountains, DSDP Leg 62, Site 463), 21°21'N/174°40'E.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test biserial throughout consisting of fifteen to seventeen chambers, which increase slowly in size as added. The proloculus is small-sized and is followed by the slightly large-side [sic] second chambers. Earlier chambers are subglobular in shape, then subrectangular, the last-formed ones being reniform and tilted and with a small test wall flexure oriented towards the zigzag suture. The resulted chamber inflation is attached to the previous formed chamber of the row in the morphologically advanced specimens. Test axis of growth can be slightly twisted in the plane of symmetry. Sutures are distinct, depressed, straight between the earlier chambers and curved between the last-formed ones, oblique to the test axis of growth. The test is symmetrical in edge view, with broadly rounded periphery and without peripheral structures. Aperture is a medium to high arch situated at the base of the last-formed chamber. It is bordered by two symmetrically developed periapertural flanges. False accessory apertural openings can be present along the zigzag suture at the specimens with developed text [sic] wall flexure. Chamber surface is ornamented with fine, often discontinuous and closely spaced costae. Test wall is calcareous, hyaline and microporulate, pore diameter ranging between 0.7 and 0.9 microns. Pores are mostly situated in the narrow spaces between costae, more rarely over these ornamentation elements resulting in interrupted ornamentation feature.”

Distinguishing features. *Huberella praehuberi* is distinguished by the presence of sutural inflections on adult chambers of the test (Georgescu, 2007a) and absence of apical chamber projections.

Remarks. Original SEM images of the holotype and a paratype of *Hu. praehuberi* are illustrated here along with new X-ray images (Figs. 23.1, 23.2). Figure 23.5 is the oldest documented occurrence of *Hu. praehuberi* from the lowermost core of TDP Site 31 (TDP 31-63-2, 26–45 cm; Fig. 3; Appendix 1). *Huberella praehuberi* exhibits many traits similar to its direct descendant *Planoheterohelix postmoremani* (Georgescu et al., 2011). X-ray images of the types and a Tanzanian specimen show that both species have a reniform chamber morphology (Figs. 23.1b, 23.2b, 23.6c). In addition, both have slender tests, symmetrical flanges, and a smooth test surface early in ontogeny that later becomes finely striate (Fig. 10). *Huberella praehuberi* differs in having chambers that increase in size slightly

faster (Fig. 7), well-developed sutural inflections (Figs. 10, 24), and pockets that occasionally appear on the apertural margin (Figs. 10, 24). The transition between the two species proposed by Georgescu et al. (2011) could not be documented in Tanzania as much of the lower *Whiteinella archaeocretacea* Zone was not recovered. The sutural inflection (also referred to as sutural depression or test wall flexure) on *Hu. praehuberi* is always near the medial suture and is occasionally present on the juvenile portion of the test (Figs. 10, 23.4c, 24). The excellent preservation of wall texture and chamber surface ornamentation of Tanzanian specimens has made it possible to identify fine-scale details that help further characterize this species. For example pore mounds are present on all *Hu. praehuberi* specimens from Tanzanian sites but are variably expressed (Fig. 10). The absence of fine costae on the earliest chambers is another characteristic that was not previously documented, probably because of inadequate preservation (e.g., Figs. 23.6, 23.9, 23.16). Some specimens assigned to this species are nearly smooth throughout their ontogeny (Fig. 23.11). Although individuals with smooth test walls are rare, the trait is characteristic of forms that are transitional between *Hu. praehuberi* and *Laeviheterohelix reniformis*. Smooth-walled forms of *Hu. praehuberi* have also been documented in middle Turonian sediments from Hamilton County, Kansas (Georgescu, 2013, figs. 5.6–5.9, which are reillustrated specimens from Eicher & Worstell, 1970a, 1970b).

Similar species. *Huberella praehuberi* differs from *Laeviheterohelix pulchra* in having 1) sutural inflections, 2) continuous fine costae on the middle to later portions of the test, and 3) chambers that less strongly overlap previously formed chambers. It differs from *Lv. reniformis* in 1) always having a biserial chamber arrangement and having 2) more poorly developed pore mounds and 3) narrower sutural inflections; and from *Hu. huberi* in 1) being less tapered in side view and 2) not having posterior chamber projections near the medial suture.

Phylogenetic relationships. *Huberella praehuberi* evolved from *Pl. postmoremani* in the early Turonian *Wh. archaeocretacea* Zone and is the direct ancestor of *Hu. huberi* and *Lv. reniformis* (Figs. 3, 8).

Stratigraphic range. The first occurrence of *Hu. praehuberi* is likely in the early Turonian (*Wh. archaeocretacea* Zone); however, because no complete Cenomanian–Turonian boundary sections containing this species have yet been identified, the transition between the presumed ancestor, *Pl. postmoremani*, and *Hu. praehuberi* has not been documented (Fig. 23.3; Appendices 1, 2). The last occurrence is in the middle Turonian (*Mg. schneegansi* Zone) and was recorded at TDP Site 31 (Fig. 3; Appendix 1). Georgescu (2007a) extended *Hu. praehuberi* into the upper *Mg.*

←
Pillawara Hill, Australia, near the type level of *Pl. papula*, Spl. 7164-0040 collected by D. J. Belford; 7, Spl. TDP 21-7-1, 24–38 cm (image taken by M. R. Petrizzo); 8, Paratype (USNM 606425), Spl. TDP 31-19-1, 2–20 cm; 9, Spl. TDP 31-19-1, 2–20 cm, transitional; 10, Paratype (USNM 606426), Spl. TDP 31-18-1, 40–52 cm; 11, Paratype (USNM 606427), Spl. TDP 31-8-1, 58–76 cm (image taken by M. R. Petrizzo); 12, Paratype (USNM 606428), upper Turonian (*Dicarinella concavata* Zone), Spl. TDP 31-2-1, 29–34 cm (image taken by M. R. Petrizzo); 13, Coniacian (*Di. concavata* Zone), Spl. TDP 39-33-3, 1–25 cm (image taken by M. R. Petrizzo). **14, 15** *Ps. nuttalli*: 14, Lectotype, side and edge view drawings from Nederbragt (1989, figs. 9a, b); 15, Coniacian–Santonian (*Di. concavata* Zone), Spl. TDP 39-31-1, 1–25 cm (image taken by M. R. Petrizzo).

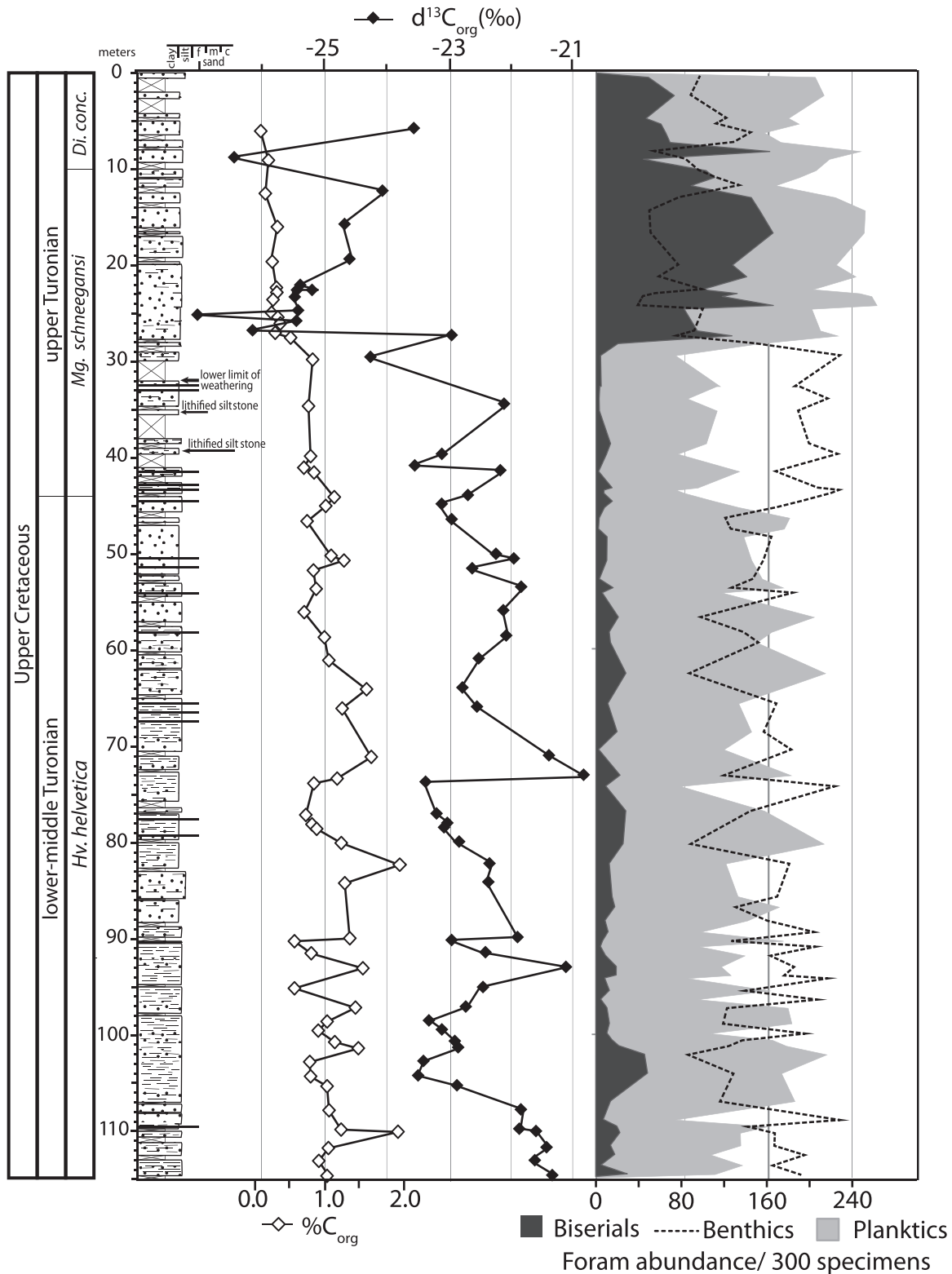


FIGURE 20. Depth profiles of TDP Site 31, bulk $\delta^{13}\text{C}_{\text{org}}$ isotopes, % total organic carbon, and relative abundance of biserial and non-biserial planktic species and benthic species normalized to 300 total specimens.

schneegansi Zone (*Mg. sigali* Zone), but we did not find it above the lower *Mg. schneegansi* Zone in Tanzania.

Geographic distribution. United States (Kansas), Africa (Tanzania, Tunisia, Senegal), and equatorial Pacific Ocean (Mid-Pacific Mountains).

Stable isotope paleoecology. As observed for other heterohellicids at TDP Site 31, *Hu. praehuberi* has lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values relative to co-occurring trochospiral planktic foraminifera. It has similar $\delta^{18}\text{O}$ values but slightly lower $\delta^{13}\text{C}$ values (on average) than other TDP 31

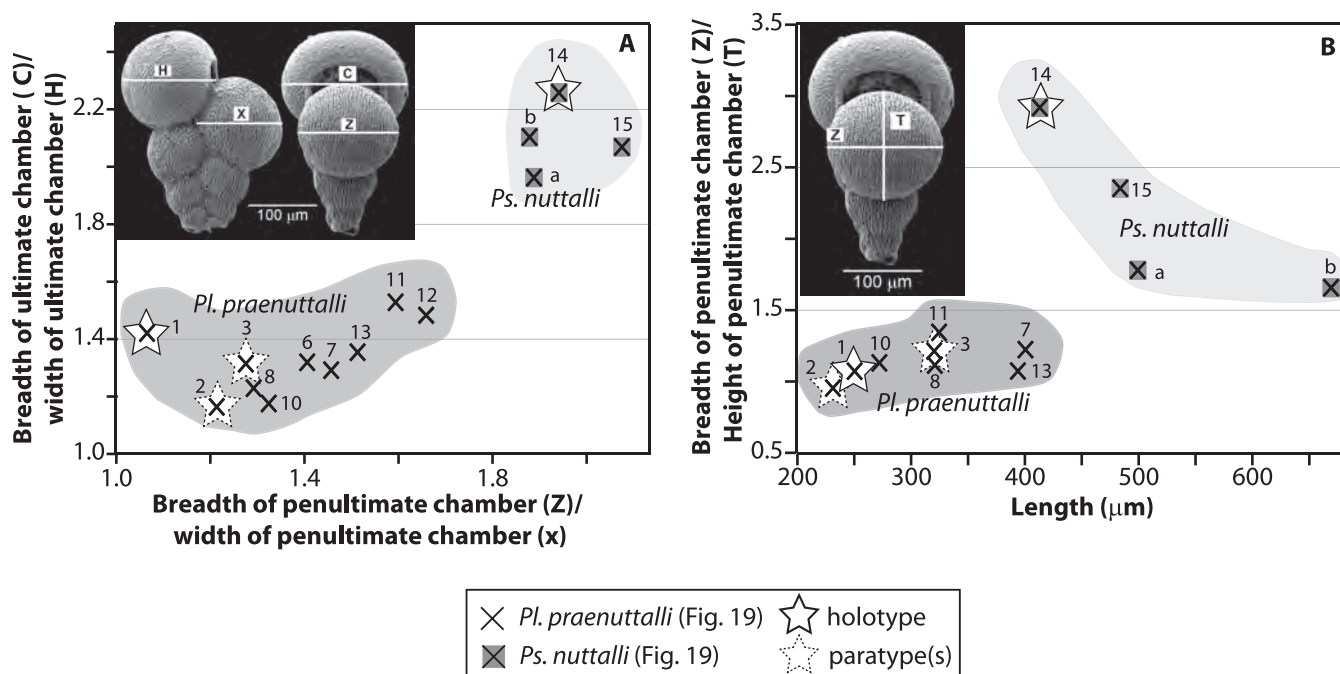


FIGURE 21. Breadth and width measurements of *Pseudotextularia nuttalli* vs. *Planoheterohelix praenuttalli*. Point marker numbers represent the illustration number of the specimen on its respective figure. For *Ps. nuttalli* the markers labeled “a” and “b” are not figured on the plate, but represent hypotypes from Nederbragt (1991 and 1989, respectively). **A** Breadth of penultimate chamber (Z)/width of penultimate chamber (x) vs. breadth of ultimate chamber (C)/width of ultimate chamber (H) for *Ps. nuttalli* and *Pl. praenuttalli*. **B** Length vs. breadth of penultimate chamber (Z)/height on the penultimate chamber for *Ps. nuttalli* and *Pl. praenuttalli*.

biserial species that have been analyzed, but differences may be an artifact of small sample size (Fig. 16).

Huberella huberi Georgescu, 2007a
Figs. 22.1–22.18

Pseudoguembelina costellifera Masters. Nederbragt, 1991, p. 358, pl. 8, fig. 1 only [early Santonian (later revised to Turonian), DSDP Leg 10, Site 95, western North Atlantic (Yucatan Shelf)]; Wilson et al., 2002, fig. 1:6 [Turonian, western Atlantic Ocean (Demerara Rise, DSDP Leg 14, Hole 144A)].

Laeviheterohelix pulchra (Brotzen). Lamolda et al., 2007, fig. 4.F [early Santonian, northern Spain (Olazagutia)].

Heterohelix sp. in Lamolda et al., 2007, fig. 4.G [early Santonian, northern Spain (Olazagutia)].

Huberella huberi, Georgescu, 2007a, p. 214, pl. 2, fig. 1 [late Turonian (*Dicarinella concavata* Zone), southern North Atlantic Ocean (Venezuelan Basin, DSDP Leg 10, Site 150)], figs. 2–6 [late Turonian (*Marginotruncana sigali* Zone), southern North Atlantic Ocean (Venezuelan Basin, DSDP Leg 10, Site 150)], pl. 3, fig. 1 [late Turonian (*Mg. sigali* Zone), southern North Atlantic Ocean (Venezuelan Basin, DSDP Leg 10, Site 150)]; Egger et al., 2013, p. 103, figs. 13.28–13.30 [Santonian, Morzg, Salzburg, Austria (Gosau Group, northern Alps)].

Type specimens. Holotype: USNM 534389, paratypes: USNM 534390 (measured but not figured).

Type level. Middle Turonian (*Marginotruncana schneegansi* Zone).

Type locality. Caribbean (Venezuelan Basin, DSDP Leg 15, Site 150), 14°51'N/69°35'W.

Repository. National Museum of Natural History, Washington, D.C.

Original description. “Test is biserial throughout, consisting of thirteen to fourteen chambers, initiated with a small-sized proloculus, which is followed by a slightly larger second chamber. Earlier chambers are subrectangular,

becoming reniform in the adult stage, tilted to the test axis of growth and increasing gradually in size as added. Later chambers present a posterior projection, which is attached to the previous chamber in the row and the periapertural flange of the previous-formed chamber. Sutures are distinct, depressed and oblique to the axis of growth. Test is symmetrical in edge view, with broadly rounded periphery and without peripheral structures. Aperture is situated at the base of the last-formed chamber and is bordered by two symmetrically developed periapertural flanges. False accessory apertures can be developed along the zigzag suture due to the test-wall folding in the proximity of the cameral projections and periapertural structures. Chamber surface is covered throughout by quasi-longitudinal fine costae. Test wall is calcareous, hyaline, and micropore. Pores are mostly situated in the spaces between the costae or, more rarely, onto these strictures resulting in discontinuous costate ornamentation. Pore diameter is in the range of 0.7–1.0 microns.”

Distinguishing features. *Huberella huberi* is easily distinguished from other Turonian heterohelid species by the tube-like extension that projects in the apical direction from the ultimate and, sometimes, penultimate chambers.

Remarks. Scanning electron microscope images of the holotype and a topotype of *Hu. huberi* were originally published in Georgescu (2007a) and new X-ray images of those specimens are presented in Figures 22.1 and 22.2. The new X-ray images accentuate the ovate shape of the chambers with the tube-like projection, directed apically from the adult chambers (Figs. 22.1b, 22.2b, 22.5b). The juvenile portion of *Hu. huberi* is slender and the adult

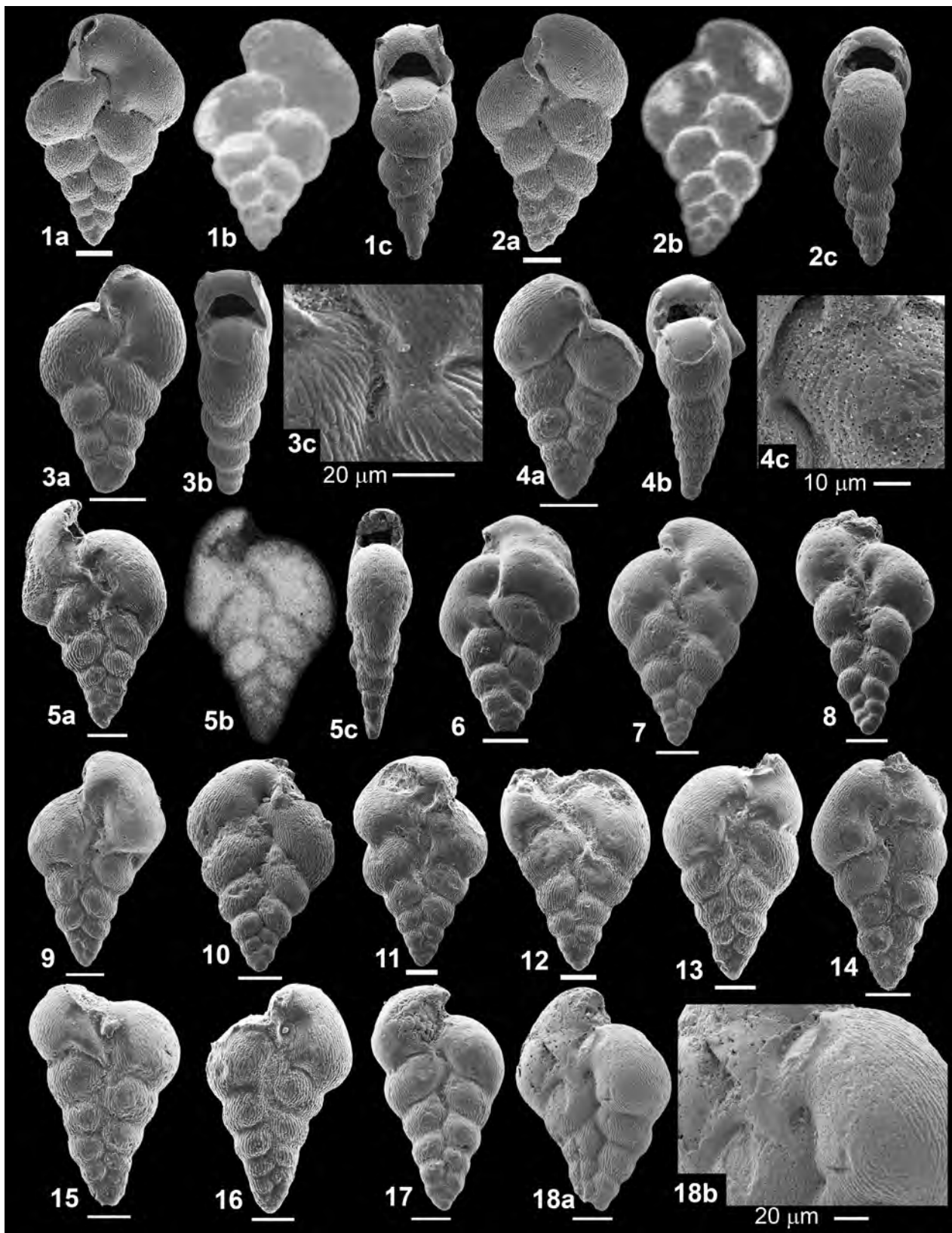


FIGURE 22. 1–18 *Huberella huberi* Georgescu, 2007a; unless otherwise noted, scale bars = 50 μm; all SEMs were taken at the National Museum of Natural History, Washington, D.C., and specimens come from the upper Turonian (*Marginotruncana schneegansi* Zone): 1, Holotype (USNM 534389), middle-upper Turonian [*Mg. sigali* (= *Mg. schneegansi*) Zone], Venezuelan Basin (Caribbean), DSDP Site 150, Spl.10-2, 48–62 cm, SEM images (1a, c) from Georgescu (2007a, pl. 2, figs. 6a, b) and X-ray (1b) taken at the National Museum of Natural History, Washington, D.C.; 2, Topotype, upper Turonian (*Dicarinella concavata* Zone), Venezuelan Basin (Caribbean), DSDP Site 150, Sample 10-1, 58–79 cm, SEM images (2a, c)

portion is commonly rapidly tapering, giving it a fan-shaped outline (Figs. 10, 22). Chamber size increases rapidly through ontogeny (Fig. 7D). Unlike *Hu. praehuberi*, the chamber surface is ornamented with fine costae that cover the entire test. The thickness of the costae remains constant throughout the entire test with the exception of the ultimate and occasionally the penultimate chambers, where the costae appear to be more weakly expressed.

The presence of the apical projection on later chambers of *Hu. huberi* represents an important evolutionary transition from *Hu. praehuberi* to *Hu. huberi* (Figs. 10, 24). This projection is likely the result of elongation and rotation of the final chamber of *Hu. praehuberi* and appears as a folded apertural flap on well-preserved forms of *Hu. huberi* (Fig. 22.1). Illustration of five regions of *Huberella* chamber sutures (Fig. 24: top panel = *Hu. praehuberi*, bottom panel = *Hu. huberi*) helps show the evolutionary transition from *Hu. praehuberi* to *Hu. huberi*. Segment “c” (the apertural rim or lip of *Hu. praehuberi*) becomes more inflated, in turn, making a pronounced depression “e,” causing the chamber to appear continuous and reniform. In stretching to accommodate this step, “d” (the depression between points “a” and “b”) becomes less pronounced and “b” becomes the tube-like projection, pointing towards the apical region that is visible in the X-ray images (e.g., the penultimate chamber of Fig. 22.5b). In the most fully developed forms of *Hu. huberi* a second tube opens at the base of the aperture (“c” on the lower *Hu. huberi* panel of Fig. 24).

Georgescu (2007a) recorded the first appearance of *Hu. huberi* within the *Hv. helvetica* Zone, overlapping the stratigraphic range of *Hu. praehuberi*. In Tanzania, however, there is a gap of about 5–8 m between the last occurrence of *Hu. praehuberi* and the first occurrence of *Hu. huberi* (Fig. 3). In a later work Georgescu et al. (2011) updated the biserial assemblage record by reassigning one specimen originally identified as *Hu. huberi* to *Hu. praehuberi* (Georgescu, 2007a, pl. 3, fig. 3). The latter specimen does not fit well into our concept of *Hu. praehuberi* or *Hu. huberi*, as it does not have well-defined sutural indentations or an apically directed projection. This specimen is likely either a transitional form or a different species. It was found in TDP Site 31 core 25 in the lower *Mg. schneegansi* Zone (Fig. 23.16; Appendix 1).

Similar species. See “*Similar species*” presented for *Hu. praehuberi* above.

Phylogenetic relationships. *Huberella huberi* evolved from *Hu. praehuberi* in the mid-Turonian (Figs. 3, 8).

Stratigraphic range. At TDP Site 31 (Fig. 3) *Hu. huberi* ranges from the middle Turonian *Mg. schneegansi* Zone (core 18; Appendix 1) to the uppermost Turonian *Di. concavata* Zone. Georgescu et al. (2011) proposed that *Hu.*

huberi became extinct at the Turonian-Coniacian boundary and can be used as a datum to mark that boundary. However, we could not confirm that proposition because the cores did not reach that boundary.

Geographic distribution. Africa (Tanzania), Austria (northern Alps), western North Atlantic Ocean (Yucatan Shelf), North Atlantic (Demerara Rise), and Caribbean (Venezuelan Basin).

Stable isotope paleoecology. There are no species-specific stable-isotopic analyses of *Hu. huberi* from the Tanzanian sites. However, Wilson et al. (2002, p. 608, fig. 2) presented single-species analyses for “*Pseudoguembelina costellifera*” collected from Demerara Rise, which is here identified as *Hu. huberi*. Cross-plots of their $\delta^{18}\text{O}$ vs. $\delta^{13}\text{C}$ values indicate that, compared to *Pl. globulosa* (referred to in Wilson et al., 2002, as *Heterohelix globulosa*), *Hu. huberi* lived in water that was slightly cooler and/or more enriched in ^{18}O and slightly depleted in ^{13}C relative to the waters in which *Pl. globulosa* calcified.

Genus *Laeviheterohelix* Nederbragt, 1991

Type species: *Gumbelina pulchra* Brotzen, 1936

Steineckia Georgescu, 2009a, p. 325.

Original description. “Test calcareous, biserial throughout or with an initial planispiral coil; wall microporulate and smooth with scattered pustules, or with pores situated in the center of a pore mound. Aperture a simple arch, bordered by distinct flanges.”

Remarks. The oldest species of this lineage was previously proposed to be *Lv. pulchra* (Nederbragt, 1991) from the Turonian (Fig. 8). However, we have documented *Lv. reniformis* in the middle Turonian (*Helvetoglobotruncana helvetica* Zone) well before the reported first occurrence of *Lv. pulchra* (Fig. 8). The transition from *Huberella* to *Laeviheterohelix* is marked by a complete loss of costae, the appearance of well-developed pore mounds, and a widening of sutural inflections. Figure 23.11 illustrates an early transitional form that is almost entirely smooth and is ornamented with faint pore mounds.

The monospecific genus *Steineckia* Georgescu, 2009a, was created to accommodate forms with pore mounds that are biserial throughout (i.e., do not become multiserial) and do not have a periapertural pustulose area. *Steineckia* is here considered a junior synonym of *Laeviheterohelix* as it also includes a species that is biserial throughout with pore mounds such as *Lv. pulchra*. Absence of a periapertural pustulose area is not considered useful for genus-level distinction.

Phylogenetic relationships. We propose that the common ancestor of *Laeviheterohelix* species is *Hu. praehuberi* (Fig. 8) based on the presence of sutural inflections and pore mounds on transitional forms (Figs. 25.3–25.5).

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from Georgescu (2007a, pl. 2, fig. 1) and X-ray (2b) taken at the National Museum of Natural History, Washington, D.C.; 3, Spl. TDP 31-25-1, 77–88 cm, transitional from *Hu. praehuberi*; 4, Spl. TDP 31-21-2, 40–50 cm, transitional from *Hu. praehuberi*, no true tube formed; 5, TDP 31-7-1, 75–90 cm; 6, Spl. TDP 31-16-2, 10–20 cm; 7, Spl. TDP 31-16-1, 10–30 cm; 8, Spl. TDP 31-17-1, 2–22 cm; 9, Spl. TDP 31-9-1, 34–51 cm; 10, Spl. TDP 31-18-1, 67–89 cm; 11, Spl. TDP 31-14-2, 5–25 cm; 12, Spl. TDP 31-11-1, 0–20 cm; 13, 14, Spl. TDP 31-10-1, 19–39 cm; 15, Spl. TDP 31-9-1, 34–51 cm; 16, Spl. TDP 31-8-1, 58–76 cm; 17, upper Turonian (*Di. concavata* Zone), Spl. TDP 31-1-1, 34–50 cm; 18, Spl. TDP 31-156-1, 26–40 cm.

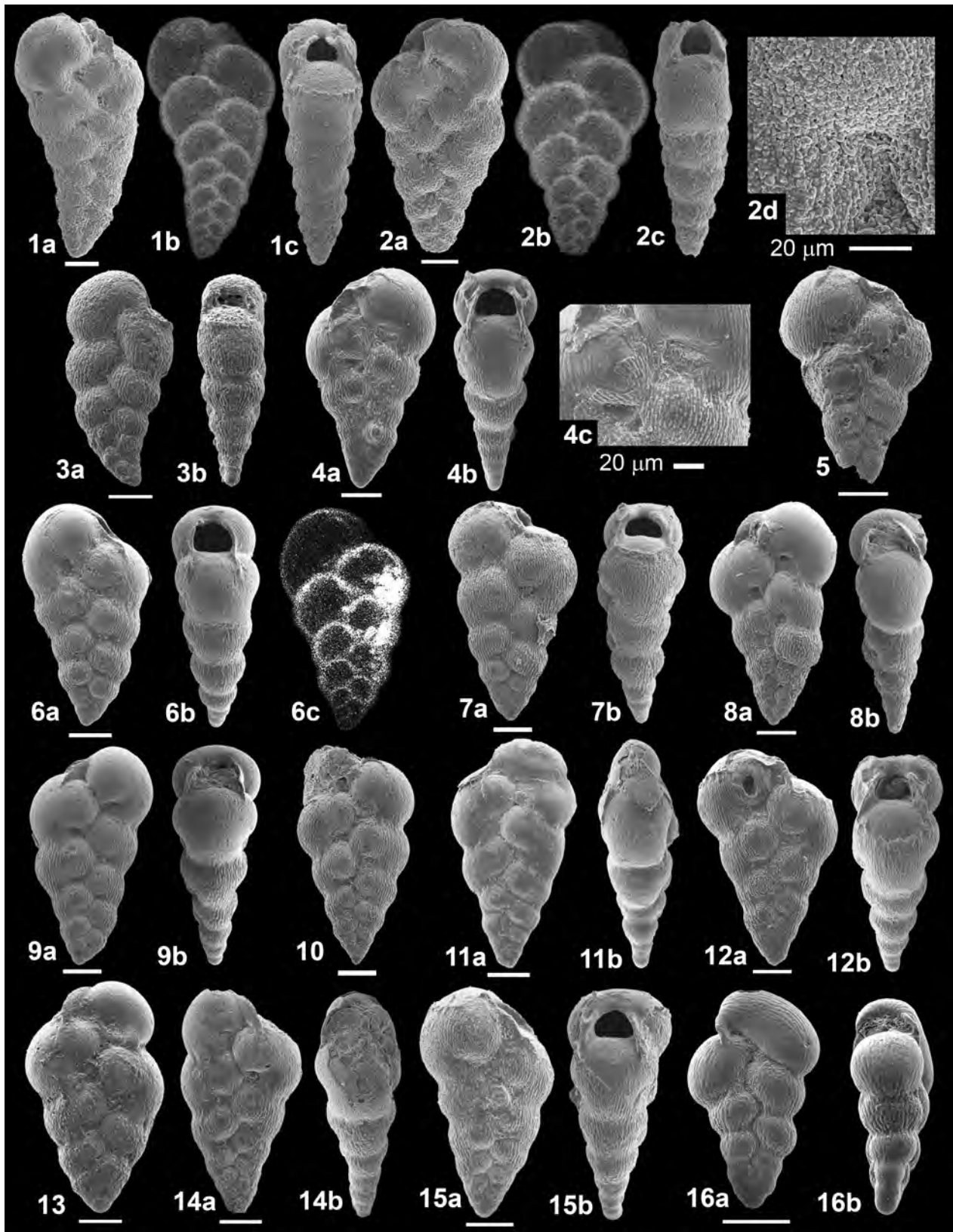


FIGURE 23. 1–16 *Huberella praehuberi* Georgescu, 2007a; unless otherwise noted, scale bars = 50 μ m, all SEMs were taken at the National Museum of Natural History, Washington, D.C., and specimens come from the lower-middle Turonian (*Helvetoglobotruncana helvetica* Zone): 1, Holotype (USNM 534391) and 2, Paratype (USNM 534392), lower Turonian, equatorial Pacific Ocean (Mid-Pacific Mountains), DSDP Site 463, Spl. 35-1, 17–19 cm, SEM images (1a, c and 2a, c, d) from Georgescu (2007a, pl. 3, figs. 4a, b and 5a–c, respectively) and X-rays (1b, 2b) taken at the National Museum of Natural History, Washington, D.C.; 3, upper Cenomanian (*Rotalipora cushmani* Zone), western North Atlantic Ocean (Blake

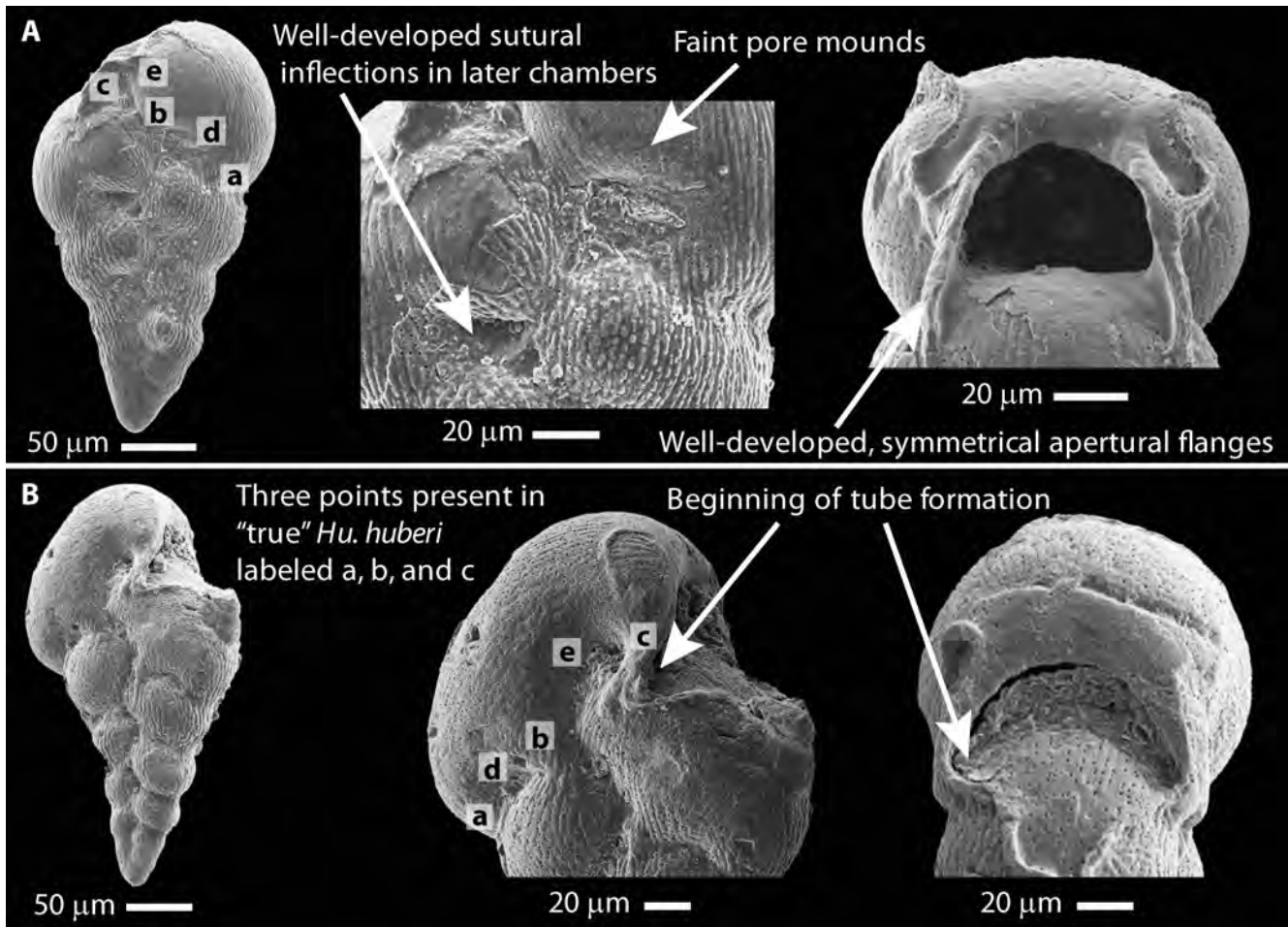


FIGURE 24. Apertural structures of **A** *Huberella praehuberi*, Spl. TDP Site 31-40-1, 29–40 cm and. **B** *Hu. huberi*, side view and close up of aperture (left and center), Spl. TDP 31-9-1, 34–51 cm, and edge view close up of aperture (right), Spl. TDP 31-10-1, 19–39 cm. Lower case letters indicate important chamber features which provide an evolutionary link between the ancestral form (*Hu. praehuberi*) and the descendant (*Hu. huberi*).

Laeviheterohelix reniformis (Marie, 1941)
Figs. 25.1–25.6

Ventrilabrella reniformis Marie, 1941, p. 264, pl. 28, fig. 277 [Campanian, France (Paris Basin)].

Laeviheterohelix reniformis (Marie). Georgescu, 2009a, p. 325, fig. 8.4 [early Campanian (*Archaeoglobigerina cretacea* Zone), South Atlantic Ocean (Falkland Plateau, DSDP Leg 79, Site 511)].

Type specimens. Not cataloged and not identified in the Marie collection deposited at the Paris Museum of Natural History (A. Bartonlini communication, 2013).

Type level. Campanian.

Type locality. France (Seine-et-Marne, Paris Basin).

Repository. Not given in original publication but now at the Paris Museum of Natural History.

Original description translated from French. “Test showing a reduced and fringed initial part, with chambers increasing sharply in size as added; mature chambers

enlarging as added, almost globular and fairly regular at the periphery of the sides, sharply elongated and reniform in their internal part. Surface finely striated longitudinally. Dimensions: very small individual made of six rows of chambers, height: 0.200 mm, width: 0.230 mm, thickness: 0.100 mm.”

Emended description. Test size ranges from 210–306 µm in length ($n = 6$) and consists of 10–14 chambers that are biserially arranged in the earlier portion of the test and may become multichambered in final growth stage. Globular early chambers become reniform later in ontogeny. Proloculus size ranges from 15–25 µm in diameter ($n = 5$); early chambers increase gradually in size and then more rapidly later, becoming fan-shaped in side view. In edge view, tests generally remain compressed throughout ontogeny. Sutures are depressed and oblique to the central axis, and they widen to create a flattened indentation of the intercameral area on

Nose), ODP Hole 1050C, Spl. 21-2, 99–102 cm, transitional from *Planoheterohelix postmoremani*; 4, Spl. TDP 31-40-1, 29–40 cm; 5, Spl. TDP 31-63-2, 26–45 cm, first occurrence; 6–9, Spl. TDP 31-53-3, 10–30 cm; 10, Spl. TDP 31-55-1, 73–90 cm; 11, Spl. TDP 31-40-1, 29–40 cm; 12, Spl. TDP 31-38-1, 29–49 cm; 13, Spl. TDP 31-32-1, 40–50 cm; 14, 15, Spl. TDP 31-30-1, 40–60 cm; 16, upper Turonian (*Marginotruncana schneegansi* Zone), Spl. TDP 31-25-1, 77–88 cm, transitional to *Hu. huberi*.

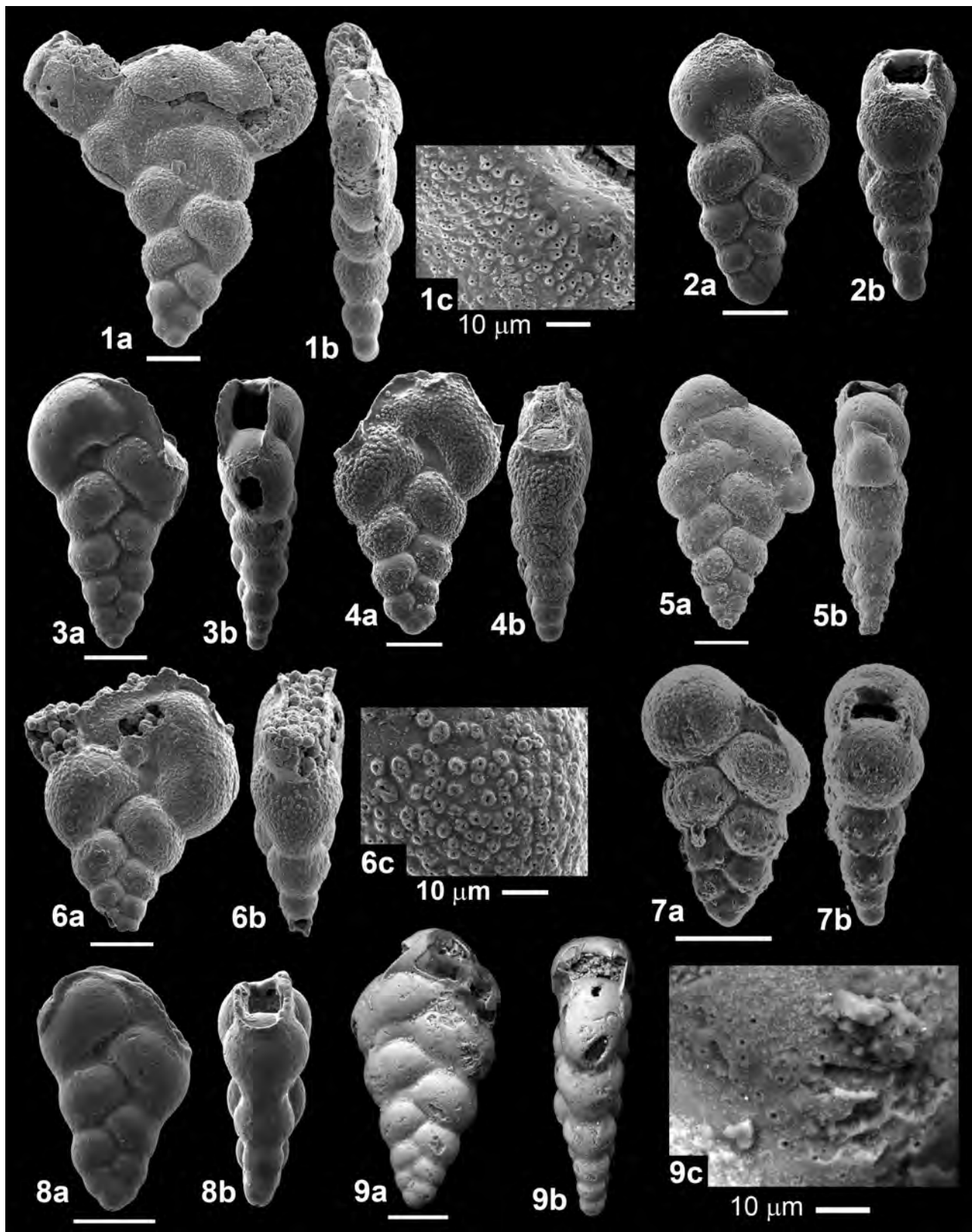


FIGURE 25. Transition of *Laeviheterohelix reniformis* (Marie, 1941) to *Lv. pulchra* (Brotzen, 1936); unless otherwise noted, scale bar = 50 μ m; all SEMs were taken at the National Museum of Natural History, Washington, D.C. and specimens come from the upper Turonian (*Marginotruncana schneegansi* Zone or equivalent) unless otherwise noted. 1–6 *Lv. reniformis*: 1, Spl. TDP 31-26-1, 73–75 cm; 2, Spl. TDP 31-25-1, 77–88 cm, transitional from *Hu. praehuberi* to *Lv. reniformis* (sutural depression becomes broader and flatter; test becomes smooth with more distinct pore mounds); 3, 4, Spl. TDP 31-25-1, 77–88 cm; 5, Turonian (*Whiteinella baltica* Zone of Huber et al., 1995, correlated with the *Mg. schneegansi* Zone of

the later chambers. Aperture is a symmetrical, high-arch at the base of the final chamber, with symmetrical apertural flanges and an imperforate margin. Test wall is calcitic and hyaline, and the surface absent of costae. Early-formed chambers are smooth, whereas later chambers are ornamented with distinct, well-developed pore mounds that are randomly distributed over the test. Pores (0.6–0.8 μm in diameter, $n = 5$) are microperforate and pore mound rims are 2.2–3.3 μm ($n = 5$) in thickness.

Distinguishing features. *Laeviheterohelix reniformis* has early biserial chambers followed by overlapping adult chambers that become multiserial; intercameral areas widen in the intermediate growth stage; and pore mounds are well-developed, appearing as small, randomly scattered pustules across the test surface.

Remarks. Turonian specimens of *Lv. reniformis* from TDP Site 31 and DSDP Site 511 (Figs. 25.1–25.6) are very similar to the Campanian specimens of Georgescu (2009a; figs. 8:4a, b), also from DSDP Site 511, although the intercameral areas on specimens collected from TDP Site 31 (Figs. 10, 25.1–25.5) are larger and flatter than that observed on specimens from DSDP Site 511 (Georgescu, 2009a, figs. 8:4a, b; Figs. 25.5a, b). This species is very rare at all described localities, including the type locality.

Laeviheterohelix flabelliformis Nederbragt, 1991, is similar to the most advanced multiserial forms documented at TDP Site 31 (e.g., Fig. 25.1). Pore mounds are not mentioned in Nederbragt's type description and are not evident in her illustrations, perhaps due to inadequate preservation. Despite uncertainty in the wall type and the greater number of multiserial chambers in Nederbragt's type specimens, we regard *Lv. flabelliformis* to be within the range of phenotypic variation of *Lv. reniformis*, and it is, therefore, considered as a junior synonym.

Similar species. See "Similar species" presented for *Hu. praeuberi* above.

Phylogenetic relationships. *Laeviheterohelix reniformis* descended from *Hu. praeuberi* and is likely the direct ancestor of *Lv. pulchra* (Figs. 3, 8).

Stratigraphic range. *Laeviheterohelix reniformis* evolved during the middle Turonian (uppermost *Hv. helvetica* Zone) and ranges into the early Campanian (*Ar. cretacea* Zone of Huber, 1992; Figs. 3, 8; Appendix 1).

Geographic distribution. Africa (Tanzania), southern South Atlantic (Falkland Plateau), and France (Paris Basin).

Stable isotope paleoecology. No data available.

Laeviheterohelix pulchra (Brotzen, 1936)
Figs. 25.7–25.9

Guembelina pulchra Brotzen, 1936, p. 121, pl. 9, figs. 2, 3 (Campanian, Eriksdal, Sweden).

Laeviheterohelix pulchra (Brotzen), Nederbragt, 1991, p. 352, pl. 6, fig. 1 [Santonian (*Dicarinella asymetrica* Zone), El Kef, Tunisia]; Bice et al., 2003, fig. 2.f [Turonian, South Atlantic Ocean (Falkland Plateau, DSDP Leg 79, Site 511)]; Lamolda et al., 2007, p. 23, fig. 4-E [early Santonian, northern Spain (Olazagutia)].

Steineckia steinecki Georgescu, 2009a, p. 325, figs. 9.1–9.5 [upper Turonian (*Whiteinella baltica* Zone), South Atlantic Ocean (Falkland Plateau, DSDP Leg 79, Site 511)].

Type specimens. Holotype: Cat. No. 188, paratype: USNM 24391.

Type level. Campanian.

Type locality. Eriksdal, Sweden.

Repository. Holotype is at the Naturhistoriska Riksmuseet, Stockholm, Sweden. Paratype is located at the National Museum of Natural History, Washington, D.C.

Original description. "Test biserial, surface smooth or with pore mounds. Periphery rounded, chambers reniform. Aperture bordered by elongate flanges, which extend to the opposite periphery. Relict flanges of preceding chambers are visible along the edges of the test."

Distinguishing features. Pore mounds are present on test surface, and chambers are reniform and overlap the previous ones.

Remarks. The paratype of *Lv. pulchra* illustrated on Figure 25.9 has strongly overlapping reniform chambers and faint pore mounds that are only visible under high magnification (Fig. 25.9c). Pore mounds are a key characteristic of this species and their size is variable, with some becoming large and well-developed (e.g., Fig. 25.7; Georgescu, 2009a, fig. 9). Nederbragt (1989, 1991) suggested that pore mounds are expressed only on smooth-walled individuals that lived in tropical locations, and therefore, were considered a poor characteristic to define a species. Recent studies, however, show that smooth-walled forms with well-developed pore mounds occur at high latitude sites such as the Falkland Plateau (DSDP Site 511; Fig. 25.7; Bice et al., 2003; Georgescu, 2009a).

Steineckia steinecki Georgescu, 2009a, differs from *Lv. pulchra* in having larger pore mounds, no periapertural pustulose area, and no evidence of vestigial costae (Georgescu, 2009b). The paratype of *Lv. pulchra* and two other specimens illustrated here (Figs. 25.7–25.9) lack both vestigial costae and periapertural pustulose areas. They also show a large range of variability in terms of pore mound size, suggesting that these features are not suitable to characterize a separate species; therefore, we consider *St. steinecki* to be a junior synonym of *Lv. pulchra*.

Similar species. *Laeviheterohelix pulchra* differs from *Lv. reniformis* in 1) being biserial throughout and 2) having inflated chambers with no evidence of sutural inflections.

Phylogenetic relationships. *Laeviheterohelix pulchra* descended from *Lv. reniformis* in the Turonian.

Stratigraphic range. The species first occurs in the Turonian (*Wh. baltica* Zone of Huber, 1992) at DSDP Site

←

Robaszynski & Caron, 1995), southern South Atlantic Ocean (Falkland Plateau), DSDP Site 511, Spl. 47–6, 38–40 cm; 6, Spl. TDP 31–26–1, 40–60 cm. 7–9 *Lv. pulchra*: 7, Coniacian–Santonian (*Wh. baltica* Zone of Huber et al., 1995, correlated with the *Dicarinella concavata* Zone of Robaszynski & Caron, 1995), southern South Atlantic Ocean (Falkland Plateau), DSDP Site 511, Spl. 45–1, 90–92 cm; 8, Spl. TDP 31–20–1, 70–88 cm, pore mounds are faint but present; 9, Paratype (USNM 24391), Upper Cretaceous, Eriksdal, Sweden (Georgescu, 2009a, p. 324, fig. 8.2a, illustrated the other side of the specimen).

511 and middle Turonian (*Marginotruncana schneegansi* Zone) at TDP Site 31 (Fig. 3, Appendix 1), and ranges into the lower Campanian (Georgescu, 2009a).

Geographic distribution. Cosmopolitan.

Stable isotope paleoecology. No data available.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS INFERRED FROM STRATOPHENETIC OBSERVATIONS

Background

Previous studies (e.g., Hemleben et al., 1991; Olsson et al., 1999; Pearson et al., 2006; Petrizzo & Huber, 2006a, b; Georgescu & Huber, 2009; Pearson & Coxall, 2014) have demonstrated the importance of using stratigraphically ordered samples with well-preserved foraminiferal assemblages to establish a framework for higher-level taxonomic classification and interpretation of phylogenetic relationships. The remarkably high quality of preservation of TDP foraminifera and the availability of closely spaced samples obtained from multiple boreholes afford a valuable opportunity to observe stratophenetic changes in shell morphology and wall microstructure that are generally obscured because of diagenetic alteration at other sites. Study of the TDP biserial distributions also provides a basis for establishing a biostratigraphic framework with well-constrained first and last appearance events for biserial species, and it enables morphometric characterization of their phenotypic variability.

Morphological Trends

Wall texture is clearly important for higher-level classification of biserial taxa. Exclusively smooth-walled forms followed by forms with weakly developed and discontinuous costae occur in the oldest part of the lineages. Younger branches of the lineages include forms with more coarsely developed and continuous costae as well as new smooth-walled forms ornamented with pore mounds. However, the expression of surface texture may be quite variable within species populations. Costae vary in thickness and extent, pore mounds vary in density and rim thickness, and some tests have weakly developed pore mounds with or without costae (e.g., Figs. 19, 23, 25).

Although proloculus size was used by Georgescu & Huber (2009) for genus-level distinction of Cretaceous biserial planktic foraminifera, we document considerable variability and overlap in proloculus diameters for *Planoheterohelix globulosa*, *Pl. paraglobulosa*, and *Pl. praenuttalli*. Therefore, this character alone is not considered useful for species or generic distinction.

Late Albian–Coniacian Biserial Evolution

Five biserial planktic lineages are identified within the late Albian–early Coniacian interval (Fig. 8). The oldest lineage, *Protoheterohelix*, evolved during the late Albian with the appearance of *Pr. washitensis* (Fig. 8). This species is characterized by primitive evolutionary traits that include an asymmetrical aperture and a smooth test wall (Fig. 4).

Although Georgescu (2009b) suggested *Pr. washitensis* evolved directly from the benthic ancestor *Praeplanctonia globifera* Georgescu, 2009b, this interpretation is considered unlikely because of significant differences in wall microstructure and apertural characteristics and absence of transitional forms that would support an evolutionary link. *Protoheterohelix washitensis* gave rise to *Pr. obscura* in the early–middle Cenomanian, but the lineage terminated in the late Cenomanian.

The *Planoheterohelix* lineage split from *Protoheterohelix* with the evolution of *Pl. moremani* during the middle Cenomanian, as recognized by the appearance of a finely costate surface and a symmetrical aperture (Figs. 8–10). The *Planoheterohelix* lineage underwent three diversifications: one during the late Cenomanian (*Rotalipora cushmani* Zone) with first appearances of *Pl. postmoremani*, *Pl. globulosa*, and *Pl. paraglobulosa*; one in the mid-late Turonian (upper *Helvetoglobotruncana helvetica* Zone) with the first appearance of *Pl. reussi*; and the last in the late Turonian (*Marginotruncana schneegansi* Zone) with the first appearance of *Pl. praenuttalli*. The latter diversification is correlated with a sudden increase in the relative abundance of biserial taxa in the middle–upper *Mg. schneegansi* Zone, and the new taxa comprise $\leq 80\%$ of the total biserial species present in this interval (Fig. 3). *Planoheterohelix praenuttalli* remains abundant throughout the Turonian and gradually increases its test breadth as it becomes morphologically transitional to *Pseudotextularia nuttalli*, which is a useful stratigraphic marker that first occurs in the upper Coniacian portion of the *Dicarinella concavata* Zone (Nederbragt, 1989; M. R. Petrizzo, communication, 2013). Further study of the *Planoheterohelix* lineage is needed to characterize its post-Turonian evolutionary history.

Following the taxonomic framework proposed by Georgescu & Huber (2009), the genus *Heterohelix* is here considered to be monospecific with the type species, *Hx. americana*, characterized by a trapezoidal projection extending from the final chamber. This taxon is generally rare with sporadic occurrences. It has been documented from lower Turonian–Santonian strata, but it was not observed in any of the material studied.

The *Huberella* lineage separated from *Planoheterohelix* during the latest Cenomanian with the appearance of *Hu. praehuberi*, which is easily identified by the presence of a sutural inflection on adult chambers. The other *Huberella* species, *Hu. huberi*, is a useful biostratigraphic marker for the middle *Mg. schneegansi* Zone, as it has distinctive tube-like projections extending from its final chambers (Fig. 22).

The *Laeviheterohelix* lineage evolved from *Huberella* during the late Turonian with the complete loss of costate ornamentation and appearance of tests with well-defined pore mounds. The TDP record reveals, for the first time, a gradual evolutionary transition from *Hu. praehuberi* to *Lv. reniformis* in the lower *Mg. schneegansi* Zone. This transition is expressed as an increase in the density and size of pore mounds, appearance of an overlapping terminal chamber, and multiserial chambers. The subsequent appearance of *Lv. pulchra* in the middle *Mg. schneegansi* Zone marks an unusual character reversal from the wholly biserial *Hu. praehuberi* ancestor to biserial-multiserial *Lv. reniformis* descendant and a return to the wholly biserial *Lv. pulchra*.

Late Turonian Biserial Turnover

The abundance of biserial heterohellicids shows little change throughout most of the lower-middle Turonian (*Helvetoglobotruncana helvetica*–lowermost *Marginotruncana schneegansi* Zone) at TDP Site 31, varying between 2–14% of the total planktic assemblage (Figs. 3, 20; Appendix 1). The biserial taxa within this interval are dominated by *Pl. globulosa*, but include, in decreasing relative abundance, *Pl. paraglobulosa*, *Hu. praeuberi*, and *Pl. postmoremani*. This period of assemblage stasis terminates at 43.34 mbs (TDP 31-25-1, 73–75 cm), where *Hu. praeuberi* becomes extinct, *Pl. postmoremani* and *Pl. paraglobulosa* significantly decrease in relative abundance, and *Pl. praenuttalli* and *Lv. reniformis* appear. It also corresponds with the extinction of *Hv. helvetica* and several species of *Whiteinella* (Huber & Petrizzo, 2014).

The abundance of biserial taxa abruptly increases with biserials becoming dominant over the total foraminiferal assemblage beginning at 27.3 mbs (TDP 31-18-2, 20–40 cm) within the lower *Mg. schneegansi* Zone (Fig. 20). The abundance shift largely reflects a dramatic increase in the relative abundance of *Pl. praenuttalli*, and the increase corresponds with 1) the first appearance of *Hu. huberi*, 2) a >3‰ decrease in $\delta^{13}\text{C}_{\text{org}}$ values (Jiménez Berrocoso et al., 2015; Fig. 20), 3) a decrease in total organic carbon by ~0.5%, 4) a >20% decrease in the relative abundance of benthic foraminifera (Fig. 20), 5) a >30% increase in the percent sand fraction (J. Wendler, communication, 2013), 6) a significant change in benthic foraminiferal species composition (I. Wendler, communication, 2013), and 7) foraminiferal test infilling by secondary calcite.

The cause for the dramatic shifts in the biserial planktic assemblages and the simultaneous changes in the bottom water and mixed-layer environments is not clear. The oxygen-isotope record in MacLeod et al. (2013) and the observation of increasing diversity of planktic species through the section suggest that changes in surface-water salinity were not a contributing factor. The diagenetic shift could be explained by an increase in sand fraction of the bulk sediment that increased sediment porosity and the flow of meteoric water, promoting shell infilling. The increase in grain size could also be interpreted as an indication of decreasing water depth, but the latter is inconsistent with an increase in the planktic/benthic ratio, which generally occurs with increasing water depth. The abrupt increase in the abundance of biserial planktics and decrease in benthics might also have been caused by an increase in surface-water productivity or other oceanographic changes. The decrease in $\delta^{13}\text{C}_{\text{org}}$ values is likely the result of changes in the local carbon budget, including a possible change in the source of preserved organic matter. Increased productivity seems inconsistent with the simultaneous decrease in total organic carbon (TOC) content, but if the rate of remineralization of organic matter increased faster than productivity (e.g., due to increased ventilation or decreased sedimentation rate), this paradox might be resolved. Existing observations are insufficient to distinguish among these alternatives and sorting out the causes will require much further investigation.

ISOTOPE PALEOECOLOGY

Available stable isotopic data for Turonian biserial planktic foraminifera indicate these species do not fit a simple depth-stratified ecological model (e.g., Hart, 1980). Analyses of TDP samples provide results based on the same species concepts as described here (MacLeod et al., 2013; Wendler et al., 2013). The number of samples analyzed in these studies is too small to evaluate whether observed differences among biserial species are meaningful, but all three species analyzed here (*Planoheterohelix moremani*, *Pl. globulosa*, and *Pl. paraglobulosa*) plot with distinctly lower $\delta^{13}\text{C}$ and lower $\delta^{18}\text{O}$ values than co-occurring planktic taxa (Fig. 16A). Low $\delta^{18}\text{O}$ values suggest very warm and/or ^{18}O -depleted waters that might be expected at the sea surface, but, if so, the very low $\delta^{13}\text{C}$ values in the same specimens require some disequilibrium processes, such as incorporation of metabolic CO_2 associated perhaps with nutrient-rich waters and rapid growth (Wendler et al., 2013). Direct comparison of these results to other isotopic studies of Cretaceous biserial taxa is complicated by the fact that species concepts have been emended in this paper. However, it is clear that isotopic separation between Turonian biserial heterohellicids and other planktic taxa are not always observed. Among individuals that lived during a warm interval at DSDP Site 511, specimens identified as *Heterohelix moremani* in Bice et al. (2003; here considered *Pl. globulosa*) have $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values that are relatively low but overlap with values from other taxa (Bice et al., 2003; Fig. 16B), whereas on Demerara Rise reported *Heterohelix globulosa* $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values effectively fill the entire field of values exhibited by other planktic taxa (Bornemann et al., 2008; Fig. 16C). Analyses of Campanian and Maastrichtian *Heterohelix globulosa* (MacLeod & Huber, 1996; MacLeod et al., 2000; Abramovich et al., 2003) add examples of specimens with high $\delta^{18}\text{O}$ values compared to other planktics to the variety of isotopic patterns exhibited by biserial specimens presumed to fall within the *Planoheterohelix* lineage.

The variety of patterns observed is consistent with the proposed placement of biserial heterohellicids in an epicontinental-sea fauna that has a different ecology from, but sometimes co-occurs with, open-ocean, shallow- and deep-water faunas (Leckie, 1987). This categorization, though, begs the question of how to interpret the stable isotopic patterns. Different patterns exhibited by related taxa at different sites or at different times might indicate an ability of a eurytrophic group to adapt its ecology to exploit transient resources. Alternatively, the group might be opportunists able to out compete more oligotrophic taxa in open-ocean settings anywhere conditions locally become more like those found in epicontinental seas, regardless of depth or temperature. For example, high nutrient and food availability at one site might occur episodically at the sea surface during unusually hot intervals with high runoff from adjacent continents. At another site, nutrient recycling from a mid-water oxygen-minimum zone might create similarly favorable conditions in relatively deep, cool waters. Heterohellicids at both sites might have the same ecology but would have very different stable isotopic ratios in their tests. Unfortunately, stable isotopes are currently

the best tool for inferring the paleoecology of foraminifera. Until other independent techniques to infer planktic foraminiferal ecology are developed, explanations for the variety of isotopic patterns exhibited by biserial heterohelids will remain difficult to test.

SUMMARY

Detailed study of excellently preserved Cenomanian–Coniacian foraminifera from southeast Tanzania, in parallel with examination of age-correlative samples from the central Pacific and western North Atlantic oceans and accompanied by comparisons with primary type specimens, provides the basis for a number of taxonomic revisions and emendations for late Albian–Coniacian Cretaceous heterohelids. The following taxonomic changes are presented: 1) *Protoheterohelix washitensis* and *Pr. obscura* cannot be consistently distinguished from each other on the basis of a straight vs. twisted central axis, but can be discriminated by their adult chambers that are reniform and overlap one another (*Pr. obscura*) vs. chambers that are globular and do not overlap (*Pr. washitensis*); 2) *Globoheterohelix* is now considered to be a junior synonym of *Planoheterohelix* as proloculus size is not considered, on its own, to be a generic characteristic; 3) faint striations are observed on the holotype and paratypes of *Pl. moremani*, resulting in revision of the species concept to include weakly striated forms; 4) the description of the genus *Planoheterohelix* has been emended to include species that would otherwise be assigned to *Heterohelix* (*Pl. moremani*, *Pl. postmoremani*, *Pl. globulosa*, *Pl. reussi*, and the new species *Pl. praenuttalli*), because they do not have a trapezoidal projection from the final chamber and have a symmetrical aperture; 5) the definition of *Pl. paraglobulosa* has been expanded to include forms with 5–9 chambers (rather than 6–8 as originally described), and the maximum diameter of the proloculus increased from 56 μm to 72 μm ; 6) Pore mounds are documented for the first time on both *Huberella praehuberi* and *Hu. huberi*, being particularly common to abundant on the early portions of the former; 7) a new species, *Pl. praenuttalli*, is described to accommodate broadly tapering forms with a breadth/width ratio <1 that were previously considered to be transitional between *Pl. globulosa* and *Ps. nuttalli*; 8) *Laeviheterohelix reniformis* is now considered to have evolved from *Hu. praehuberi* and given rise to subsequent species in the *Laeviheterohelix* lineage; 9) *Lv. reniformis* is here considered directly ancestral to *Lv. pulchra*, and its first occurrence is documented in the late Turonian, which predates its previously recognized oldest occurrence in the Santonian; 10) the genus *Steineckia* is considered to be a junior synonym of *Laeviheterohelix*; and 11) the species *St. steinecki* is now considered to be a junior synonym of *Lv. pulchra*.

These revisions, based largely on study of exceptionally well-preserved specimens, result in an internally consistent and relatively objective classification scheme that suggests Albian–Santonian biserials have considerable biostratigraphic utility. Identifying and placing *Textularia globulosa* Ehrenberg, 1840, in the genus *Planoheterohelix* Georgescu

& Huber, 2009, resolves a persistent debate about where to place this common and long-ranging species. Stratophenetic determination of key features that reveal ancestor-descendant relationships provide the basis for genus-level groupings and reconstruction of the phylogenetic history of the heterohelids.

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REFERENCES

- Abramovich, S., Keller, G., Stuben, D., and Berner, Z., 2003, Characterization of late Campanian and Maastrichtian planktonic foraminiferal depth habitats and vital activities based on stable isotopes: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 202, p. 1–29.
- Ando, A., Nakano, T., Kobayashi, T., Kokado, E., and Khim, B.-K., 2009, Onset of seawater $^{87}\text{Sr}/^{86}\text{Sr}$ excursion prior to Cenomanian–Turonian Oceanic Anoxic Event 2? New Late Cretaceous strontium isotope curve from the central Pacific Ocean: *Journal of Foraminiferal Research*, v. 39, p. 322–334.
- Belford, D. J., 1960, Upper Cretaceous foraminifera from the Toolongal Calcilutite and Gingin Chal, Western Australia: Bureau of Mineral Resources, Geology and Geophysics, Bulletin, v. 57, p. 1–198.
- Bergstresser, T. J., and Frerichs, W. E., 1982, Planktonic foraminifera from the Upper Cretaceous Pierre Shale at Red Bird, Wyoming: *Journal of Foraminiferal Research*, v. 12, p. 353–361.
- Bice, K. L., Huber, B. T., and Norris, R. D., 2003, Extreme polar warmth during the Cretaceous greenhouse? Paradox of the late Turonian $\delta^{18}\text{O}$ record at Deep Sea Drilling Project Site 511: *Paleoceanography*, v. 18, p. 9.1–9.7.
- Bornemann, A., Norris, R. D., Friedrich, O., Beckmann, B., Schouten, S., Sinninghe Damste, J. S., Vogel, J., Hofmann, P., and Wagner, T., 2008, Isotopic evidence for glaciation during the Cretaceous supergreenhouse: *Science*, v. 319, p. 189–192.
- Brotzen, F., 1936, Foraminiferen aus dem schwedischen unterer Senon von Eriksdal in Schonen: *Sveriges Geologiska Undersökning*, ser. C, v. 396, p. 1–69.
- Caron, M., 1985, Cretaceous planktic foraminifera, in Bolli, H. M., et al. (eds.), *Plankton Stratigraphy*: Cambridge University Press, Cambridge, p. 17–86.

- Caron, M., Dall' Agnolo, S., Accarie, H., Barrera, E., Kauffman, E. G., Amédéo, F., and Robaszynski, F., 2006, High-resolution stratigraphy of the Cenomanian-Turonian boundary interval at Pueblo (U.S.A.) and wadi Bahloul (Tunisia): stable isotope and bio-events correlation: *Géobios*, v. 39, p. 171–200.
- Cavalier-Smith, T., 2002, The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa: *International Journal of Systematic and Evolutionary Microbiology*, v. 52, p. 297–354.
- Cushman, J. A., 1927, An outline of a re-classification of the Foraminifera: Contributions from the Cushman Laboratory for Foraminiferal Research, v. 3, p. 1–105.
- Cushman, J. A., 1938, Cretaceous species of *Gümbelina* and related genera: Contributions from the Cushman Laboratory for Foraminiferal Research, v. 14, p. 2–28.
- Cushman, J. A., 1946, Upper Cretaceous foraminifera of the Gulf coastal region of the United States and adjacent areas: United States Geological Survey Professional Paper, v. 206, p. 1–241.
- de Klasz, I., de Klasz, S., and Saint-Marc, P., 1995, Heterohellicids from the Turonian of Senegal (West Africa) with particular emphasis on *Heterohelix americana* (Ehrenberg): *Journal of Micropaleontology*, v. 41, p. 359–368.
- Delage, Y., and Hérourard, E., 1896, *Traité de Zoologie Concrète Tome I: la Cellule et les Protozoaires*: Schleicher Frères, Paris, 584 p.
- D'Hondt, S., and Arthur, M. A., 1995, Interspecies variation in stable isotopic signals of Maastrichtian planktonic foraminifera: *Paleoceanography*, v. 10, p. 123–135.
- d'Orbigny, A. D., 1826, *Tableau méthodique de la classe des Céphalopodes*: Annales de Sciences Naturelles, ser. 1, v. 7, p. 245–314.
- Douglas, R. G., 1969, Upper Cretaceous planktic foraminifera in northern California; part 1, systematics: *Micropaleontology*, v. 15, p. 151–209.
- Egger, H., Mohamed, O., and Rögl, F., 2013, Plankton stratigraphy of the Santonian at Morzg, Salzburg (Gosau Group, northern calcareous Alps, Austria): *Austrian Journal of Earth Sciences*, v. 106, p. 89–114.
- Egger, J. G., 1899, Foraminiferen und Ostrakoden aus den Kreidemergeln der oberbayerischen Alpen: Abhandlungen der königlichen bayerischen Akademie der Wissenschaften zu München, Mathematische-Naturwissenschaftliche Klasse, v. 21, p. 3–230.
- Ehrenberg, C. G., 1840, Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen: Abhandlungen der königlichen preussischen Akademie der Wissenschaften zu Berlin (1838), p. 59–147.
- Ehrenberg, C. G., 1843, Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord America: Abhandlungen der königlichen preussischen Akademie der Wissenschaften zu Berlin, v. 1, p. 291–446.
- Ehrenberg, C. G., 1844, Über zwei neue Lager Gebirgsmassen aus Infusorien als Meers-Absatz in Nord-Amerika und eine Vergleichung derselben mit den organischen Kreide-Gebilden in Europa und Afrika: Abhandlungen der königlichen preussischen Akademie der Wissenschaften zu Berlin, p. 57–98.
- Eicher, D. L., and Worstell, P., 1970a, Cenomanian and Turonian Foraminifera from the Great Plains, United States: *Journal of Micropaleontology*, v. 16, p. 269–324.
- Eicher, D. L., and Worstell, P., 1970b, *Lunatriella*, a Cretaceous heterohellicid foraminifer from the western interior of the United States: *Journal of Micropaleontology*, v. 16, p. 117–121.
- Frerichs, W. E., and Gaskill, C. H., 1978, *Textilaria americana* Ehrenberg: type species of *Heterohelix*: *Journal of Foraminiferal Research*, v. 8, p. 143–146.
- Georgescu, M. D., 2007a, A new planktonic heterohellicid foraminiferal genus from the Upper Cretaceous (Turonian): *Journal of Micropaleontology*, v. 53, p. 212–220.
- Georgescu, M. D., 2007b, Taxonomic re-evaluation of the Late Cretaceous serial planktonic foraminifer *Gümbelina punctulata* Cushman, 1938 and related species: *Revista Española de Micropaleontología*, v. 39, p. 155–176.
- Georgescu, M. D., 2009a, Taxonomic revision and evolutionary classification of the biserial Cretaceous planktic foraminiferal genus *Laeviheterohelix* Nederbragt, 1991: *Revista Mexicana de Ciencias Geológicas*, v. 26, p. 315–334.
- Georgescu, M. D., 2009b, On the origins of Superfamily Heterohellicacea Cushman, 1927 and the polyphyletic nature of planktic foraminifera: *Revista Española de Micropaleontología*, v. 41, p. 107–144.
- Georgescu, M. D., 2010, Origin, taxonomic revision and evolutionary classification of the late Coniacian-early Campanian (Late Cretaceous) planktic foraminifera with multichamber growth in the adult stage: *Revista Española de Micropaleontología*, v. 42, p. 59–118.
- Georgescu, M. D., 2012, Origin, evolutionary classification, and biostratigraphic of the Late Cretaceous planktic foraminiferal directional lineage *Bollitruncana* O. A. Korchagin, 2001: *Studia UBB Geologia*, v. 57, p. 3–16.
- Georgescu, M. D., 2013, New advances in understanding the heterohellicid planktic foraminifer early evolution: *Studia UBB Geologia*, v. 58, p. 19–28.
- Georgescu, M. D., and Abramovich, S., 2008, Taxonomic revision and phylogenetic classification of the Late Cretaceous (upper Santonian-Maastrichtian) serial planktonic foraminifera (Family Heterohellicidae Cushman, 1927) with peripheral test wall flexure: *Revista Española de Micropaleontología*, v. 40, p. 97–114.
- Georgescu, M. D., and Abramovich, S., 2009, A new Late Cretaceous (Maastrichtian) serial planktic foraminifer (Family Heterohellicidae) with early planispiral coil and revision of *Spiroplecta* Ehrenberg, 1844: *Géobios*, v. 42, p. 687–698.
- Georgescu, M. D., and Huber, B. T., 2009, Early evolution of the Cretaceous serial planktonic foraminifera (late Albian-Cenomanian): *Journal of Foraminiferal Research*, v. 39, p. 335–360.
- Georgescu, M. D., Saupe, E. E., and Huber, B. T., 2008, Morphometric and stratophenetic basis for phylogeny and taxonomy in Late Cretaceous gublerinid planktonic foraminifera: *Micropaleontology*, v. 54, p. 397–424.
- Georgescu, M. D., Quinney, A. E., and Anderson, K. D., 2011, New data on the taxonomy, evolution and biostratigraphical significance of the Turonian-Coniacian (Late Cretaceous) planktic foraminifer *Huberella* Georgescu 2007: *Micropaleontology*, v. 57, p. 247–254.
- Hart, M. B., 1980, A water depth model for the evolution of the planktonic Foraminifera: *Nature*, v. 286, p. 252–254.
- Hay, W. W., Deconto, R. M., Wold, C. N., Wilson, K. M., Voigt, S., Schulz, M., Wold, A. R., Dullo, W. C., Ronov, A. B., Balukhovskiy, A. N., and Söding, E., 1999, An alternative global Cretaceous paleogeography, in Barrera, E., and Johnson, C. C. (eds.), *Evolution of the Cretaceous Ocean-Climate System*: Geological Society of America, Special Publication, v. 332, p. 1–47.
- Hemleben, C., Muhlen, D., Olsson, R. K., and Berggren, W. A., 1991, Surface texture and the first occurrence of spines in planktonic foraminifera from the Early Tertiary: *Geologisch Jahrbuch*, v. 128, p. 117–146.
- Huber, B. T., and Petrizzo, M. R., 2014, Evolution and taxonomic study of the Cretaceous planktonic foraminiferal Genus *Helvetoglobotruncana* Reiss, 1957: *Journal of Foraminiferal Research*, v. 44, p. 40–57.
- Huber, B. T., Hodell, D. A., and Hamilton, C. P., 1995, Middle-Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients: *Geological Society of America Bulletin*, v. 107, p. 1164–1191.
- Huber, B. T., Leckie, M., Norris, R. D., Bralower, T. J., and Cobabe, E., 1999, Foraminiferal assemblage and stable isotopic changes across the Cenomanian-Turonian boundary in the subtropical North Atlantic: *Journal of Foraminiferal Research*, v. 29, p. 392–417.
- Jiménez Berrocoso, Á., MacLeod, K. G., Huber, B. T., Lees, J. A., Wendler, I., Bown, P. R., Mweneinda, A. K., Isaza Londono, C., and Singano, J. M., 2010, Lithostratigraphy, biostratigraphy and chemostratigraphy of Upper Cretaceous sediment from southern Tanzania: Tanzania Drilling Project Sites 21–26: *Journal of African Earth Sciences*, v. 57, p. 47–69.
- Jiménez Berrocoso, Á., Huber, B. T., MacLeod, K. G., Petrizzo, M. R., Lees, J. A., Wendler, I., Coxall, H., Mweneinda, A. K., Falzoni, F., Birch, H., Singano, J. M., Haynes, S., Cotton, L., Wendler, J., Bown, P. R., Robinson, S. A., and Gould, J., 2012, Lithostratigraphy, biostratigraphy and chemostratigraphy of Upper Cretaceous and Paleogene sediments from southern

- Tanzania: Tanzania Drilling Project Sites 27 to 35: *Journal of African Earth Sciences*, v. 70, p. 36–57.
- Jiménez Berrocoso, Á., Huber, B. T., MacLeod, K. G., Petrizzo, M. R., Lees, J. A., Wendler, I., Coxall, H., Mweneinda, A. K., Falzoni, F., Birch, H., Haynes, S. J., Bown, P. R., Robinson, S. A., and Singano, J. M., 2015, Lithostratigraphy, biostratigraphy and chemostratigraphy of Upper Cretaceous and Paleogene sediments from southern Tanzania: Tanzania Drilling Project Sites 36 to 40: *Journal of African Earth Sciences*, v. 101, p. 282–308.
- Kent, P. E., Hunt, J. A., and Johnstone, D. W., 1971, The geology and geophysics of coastal Tanzania: HM Stationary Office, London, Institute of Geological Sciences, Geophysical Paper No. 6, p. 1–101.
- Kuntz, O., 1895, Sind Carbonkohlen autochthon, allochthon oder pelagochthon?, in *Geogenetische Beiträge*: Druck von Gressner und Schramm, Leipzig, p. 42–77.
- Lamolda, M. A., Peryt, D., and Ion, J., 2007, Planktonic foraminiferal bioevents in the Coniacian/Santonian boundary interval at Olazagutia, Navarra province, Spain: *Cretaceous Research*, v. 28, p. 18–29.
- Leckie, R. M., 1987, Paleocology of Mid-Cretaceous planktonic foraminifera: a comparison of open ocean and epicontinental sea assemblages: *Micropaleontology*, v. 33, p. 164–176.
- Loeblich, A. R., Jr., 1951, Coiling in the *Heterohelidae*: Contributions from the Cushman Foundation for Foraminiferal Research, v. 2, p. 106–110.
- Loeblich, A. R., Jr. and Tappan, H., 1961, The genera *Microaulopora* Kuntz, 1895, and *Guembelina* Kuntz, 1895, and the status of *Guembelina* Egger, 1899: *Journal of Paleontology*, v. 35, p. 625–627.
- MacLeod, K. G., and Huber, B. T., 1996, Reorganization of deep ocean circulation accompanying a Late Cretaceous extinction event: *Nature*, v. 380, p. 422–425.
- MacLeod, K. G., Huber, B. T., and Ducharme, M. L., 2000, Paleontological and geochemical constraints on the deep ocean during the Cretaceous Greenhouse interval, in Huber, B. T., et al. (eds.), *Warm Climates in Earth History*: Cambridge University Press, Cambridge, p. 241–274.
- MacLeod, K. G., Huber, B. T., Jiménez Berrocoso, Á., and Wendler, I., 2013, A stable and hot Turonian without glacial $\delta^{18}\text{O}$ excursions is indicated by exquisitely preserved Tanzanian foraminifera: *Geology*, v. 41, p. 1083–1086.
- Marie, P., 1941, Les foraminifères de la craie a *Belemnitella mucronata* du Bassin de Paris: *Mémoires du Muséum National d'Histoire Naturelle*, v. 12, p. 1–296.
- Masters, B. A., 1980, Reevaluation of selected types of Ehrenberg's Cretaceous planktonic foraminifera: *Eclogae Geologicae Helveticae*, v. 73, p. 95–107.
- Montanaro Gallitelli, E., 1957, A revision of the foraminiferal family Heterohelidae, in Loeblich, A. R., Jr. (ed.), *Studies in Foraminifera*; Part 1—Planktonic Foraminifera: United States National Museum Bulletin, v. 215, p. 133–154.
- Nash, S., 1981, A neotype for the Cretaceous genus *Pseudotextularia* Rzehak, 1891: *Journal of Foraminiferal Research*, v. 11, p. 70–75.
- Nederbragt, A. J., 1989, Maastrichtian Heterohelidae (planktonic Foraminifera) from the north west Atlantic: *Journal of Micropaleontology*, v. 8, p. 183–206.
- Nederbragt, A. J., 1991, Late Cretaceous biostratigraphy and development of Heterohelidae (planktonic Foraminifera): *Journal of Micropaleontology*, v. 37, p. 329–372.
- Nederbragt, A. J., and Koning, J. A., 1994, Morphologic variation in Turonian to Maastrichtian *Heterohelix globulosa* (Ehrenberg): Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Biological, Chemical, Geological, Physical, and Medical Sciences, v. 97, p. 429–444.
- Nederbragt, A. J., Erlich, R. N., Fouke, B. W., and Ganssen, G. M., 1998, Palaeoecology of the biserial planktonic foraminifer *Heterohelix moremani* (Cushman) in the late Albian to middle Turonian circum-North Atlantic: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 144, p. 115–133.
- Nicholas, C. J., Pearson, P. N., Mcmillan, I. K., Ditchfield, P. W., and Singano, J. M., 2007, Structural evolution of southern coastal Tanzania since the Jurassic: *Journal of African Earth Sciences*, v. 48, p. 273–297.
- Norris, R. D., and Wilson, P. A., 1998, Low-latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktonic foraminifera: *Geology*, v. 26, p. 823–826.
- Olsson, R. K., Hemleben, C., and Huber, B. T., 1999, *Atlas of Paleocene Planktonic Foraminifera*: Smithsonian Institution Press, Washington, D.C., 252 p.
- Pearson, P. N., and Coxall, H. K., 2014, Origin of the Eocene planktonic foraminifer *Hantkenina* by gradual evolution: *Palaeontology*, v. 57, p. 243–267.
- Pearson, P. N., Olsson, R. K., Hemleben, C., Huber, B. T., and Berggren, W. A., 2006, *Atlas of Eocene Planktonic Foraminifera*: Cushman Foundation for Foraminiferal Research, Special Publication 41, p. 1–513.
- Pessagno, E. A., Jr., 1967, Upper Cretaceous planktonic foraminifera from the western Gulf coastal plain: *Palaeontographica Americana*, v. 5, p. 244–441.
- Petrizzo, M. R., and Huber, B. T., 2006a, Biostratigraphy and taxonomy of late Albian planktonic foraminifera from ODP Leg 171B (western North Atlantic Ocean): *Journal of Foraminiferal Research*, v. 36, p. 166–190.
- Petrizzo, M. R., and Huber, B. T., 2006b, On the phylogeny of the late Albian genus *Planomalina*: *Journal of Foraminiferal Research*, v. 36, p. 233–240.
- Postuma, J. A., 1971, *A Manual of Planktonic Foraminifera*: Elsevier, New York, 420 p.
- Robaszynski, F., and Caron, M., 1995, Foraminifères planctoniques du Crétacé: commentaire de la zonation Europe-Méditerranée: *Bulletin de la Société Géologique de France*, v. 166, p. 681–692.
- Robaszynski, F., Caron, M., Gonzalez Donoso, J. M., and Wonders, A. A. H., 1984, *Atlas of the Late Cretaceous globotruncanids*: *Revue de Micropaléontologie*, v. 26, p. 1–305.
- Rzehak, A., 1891, Die Foraminiferen-Fauna der alttertiären Ablagerungen von Brunderndorf in Niederösterreich mit Berücksichtigung des angeblichen Kreidevorkommens von Leitersdorf: *Annalen des k. k. naturhistorischen Hofmuseums Wien*, v. 6, p. 1–12.
- Said, R., and Kenawy, A., 1956, Upper Cretaceous and Lower Tertiary foraminifera from northern Sinai, Egypt: *Micropaleontology*, v. 2, p. 105–173.
- Said, R., and Sabry, H., 1964, Planktonic foraminifera from the type locality of the Esna Shale in Egypt: *Micropaleontology*, v. 10, p. 375–395.
- Smith, C. C., and Pessagno, E. A., Jr., 1973, Planktonic foraminifera and stratigraphy of the Corsicana Formation (Maestrichtian) north-central Texas: Cushman Foundation for Foraminiferal Research, Special Publication 12, p. 1–68.
- Tappan, H., 1940, Foraminifera from the Grayson Formation of northern Texas: *Journal of Paleontology*, v. 14, p. 93–126.
- Theide, J., Boersma, A., Schmidt, R. R., and Vincent, E., 1981, Reworked fossils in Mesozoic and Cenozoic pelagic central Pacific Ocean sediments, Deep Sea Drilling Project Sites 463, 464, 465, and 466, Leg 62, in Stout, L. N. (ed.), *Initial Reports of the Deep Sea Drilling Project*, v. 62: U.S. Government Printing Office, Washington, D.C., p. 495–512.
- Voorwijk, G. H., 1937, Foraminifera from the Upper Cretaceous of Habana, Cuba: *Koninklijke Akademie van Wetenschappen, Amsterdam, Proceedings of the Section of Sciences*, v. 40, p. 190–198.
- Walaszczyk, I., Lees, J. A., Peryt, D., Cobban, W. A., and Wood, C. J., 2012, Testing the congruence of the macrofossil versus microfossil record in the Turonian-Coniacian boundary succession of the Wagon Mound-Springer composite section (NE New Mexico, USA): *Acta Geologica Polonica*, v. 62, p. 581–594.
- Wendler, I., Huber, B. T., MacLeod, K. G., and Wendler, J. E., 2011, Early evolutionary history of *Tubulogenerina* and *Colomia*, with new species from the Turonian of East Africa: *Journal of Foraminiferal Research*, v. 41, p. 384–400.
- Wendler, I., Huber, B. T., MacLeod, K. G., and Wendler, J., 2013, Stable oxygen and carbon isotope systematics of exquisitely preserved Turonian foraminifera from Tanzania—understanding isotopic signatures: *Marine Micropaleontology*, v. 102, p. 1–33.
- Wilson, P. A., Norris, R. D., and Cooper, M. J., 2002, Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal

calcite from the core of the Turonian tropics on Demerara Rise: *Geology*, v. 30, p. 607–610.

Winterer, E. L., and Sager, W. W., 1995, Synthesis of drilling results from the Mid-Pacific Mountains: regional context and implications, *in* Winterer, E. L., et al. (eds.), *Proceedings of the Ocean*

Drilling Program, Scientific Results, v. 143: Ocean Drilling Program, College Station, Texas, p. 497–535.

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APPENDIX 1

Tanzania Drilling Project Site 31 biostratigraphy and species abundances. For this site, a microsplit of one sample/core was counted for benthic, non-biserial planktic, and biserial planktic foraminifera, and the number of specimens were normalized to 300/sample. This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2015001.

APPENDIX 2

Tanzania Drilling Program Site 24 biostratigraphy. This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2015001.

APPENDIX 3

Deep Sea Drilling Program Site 463 biostratigraphy. This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2015001.

APPENDIX 4

Ocean Drilling Program Hole 1050C biostratigraphy. Foraminiferal zonation is based on Huber et al. (1999) and Petrizzo & Huber (2006). This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2015001.

APPENDIX 5

Measurements of all illustrated specimens that are used for plots. Data presented in this appendix are used in various figures throughout the manuscript. Specimens noted as transitional or juvenile in figure captions are not included in averages of species measurements. This appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR_DR2015001.