

Morphometric and stratophenetic basis for phylogeny and taxonomy in Late Cretaceous gublerinid planktonic foraminifera

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ABSTRACT: Taxonomic revision of the gublerinid serial planktonic foraminifera of the Late Cretaceous (late Campanian-Maastrichtian) reveals that the group consists of two genera, *Gublerina* Kikoïne 1948 and *Praegublerina* gen. nov., which evolved from the finely costate, biserial species *Heterohelix planata* (Cushman 1938). Three species are included within *Praegublerina*: *P. pseudotessera* (Cushman 1938), *P. acuta* (de Klasz 1953) and *P. robusta* (de Klasz 1953), the first being the oldest of the genus and a descendant of *Heterohelix planata* (Cushman 1938). *Gublerina cuvillieri* Kikoïne 1948 and *G. rajagopalani* Govindan 1972 are retained within *Gublerina*. The two lineages are recognized based on gross test architecture, test ornamentation, pore size and internal test morphology. Our study reveals the existence of an evolutionary continuum between lineages in which the gublerinid-type chamber proliferation is independently developed in *Gublerina* and *Praegublerina*. The new taxonomic framework reflects the iterative pattern of planktonic foraminiferal evolution and it results in a better understanding of the stratigraphic and geographic distribution of the gublerinid taxa. Stable isotopic comparison of *G. rajagopalani* and *G. cuvillieri* with co-occurring late Maastrichtian benthic and planktonic species indicates that the two *Gublerina* species shared the same depth habitat near the thermocline.

INTRODUCTION

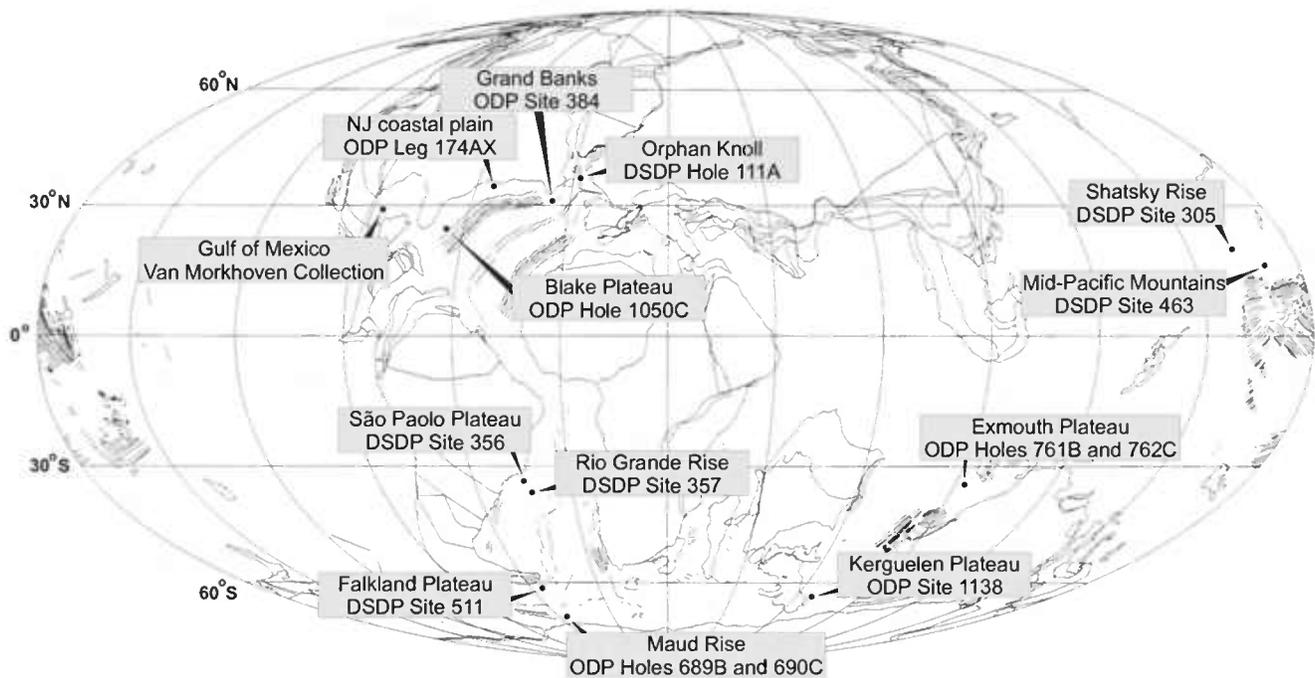
The first report of a Late Cretaceous planktonic foraminifer with chamber proliferation in the adult stage, which largely resembles that of the gublerinids, was made by Marie (1941). The specimen described by Marie (1941) came from a white chalk containing the belemnite *Belemnitella mucronata* in the Paris Basin, which is late Campanian in age and is approximately the stratigraphic equivalent of the *Radotruncana calcarata* planktonic foraminiferal Biozone. *Ventilabrella reniformis* Marie 1941 was later placed in *Gublerina* and considered valid in two taxonomic revisions by Brown (1969) and Masters (1977). No additional material was studied to clarify its detailed morphological features and taxonomic position. The taxonomic status of this species is discussed in Appendix 1.

The serial planktonic foraminiferal genus *Gublerina* Kikoïne 1948 was proposed to accommodate late Campanian-Maastrichtian tests with diverging rows of alternating chambers and a proliferating chamber stage later in ontogeny. The genus was considered monotypic in the initial report and included only *Gublerina cuvillieri* Kikoïne 1948. Subsequent studies of planktonic foraminifera from southern Germany (de Klasz 1953) and Cuba (Brönnimann and Brown 1953) showed the genus is more diverse with two other species being described: *Gublerina acuta* and *G. acuta robusta*. The degree of development of the portion of the test with proliferating (=incipient or developing) chambers and gross test characteristics, such as test thickness, were considered valid taxonomic criteria at the species level.

The status of the type species *Gublerina cuvillieri* was re-evaluated in the first taxonomic revision of the genus by Montanaro Gallitelli (1957), who considered it to be a junior synonym of *Ventilabrella ornatissima* Cushman and Church (1929). This synonymy was contested by Brown (1969) who, after examination of topotypes of *Gublerina cuvillieri* and the holotype of *Ventilabrella ornatissima*, concluded that “Montanaro Gallitelli (1957, p.140, pl.32, figs.1-6) was mistaken in regarding the two species as synonyms or even congeneric” (Brown 1969, p. 59). A discussion of the status of *Ventilabrella ornatissima* is presented in Appendix 2.

A major breakthrough in understanding the morphological variability, and therefore taxonomy, of *Gublerina* occurred when Govindan (1972) described *Gublerina rajagopalani*, a species which lacks a multiserial growth stage in the adult portion of the test. In his original description Govindan (1972, p.170) noted the presence of “coarse costae in the earlier portion of test.” He also mentioned that the test periphery is “truncate, moderately lobulate, ornamented with thick, strongly raised, longitudinal costae.” Govindan’s decision to include *G. rajagopalani* in the genus *Gublerina* is significant because he used test ornamentation as a feature of primary importance at the species level. This generic assignment was later contested by Masters (1977), Nederbragt (1991) and Wonders (1992) due to the absence of multiserial chambers in the adult stage, and *Gublerina rajagopalani* was assigned to the biserial genus *Heterohelix*.

The most recent taxonomic review of *Gublerina* was presented by Nederbragt (1991) who retained only two species within the



TEXT-FIGURE 1

Location of Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites from where material for this study was collected. The approximate location of material from the Van Morkhoven Collection (NMNH) is also included.

genus: *Gublerina acuta* and *G. cuvillieri*. *Gublerina cuvillieri* was considered the descendant of *G. acuta*. This revision and phylogenetic interpretation has received wide acceptance among the scientific community.

Our study shows that *Gublerina cuvillieri*, on one hand, and *G. acuta* and *G. robusta* on the other, are the result of divergent evolution and originated from two distinct, completely biserial species. Here we demonstrate that the biserial species *Gublerina rajagopalani* is the ancestor of the multiserial *G. cuvillieri*. The two species formerly assigned to *Gublerina*, namely *G. acuta* and *G. robusta* are included in a distinct genus, *Praegublerina* nov. gen., together with their ancestor, *P. pseudotessera* (Cushman 1938). *Gublerina* and *Praegublerina* are thus defined to include both completely biserial species and species with chamber proliferation in the adult stage. Separation of the two genera is based on test ornamentation and patterns in chamber addition in the adult chamber proliferation stage.

MATERIAL AND METHODS

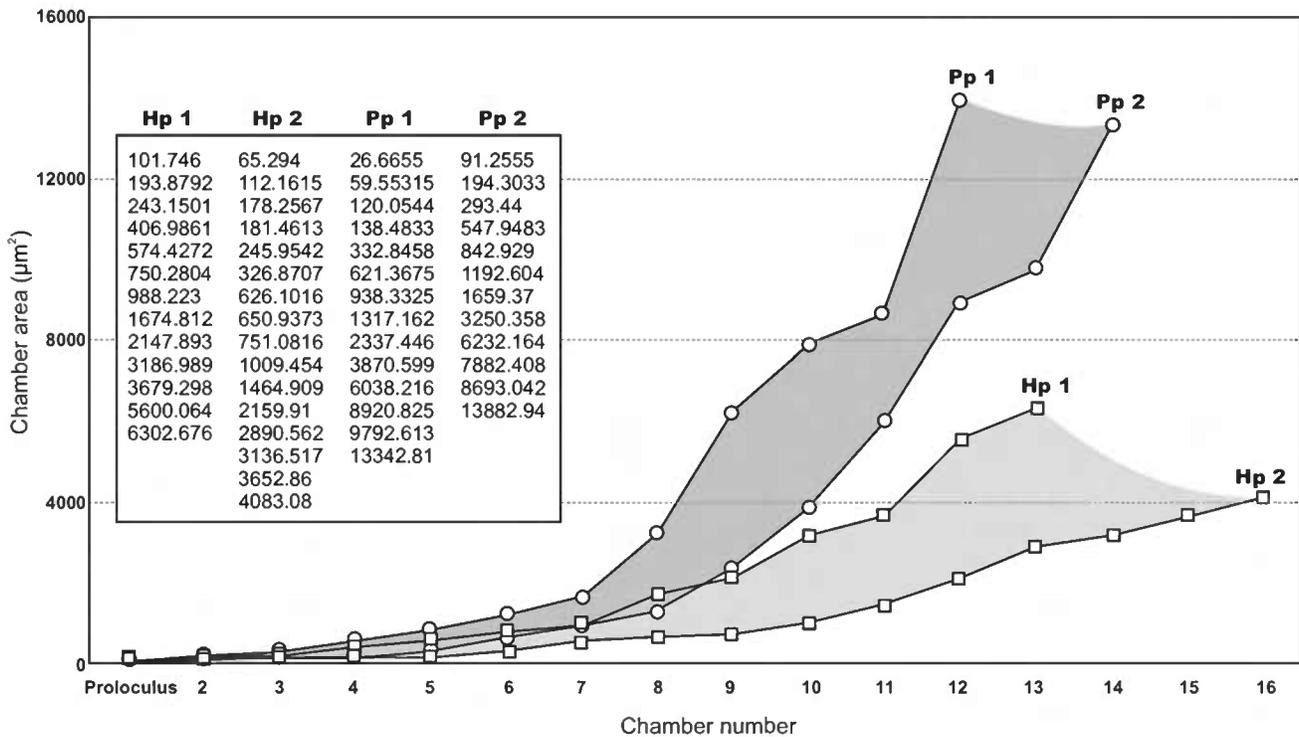
Type collections and new material were investigated during our study. All of the collection types are deposited at the National Museum of Natural History, Washington D.C. Additional material comes from a number of DSDP/ODP sites (text-figure 1). The samples examined are deposited in the Micropaleontological Reference Center Collection at the NMNH.

The holotype of *Praegublerina pseudotessera* (USNM 299326) was analyzed and photographed under the SEM along with seven topotypes from the Loeblich and Tappan Collection, including *Spiroplecta pseudotessera* (USNM 478612 and USNM 473282), two paratypes of *P. acuta* (USNM 370117 and USNM 370118), and four paratypes of *P. robusta* (USNM 370119). No

type specimens of *Gublerina rajagopalani* Govindan 1972 were available for our observation. Two topotypes of *Gublerina cuvillieri* Kikoïne 1948 from the Loeblich and Tappan Collection (USNM 473130) were observed and photographed under the ESEM (Environmental Scanning Electron Microscope). These specimens were also examined by Montanaro Gallitelli (1957) and Brown (1969) in their taxonomic revisions of Cretaceous serial planktonic foraminifera.

Additional new material was collected and examined from the upper Campanian-Maastrichtian of ODP Holes 761B and 762C (Exmouth Plateau, offshore northwest Australia). These are the only sites we studied with *Gublerina cuvillieri* present.

Gublerina rajagopalani was studied from three other sites in the Southern Hemisphere: DSDP Sites 356 (São Paulo Plateau) and 357 (Rio Grande Rise), and ODP Hole 113 8A (Kerguelen Plateau). *Praegublerina robusta* specimens were collected and investigated from upper Campanian-lower Maastrichtian sediments from the following sites: DSDP Hole 111A (Orphan Knoll, North Atlantic Ocean), DSDP Site 463 (Shatsky Rise, Pacific Ocean), DSDP Site 384 (Grand Banks, Atlantic Ocean), and ODP Holes 1049B, 1050C, and 1052E (Blake Plateau, western North Atlantic Ocean). *Praegublerina acuta* material consists of specimens from upper Campanian-Maastrichtian sediments from the following sites: DSDP Site 111A (Orphan Knoll, Atlantic Ocean), DSDP Site 463 (Mid-Pacific Mountains, Pacific Ocean), DSDP Site 384 (Grand Banks, Atlantic Ocean), ODP Holes 761B, and 762C (Exmouth Plateau, Indian Ocean), and ODP Holes 1049B, 1050C, and 1052E (Blake Plateau, western North Atlantic Ocean). *Praegublerina pseudotessera* material consists of approximately fifty specimens from the lower Campanian-middle Maastrichtian of DSDP Site 384



TEXT-FIGURE 2

Comparison between the chamber area growth trajectories in *Praegublerina pseudotessera* (Pp 1 and Pp 2) and *Heterohelix planata* (Hp 1 and Hp 2). Note that the two areas overlap in the earlier stages, demonstrating a phylogenetic relationship between the two species, *H. planata* as ancestor and *P. pseudotessera* as descendant. The well defined higher rate of chamber growth in *P. pseudotessera*, which is the oldest gublerinid species, is also due to the development of the wide periapertural flanges. Only the trajectories of two specimens are illustrated, namely the lowest and highest ones, which define the characteristic area for each species.

(Grand Banks, North Atlantic Ocean), DSDP Site 356 (São Paulo Plateau, western South Atlantic Ocean), and DSDP Site 357 (Rio Grande Rise, western South Atlantic Ocean). Well-preserved specimens of *Heterohelix planata* were studied in three additional wells, namely ODP Holes 689B and 690C (Weddell Sea, Antarctica) and ODP Leg 174AX at Bass River Site (New Jersey coastal plain).

Deep-sea sample designation follows the standard format including leg, site, hole, core, drilling tool (H = hydraulic piston corer; X = extended core barrel; R = rotary), core-section and centimeter interval. The only exception is represented by ODP Leg 174AX at Bass River Site (New Jersey coastal plain), where the samples are designated as follows: leg number followed by the sample depth below surface. Multiple approaches were used in the study of the gublerinid tests. External test morphology was studied under the optical microscope. Gross test architecture, ornamentation, and pores were extensively studied with the aid of the scanning electron microscope (SEM). Internal test architecture and ontogenetic morphometry were analyzed using x-ray micrographs. Over three hundred SEM micrographs and one hundred x-rays were used in this study.

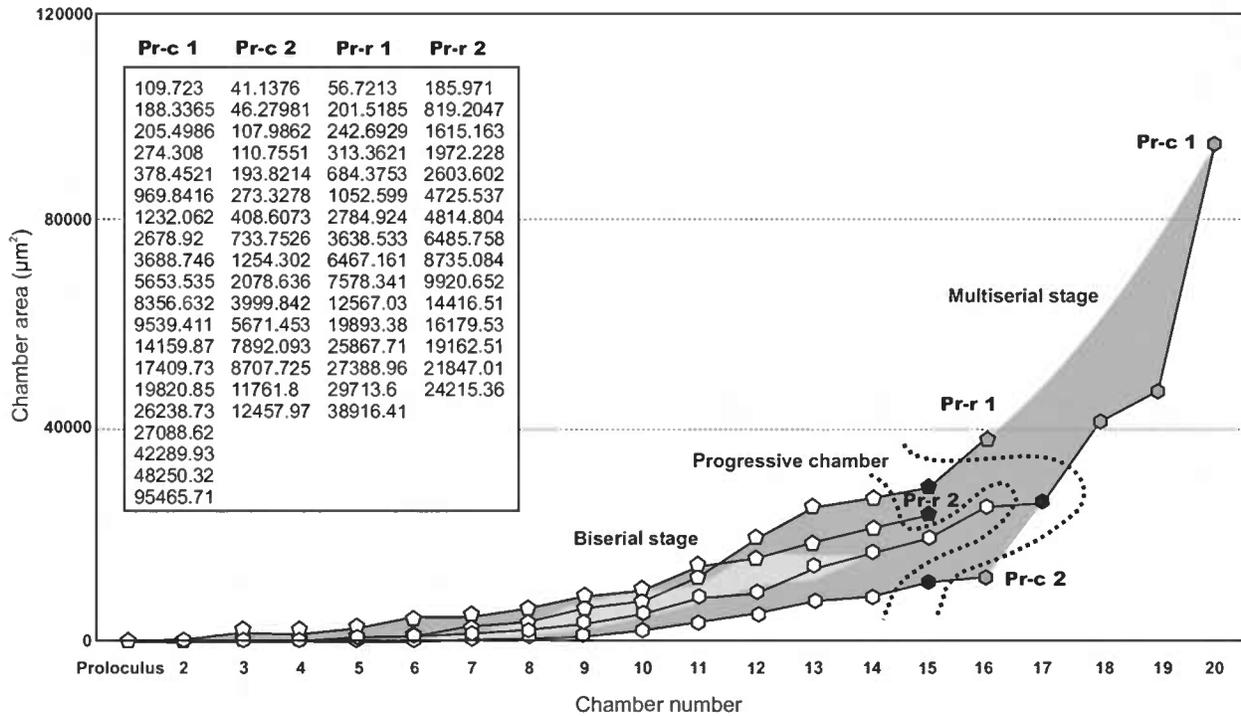
The x-rays were taken on SO-253 High Speed Holographic Film for an exposure time of 2 minutes and 30 seconds at 20 kilovolts. They were developed with D-19 developer for 5 min-

utes, rinsed for 30 seconds in a stop bath, and fixed for one minute in an F-5 fixing bath.

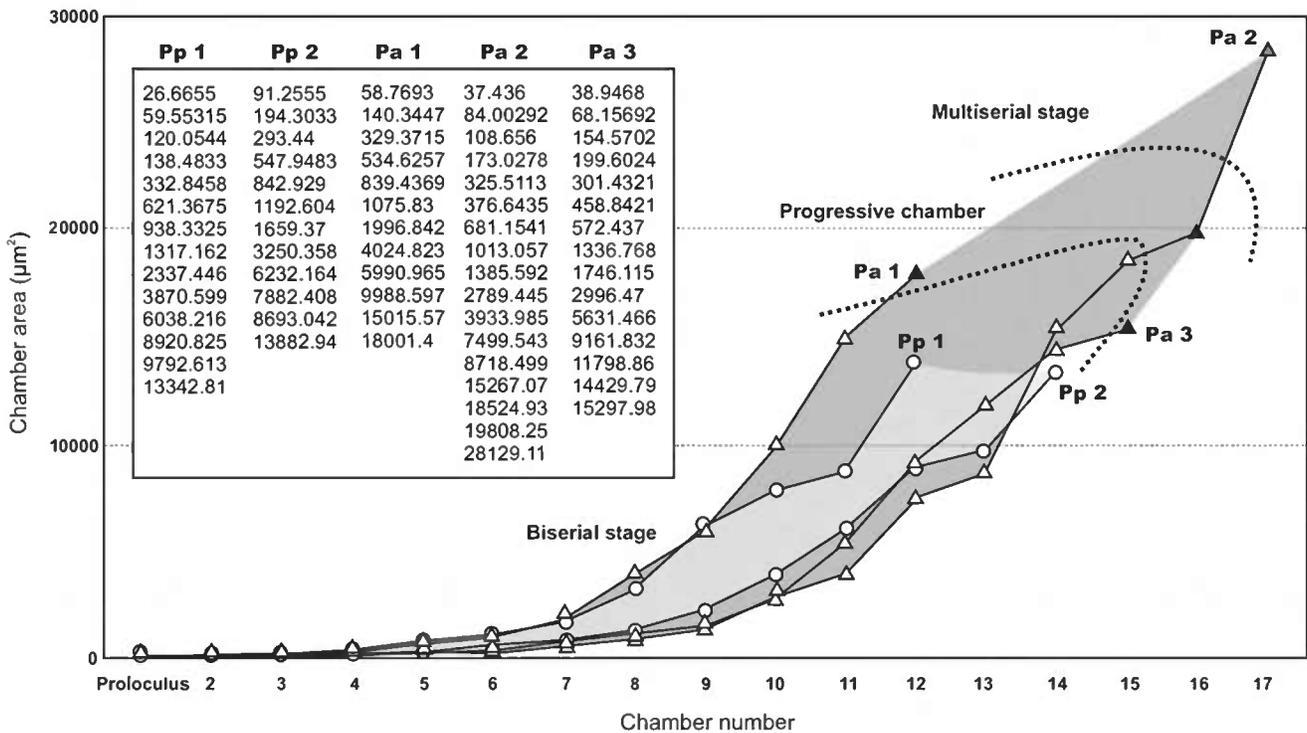
Late Maastrichtian foraminiferal samples for stable isotopic analyses were obtained from ODP Core-sections 761B-24-1, -24-2, and -23-4. Foraminiferal shells from these samples are well preserved, showing no adhering secondary calcite and minimal recrystallization of the shell wall. These data are presented in Table 1. Stable isotopes were analyzed from narrow size fractions of one epifaunal benthic foraminifera and three planktonic foraminiferal species. Replicate analyses were run for all species from core-section 761B-24X-2 and for one species in core-section 761B-23X-4. All samples were analyzed in individual reaction vials using a Kiel III carbonate device-ThermoFinnigan DeltaPlus isotope ratio mass spectrometer at the University of Missouri. Results are reported in standard δ -notation relative to the Vienna PDB standard. External precision is estimated at <0.03% and <0.06% for $\delta^{13}C$ and $\delta^{18}O$ (one standard deviation) based on replicate analyses of NBS-19 and internal lab standards (Table 1).

SYSTEMATIC CLASSIFICATION

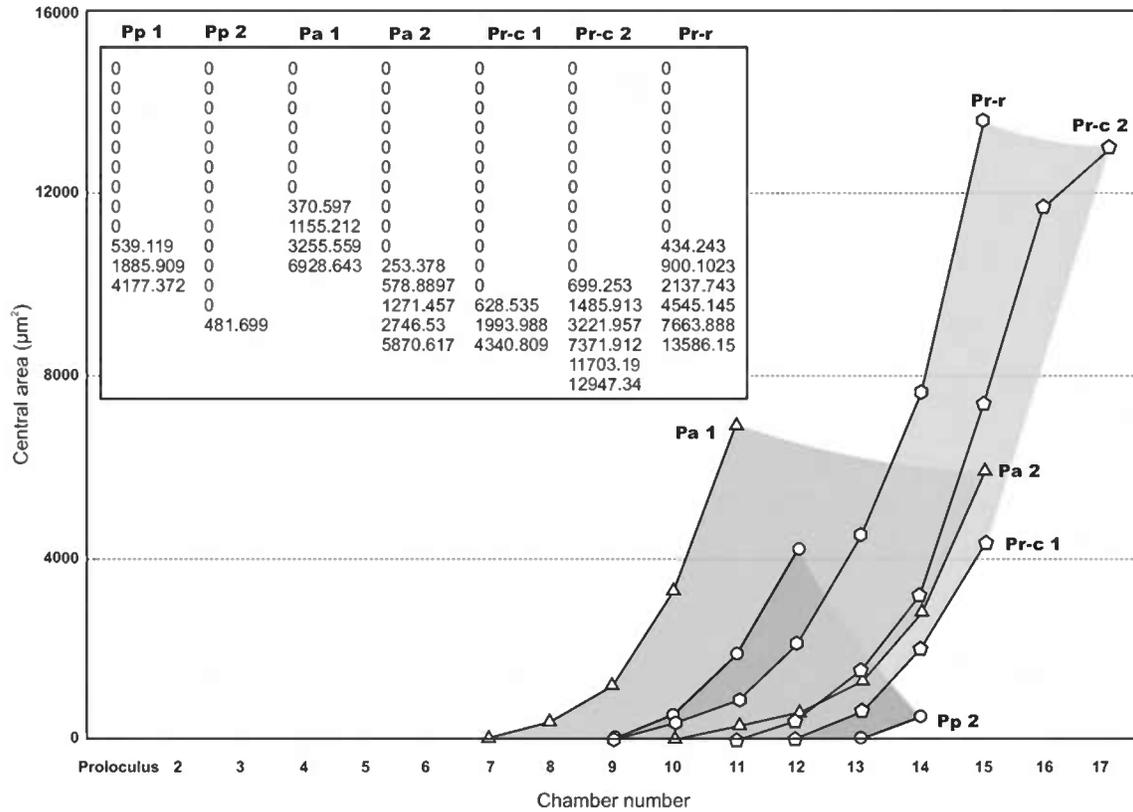
The higher taxonomic categories presented below are based on Loeblich and Tappan (1984, 1987). The genus *Heterohelix* Ehrenberg 1843 is not discussed in detail. We analyzed only *Heterohelix planata* (Cushman 1938), the ancestor of the genus



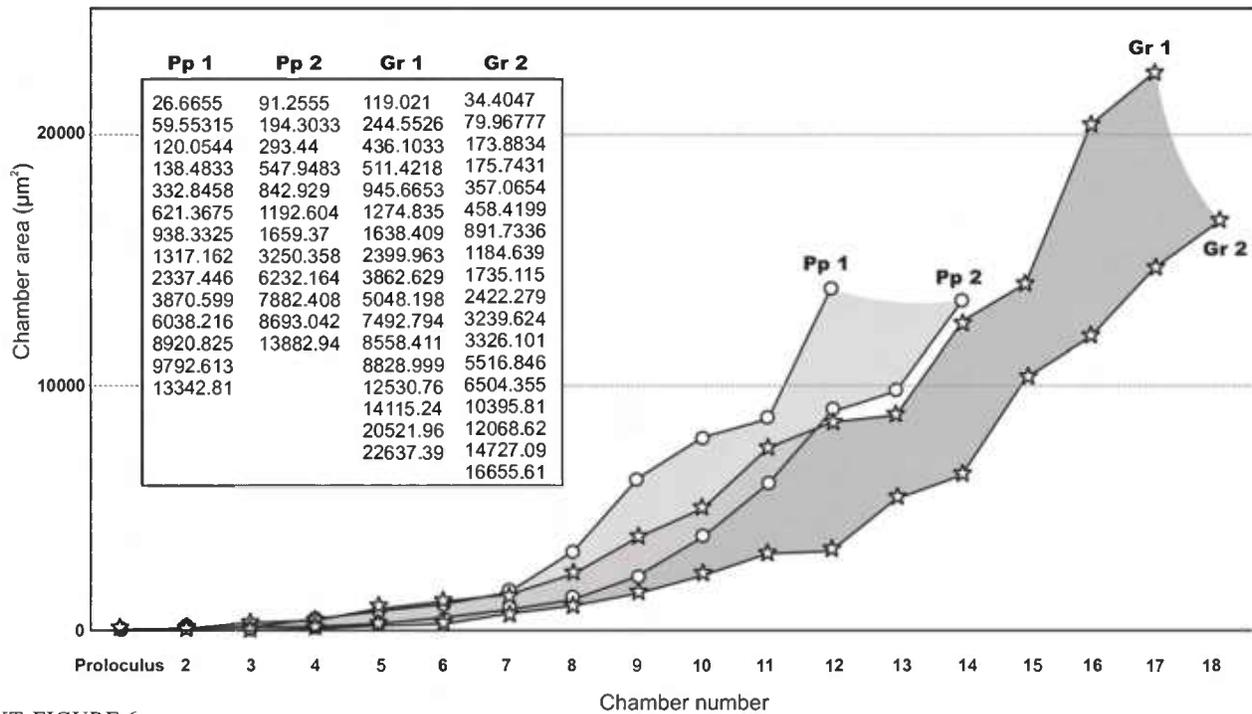
TEXT-FIGURE 3
 Ontogenetic morphometric trajectories of cross-sectional chamber areas for *Praegublerina robusta* (dark grey) and its ancestor *P. pseudotessera* (light grey). Tests with costate (pentagons, Pr-c) and reticulate (hexagons, Pr-r) ornamentation patterns are included. The dotted curved lines delineate the biserial stage (empty symbols), progressive chamber (solid symbols) and multiserial stage sets (dark grey symbols). Notice the sharp increase in test area with the development of the multiserial stage.



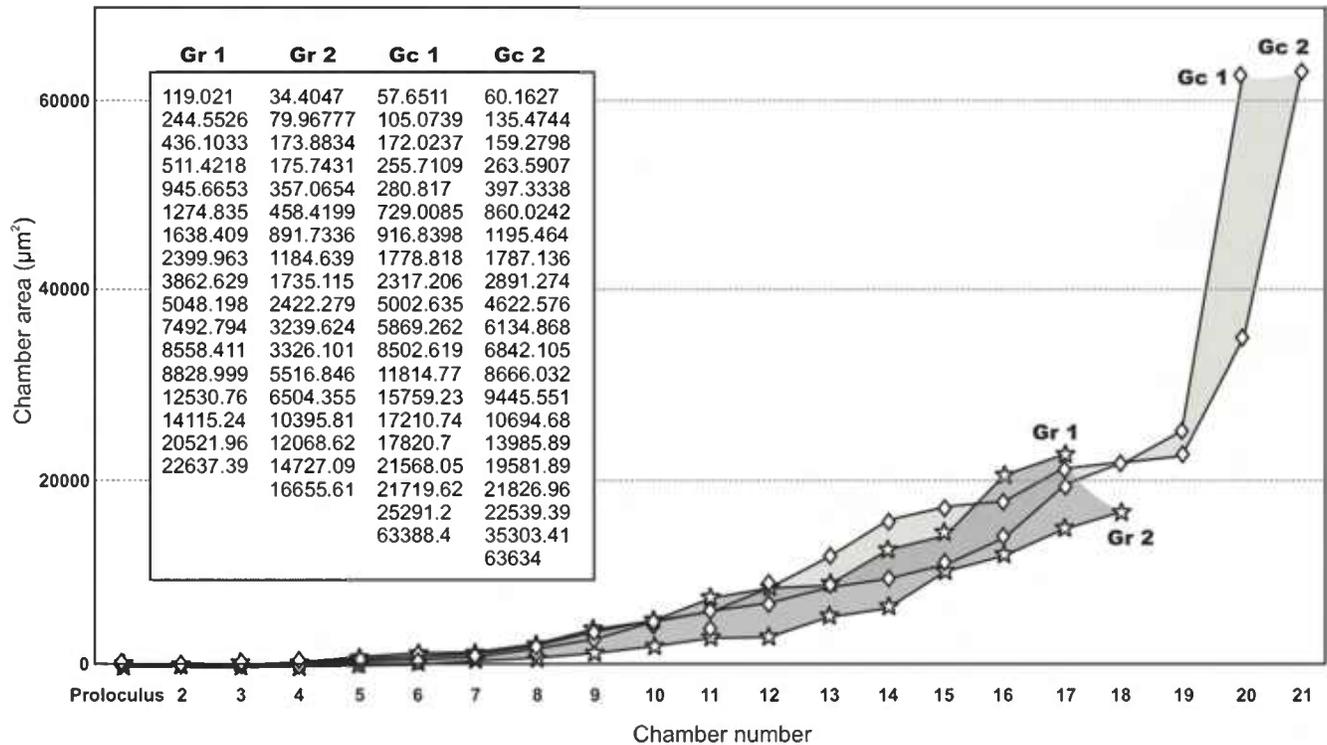
TEXT-FIGURE 4
 Ontogenetic morphometric trajectories of cross-sectional chamber areas for *Praegublerina pseudotessera* (light grey area, circles)-*P. acuta* (dark grey area, triangles) lineage. Only the specimens which define the area are presented in the diagram. The dotted lines delineate the biserial stage chambers (empty symbols), progressive chamber (solid symbols) and multiserial sets (dark grey symbols). The similarities between the growth patterns document the phylogenetic relationship between the two species.



TEXT-FIGURE 5
 Ontogenetic morphometric trajectories showing the development of the central area in the three species of the genus *Praegublerina* nov. gen.: *P. pseudotessera* (circles), *P. acuta* (triangles), and *P. robusta* (costate variety-pentagons and reticulate variety-hexagons). Defined areas for each species are marked with different shades of grey.



TEXT-FIGURE 6
 Comparative chamber increase trajectories in the *Praegublerina pseudotessera* (light grey area, circles)-*Gublerina rajagopalani* lineage (dark grey area, stars). The similar values in the earlier stages document the phylogenetic relationship existing between the two species. The sharp differences in the increasing chamber area in *Gublerina rajagopalani* when compared to its ancestor *Praegublerina cuvillieri* is partly due to the development of the periapertural flanges.



TEXT-FIGURE 7

Chamber area ontogenetic morphometry trajectories in the *Gublerina rajagopalani* (dark grey area, stars)–*G. cuvillieri* (light grey area, diamonds) lineage. Note the sharp increase in test surface with the development of the multiserial chamber sets (terminal values in *Gublerina cuvillieri* trajectories). Only the first multiserial set is included due to the constant poor preservation of this species. The similarity of the biserial stages demonstrates that *Gublerina rajagopalani* is the ancestor of *G. cuvillieri*.

Praegublerina nov. gen. The species concept used is that given by Georgescu and Huber (2007).

Order Foraminiferida Eichwald 1830
 Suborder Globigerinina Delage and Hérouard 1896
 Superfamily Heterohelicacea Cushman 1927
 Family Heterohelicidae Cushman 1927
 Genus *Heterohelix* Ehrenberg 1843
 Type species: *Textilaria americana* Ehrenberg 1843, p. 429.

Heterohelix planata (Cushman) 1938
 Plate 1, figure A(1), plate 3, figures 1-5

Guembelina planata CUSHMAN 1938, p. 12, pl. 2, figs. 13-14. – CUSHMAN 1944, p. 10, pl. 2, fig. 20. – CUSHMAN 1946, p. 105, pl. 45, figs. 6-7.

Heterohelix planata (Cushman), PESSAGNO 1967, pl. 86, figs. 3-4, pl. 89, figs. 6-7. – PETTERS 1977, pl. 1, fig. 9. – PERYT 1980, p. 36, pl. 2, figs. 9-10, pl. 3, figs. 13-14. – NEDERBRAGT 1989b, p. 198, pl. 2, fig. 8, pl. 3, figs. 1-2. – HUBER 1990, p. 503, pl. 1, figs. 5-6. – NEDERBRAGT 1991, p. 346, pl. 3, fig. 3. – GEORGESCU 1995, p. 96, pl. 1, figs. 9-11. – GEORGESCU 2006, fig. 1: 4-5.

Heterohelix pulchra (Brotzen). – KRASHENINNIKOV and BASOV 1983, p. 807, pl. 12, figs. 6-8.

Material. Over 500 specimens.

Description. The test is biserial throughout. The earliest chambers are globular then subrectangular; the later chambers may be reniform in some specimens. Chambers increase gradually in size as added. Sutures are distinct, straight and depressed and

slightly oblique to the test axis of growth. The two rows of alternating chambers may diverge in the adult stages of some specimens, but no central area is consistently developed. The periphery of the test is rounded. The aperture is situated at the base of the last-formed chamber and has a medium high to high arch. It is bordered by two small flanges, which are rarely rimmed. Chamber surface is ornamented with fine costae that are 1.8 to 2.5µm thick. The test wall is microperforate with pore diameters ranging from 0.6 to 0.8µm. Pores are distributed in the spaces between the costae or can penetrate through the costae.

Remarks. *Heterohelix planata* presents a wide range of morphological variability, expressed in the presence or absence of an incipient planispiral coil in the juvenile stage, test wall flexure in the earlier portion of the test periphery, reniform final chambers, an incipient central area in the adult stage of some (rare) specimens, and rimmed periapertural flanges.

Stratigraphic range. Upper Santonian-Maastrichtian [from the *Dicarinella asymetrica* Biozone (e.g., 10-95-16-3, 97.5-99cm) throughout *Pseudoguembelina hariaensis* Biozone (e.g., 113-689B-25X-5, 105-107cm)].

Geographic distribution. Cosmopolitan.

Genus *Praegublerina* Georgescu, Saupe and Huber, n. gen.
 Type species: *Gublerina acuta robusta* de Klasz 1953, p. 246.

TEXT-FIGURE 8

Diagram presenting the ontogenetic morphometric trajectories in the *Praegublerina pseudotessera* (circles)-*Gublerina rajagopalani* (stars)-*G. cuvillieri* (diamonds) lineage. The defined areas for the three species are given in different shades of grey.

Diagnosis. Tests are biserial throughout or with a multiserial chamber stage in the adult portion; a chamber proliferation stage follows the biaperturate progressive chamber; maximum of three multiserial chamber sets that gradually increase their number by one; test ornamentation costate or reticulate throughout, or a combination of the two kinds.

Description. Test is biserial throughout in earlier species of the lineage with chamber proliferation in the adult stage in the more highly evolved forms. Test outline is subtriangular to flaring due to the addition of chambers in the proliferation stage. The earlier biserial stage presents a central nonseptate area bounded by two rows of divergent chambers. The chamber proliferation stage initiates with the progressive chamber, which is the first biaperturate chamber of the test, and is followed by up to three multiserial chamber sets, the latter increasing the chamber number by one as new sets are added (i.e., two, then three, then four additional chambers in successive multiserial chamber sets). The test periphery is broadly rounded without peripheral structures. The aperture is single at the base of the last-formed chamber in the biserial stage and multiple due to the presence of both mono- and biaperturate chambers in the multiserial stage. Apertures are bordered by wide flanges that are occasionally rimmed. Transverse biaperturate walls can be developed between the chambers in the multiserial portion of the test. Chamber surface is costate or reticulate or a combination of the two. The reticulate ornamentation occurs later in the genus history, being derived from costate forms. Test wall is calcareous, hyaline, and microperforate to finely perforate.

Remarks. *Praegublerina* nov. gen. differs from *Heterohelix* in having (i) a central nonseptate area between the two rows of diverging chambers, (ii) a chamber proliferation stage in the evolved taxa (e.g., *P. acuta*, *P. robusta*) and (iii) coarser costae than in *H. planata*, its ancestral species, and reticulate ornamentation, the latter being present either on distinct parts of the test or all over the test surface. *Praegublerina* differs from *Gublerina* in having (i) a multiserial stage with chamber sets increasing their number by one chamber at a time rather than three chambers with each successive chamber set, (ii) finer costae (when present) and reticulate ornamentation without smooth sutures and unornamented portions and (iii) transverse biaperturate walls between the chambers of the multiserial chamber stage (text-figure 4).

Species included.

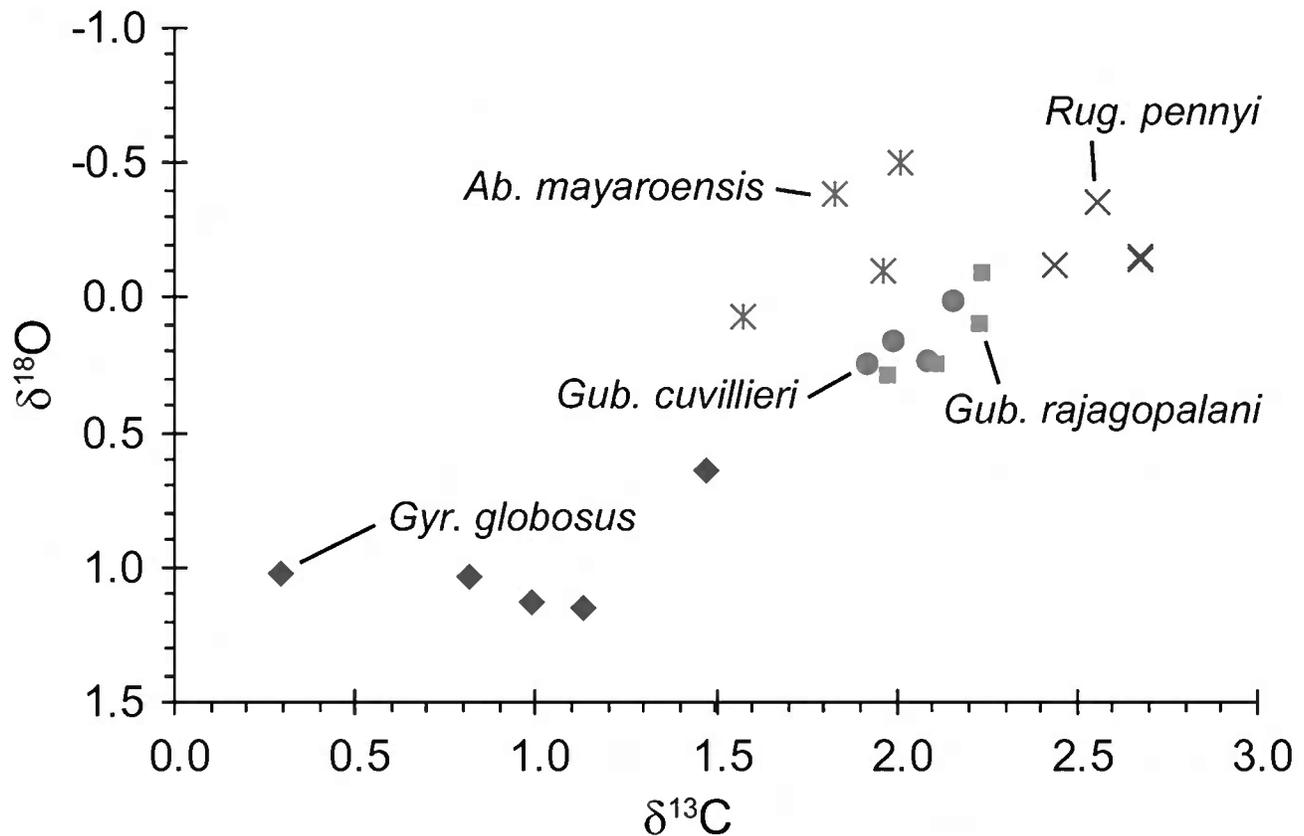
Praegublerina pseudotessera (Cushman) 1938, p. 14, pl. 2, figs. 19-20.

Praegublerina robusta (de Klasz) 1953, p. 247, pl. 8, figs. 4-5.

Praegublerina acuta (de Klasz) 1953, p. 246, pl. 8, fig. 3.

Etymology. The prefix “*Prae-*” (= before, anterior to) is added to the pre-existing genus name *Gublerina*.

Phylogenetic relationships. *Praegublerina* nov. gen. is the oldest gublerinid genus and it evolved from *Heterohelix* through development of (i) a central nonseptate area between the two rows of divergent chambers and (ii) coarsening of costae. These trends are apparent in the *Heterohelix planata*-*Praegublerina pseudotessera* lineage.



TEXT-FIGURE 9

Oxygen and carbon isotope cross-plot of benthic and planktonic foraminifera from ODP Core-sections 761B-24X-1, -24X-2, and -23X-4. See Table 1 for presentation of data.

Stratigraphic range. Campanian-Maastrichtian (from the *Globotruncanita elevata* Biozone to and throughout the *Pseudoguembelina hariaensis* Biozone).

Geographic distribution. Cosmopolitan.

Praegublerina pseudotessera (Cushman) 1938 emended Plate 1, figure A(2), plate 3, figures 6-12

Guembelina pseudotessera CUSHMAN 1938, p. 14, pl. 2, figs. 19-20. – CUSHMAN 1946, p. 106, pl. 45, figs. 16-17. – HAMILTON 1953, p. 234, pl. 30, fig. 14. – FRIZZELL 1954, p. 109, pl. 15, figs. 33-34.

Guembelina conjakica GEODAKCHAN in GEODAKCHAN and ALIYULLA 1959, p. 58, pl. 1, figs. 7-8.

Heterohelix pseudotessera (Cushman) BARR 1968, pl. 1, figs. 12-13. – MASTERS 1977, p. 349, pl. 1, figs. 10-11. – SCHREIBER 1979, p. 38, pl. 3, fig. 8, pl. 4, fig. 5.

Heterohelix pulchra (Brotzen) SLITER 1968, p. 95, pl. 14, fig. 9.

Heterohelix planata (Cushman) NEDERBRAGT 1991, p. 346, pl. 3, fig. 4.

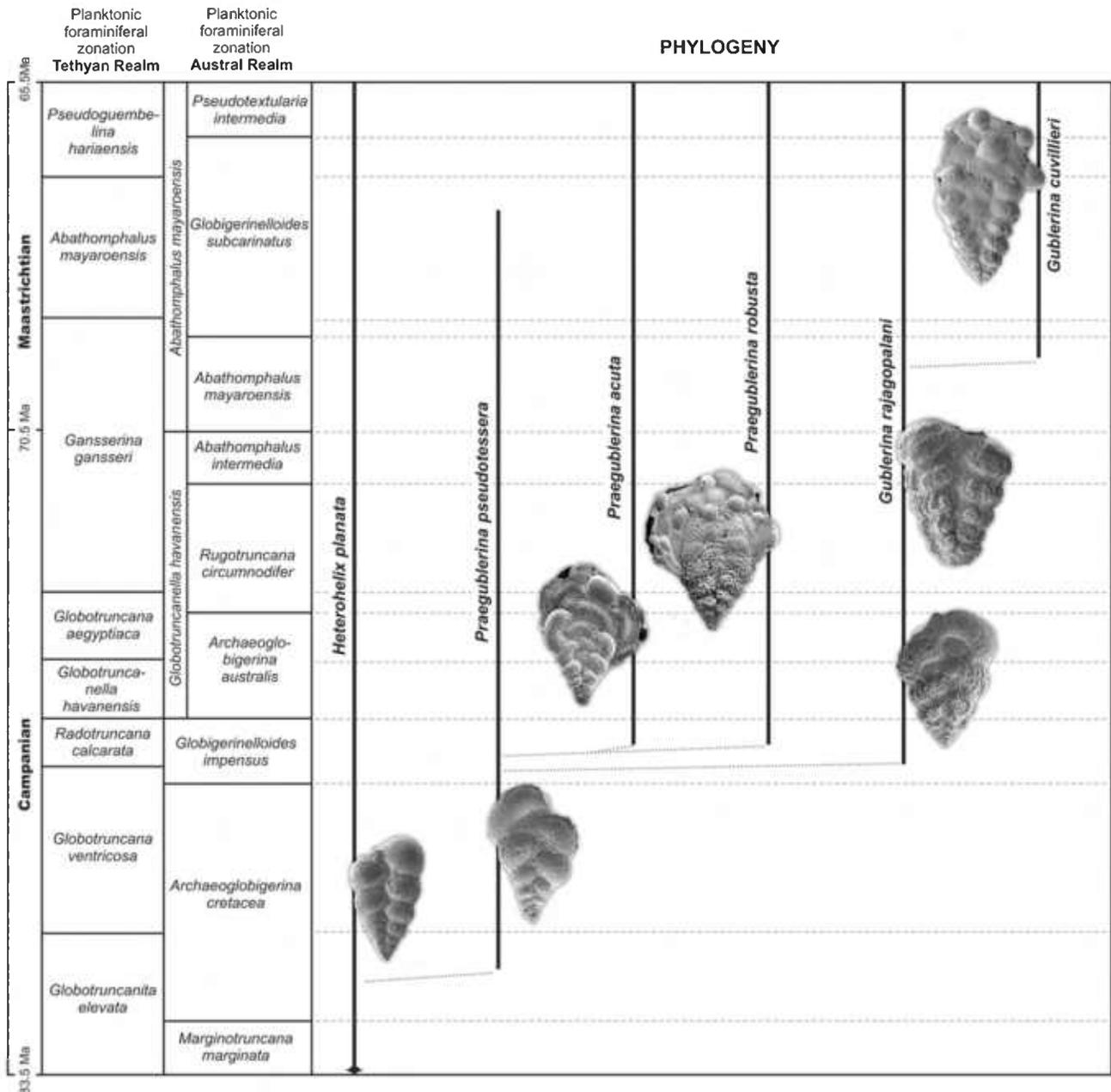
Material. Approximately 50 specimens.

Original description. “Test compressed, 1 1/2 - 2 times as long as broad, rapidly tapering with greatest breadth at the last pair of chambers, periphery indented throughout; chambers somewhat inflated, broader than high throughout, in the adult somewhat curved and broader; sutures depressed, somewhat curved in the last portion; wall smooth and polished, very finely perforate; aperture, a very high, arched opening with a slight lip and distinct

flanges, but not extending far onto the preceding chamber.” (Cushman 1938, p. 14).

Emended description. Test biserial throughout. The chambers are subrectangular in the earlier part of the test and become reniform in the adult stages. The periphery is broadly rounded without peripheral structures. Sutures are distinct, depressed, and oblique to the longitudinal axis of the test. There are distinctly depressed subtriangular areas on each side of the central zigzag suture, which are generated by the divergent rows of biserial chambers and gradual development of the periapertural flaps (Pl. 3, figs. 6a, 7a, 8a, 9a, 10b, 11a, 12a). Aperture is a low or medium high arch at the base of the apertural face of the final chamber, bordered by two well-developed flanges. The test is ornamented with fine and discontinuous costae, which are 2.5 to 4.0µm in width. Test wall is microperforate, pore diameter ranging between 0.4 and 0.8µm.

Remarks. *Praegublerina pseudotessera* differs from *Heterohelix planata* by having (i) divergent rows of biserial chambers resulting in the development of a central nonseptate area in the adult part of the test, (ii) reniform chambers in the adult part of the test, (iii) larger periapertural flanges and (iv) coarser costae. It differs from *Gublerina rajagopalani* in that it has an entirely finely costate test and lacks pseudokeels on the lateral sides of the test. *Praegublerina pseudotessera* differs from *Laeviheterohelix pulchra* (Brotzen 1936) in (i) being completely costate rather than ornamented with pore mounds and (ii) in having a central



TEXT-FIGURE 10
 Phylogeny of the planktonic foraminiferal gublerinid lineages. Note that *Gublerina rajagopalani* is illustrated with both “primitive” (below) and “evolved” (above) tests. Both test varieties are recorded throughout the stratigraphic range of the species. Notice the morphological resemblance between the “primitive” tests of *G. rajagopalani* and its ancestor, *Praegublerina pseudotessera*, and between the “evolved” tests and *Gublerina cuvillieri*, its only known descendant. Planktonic foraminiferal zonation for the Tethyan Realm after Robaszynski & Caron (1995) and after Huber (1992) for the Austral Realm. Absolute ages after Gradstein and others (2004).

nonseptate area between the two rows of diverging chambers in the adult portion of the test.

Phylogenetic relationships. *Praegublerina pseudotessera* evolved from *Heterohelix planata* with the development of the central nonseptate area, periapertural flanges and increase in costae thickness. Chamber area variability increases early in ontogeny and presents similar growth trajectories as its ancestor, *H. planata*. There is a marked increase in the chamber size later in ontogeny which results from the development of periapertural

flanges in *P. pseudotessera*. The two species present distinct ontogenetic trajectories of chamber size increase by the early half of the ontogeny (text-figure 2).

Stratigraphic range. Campanian-Maastrichtian [from the lower part of the *Globotruncanita elevata* Biozone (e.g., 174AX, 493.47-493.50 m) throughout the top of the *Abathomphalus mayaroensis* Biozone (e.g., 39-357-31-3, 80-94cm)].

Species and phylogeny	Formula to calculate the test number of chambers			
	Total number	Biserial stage	Progressive chamber	Multiserial stage
<i>Heterohelix planata</i> (Cushman, 1938)	$N = \sum_{i=14}^{17} N_i$			
<i>Praegublerina pseudotessera</i> (Cushman, 1938)	$N = \sum_{i=12}^{14} N_i$			
<i>Praegublerina acuta</i> (de Klasz, 1953)	$N = \sum_{i=11}^{13} N_i + P + \sum_{n=2}^2 n$			
<i>Praegublerina robusta</i> (de Klasz, 1953)	$N = \sum_{i=13}^{17} N_i + P + \sum_{n=2}^4 n$			
<i>Gublerina rajagopalani</i> Govindan, 1972	$N = \sum_{i=14}^{17} N_i$			
<i>Gublerina cuvillieri</i> Kikoïne, 1948	$N = \sum_{i=19}^{23} N_i + P + \sum_{n=1}^3 4n$			

Biserial throughout species
 Multiserial species

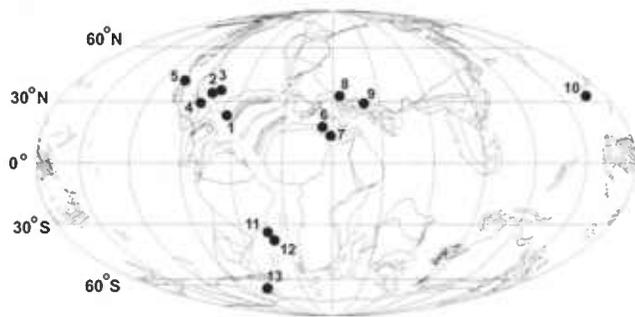
TEXT-FIGURE 11
 Formulas for chamber number (N) calculation in the gublerinid planktonic foraminifera. Notice that the total number of chambers in the multiserial species of *Praegublerina* and *Gublerina* can be calculated with similar formulas, demonstrating their common ancestry and parallel development. The three species differ in the number of chambers in the biserial stage and multiserial stage, which follows the progressive chamber (P).

Geographic distribution. Northern Hemisphere: United States (Gulf region, Western Interior, California), Mexico, South Atlantic Ocean (São Paulo Plateau and Rio Grande Rise), Europe (Germany, Austria), central Asia (Azerbaijan), northern Africa (Libya, Tunisia) and northern Atlantic Ocean (Grand Banks).

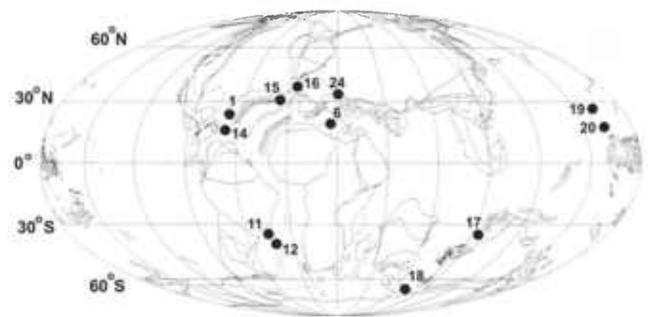
Praegublerina robusta (de Klasz) 1953 emended
 Plate 1, figure 4, plate 2, figures A(1-2), plate 4, figures 5-12, plate 6, figures 1-3

Gublerina acuta robusta DE KLASZ 1953, p. 247, pl. 8, figs. 4-5. – MONTANARO GALLITELLI 1957, pl. 32, fig. 9. – SALAJ and SAMUEL 1966, p. 227, pl. 26, figs. 5-6. *Gublerina* aff. *cuvillieri* Kikoïne. DE KLASZ 1953, p. 246, pl. 8, fig. 2.
Gublerina glaessneri BRÖNNIMANN and BROWN 1953, p. 155, text-figs. 13-14.
Gublerina robusta de Klasz. BRÖNNIMANN AND BROWN 1954, p. 62. – PETERS 1977, pl.2, fig. 5. – HUBER 1990, p. 503, pl. 1, fig. 7.
Gublerina ornatissima (Cushman and Church). BRÖNNIMANN and RIGASSI 1963, pl. 17, fig. 4. – SALAJ and SAMUEL 1966, p. 229, text-fig. 18.

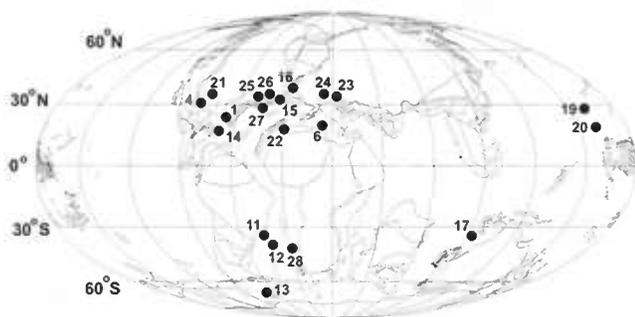
A. *Praegublerina pseudotessera*



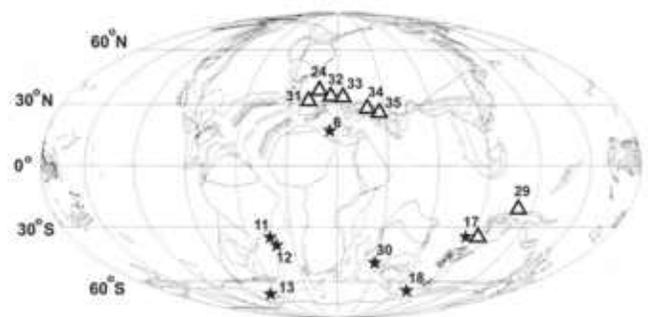
B. *Praegublerina acuta*



C. *Praegublerina robusta*



D. *Gublerina rajagopalani* and *G. cuvillieri*



Legend

- *Praegublerina*
- ★ *Gublerina rajagopalani*
- △ *Gublerina cuvillieri*

TEXT-FIGURE 12

Occurrence distribution of the gublerinid species. Cipher significance: 1-Blake Plateau (this study), 2 and 3-Texas, USA (Cushman 1938, 1944, 1946; Pessagno 1967; this study), 4-Nicaragua Rise (this study), 5-California, USA (Sliter 1968), 6-El Kef section, Tunisia (Nederbragt 1991), 7-Libya (Barr 1968), 8-Austria (Schreiber 1979), 9-Azerbaijan (Geodakhan and Aliyulla 1959), 10-Central pacific (Hamilton 1953), 11-São Paulo Plateau (this study), 12-Rio Grande Rise (this study), 13-Weddell Sea (Huber 1990; this study), 14-Cuba (Brönnimann and Brown 1953), 15-Grand Banks (this study), 16-Orphan Knoll (this study), 17-Exmouth Plateau (Wonders 1992; Zapeda 1998; this study), 18-Kerguelen Plateau (Petrizzo, 2001), 19-Mid-Pacific mountains (this study); 20-Shatsky Rise (this study), 21-Texas, USA (Smith & Pessagno 1973), 22-Morocco (Lehmann 1966), 23-Western Carpathians (Salaj and Samuel 1966), 24-southern Germany (de Klasz 1953), 25-New Jersey coastal plain (Petters 1977), 26-Long Island, New York (Perlmutter and Todd 1965), 27-offshore New Jersey (Jensen and Kroon 1987), 28-Walvis Ridge (Todd 1970), 29-Ceram Island (Van der Sluis 1950), 30-south India (Govindan 1972), 31-Pyrenees, southern France (Kikoïne 1948), 32-Austria (Butt 1981), 33-Slovakia (Hanzliková), 34-Romania (Neagu 1970) and 35-Western Black Sea (Georgescu 1995). Paleogeographic reconstruction after Hay and others (1999).

Gublerina acuta de Klasz. PERLMUTTER and TODD 1965, p. 114, pl. 2, fig. 18. – TODD 1970, p. 151, pl. 5, fig. 4. NEDERBRAGT 1991, p. 339, pl. 1, fig. 2.
Gublerina cuvillieri Kikoïne. LEHMANN 1966, p. 315, pl. 2, fig. 5. – SALAJ 1983, pl. 1, figs. 44-45. – JANSEN and KROON 1987, p. 565, pl. 9, fig. 11. – NEDERBRAGT 1989b, p. 194, pl. 1, figs. 2-3. – NEDERBRAGT 1991, p. 339, pl. 1, figs. 3-4.
Gublerina reniformis (Marie). CITA and GARTNER 1971, pl. 5, fig. 2.

Material. Over 200 specimens.

Original description. “Similar to *Gublerina acuta*, but contrary to it generally larger, with bigger, more globular chambers, which are usually even more inflated in the middle of the lateral rows of chambers than the others. Both lateral rows are some-

times connected with two calcareous lamellas instead of one. The sutures are deeper than with *G. acuta*.” (de Klasz 1953, p. 247).

Emended description. The test is biserial in the younger stage and multiserial in the adult stage. The small proloculus is followed by a biserial stage with two rows of divergent alternating chambers. The earliest chambers of the biserial stage are subglobose and become rounded to subrectangular. The latest formed chambers are reniform and distinctly tilted. The multiserial stage begins after the biaperturate progressive chamber and consists of a maximum of three sets of chambers, the earlier one presenting two chambers beyond the progressive chamber (P) and the number of chambers increasing by one for

TABLE 1

Oxygen and carbon isotope data expressed as the per mil deviation from for the benthic foraminifer *Gyroidinoides globosus*, and the planktonic foraminifera *Rugoglobigerina pennyi*, *Gublerina cuvillieri*, *G. rajagopalani*, and *Abathomphalus mayaroensis* from the upper Maastrichtian of ODP Hole 761B (southeast Indian Ocean). n = number of specimens analyzed per sample run. Results are reported in standard δ notation relative to the Vienna PDB standard.

Sample	<i>G. cuvillieri</i>			<i>G. rajagopalani</i>			<i>G. globosus</i>			<i>R. pennyi</i>			<i>A. mayaroensis</i>		
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	n	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	n	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	n	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	n	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	n
761B-23X-4, 61 cm	2.16	0.01	4	2.24	-0.09	12	1.47	0.64	5	2.56	-0.36	8	1.83	-0.39	3
761B-23X-4, 61 cm													2.01	-0.50	4
761B-24X-1, 71 cm	2.09	0.24	5	2.12	0.25	11	0.82	1.04	4	2.44	-0.12	9	1.96	-0.10	4
761B-24X-2, 125 cm	2.00	0.16	5	1.98	0.29	7	1.13	1.15	1	2.68	-0.15	6	1.58	0.07	5
761B-24X-2, 125 cm	1.92	0.25	5	2.24	0.11	5	0.99	1.13	1	2.67	-0.14	6			
761B-24X-2, 125 cm							0.29	1.03	1						

each newly added chamber set (pl. 1, fig. B-C). Sutures are distinct and depressed, consistently oblique with respect to the longitudinal axis of the test. The main aperture in the biserial part of the test is single, a medium-high arch at the base of the last formed chambers. The progressive chamber is the first biaperturate chamber of the test; remaining chambers of the multiserial stage being either monoaperturate if they are situated adjacent to the test periphery or biaperturate if they are towards the central parts of the multiserial stage. Apertures are bordered by well developed periapertural flanges, which are generally flat or gently folded. The flanges bound the central nonseptate area between the two diverging rows of chambers. Biaperturate transverse walls are present in well-preserved specimens (pl. 2, figs. A1-2, pl. 4, fig. 6b). Test surface is costate to reticulate with the costae thickness varying between 2.9 and 4.0 μm in the adult specimens; ornamentation may be thicker over the chamber in the earlier part of the test (pl. 4, figs. 7a, 8a, 9a, 10a, 12a). Pore diameter can be up to 1.9 μm in the portions of the tests with reticulate ornamentation; however, the last added chambers present smaller pores with diameters between 0.6 and 0.9 μm (pl. 6, figs. 1-2).

Remarks. This species differs from *Praegublerina acuta* by having (i) a multiserial stage consisting of up to three chamber sets following the progressive chamber, (ii) test ornamentation that is not arranged in quasi-longitudinal bands but developed along the growth axis of the test, and (iii) transverse biaperturate walls between the chambers of the multiserial stage. *Praegublerina robusta* presents a wide range of variability with respect to test ornamentation, from costate to reticulate. Specimens with intermediate ornamentation patterns between the two are known in the upper Campanian and Maastrichtian (Pl. 4, fig. 12). The reticulate tests appear to be dominant in the tropical regions, whereas the costate tests are the only ones known from the higher latitudes.

Phylogenetic relationships. *Praegublerina robusta* evolved from *P. pseudotessera* through (i) significant development of the central area, (ii) development of a multiserial stage initiating with the progressive chamber, which follows the earlier biserial stage and (iii) test ornamentation, which is reticulate in one of the two varieties of the species. Chamber areas were measured

in order to define the ontogenetic trajectories for various specimens. The trajectories of chamber size increase for *P. pseudotessera* (ancestor) and *P. robusta* (its descendant) are similar in the earlier portion of the test (text-figure 3).

Stratigraphic range. Upper Campanian-Maastrichtian [from the upper part of the *Radotruncana calcarata* Biozone (e.g., 15-152-21-1, 67-8 1cm) throughout the top of the *Pseudoguembelina hariaensis* Biozone (e.g., 171B-1050C-1 1R-1, 22-25cm)].

Geographic distribution. Cosmopolitan.

Praegublerina acuta (de Klasz) 1953 emended
Plate 1, figure A(3), plate 4, figures 1-4, plate 6, figures 4-6

Gublerina acuta DE KLASZ 1953, p. 246, pl. 8, fig. 3. – BRÖNNIMANN and BROWN 1954, p. 62. – NEDERBRAGT 1989b, p. 194, pl.1, fig. 1. – NEDERBRAGT 1991, p. 339, pl. 1, fig. 1. – PETRIZZO 2001, p. 851, fig. 10.8.
Gublerina hedbergi BRÖNNIMANN and BROWN 1953, p. 155, text-figs. 11-12.

Material. Over 100 specimens.

Original description. "Test consists of two divergent rows of more or less globular chambers connected with each other by a calcareous lamella. The latter also contains a varying number of irregularly dispersed, often partly reniform, chambers filling almost the whole space between the two lateral rows of chambers of some of the specimens. The chambers of the lateral divergent rows are separated from each other by depressed sutures. Their size is generally increasing from the first to the last, although this increase in size is not always regular. The size of the initial chambers is increasing more slowly than of theseone of *G. cuvillieri*. The last chambers are often elongating a little towards the centre of the test. The whole test is sometimes compressed in the vertical direction towards the symmetric plane of both divergent rows of chambers. The calcareous lamella, filling the space between these rows, occasionally encloses the upper end of the test and part of its flanks." (de Klasz 1953, p. 246).

Emended description. The test has a subtriangular outline and is biserial in the early stage and multiserial when adult. Chambers

of the biserial stage are rounded, subrectangular to reniform. There is a gradual tilting of the chambers with respect to the test growth axis. The test is compressed with the two sides of the test being quasi-parallel in edge view. Sutures in the biserial part of the test are depressed, straight and oblique to the test axis of growth and curved in the adult stage (pl. 4, figs. 1a, 2a, 3a, 4a). The aperture in the earlier biserial chambers has a medium high arch at the base of the last formed chamber; it is bordered by long, wide periapertural flaps that are attached to the previous chamber. The periapertural flanges in the multiserial stage may be gently folded. The two rows of alternating chambers are divergent resulting in the development of a central nonseptate area. The early biserial stage is followed by the progressive chamber, which is subglobose in outline. The multiserial stage is poorly developed and consists of a single set of two elongate chambers beyond the progressive chamber (pl. 1, fig. B-B). No transverse walls are present in the multiserial stage. The test is ornamented with five quasi-longitudinal bands of costae or reticulations. Two finely costate bands are developed at the test periphery with costae thickness between 3.0 and 3.4 μ m. Pores are present in the spaces between the costae; their diameter ranges between 0.6 and 0.8 μ m. The ornamentation over the chambers is incipiently reticulate with pore sizes ranging between 2.0 and 4.9 μ m (pl. 6, figs. 4-6). The fifth band is centrally located over the central non-septate area and is finely costate with pores between 0.6 and 0.7 μ m.

Remarks. *Praegublerina acuta* differs from *P. pseudotessera* by (i) presence of the multiserial growth stage with a single set of two chambers and (ii) test ornamentation consisting of five quasi-longitudinal bands of alternating costate and reticulate patterns.

Phylogenetic relationships. *Praegublerina acuta* evolved from *P. pseudotessera* through (i) development of a multiserial stage consisting of one set of two chambers that initiate with the progressive chamber and follow the earlier biserial stage, (ii) increase in size of the central nonseptate area and (iii) development of reticulate ornamentation above the chambers leaving only the peripheral regions and central area ornamented with a costate pattern. The ontogenetic trajectories of *P. pseudotessera* as ancestor and *P. acuta* as descendant are similar in the earlier part of ontogeny (text-figure 4). The ontogenetic development of the central nonseptate area in *Praegublerina acuta* presents wider variability when compared to the other two species of the genus, namely *P. pseudotessera* and *P. robusta* (text-figure 5).

Stratigraphic range. Upper Campanian-Maastrichtian [from the upper part of the *Radotruncana calcarata* Biozone (e.g., 15-152-21-1, 67-81cm) throughout the top of the *Pseudoguembelina hariaensis* Biozone (e.g., 171B-1050C-1 1R-1, 22-25cm)].

Geographic distribution. Cosmopolitan.

Genus *Gublerina* Kikoïne 1948 emended

Type species: *Gublerina cuvillieri* Kikoïne 1948, p. 26.

Gublerina Kikoïne 1948, p. 26. – MONTANARO GALLITELLI 1957, p. 140. – BROWN 1969, p. 57. – LOEBLICH and TAPPAN 1987, p. 457. – NEDERBRAGT 1 989a, p. 111. – NEDERBRAGT 1991, p. 339.

Diagnosis. The test is biserial throughout or with chamber proliferation later in ontogeny; the multiserial stage consists of a maximum of three chamber sets; chamber number in the multiserial

TABLE 2

Apical angle and chamber proliferation angle ranges of variability in the investigated species. Only the values measured on X-ray micrographs are included.

SPECIES	Apical	Progressive
	angle (°) (4)	chamber angle (°) (5)
<i>Heterohelix planata</i> (Cushman, 1938)	40° to 54°	N/A
<i>Praegublerina pseudotessera</i> (Cushman, 1938)	52° to 65°	N/A
<i>Praegublerina acuta</i> (de Klasz, 1953)	55° to 67°	6° to 10°
<i>Praegublerina robusta</i> (de Klasz, 1953)	57° to 73°	3° to 11°
<i>Gublerina rajagopalani</i> Govindan, 1972	51° to 64°	N/A
<i>Gublerina cuvillieri</i> Kikoïne, 1948	49° to 57°	7° to 16°

sets gradually increases by three; the test is ornamented with strong, blunt costae in the earlier species and with irregular, non-costate areas over the chambers; sutures remain flush in the evolved species; the test wall is calcareous and microperforate.

Emended description. Test biserial throughout and with a proliferating stage in adults. Biserial chambers are arranged in two diverging rows bounding a nonseptate central subtriangular cavity. Test periphery is rounded with pseudokeels formed by fused, coarse costae in the earlier species and with transverse keels over the chambers across the periphery in the evolved species. Sutures are depressed and flush in the evolved species. Chamber proliferation follows the biaperturate progressive chamber and consists of two to four sets in which chamber number increases by three. Aperture is single in the biserial part of the test, situated at the base of the last-formed chamber and multiple in the adult, multiserial portion. Apertures are bordered by wide periapertural flanges. There are no transverse walls in the multiserial stage. Chamber surface is ornamented with coarse costae in the earlier species and massive ornamented areas over the chambers connected by transverse peripheral keels. Ornamentation is absent in the central part of the test in the evolved species. Test wall is calcitic, hyaline and microperforate.

Remarks. This emendation is proposed to accommodate the *Gublerina rajagopalani*-*G. cuvillieri* lineage, which initiated in the late Campanian (*Radotruncana calcarata* Biozone) from *Praegublerina pseudotessera* with development of strong and blunt costae, enlargement of the central nonseptate area and development of peripheral pseudokeels. Coarser ornamentation in the earlier species, absence of transverse walls in the multiserial portion and rate of numerical increase of chambers in the proliferating stage separate *Gublerina* from its ancestor *Praegublerina*.

Species included.

Gublerina rajagopalani Govindan 1972, p. 170, pl. 2, figs. 1-5.
Gublerina cuvillieri Kikoïne 1948, p. 26, pl. 2, fig. 10.

Phylogenetic relationships. *Gublerina* evolved from *Praegublerina*, which is documented in the *Praegublerina pseudotessera*-*Gublerina rajagopalani* lineage.

Stratigraphic range. Upper Campanian-Maastrichtian, from the upper part of the *Radotruncana calcarata* Biozone to and throughout *Pseudoguembelina hariaensis* Biozone.

Geographical distribution. Europe (southern France, southern Germany, Austria, Slovakia, Romania, Tunisia), southern India, South Atlantic Ocean (Rio Grande Rise, São Paulo Plateau) and Indian Ocean (Exmouth Plateau).

Gublerina rajagopalani Govindan 1972

Plate 5, figures 1-5

Gublerina rajagopalani GOVINDAN 1972, p. 170, pl. 2, figs. 1-5.
Gublerina cuvillieri Kikoïne. – WRIGHT and APHORPE 1976, p. 238, pl. 1, fig. 1. *Heterohelix rajagopalani* (Govindan). – NEDERBRAGT 1991, p. 348, pl. 4, figs. 1, 3. – WONDERS 1992, p. 591, pl. 1, figs. 7-9, pl. 2, figs. 5-13. – ZAPEDA 1998, p. 137, fig. 10.1. – PETRIZZO 2001, p. 851, figs. 10.9-10.

Material. Over 700 specimens.

Description. Test is biserial throughout and has a subtriangular outline in lateral view and is slightly compressed in edge view. Chambers are subrectangular in the earlier part of the test and variable in the adult portion, ranging from reniform in the primitive tests (pl. 5, fig. 1) to subrectangular in the evolved ones (pl. 5, fig. 4). Test periphery is broadly rounded to subangular. Sutures are distinct, depressed, slightly oblique to almost perpendicular on the test axis of growth in the evolved specimens. The central suture may be bordered by subtriangular depressed areas. The two rows of biserial chambers are symmetrically divergent with respect to the growth axis of the test. Test periphery

has one or two more or less continuous strong costae, resulting in a keeled appearance (pl. 5, figs. 1b, 2b, 3b, 4b). Aperture is a low to medium high arch at the base of the last formed chamber. It is bordered by two well-developed flanges, which are rarely fused above the aperture. Test wall is coarsely costate on the earlier part of the test with amorphous agglomerations of fused ornamentation elements over the last-formed chambers, leaving the sutures flush. The last-formed chamber or, rarely, several chambers may be finely costate. Test wall calcitic, hyaline and microperforate.

Remarks. *Gublerina rajagopalani* differs from its ancestor *Heterohelix pseudotessera* in (i) being coarsely ornamented rather than costate, (ii) having strong costae on the test periphery, resulting in a keeled appearance when seen in edge view, (iii) having weaker ornamentation over the sutures and (iv) presenting a well-developed nonseptate central area.

Phylogenetic relationships. *Gublerina rajagopalani* evolved from *Praegublerina pseudotessera* as indicated by the similarity in the primitive tests of the former species to the latter and the similar ontogenetic morphometry in the earlier stage of the tests. Tests with intermediate features between the two species occur frequently throughout the Maastrichtian (pl. 5, figs. 1-2), but they have not been observed in the Upper Campanian (*Radotruncana calcarata* Biozone). The rate of chamber size increase is smaller in *G. rajagopalani* when compared with *P. pseudotessera* (text-figure 6).

PLATE 1

Type specimens and morphological features in *Praegublerina* nov. gen. and *Gublerina* Kikoïne 1948.

PART A. Type specimens from the National Museum of Natural History investigated in the course of this study.

- | | |
|--|--|
| 1 Holotype of <i>Heterohelix planata</i> (Cushman 1938), USNM 24376. | 4 Paratype of <i>Praegublerina robusta</i> (de Klasz 1953), USNM 370119. |
| 2 Holotype of <i>Heterohelix pseudotessera</i> (Cushman 1938), USNM 24380. | 5-6 Topotypes of <i>Gublerina cuvillieri</i> Kikoïne 1948 from the Loeblich and Tappan Topotype Collection, USNM 473111. |
| 3 Paratype of <i>Praegublerina acuta</i> (de Klasz 1953), USNM 370118. | |

PART B. Chamber proliferation in *Praegublerina* nov. gen. and *Gublerina* Kikoïne 1948 illustrated in x-ray micrographs.

Symbols: P-progressive chamber, 1 to 3-multiserial sets, a to d-chambers in the multiserial sets.

Note that the first multiserial set is formed by two chambers in the multiserial species of *Praegublerina*, namely *P. acuta* (B) and *P. robusta* (C) and by four chambers in *Gublerina cuvillieri* (E).

This demonstrates the different patterns in development of the multiserial growth stage and represents the major basis for separating the two genera.

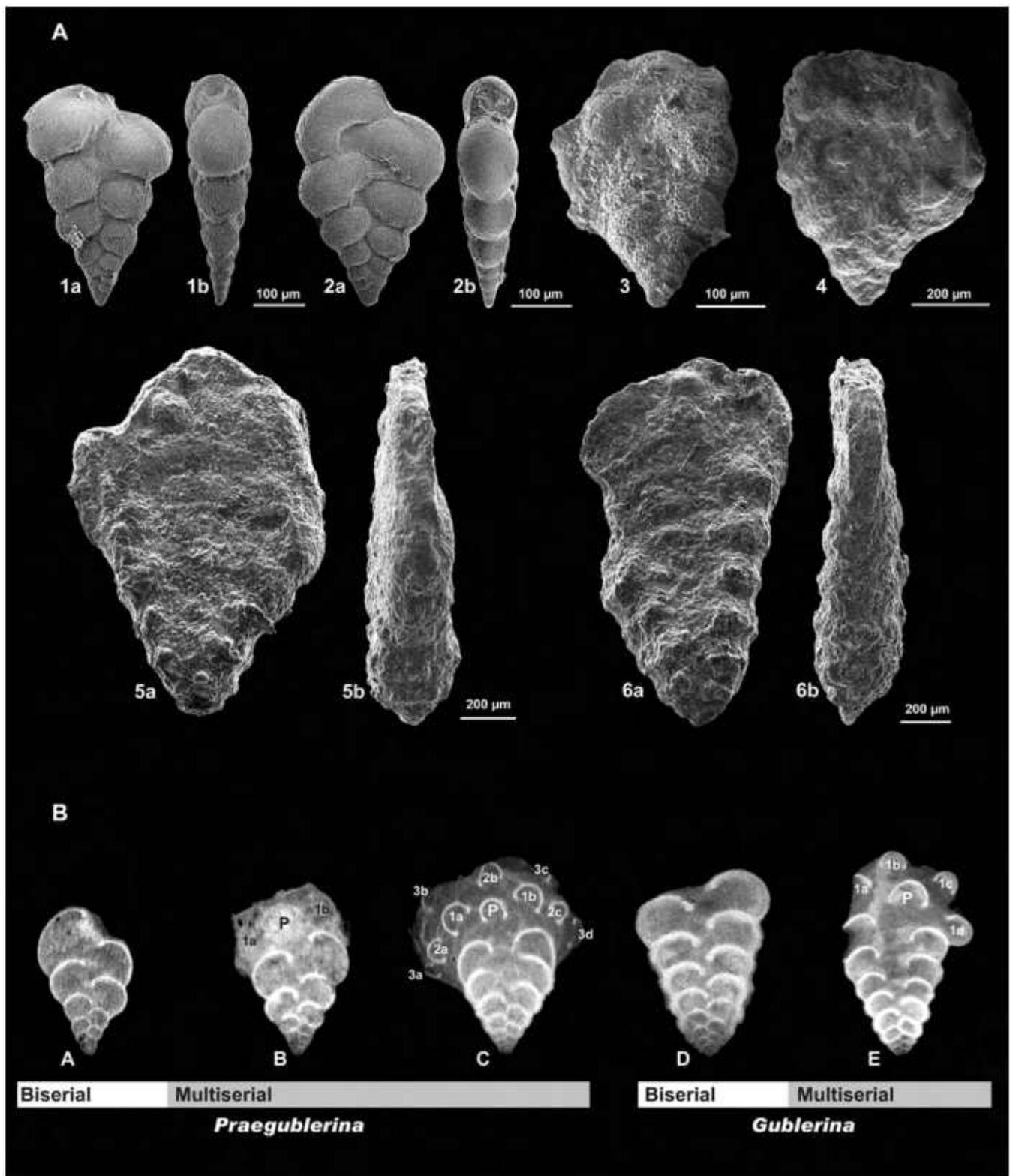
A *Praegublerina pseudotessera* (Cushman 1938);

B *P. acuta* (de Klasz 1953);

C *P. robusta* (de Klasz 1953);

D *Gublerina rajagopalani* Govindan 1972;

E *G. cuvillieri* Kikoïne 1948.



Stratigraphic range. Upper Campanian – Maastrichtian [from the lower part of the *Radotruncana calcarata* Biozone to the top of the *Abathomphalus mayaroensis* Biozone (122-761B-22X-4, 75-76cm)]. The first occurrence of this species in the Upper Campanian (*Radotruncana calcarata* Biozone) was documented in the El-Kef Section (Tunisia) by Nederbragt (1991).

Geographic distribution. South Atlantic Ocean (São Paulo Plateau and Rio Grande Rise), Indian ocean (Exmouth Plateau and Kerguelen Plateau) and north Africa (Tunisia).

Gublerina cuvillieri Kikoïne 1948 emended

Plate 1, figures A(5-6), plate 5, figures 6-11, plate 6, figures 7-9

Gublerina cuvillieri KIKOÏNE 1948, p. 26, pl. 2, fig. 10. – DE KLASZ 1953, pl. 8, fig. 1. – BETTENSTAEDT and WICHER 1955, p. 502, pl. 2, fig. 15. – SACAL and DEBOURLE 1957, p. 13, pl. 3, fig. 6. – BROWN 1969, p. 57, pl. 2, fig. 7, pl. 3, fig. 5, pl. 4, fig. 5. – HANZLIKOVÁ 1972, pl. 93, figs. 13-14. – MASTERS 1977, p. 333. – BUTT 1981, pl. 19, fig. F. – WONDERS 1992, p. 591, pl. 1, figs. 5-6. – ZAPEDA 1998, p. 136, fig. 10-3.

Ventilabrella compressiformis VANDER SLUIS 1950, p. 20, pl. 1, fig. 1. *Gublerina ornatissima* (Cushman and Church). – MONTANARO GALLITELLI 1957, pl. 32, figs. 1-6. NEAGU 1970, pl. 14, fig. 11. *Gublerina glaessneri* Brönnimann and Brown. – SALAJ and SAMUEL 1966, p. 228, pl. 26, fig. 3.

Material. Over 500 specimens.

Diagnosis. Test biserial in the earlier stage, multiserial when adult; chamber number in multiserial sets increases by three as new sets are added; ornamentation concentrated over the chambers, those of the same chamber connected across the periphery by transverse keels.

Emended description. Test is flaring and biserial early in ontogeny and multiserial in adult stage. There are up to twenty-three chambers in the biserial portion of the test. Chambers are subrectangular with width greater than height. Sutures are depressed and straight to slightly oblique to the test axis of growth. Test compressed in edge view with the earlier portion thicker than the later portion due to the addition of successive layers of calcite. The two rows of biserially arranged chambers are divergent, resulting in the development of a central, subtriangular nonseptate area. Aperture has a medium, high arch situated at the base of the last-formed chamber and is bordered by two thin, wide flanges that extend and attach to the previously formed chamber. Successive flanges merge and border the central nonseptate area. The earlier stage is followed by the progressive chamber, which is the first biaperturate chamber of the test. The progressive chamber is globular to subglobular. The first chamber set consists of four chambers of variable shape. The shape of the chambers in the first multiserial test varies from subglobular to subrectangular, being intermediate between the shape of the

PLATE 2

Morphological features and measurements in *Praegublerina* nov. gen. and *Gublerina* Kikoïne 1948 (A-B) and species with taxonomic status reconsidered in Appendix 1 and 2 (C-D).

PART A. Transverse wall in a well-preserved specimen of *Praegublerina robusta* (de KLASZ 1953) from the Maastrichtian (*Racemiguembelina fructicosa* Biozone) of the Orphan Basin, northern Atlantic (11 1A- 11-4, 124-13 8cm). *Praegublerina robusta* is the only species of the genus that presents this feature. Such structures are absent in the *Gublerina rajagopalani*-*G. cuvillieri* lineage.

1 Oblique edge view.

2 Detail showing the transverse walls.

PART B. Measurements applied on gublerinid tests (CHA-chamber area, CA-central area, MCSA-multiserial chamber set area, A-apical angle, PCA-progressive chamber angle). CHA and MCSA also include the periapertural flange surface, as they were formed at the same time with the chamber in a single growth stage. The progressive chamber angle (PCA) was measured between the test axis of growth and an imaginary line that passes through the test apex and the middle of the progressive chamber basis.

PART C. *Ventilabrella ornatissima* (Cushman and Church 1929).

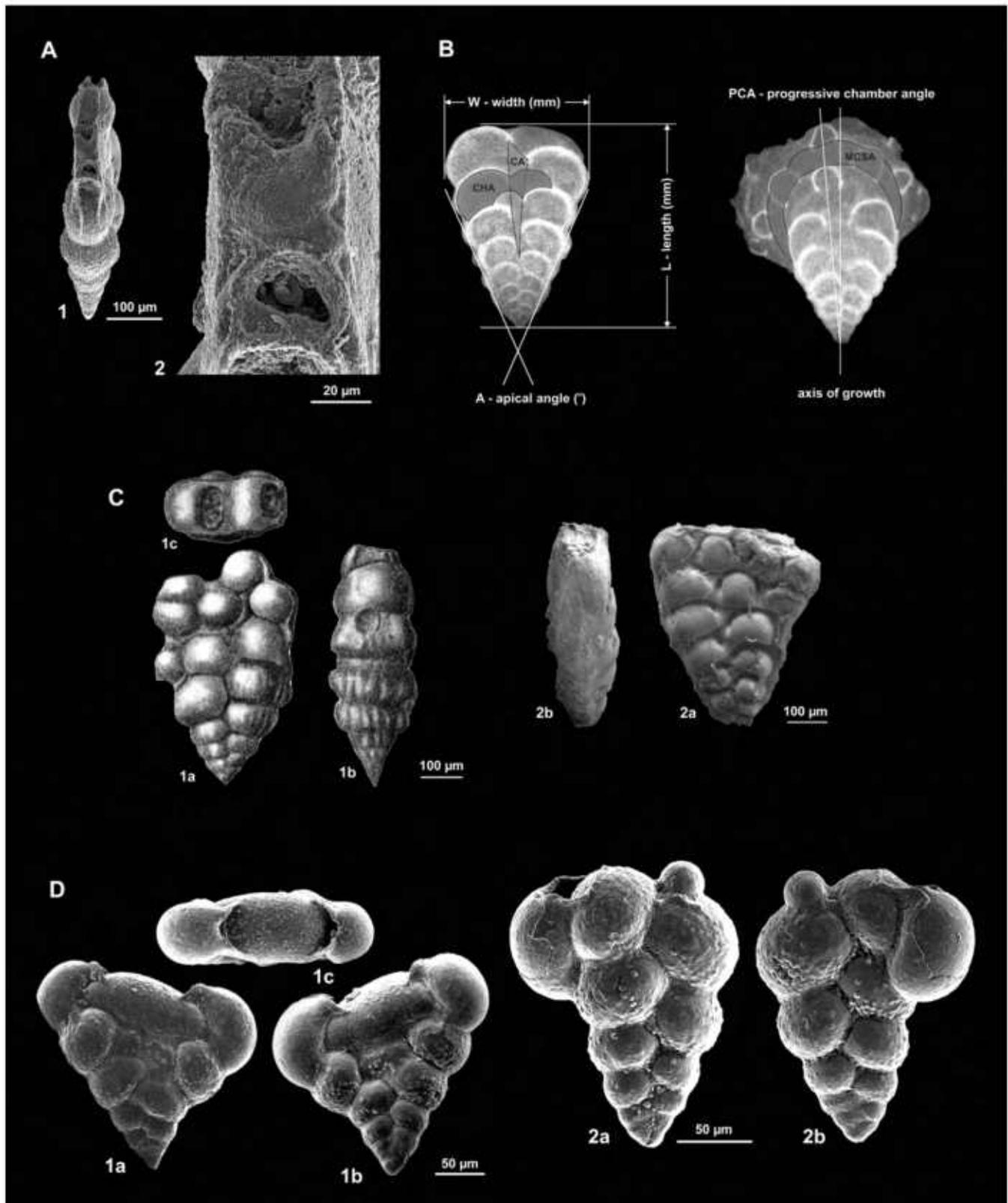
1 Holotype of *Ventilabrella ornatissima* figured by Cushman and Church (1929, pl. 39, figs. 12-14) from the Upper Cretaceous of San Joaquin Valley (California).

2 Paratype of *Ventilabrella ornatissima* deposited at the National Museum of Natural History, Washington D.C. (Cushman Collection 10038).

PART D. *Laeviheterohelix reniformis* (Marie 1941) from Campanian sediments of the Falkland Plateau, DSDP Site 511.

1 Hypotype from the upper lower Campanian (*Archaeoglobigerina cretacea* Biozone), Sample 511-32-CC.

2 Hypotype from the lowermost Campanian (uppermost part of the *Archaeoglobigerina cretacea* Biozone), Sample 511-36-4, 23-27cm. Planktonic foraminiferal zonation after Huber and others (1995).



progressive chamber and that of the earlier stage. Additional incomplete multiserial chamber sets occasionally occur. The lateral chambers of the multiserial chamber sets are mono-aperturate and those of the central part biaperturate. Test surface is ornamented with coarse, irregular areas that can be nodular in appearance or with vestiges of coarse costae and are usually present on the earlier chamber surfaces of the test due to the addition of successive layers of calcite (pl. 5, figs. 6a, 7a, 8a, 9a, 10a, 11a, pl. 6, figs. 7-9). They are absent in the central part of the test as seen in lateral view, but those of the same chamber are connected across the periphery by transverse keels (pl. 5, figs. 6b, 7b, 9b, 10b). Ornamentation in the suture areas is strongly reduced, resulting in a smooth appearance (pl. 6, figs. 7-9). The surface of the multiserial test presents very low costae, ranging in thickness from 2.8 to 3.6µm. Test wall is microporulate with pore size ranging between 0.7 and 0.9µm. The pores are situated between the ornamentation structures.

Remarks. *Gublerina cuvillieri* differs from *G. rajagopalani* by (i) the presence of a proliferating chamber stage later in ontogeny, (ii) a wider nonseptate central area, (iii) ornamentation concentrated over the chambers and extending to the periphery of the test (giving the appearance of prominent shoulders on the earlier formed chambers) while absent over the zigzag suture in the central part of the test, (iv) having more chambers in the biserial part of the test, and (v) lacking coarse peripheral costae. *Gublerina cuvillieri* differs from *Praegublerina acuta* by (i) a chamber proliferation stage in which the progressive chamber is followed by four rather than two chambers, (ii) multiserial chambers that are variable in shape rather than elongate, (iii) test ornamentation consisting of strongly ornamented areas concentrated over the chambers, rather than five quasi-longitudinal bands of alternating costate and reticulate ornamentation, (iv) absence of reticulate ornamentation over the test surface, (v) having more chambers in the biserial part of the test, and (vi) a wider central area. *Gublerina cuvillieri* differs from *Prae-*

gublerina robusta in (i) chamber proliferation pattern (the number of chambers in the multiserial sets increase by three in the former and by one in the latter species), (ii) test ornamentation, which is concentrated over the chambers, with the remaining part of the test smooth or finely costate in *G. cuvillieri* and costate to reticulate in *P. robusta* and (iii) complete absence of transverse walls.

Phylogenetic relationships. *Gublerina cuvillieri* is the only descendant of *G. rajagopalani*. This phylogenetic relationship is demonstrated by the gradual development of the central area and the occurrences of specimens with intermediate test ornamentation, which present both transverse keels and coarse longitudinal costae over the periphery. Chamber growth rate in the biserial stage of *Gublerina cuvillieri* is similar to that of *G. rajagopalani*. The two species differ in the late stage of ontogeny with development of multiserial chamber growth (text-figure 7). The ontogenetic development of the central nonseptate area shows increased rates in *Gublerina cuvillieri* when compared to its ancestor, *G. rajagopalani*.

Stratigraphic range. Upper Maastrichtian [from the upper part of the *Gansserina gansseri* Biozone (122-761B-24X-4, 104-105cm) to the uppermost part of the *Abathomphalus mayaroensis* Biozone (122-761B-22X-4, 75-76cm)].

Geographic distribution. Europe (southern France, southern Germany, Austria, Slovakia, Romania) and Indian Ocean (Exmouth Plateau).

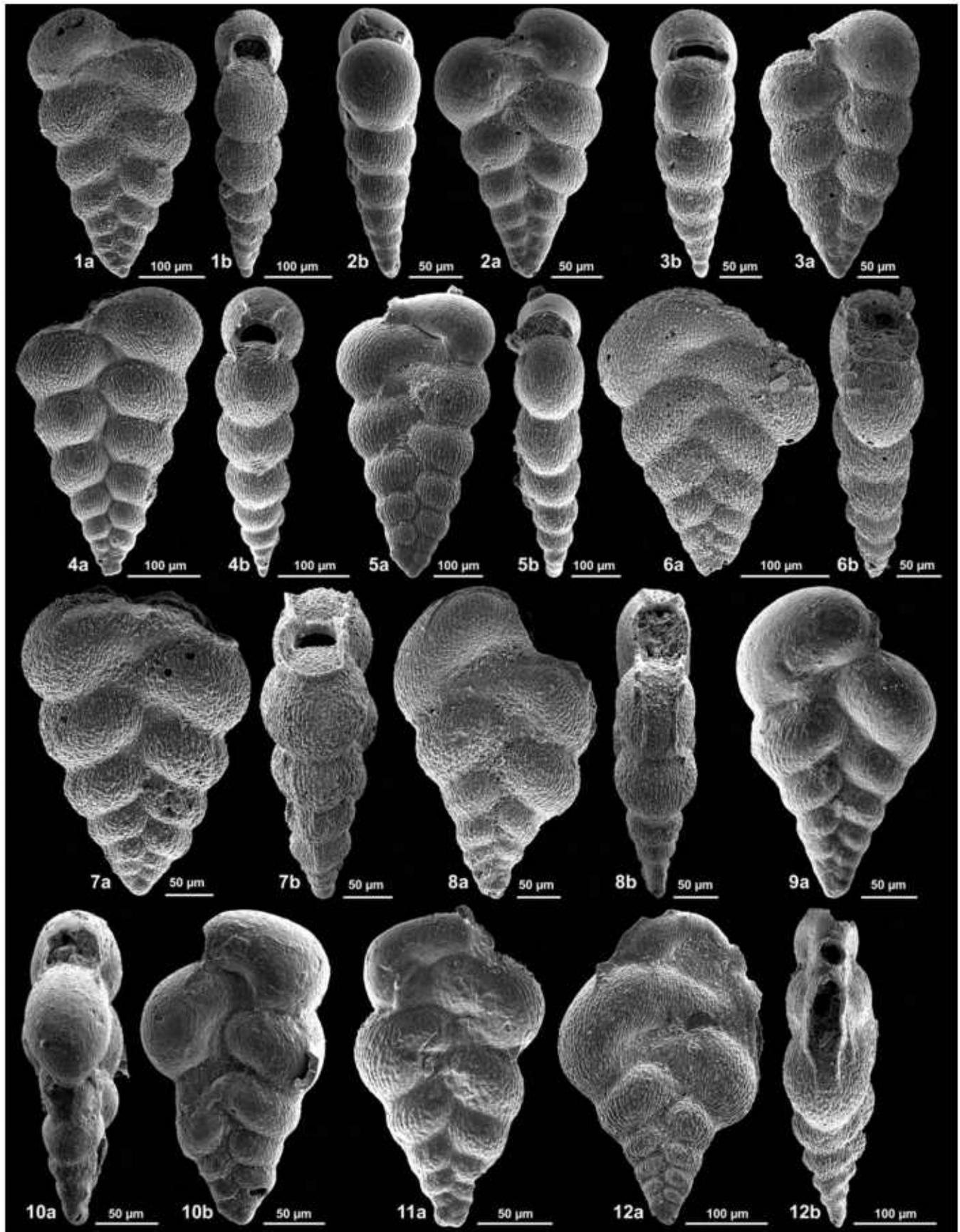
DEPTH ECOLOGY OF GUBLERINA CUVILLIERI AND G. RAJAGOPALANI

Depth habitats of planktonic foraminifera can be inferred by comparing interspecies differences in carbon and oxygen isotope values among taxa from the same sample (text-figure 9; Table 1). Because the $\delta^{18}\text{O}$ of calcite precipitated in equilibrium with ambient seawater is temperature dependent, and temperature most

PLATE 3

Hypotypes of *Heterohelix planata* (Cushman 1938) and *Praegublerina pseudotessera* (Cushman 1938).

- | | |
|---|--|
| <p>1 <i>Heterohelix planata</i> from the upper Maastrichtian (<i>Abathomphalus mayaroensis</i> Biozone) of the Maud Rise, Sample 1 13-690C-16-1, 42-44cm.</p> <p>2 <i>Heterohelix planata</i> from the upper Santonian (<i>Globotruncana arca</i> Biozone) of the New Jersey coastal plain, Sample 174AX, 505.35-.38m.</p> <p>3-4 <i>Heterohelix planata</i> from the lower Maastrichtian (<i>Globotruncanella havanensis</i> Biozone) of the Maud Rise, Sample 1 13-690C-20-7, 24-25cm.</p> <p>5 <i>Heterohelix planata</i> from the lower Campanian (<i>Archaeoglobigerina cretacea</i> Biozone) of the Falkland Plateau, Sample 79-511-31-5, 33-35cm.</p> <p>6-7 <i>Praegublerina pseudotessera</i> from the Maastrichtian (<i>Abathomphalus mayaroensis</i> Biozone) sediments of</p> | <p>the Orphan Knoll (North Atlantic), Sample 12-11 1A-1 1-6, 7 1-85cm.</p> <p>8 <i>P. pseudotessera</i> from the upper Campanian (<i>Radotruncana calcarata</i> Biozone) from a well in the Gulf of Mexico for which no precise location can be given; Van Morkhoven Collection.</p> <p>9-11 <i>P. pseudotessera</i> from the Upper Taylor Marl, Onion Creek, Travis County, Texas; specimens from the Loeblich and Tappan Topotype Collection, USNM 478612; slide labeled as <i>Spiroplecta pseudotessera</i> (Cushman), HT & ARL sample #603 2.</p> <p>12 Specimen with intermediate morphological features between <i>Praegublerina pseudotessera</i> and <i>P. acuta</i>; specimen from a well from the Gulf of Mexico for which no precise location can be given; Van Morkhoven Collection.</p> |
|---|--|



commonly decreases with depth from the ocean surface to the seafloor, modern deeper dwelling planktonic foraminifera have higher $\delta^{18}\text{O}$ values than surface dwelling taxa (e.g., Emiliani 1954; Shackleton and Vincent 1978; Fairbanks et al. 1980). Preferential fixing of ^{12}C during photosynthesis in the euphotic zone and remineralization of this isotopically light carbon at depth results in decreasing $\delta^{13}\text{C}$ values from the surface mixed layer to the seafloor. Thus, consistent $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ offsets among fossil taxa assemblage can be used to infer relative depth habitats.

Problems associated with using stable isotopes to estimate the ecology of planktonic foraminifera have been reviewed by several authors (Wefer and Berger 1991; D'Hondt and Arthur 1995; Spero et al. 1997; Zeebe 1999). Our depth ecology interpretations assume: (1) no kinetic effects of varying calcification rates; (2) no depth migration through ontogeny; (3) population abundance maxima may have differed between the different taxa (4) algal symbionts were absent; (5) a small measurement error ($\sim 0.1\%$); and (6) minimal diagenetic artifacts.

Our results show that the *G. rajagopalani* and *G. cuvillieri* $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures are nearly indistinguishable from each other and they consistently plot more negative in $\delta^{13}\text{C}$ and more positive in $\delta^{18}\text{O}$ than co-occurring specimens of *Rugoglobigerina pennyi*. Both *Gublerina* species are about 0.5‰ more enriched in $\delta^{18}\text{O}$ than co-occurring *A. mayaroensis*. As expected, the benthic foraminifer *Gyroidina globosa* consistently plots with the most negative $\delta^{13}\text{C}$ and the most positive $\delta^{18}\text{O}$ of the foraminifera analyzed.

These data indicate that the evolution of *G. cuvillieri* from *G. rajagopalani* did not result from a change in its depth ecology. Both species probably lived near the thermocline and/or they were most abundant in the mixed layer during a cooler growing season than *R. pennyi* and *A. mayaroensis*.

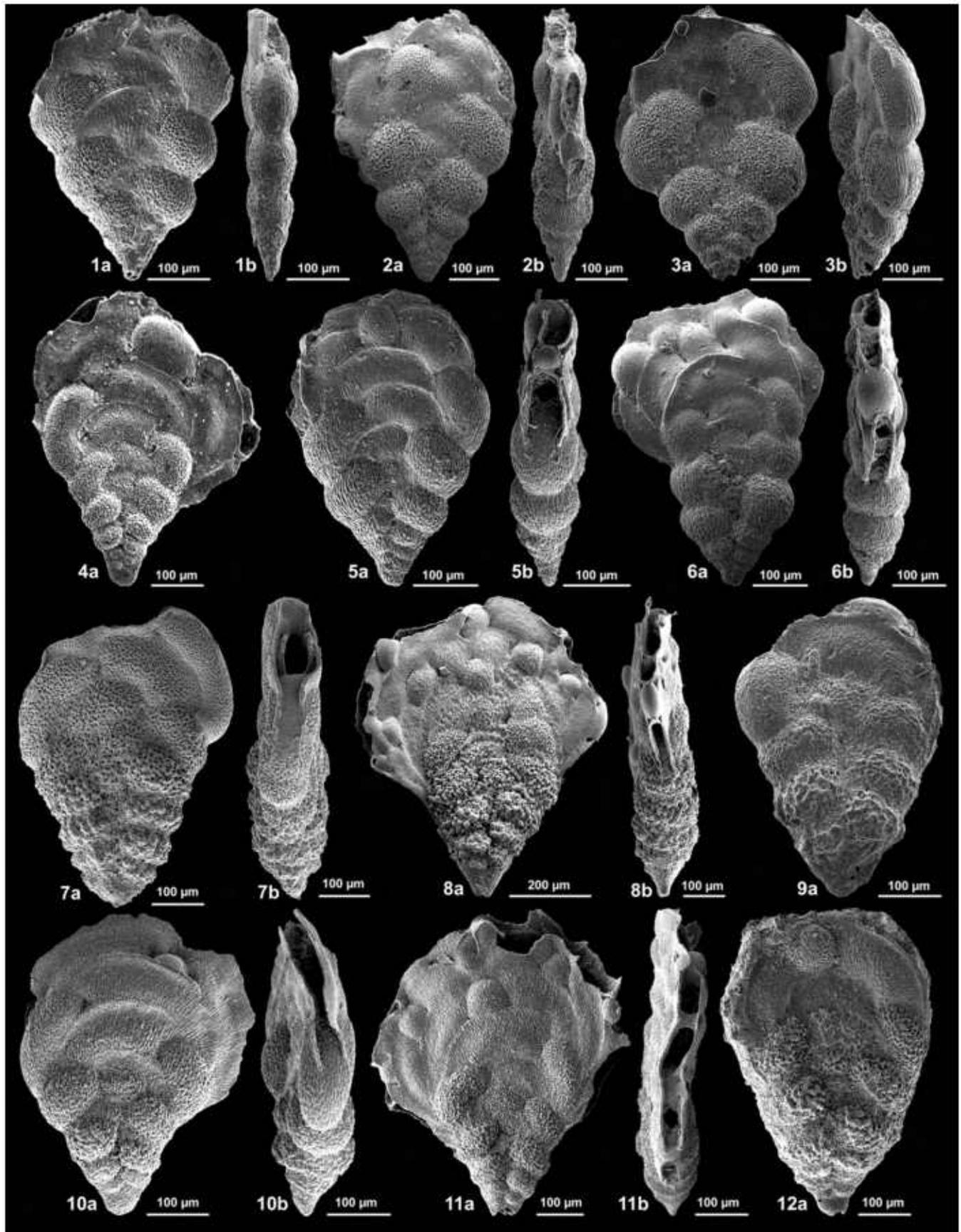
DISCUSSION AND CONCLUSIONS

The detailed morphological, morphometric and biostratigraphic study of gublerinid taxa shows that the group commenced its evolution in the lower Campanian *Globotruncanita elevata* Biozone (text-figure 10). The first representative of the group is *Praegublerina pseudotessera*. The development of a central nonseptate area between the last-formed one to three pairs of biserial chambers is a key feature for this species. This species evolved from *Heterohelix planata*. Both species are finely costate throughout and do not present chamber proliferation in the adult portion of the test. There is an evolutionary continuum between *P. pseudotessera* and *H. planata*; “evolved” tests of *Heterohelix planata* may present a poorly developed central area between the last-formed two chambers. Conversely, rare “primitive” tests of *Praegublerina pseudotessera* may lack this feature, but they are still included in this species due to the well-developed periapertural flanges and thicker costae when compared to those of the ancestor, *Heterohelix planata*. In addition to characteristics of the central area between the last-formed pair of chambers, the transition from *Heterohelix* to *Praegublerina* is marked by an increase in the costae thickness from 1-8 to 2.5 μm in *H. planata* to 2.5 to 4.0 μm in *P. pseudotessera*. Although the two species were considered synonyms by Nederbragt (1991), our study shows they are differ-

PLATE 4

Hypotypes of *Praegublerina acuta* (de Klasz 1953) and *P. robusta* (de Klasz 1953).

- 1 *Praegublerina acuta* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Blake Plateau (western North Atlantic), Sample 171B-1050C-13-6, 110-114cm.
- 2 *P. acuta* from the late Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Orphan Knoll (North Atlantic), Sample 12-11 1A-1 1-2, 5-19cm.
- 3 *P. acuta* from the upper Maastrichtian (*Pseudoguembelina hariaensis* Biozone) of the Blake Plateau (western North Atlantic), Sample 171B-1050C-1 1-1, 127-130cm.
- 4 *P. acuta* from the upper Maastrichtian (*Pseudoguembelina hariaensis* Biozone) of the Shatsky Rise (equatorial Pacific), Sample 198-1212B-13-7, 50-52cm; the specimen was made available to us by Dr. S. Abramovich (Ben Gurion University of the Negev).
- 5-6 Costate throughout specimens *P. robusta* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Orphan Knoll (North Atlantic), Samples 12-11 1A-1 1-4, 124-128cm and 12-11 1A-1 1-2, 5-19cm respectively.
- 7 Reticulate throughout specimen of *P. robusta* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Shatsky Rise (equatorial Pacific), Sample 305-16-5, 60-76cm.
- 8 Specimen of *P. robusta* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Grand Banks (North Atlantic), sample 43-384-13-5, 66-68cm.
- 9,12 *P. robusta* from the upper Maastrichtian (*Pseudoguembelina hariaensis* Biozone) of the Blake Plateau (western North Atlantic), Samples 171B-1050C-1 1-1, 127-130cm and 171B-1050C-13-6, 110-114cm respectively.
- 10-11 Specimens of *P. robusta* with incipient reticulate ornamentation from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Shatsky Rise (equatorial Pacific), Sample 32-305-16-5, 60-76cm.



ent, which is supported by their morphology, ontogenetic morphometry and distinct stratigraphic ranges.

Praegublerina pseudotessera is the oldest species of the gublerinid stock. Two evolutionary trends can be recognized in the history of this species. The first trend is represented by the continuing evolution of the finely costate tests within the genus *Praegublerina*, leading to the development of tests with chamber proliferation in the adult stage and with either costate or reticulate ornamentation or a combination of the two. The other trend corresponds to the genus *Gublerina* and is defined by the coarsening of the test ornamentation followed by the development of multiserial chamber growth.

Reticulate ornamentation and multiserial chamber growth developed in *Praegublerina acuta* and *P. robusta*. Both species first occurred in the late Campanian (*Radotruncana calcarata* Biozone). *Praegublerina robusta* presents costate or reticulate ornamentation. However, the earlier tests are costate throughout and the latest ones are dominantly reticulate; specimens with mixed ornamentation patterns have also been recorded. There is also a latitudinal zonation, with the reticulate representatives of *P. robusta* throughout the paleo-tropics and dominantly costate in the temperate latitudes. The reticulate and costate ornamentation patterns occur on the same specimens in *Praegublerina acuta*, the former pattern being present over the chambers and the latter on the flanges and in the peripheral regions. The multiserial chamber stage differs in the two species. The progressive chamber is followed by one multiserial set consisting of two chambers in *Praegublerina acuta* and by a maximum of three sets with the number of chambers gradually increasing by one in *P. robusta*. Biaperturate transverse walls are present only in *Praegublerina robusta*.

Test ornamentation is of paramount importance in defining the genus *Gublerina* due to the major change from finely costate to coarsely costate in the *Praegublerina pseudotessera*-*Gublerina rajagopalani* lineage. The coarse test ornamentation that forms

pseudo-keels on the earlier portion of the test periphery is developed in parallel with a slight increase in the nonseptate central area in *Gublerina rajagopalani* when compared with the *Praegublerina pseudotessera* ancestor. *Gublerina cuvillieri* is the only species of the genus with a proliferating chamber stage later in ontogeny. The progressive chamber is followed by a maximum of three multiserial chamber sets in which the number of chambers increases by three. No transverse walls are present in *Gublerina*.

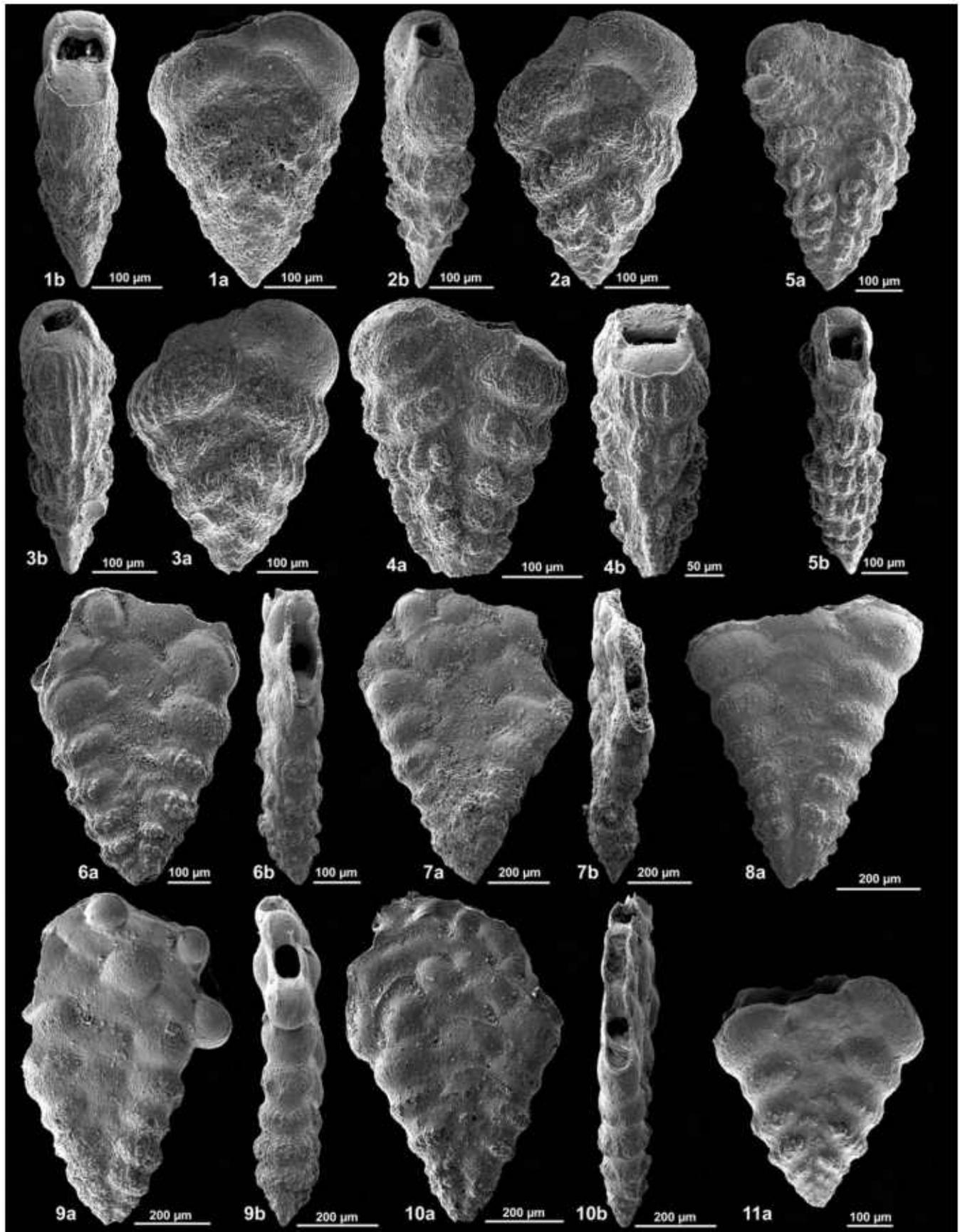
The total number of chambers can be calculated in different ways for the completely biserial species and those with multiserial growth. The number of chambers in the biserial stage is reduced with the emergence of *Praegublerina*, from 14 to 17 in *Heterohelix planata* to 12 to 14 in *P. pseudotessera*. Divergent evolution is recorded in the proliferating species of *Praegublerina*: continuing reduction to 11 to 13 in *P. acuta*, and increase to 13 to 17 in *P. robusta*. The increase in the number of chambers of the biserial stage is continuous in the *P. pseudotessera*-*Gublerina rajagopalani*-*G. cuvillieri* and at much higher rate than in *P. pseudotessera*-*P. robusta* lineage. The number of chambers in the multiserial stage differs in *Praegublerina acuta*, *P. robusta* and *Gublerina cuvillieri* and can be calculated by different formulas (text-figure 11).

Another feature with insufficiently understood significance in depicting the evolutionary patterns in the gublerinid serial planktonic foraminifera is the apical angle (Table 2). We observed an increase in the apical angle with the transition from *Heterohelix* to *Praegublerina*, from 40 to 54° in *H. planata* to 52-65° in *P. pseudotessera*. The feature shows little change in the *Praegublerina pseudotessera*-*P. acuta* lineage and increases to 57-73° in *P. robusta*. The difference in apical angles further supports *Praegublerina acuta* and *P. robusta* as distinct species. A different pattern in the evolution of the apical angle is recorded in the *Praegublerina pseudotessera*-*Gublerina rajagopalani*-*G. cuvillieri* lineage. The end species of this lin-

PLATE 5

Hypotypes of *Gublerina rajagopalani* Govindan 1972 and *G. cuvillieri* Kikoïne 1948.

- 1 *Gublerina rajagopalani* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Exmouth Plateau (Indian Ocean), Sample 122-761B-24-1, 8.9-9.0cm.
- 2 *G. rajagopalani* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the São Paulo Plateau (southern Atlantic), Sample 39-356-29-6, 11-25cm.
- 3 *G. rajagopalani* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the São Paulo Plateau, Sample 39-356-29-6, 11-25cm.
- 4 *G. rajagopalani* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Exmouth Plateau (Indian Ocean), Sample 122-761B-24-1, 25-26cm.
- 5 Specimen with intermediate features between *Gublerina rajagopalani* and *G. cuvillieri* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Exmouth Plateau (Indian Ocean), Sample 122-761B-24-1, 76-77cm.
- 6-11 *Gublerina cuvillieri* from the upper Maastrichtian (*Abathomphalus mayaroensis* Biozone) of the Exmouth Plateau (Indian Ocean): 6-Sample 122-761B-24-3, 28-29cm; 7-Sample 122-761B-23-1, 75-76cm; 8-Sample 122-761B-24-2, 25-26cm; 9-Sample 122-761B-22-4, 75-76cm; 10-Sample 122-761B-24-1, 111-112cm; 11-Sample 122-761B-24-1, 25-26cm.



eage presents lower apical angle values of 49-57°. The angle measurements present, however, wide ranges of variability.

Praegublerina and *Gublerina* present different patterns of paleobiogeographical distributions. *Praegublerina*, which is the oldest gublerinid genus, evolved from the cosmopolitan species *Heterohelix planata*. *Praegublerina pseudotessera* is restricted to the Atlantic Ocean and western Tethyan Realm. The two species with chamber proliferation, *Praegublerina acuta* and *P. robusta*, are cosmopolitan. In contrast, none of the *Gublerina* species are cosmopolitan, with *G. rajagopalani* being recorded in the Southern Hemisphere and Western Tethys, but absent in the Blake Plateau sites despite the tropical waters and open ocean conditions. *Gublerina cuvillieri* appears restricted to the Tethyan and Transitional Realms (text-figure 12).

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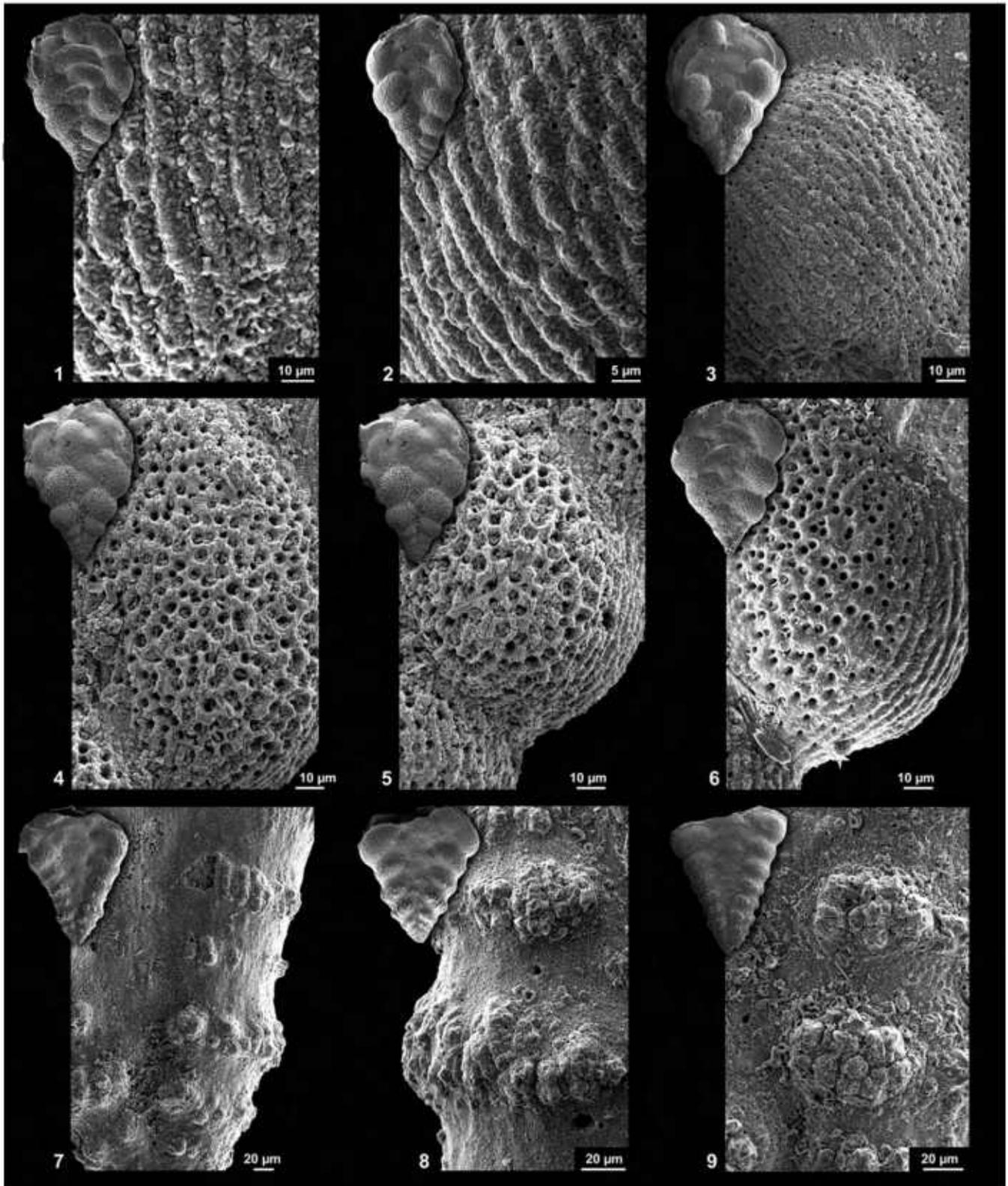
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PLATE 6

Details of the test ornamentation of the species of *Praegublerina* nov. gen. and *Gublerina* Kikoïne 1948 with multiseriate chamber growth.

- 1-3 Costate test variety of *Praegublerina robusta* (de Klasz 1953); 1-Sample 12-11 1A-11-4, 124-128cm, 2-Sample 12-11 1A-11-2, 5-19cm, 3-Sample 12-11 1A-1 1-4, 124-128cm.
- 4-6 *Praegublerina acuta* (de Klasz 1953); 4 and 5-Sample 12-11 1A-11-2, 5-19cm, 6-Sample 171B-1050C-

13-6, 110-114cm; note the incipiently reticulate ornamentation over the chamber surface and costate pattern at the periphery. 7-9 *Gublerina cuvillieri* Kikoïne 1948; 7 and 8-Sample 122-761B-24-2, 25-26cm, 9-Sample 171B-1050C-13-6, 110-114cm; note the coarse ornamentation over the chambers and the smooth test surface over the sutures.



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APPENDIX 1

The taxonomic status of *Ventilabrella reniformis* Marie 1941

Ventilabrella reniformis is a poorly documented species that was considered valid only in the taxonomic revisions of Brown (1969) and Masters (1977). Notably, no additional specimens other than the holotype have been figured in the past. The species was interpreted as having reniform chambers that increase rapidly in size in the adult part of the test. Its ornamentation was unknown, the species being described as finely striate but no ornamentation pattern is apparent in the original figuration (Marie 1941, pl. 28, figs. 277).

Examination of the holotype figures (Marie 1941, pl. 28, figs. 277) shows the chambers of the divergent biserial rows are globular and only those in the adult stage are reniform in shape. Similar specimens are now reported from the Campanian sediments of the Falkland Plateau, DSDP Site 511. The chamber surface is ornamented with pore mounds (pl. 2, figs. D1-2) similar to those known from the genus *Laeviheterohelix*. The poorly developed multiserial adult stage consists of one row of three chambers. As shown in this study, the presence of multiserial growth in the adult portion of the test is not a feature that can be consistently used at generic level, chamber proliferation being developed within different lineages that initiated with species bearing chambers that are biserially arranged throughout. Accordingly, *Ventilabrella reniformis* is assigned to the genus *Laeviheterohelix*.

APPENDIX 2

The taxonomic status of *Ventilabrella ornatissima* Cushman and Church 1929

The taxonomic status of the species *Ventilabrella ornatissima* Cushman and Church 1929 should be evaluated since it was considered a senior synonym of *Gublerina cuvillieri* Kikoïne 1948 by some authors such as Montanaro Gallitelli (1957, p.140), Loeblich and Tappan (1964, p.C654), and Loeblich and Tappan (1988, p.456).

In the original description of *Ventilabrella ornatissima*, Cushman and Church (1929, p.512) stated that it presents "...all chambers in one plane, subglobular, the early ones biserial, later ones spreading out irregularly...". Such a peculiar chamber arrangement in the adult proliferating stage is not known in any other Late Cretaceous serial planktonic foraminiferal species. It was noted by Douglas (1969, p. 160) and Brown (1969, p. 59) that this species lacks the divergent rows of biserially arranged chambers in the earlier part of the test. Thus, *Ventilabrella ornatissima* and *Gublerina cuvillieri* are two distinct species which are not even congeneric.

It was claimed in the original description of *Ventilabrella ornatissima* that the chambers of the adult stage are irregularly arranged. As the holotype is probably lost, the only primary type specimen available is a paratype from the Cushman Collection (NMNH), namely no. 10038, which was figured by Montanaro Gallitelli (1957, pl. 32, fig. 6). The SEM photographs of this specimen show that it is an internal mold with rather poor pres-

ervation (pl. 2, fig. 2). The multiserial stage consists of additional chambers that are added between the two rows of divergent chambers of the earlier biserial part of the test. Such chamber arrangement is not known in any gublerinid test. From this point of view, our observations are convergent with that of Douglas (1969) and Brown (1969) in that *Ventilabrella ornatissima* is quite different from *Gublerina cuvillieri*, even at generic level. Therefore, the two species cannot be synonymized.

A species in our material that presents similar chamber proliferation between the two rows of divergent chambers is *Pseudo-*

guembelina hariaensis Nederbragt 1991. However, the ornamentation of this species sharply differs from that of *Ventilabrella ornatissima*. The figured specimens by Cushman and Church (1929, pl. 39, figs.12-15) show rather coarse costae mainly on the earlier part of the test, whereas in *P. hariaensis* the test ornamentation is uniformly developed over the entire test surface. Accordingly, *Ventilabrella ornatissima* is here considered different from *Gublerina*. A possible synonymy between *P. hariaensis* and *V. ornatissima* must be better documented. Specimens assigned to *Planoglobulina ornatissima* by Douglas (1969, pl.1 1, figs.1-2) are here considered as *Planoglobulina acervulinoides* (Egger 1899).