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**MORPHOSTATISTICAL ANALYSIS OF MAASTRICHTIAN POPULATIONS OF *GUEMBELITRIA* FROM EL KEF, TUNISIA**

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# MORPHOSTATISTICAL ANALYSIS OF MAASTRICHTIAN POPULATIONS OF *GUEMBELITRIA* FROM EL KEF, TUNISIA

José A. Arz[1,3], Ignacio Arenillas[1] and Carolina Náñez[2]

## ABSTRACT

Three species of *Guembelitria* with regular triserial arrangement are recognized in the late Maastrichtian, based on biometric measures of specimens from El Kef (Tunisia) and morphostatistical analysis. They are mainly recognized based on their test height and rate of increase in size of the chambers. *Guembelitria blowi*, nov. sp. is proposed for the short-spired morphotypes that were previously ascribed to *Guembelitria trifolia*. *Guembelitria cretacea* Cushman, 1933, is restricted to medium-spired morphotypes, and *Guembelitria dammula* Voloshina, 1961, to high-spired morphotypes. The three morphospecies have a papillate test surface, usually with pore-mounds, but some specimens exhibit imperforate papillae. The origin of this variability in the guembelitrid test surface might be linked to ecophenotypy or ontogeny, but the presence of cryptic species cannot be ruled out.

## INTRODUCTION

The genus *Guembelitria* Cushman, 1933, comprises opportunist Aptian–Danian planktonic species that mainly had a shallow, neritic habitat (e.g., Smith and Pessagno, 1973; Kroon and Nederbragt, 1990; D'Hondt, 1991; Koutsoukos, 1994; Olsson and others, 1999). It is the emblematic survivor of the Cretaceous-Paleogene (K-Pg) extinction, and might constitute the bulk of planktic foraminiferal assemblages in the earliest Danian (Smit, 1982, among others).

*Guembelitria* was defined by Cushman (1933) to group triserial planktic foraminifera. Later, it was established that the test of *Guembelitria* s.s. is microperforate and with pore-mounds, i.e., mounds marked by one or more pores (see Loeblich and Tappan, 1987). Debatable is the number of species that lived during the Maastrichtian–Danian transition. Several *Guembelitria* species have been included, such as *G. cretacea* Cushman, 1933, *G. dammula* Voloshina, 1961, *G. trifolia* (sensu Blow, 1979), *Chiloguembelitria danica* Hofker, 1978, *G. irregularis* Morozova, 1961, *G. besbesi* Salaj, 1986, and *G. azzouzi* Salaj, 1986. Olsson and others (1999) consider all of them synonymous with *G. cretacea*, with the possible exception of *G. dammula*. Other taxonomists retain some of these names for morphospecies that occur in distinct populations, mainly *G. trifolia* (MacLeod, 1993; Arz and others, 2000), *G. dammula* (Abramovich and others, 2003; Pardo and Keller, 2008), *G. danica* (MacLeod, 1993; Arenillas and others, 2000a,b),

and *G. irregularis* (D'Hondt, 1991; Coccioni and Luciani, 2006).

Through biometric analysis, Arenillas and others (2007) delimited three *Guembelitria* morphospecies among regular triserial specimens in an El Kef Danian sample. These morphospecies were provisionally named *G.* cf. *trifolia*, *G. cretacea*, and *G. danica* for low-spired, medium-spired, and high-spired morphotypes, respectively. However, the morphological and microtextural variability of guembelitrids is greater in the early Danian than in the Maastrichtian (see Olsson and others, 1999, and Arenillas and others, 2007). After the K-Pg extinction, trochospiral and biserial guembelitrids, such as *Parvularugoglobigerina* Hofker, 1978 and *Woodringina* Loeblich and Tappan, 1957, diversified. In addition, three triserial taxa that first appear in the early Danian—*G. irregularis*, *G. besbesi*, and *G. azzouzi*—exhibit a wall surface different from that of the Maastrichtian guembelitrids (Hofker, 1978; Loeblich and Tappan, 1987; Coccioni and Luciani, 2006). Arenillas and others (2007) pointed out the possible existence of two cryptic species among Danian high-spired *Guembelitria*, both usually referred to *G. danica* but one exhibits pore-mounds (*G. danica* sensu MacLeod, 1993) and the other has imperforate papillae and rugosities (*Chiloguembelitria danica* sensu Hofker, 1978). Similarly, the morphospecies *G. irregularis* might have been a "wastebasket" taxon grouping earliest Danian cryptic species that have a smooth wall (Coccioni and Luciani, 2006) with those that have a rugose wall (Loeblich and Tappan, 1987), as well as both Maastrichtian and Danian aberrant pore-mounded forms with irregular chamber arrangement. The early Danian guembelitrids therefore require more profound research beyond the aim of this study. Nevertheless, morphologic diversity in Maastrichtian guembelitrids also seems to be greater than that believed by some authors who have assumed that *G. cretacea* is the only Maastrichtian guembelitrid.

In this study, we employ biometric measurements and morphostatistical analyses to delimit the number of *Guembelitria* species, or morphospecies, in the late Maastrichtian. We also analyze the wall microtexture of recognized morphospecies to determine the phenotypic plasticity of the wall surface, and possible cryptic or pseudocryptic species, among the Maastrichtian guembelitrids.

## MATERIAL AND METHODS

### MATERIAL

Samples from the upper Maastrichtian part of the section of the El Haria Formation at El Kef, central-northeastern Tunisia, were chosen for this study (Fig. 1). The El Haria Formation consists of marls and micritic limestones of late Maastrichtian–Paleocene age, lying between the Campanian–Maastrichtian Abiod Formation and the lower Eocene Jebel Madhkour Formation (Bourollet, 1967; Said,

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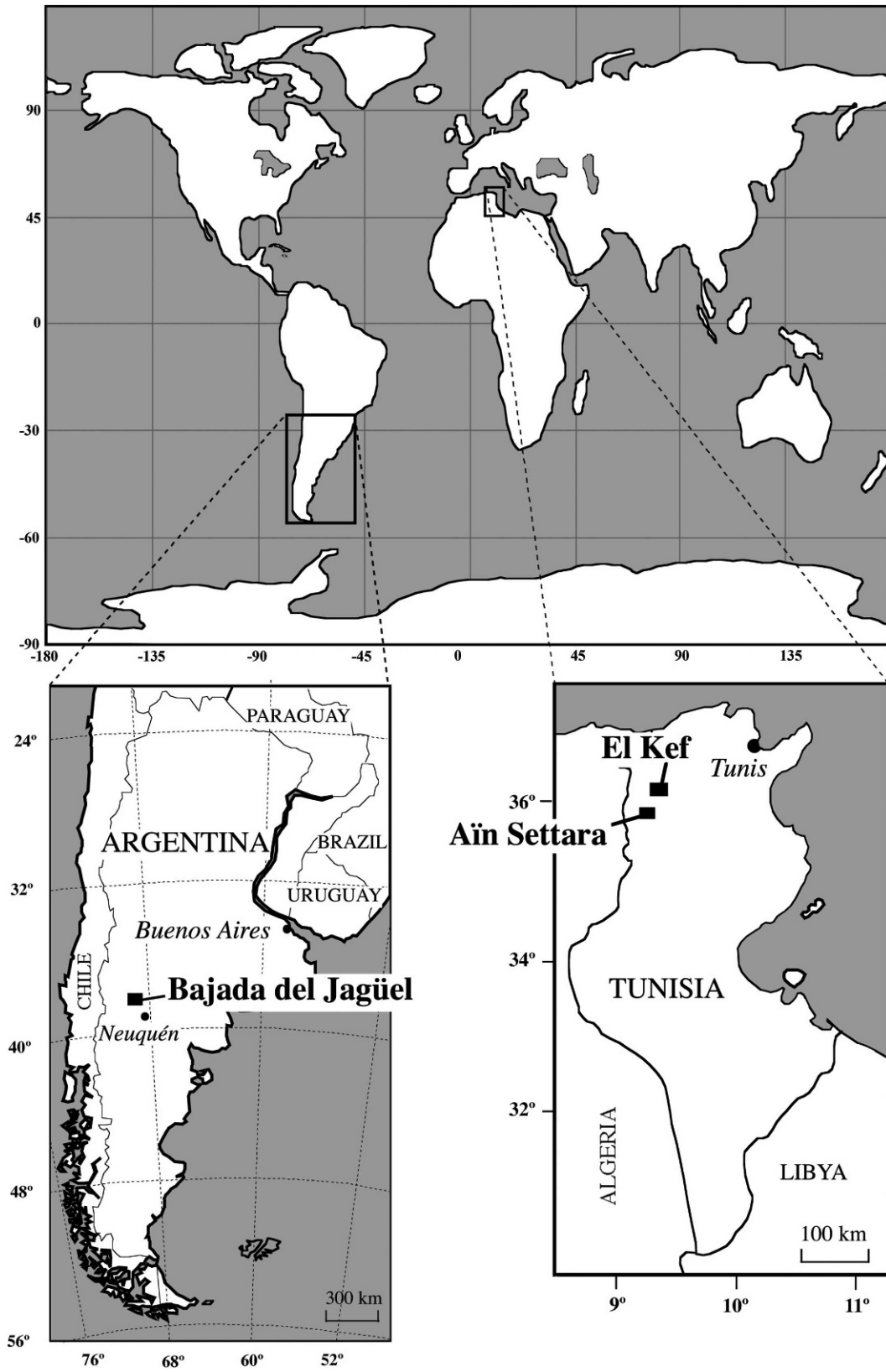[3] Correspondence author. E-mail: josearz@unizar.es

FIGURE 1.   Geographic locations of the El Kef and Aïn Settara sections (Tunisia), and the Bajada del Jagüel section (Argentina).

**Shell biometric parameters**

$L$ = length; $W$ = width;
$H$ = height; $SH$ = spiral height

**Chamber biometric parameters**
$CL$ = chamber length
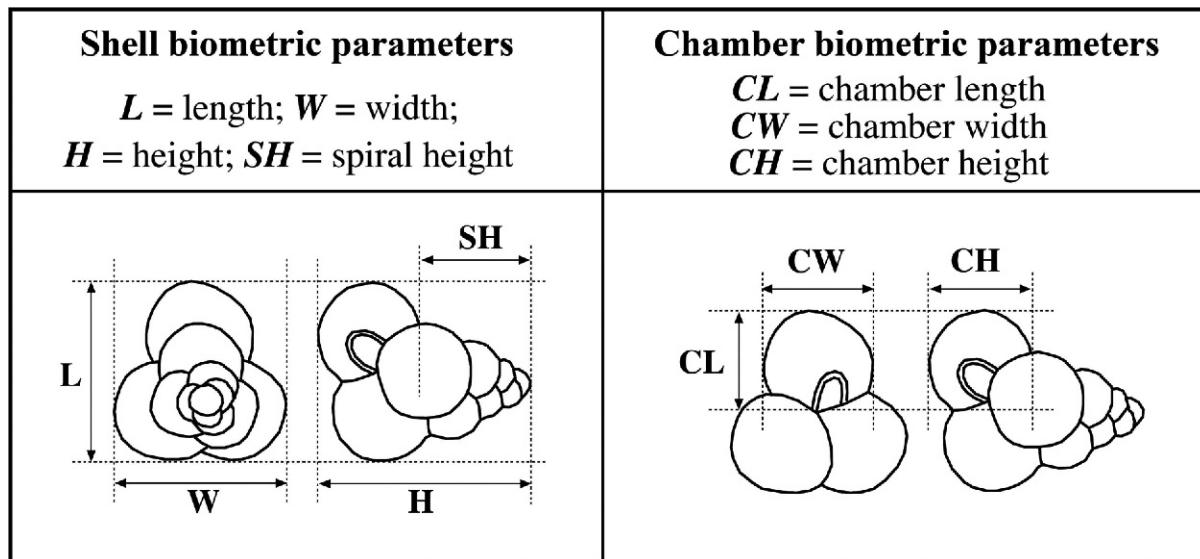$CW$ = chamber width
$CH$ = chamber height

FIGURE 2.    Biometric parameters, abbreviations, and descriptive terms used in biometric and morphologic analyses of guembelitrids.

1978). Benthic foraminifera reveal the El Kef section was deposited on the shelf and upper slope (see Peryt and others, 2002). In 1989, it was designated as the Global Boundary Stratotype Section and Point of the Cretaceous-Paleogene Boundary, primarily because of its stratigraphic continuity and high sedimentation rate (see Molina and others, 2006). Planktic foraminiferal biostratigraphic studies of El Kef section are numerous, including Smit (1982), Keller and others (1995), Li and Keller (1998), and Arenillas and others (2000a; 2004).

In addition some guembelitrid specimens from other localities and ages were shown in Figs. 8 and 9 to better reflect their paleogeographic and stratigraphic distribution. The most significant specimens shown are from the lowermost Danian part of the outer shelf to upper slope Aïn Settara section, Tunisia (Arenillas and others, 2000b; Peryt and others, 2002), and the upper Maastrichtian part of the inner to middle shelf Bajada del Jagüel section, Argentina (Náñez and others, 2002; Keller and others, 2007; Náñez, 2007).

METHODS

Rock samples were disaggregated in water with diluted $H_2O_2$, washed through a 63-μm sieve, then oven-dried at 50°C. Specimens were picked from the residues and selected for scanning electron microscopy using a JEOL JSM 6400 SEM at the Microscopy Service of the Universidad de Zaragoza (Spain), and a Philips 515 with EDAX Genesis digital imaging in the Microscopy Service of the Instituto de Investigaciones Científicas y Técnicas para la Defensa (CITEFA) (Argentina). Figured specimens are deposited in the Museo Paleontológico of the Universidad de Zaragoza (Aragon Government, Spain) and in the micropaleontological collection of the Servicio Geológico Minero Argentino (SEGEMAR, Buenos Aires, Argentina).

Seventy-five guembelitrid specimens from Maastrichtian sample KF-11, approximately 1 m below the K-Pg boundary in the El Kef section, were chosen for the morphostatistical analysis. Included were those with regular triserial arrangement belonging to the three early Danian morphotypes of *Guembelitria* recognized by Arenillas and others (2007). Multiserial and irregular specimens (assigned to *Guembelitriella postcretacea* by Pandey, 1981) were excluded from the analysis.

The biometric parameters used to delimit the *Guembelitria* species were length (L), width (W) and height (H) of the test, as well as the length (CL), width (CW) and height (CH) of the ultimate chamber (see Fig. 2). Four biometric indices were used: H/L, CAD/H, CH/H, and H/W, with the average chamber diameter CAD = $(CL \times CW \times CH)^{1/3}$ (Tables 1–3). The rate of chamber enlargement of each species also was evaluated by measuring the width of each chamber (CW) throughout their ontogeny (Table 4). Biometric measurements were made using a Zeiss SteREO Discovery V20 stereomicroscope equipt with 10× oculars and micrometer, and capable of 225× maximum magnification.

The morphostatistical study includes univariate, bivariate, and multivariate analysis. The results of the univariate analyses are displayed as histograms, using the H/L index because it is the most adequate to delimit the *Guembelitria* species (Fig. 3a). Several statistical tests (i.e., *t*-Student, Kolmogorov-Smirnov, Mann-Whitney, and ANOVA) have been applied in refuting or accepting the null hypotheses (i.e., two populations belong to the same species) by estimating the probability that the specimen population belongs to the same species. Our bivariate analyses are based on the two more adequate biometric indices: H/L index and CAD/H index (Fig. 3b). Their results are presented in scatter diagrams with 95% confidence ellipses that assume a bivariate normal distribution and convex hulls that are the smallest convex polygons containing all points.

Three types of multivariate analyses were used in this study: cluster analysis, principal component analysis (PCA), and multivariate analyses of variance (MANOVA). The R-mode cluster analyses were based on Euclidean distance measures among all specimens through the values of the four above-mentioned biometric indices in order to find groupings that might represent species (Fig. 4). The

TABLE 1. Biometric measurements (in microns) of late Maastrichtian middle-spired guembelitrid specimens (assigned to *Guembelitria cretacea* Cushman in this paper), and biometric indices H/L, CAD/H, CH/H and H/W (in percentage). Arithmetic means in bold type. The measures have been taken on 25 specimens of the stratigraphic horizon placed 1 m below the K-Pg boundary of El Kef (sample KF11). L, test length; W, test width; H, test height; CL, chamber length; CW, chamber width; CH, chamber height; CAD = $(CL \times CW \times CH)^{1/3}$.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Guembelitria cretacea* **Cushman 1933** | | | | | | | |
| Specimen | **L** | **W** | **H** | **CL** | **CW** | **CH** | **CAD** | **H/L** | **CAD/H** | **CH/H** | **H/W** |
| 1 | 109.7 | 87.1 | 134.3 | 56.0 | 66.0 | 62.8 | 61.5 | 122.4 | 45.8 | 46.8 | 154.2 |
| 2 | 100.9 | 77.5 | 119.7 | 56.1 | 64.9 | 56.0 | 58.9 | 118.6 | 49.2 | 46.8 | 154.5 |
| 3 | 98.5 | 85.8 | 117.8 | 50.8 | 62.9 | 51.6 | 54.8 | 119.6 | 46.5 | 43.8 | 137.3 |
| 4 | 89.7 | 81.9 | 111.5 | 51.7 | 58.5 | 45.8 | 51.7 | 124.3 | 46.4 | 41.1 | 136.1 |
| 5 | 97.5 | 82.8 | 113.2 | 50.7 | 60.9 | 49.9 | 53.6 | 116.1 | 47.4 | 44.1 | 136.7 |
| 6 | 79.5 | 72.6 | 98.8 | 46.6 | 52.7 | 39.7 | 46.0 | 124.3 | 46.6 | 40.2 | 136.1 |
| 7 | 90.5 | 74.7 | 110.8 | 50.3 | 64.0 | 55.2 | 56.2 | 122.4 | 50.7 | 49.8 | 148.3 |
| 8 | 89.4 | 69.8 | 109.0 | 48.7 | 63.7 | 51.9 | 54.4 | 121.9 | 49.9 | 47.6 | 156.2 |
| 9 | 101.3 | 80.4 | 120.0 | 51.9 | 64.9 | 57.7 | 57.9 | 118.5 | 48.3 | 48.1 | 149.3 |
| 10 | 99.4 | 89.3 | 122.6 | 50.3 | 63.3 | 56.0 | 56.3 | 123.3 | 45.9 | 45.7 | 137.3 |
| 11 | 95.8 | 75.0 | 116.7 | 47.1 | 66.6 | 49.6 | 53.8 | 121.8 | 46.1 | 42.5 | 155.6 |
| 12 | 94.2 | 79.6 | 113.7 | 50.3 | 64.0 | 61.7 | 58.3 | 120.7 | 51.3 | 54.3 | 142.8 |
| 13 | 107.0 | 97.5 | 127.0 | 61.7 | 68.2 | 55.2 | 61.5 | 118.7 | 48.4 | 43.5 | 130.3 |
| 14 | 97.0 | 85.4 | 113.7 | 61.6 | 60.1 | 47.9 | 56.2 | 117.2 | 49.4 | 42.1 | 133.1 |
| 15 | 99.9 | 89.9 | 115.3 | 50.3 | 62.5 | 51.8 | 54.6 | 115.4 | 47.4 | 44.9 | 128.3 |
| 16 | 99.4 | 79.3 | 118.6 | 65.0 | 64.1 | 47.1 | 58.1 | 119.3 | 49.0 | 39.7 | 149.6 |
| 17 | 91.0 | 73.1 | 110.5 | 47.1 | 56.9 | 50.3 | 51.3 | 121.4 | 46.4 | 45.5 | 151.2 |
| 18 | 93.9 | 77.1 | 113.7 | 51.2 | 58.5 | 48.7 | 52.6 | 121.1 | 46.3 | 42.8 | 147.5 |
| 19 | 101.5 | 86.0 | 121.9 | 51.2 | 71.3 | 61.7 | 60.8 | 120.1 | 49.9 | 50.6 | 141.7 |
| 20 | 100.8 | 87.4 | 118.6 | 55.2 | 69.0 | 58.5 | 60.6 | 117.7 | 51.1 | 49.3 | 135.7 |
| 21 | 89.4 | 71.4 | 105.6 | 48.7 | 55.2 | 46.3 | 49.9 | 118.1 | 47.3 | 43.8 | 147.9 |
| 22 | 95.7 | 73.2 | 112.1 | 50.3 | 59.3 | 51.9 | 53.7 | 117.1 | 47.9 | 46.3 | 153.1 |
| 23 | 103.4 | 87.0 | 125.3 | 55.3 | 65.8 | 60.3 | 60.3 | 121.2 | 48.1 | 48.1 | 144.0 |
| 24 | 104.5 | 97.5 | 128.7 | 54.2 | 69.0 | 65.0 | 62.4 | 123.2 | 48.5 | 50.5 | 132.0 |
| 25 | 122.7 | 100.0 | 147.0 | 64.4 | 67.4 | 72.3 | 68.0 | 119.8 | 46.2 | 49.2 | 147.0 |
| **Average** | **98.1** | **82.5** | **117.8** | **53.1** | **63.2** | **54.2** | **56.5** | **120.2** | **48.0** | **45.9** | **143.4** |

TABLE 2. Biometric measurements (in microns) of late Maastrichtian low-spired guembelitrid specimens (assigned to *Guembelitria blowi*, nov. sp. in this paper), and biometric indices H/L, CAD/H, CH/H and H/W (in percentage). Arithmetic means in bold type. The measures have been taken on 25 specimens of the stratigraphic horizon placed 1 m below the K-Pg boundary of El Kef (sample KF11). L, test length; W, test width; H, test height; CL, chamber length; CW, chamber width; CH, chamber height; CAD = $(CL \times CW \times CH)^{1/3}$.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Guembelitria blowi* **nov. sp.** | | | | | | | |
| Specimen | **L** | **W** | **H** | **CL** | **CW** | **CH** | **CAD** | **H/L** | **CAD/H** | **CH/H** | **H/W** |
| 1 | 124.0 | 85.8 | 111.8 | 65.6 | 77.7 | 63.9 | 68.8 | 90.2 | 61.5 | 57.2 | 130.3 |
| 2 | 101.1 | 81.0 | 104.7 | 56.8 | 72.2 | 56.2 | 61.3 | 103.6 | 58.6 | 53.7 | 129.3 |
| 3 | 116.0 | 93.2 | 116.5 | 61.1 | 74.3 | 59.2 | 64.5 | 100.4 | 55.4 | 50.8 | 125.0 |
| 4 | 117.7 | 91.3 | 119.7 | 69.0 | 77.8 | 64.9 | 70.4 | 101.7 | 58.8 | 54.2 | 131.1 |
| 5 | 113.4 | 86.0 | 108.4 | 69.3 | 76.2 | 61.5 | 68.7 | 95.6 | 63.4 | 56.7 | 126.0 |
| 6 | 102.4 | 77.1 | 98.1 | 53.4 | 70.3 | 57.8 | 60.1 | 95.8 | 61.3 | 58.9 | 127.2 |
| 7 | 84.8 | 73.7 | 89.5 | 49.8 | 64.0 | 57.3 | 56.7 | 105.5 | 63.4 | 64.0 | 121.4 |
| 8 | 112.3 | 89.4 | 115.3 | 64.9 | 78.7 | 66.8 | 69.9 | 102.7 | 60.6 | 57.9 | 129.0 |
| 9 | 105.8 | 89.6 | 110.7 | 57.9 | 66.5 | 63.3 | 62.5 | 104.6 | 56.4 | 57.2 | 123.5 |
| 10 | 109.6 | 79.3 | 101.5 | 60.9 | 65.8 | 62.5 | 63.0 | 92.6 | 62.1 | 61.6 | 128.0 |
| 11 | 119.9 | 94.6 | 122.6 | 65.0 | 81.2 | 74.7 | 73.3 | 102.3 | 59.8 | 60.9 | 129.6 |
| 12 | 118.6 | 88.7 | 115.3 | 66.6 | 69.8 | 66.6 | 67.7 | 97.2 | 58.7 | 57.8 | 130.0 |
| 13 | 86.8 | 82.7 | 92.0 | 47.7 | 56.9 | 52.8 | 52.3 | 106.0 | 56.9 | 57.4 | 111.2 |
| 14 | 143.8 | 103.1 | 142.9 | 82.8 | 96.8 | 82.8 | 87.2 | 99.4 | 61.0 | 57.9 | 138.6 |
| 15 | 104.3 | 82.8 | 106.4 | 61.7 | 67.4 | 64.1 | 64.4 | 102.0 | 60.5 | 60.2 | 128.5 |
| 16 | 127.7 | 83.7 | 104.4 | 61.7 | 67.5 | 63.3 | 64.1 | 81.8 | 61.4 | 60.6 | 124.7 |
| 17 | 120.3 | 99.9 | 114.6 | 65.0 | 86.9 | 68.2 | 72.8 | 95.3 | 63.5 | 59.5 | 114.7 |
| 18 | 102.7 | 95.0 | 109.4 | 58.5 | 69.1 | 66.6 | 64.6 | 106.5 | 59.0 | 60.9 | 115.2 |
| 19 | 113.7 | 80.6 | 104.8 | 61.7 | 65.0 | 66.7 | 64.4 | 92.2 | 61.5 | 63.6 | 130.0 |
| 20 | 102.1 | 82.1 | 105.2 | 58.5 | 66.5 | 64.9 | 63.2 | 103.0 | 60.1 | 61.7 | 128.1 |
| 21 | 98.2 | 81.2 | 100.7 | 54.4 | 67.3 | 67.4 | 62.7 | 102.5 | 62.3 | 66.9 | 124.0 |
| 22 | 91.8 | 78.5 | 95.0 | 53.3 | 63.8 | 64.6 | 60.3 | 103.5 | 63.5 | 68.0 | 121.0 |
| 23 | 105.6 | 80.2 | 103.2 | 58.7 | 73.6 | 62.3 | 64.6 | 97.7 | 62.6 | 60.4 | 128.7 |
| 24 | 122.7 | 88.2 | 113.7 | 68.3 | 72.9 | 79.6 | 73.5 | 92.7 | 64.6 | 70.0 | 128.9 |
| 25 | 113.7 | 87.7 | 110.5 | 60.1 | 68.8 | 65.3 | 64.6 | 97.2 | 58.5 | 59.1 | 126.0 |
| **Average** | **110.4** | **86.2** | **108.7** | **61.3** | **71.9** | **64.9** | **65.8** | **98.9** | **60.6** | **59.9** | **126.0** |

TABLE 3. Biometric measurements (in microns) of late Maastrichtian high-spired guembelitrid specimens (assigned to *Guembelitria dammula* Voloshina in this paper), and biometric indices H/L, CAD/H, CH/H, and H/W (in percentages). Arithmetic means in bold type. The measures have been taken on 25 specimens of the stratigraphic horizon placed 1 m below the K-Pg boundary of El Kef (sample KF11). L = test length, W = test width, H, test height, CL = chamber length, CW = chamber width, CH = chamber height, CAD = $(CL \times CW \times CH)^{1/3}$.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Guembelitria dammula* Voloshina, 1961 | | | | | | | | | | | |
| Specimen | L | W | H | CL | CW | CH | CAD | H/L | CAD/H | CH/H | H/W |
| 1 | 101.9 | 85.9 | 138.1 | 48.5 | 57.9 | 47.2 | 51.0 | 135.5 | 36.9 | 34.2 | 160.8 |
| 2 | 99.6 | 93.6 | 140.3 | 56.2 | 71.1 | 61.0 | 62.5 | 140.9 | 44.5 | 43.5 | 149.9 |
| 3 | 114.6 | 108.3 | 166.7 | 57.9 | 76.8 | 54.4 | 62.3 | 145.5 | 37.4 | 32.6 | 153.9 |
| 4 | 99.9 | 84.7 | 137.1 | 51.3 | 66.7 | 68.4 | 61.6 | 137.2 | 44.9 | 49.9 | 161.9 |
| 5 | 81.2 | 75.6 | 118.5 | 48.7 | 51.2 | 50.3 | 50.1 | 145.9 | 42.2 | 42.4 | 156.7 |
| 6 | 97.5 | 81.2 | 134.9 | 48.9 | 49.0 | 55.2 | 51.0 | 138.4 | 37.8 | 40.9 | 166.1 |
| 7 | 121.0 | 105.6 | 163.3 | 64.1 | 78.0 | 74.7 | 72.0 | 135.0 | 44.1 | 45.7 | 154.6 |
| 8 | 84.4 | 69.0 | 115.7 | 47.1 | 52.8 | 50.3 | 50.0 | 137.1 | 43.2 | 43.5 | 167.7 |
| 9 | 94.9 | 80.9 | 127.0 | 51.4 | 61.5 | 61.6 | 58.0 | 133.8 | 45.6 | 48.5 | 157.0 |
| 10 | 91.0 | 77.9 | 132.4 | 51.9 | 65.0 | 64.2 | 60.1 | 145.5 | 45.4 | 48.5 | 170.0 |
| 11 | 93.2 | 82.1 | 124.5 | 48.7 | 64.4 | 63.2 | 58.3 | 133.6 | 46.8 | 50.8 | 151.6 |
| 12 | 98.3 | 80.9 | 132.8 | 52.0 | 66.6 | 52.8 | 56.8 | 135.1 | 42.7 | 39.8 | 164.2 |
| 13 | 101.2 | 90.0 | 136.2 | 52.0 | 74.7 | 55.2 | 59.9 | 134.6 | 43.9 | 40.5 | 151.3 |
| 14 | 108.5 | 90.9 | 145.4 | 64.8 | 66.7 | 63.4 | 65.0 | 134.0 | 44.7 | 43.6 | 160.0 |
| 15 | 90.4 | 79.0 | 127.5 | 47.1 | 48.7 | 50.1 | 48.6 | 141.0 | 38.1 | 39.3 | 161.4 |
| 16 | 97.5 | 82.9 | 131.6 | 48.9 | 70.7 | 59.7 | 59.1 | 135.0 | 44.9 | 45.4 | 158.7 |
| 17 | 96.3 | 81.5 | 133.0 | 55.2 | 66.1 | 60.7 | 60.5 | 138.1 | 45.5 | 45.6 | 163.2 |
| 18 | 109.1 | 103.8 | 156.8 | 52.8 | 62.0 | 63.4 | 59.2 | 143.7 | 37.8 | 40.4 | 151.1 |
| 19 | 93.4 | 84.4 | 131.6 | 48.7 | 67.0 | 50.4 | 54.8 | 140.9 | 41.6 | 38.3 | 155.9 |
| 20 | 100.7 | 89.5 | 147.8 | 52.0 | 68.2 | 50.8 | 56.5 | 146.8 | 38.2 | 34.4 | 165.1 |
| 21 | 95.6 | 81.2 | 130.0 | 51.7 | 63.4 | 50.1 | 54.8 | 136.0 | 42.1 | 38.5 | 160.1 |
| 22 | 110.2 | 98.5 | 148.2 | 61.7 | 74.7 | 65.9 | 67.2 | 134.5 | 45.4 | 44.5 | 150.5 |
| 23 | 124.6 | 110.5 | 172.2 | 65.0 | 82.9 | 81.2 | 75.9 | 138.2 | 44.1 | 47.2 | 155.8 |
| 24 | 104.8 | 91.0 | 144.6 | 52.0 | 68.2 | 65.0 | 61.3 | 138.0 | 42.4 | 45.0 | 158.9 |
| 25 | 99.1 | 82.1 | 138.8 | 49.6 | 60.8 | 59.1 | 56.3 | 140.1 | 40.5 | 42.6 | 169.1 |
| **Average** | **100.2** | **87.7** | **138.8** | **53.3** | **65.5** | **58.9** | **58.9** | **138.5** | **42.5** | **42.5** | **158.6** |

PCA was applied to the values of the four biometric indices (original variables). It finds hypothetical variables (components) that account for as much of the variance in the multidimensional data as possible by reducing the data set to two variables (the two most important components) through a routine that finds eigenvalues and eigenvectors (i.e., components) of the variance-covariance correlation matrix. All original data points were plotted as an XY graph in the coordinate system given by the two most important components (PC1 and PC2) to enhance visualization of the data sets representing the possible species (Fig. 5). The MANOVA were applied two by two to pairs of more similar specimen populations (Figs. 6a,b) and to the whole data set (Fig. 6c) for Wilk's lambda and Pillai trace statistical tests. MANOVA include scatter plots obtained using canonical variates analyses (CVA).

## RESULTS OF MORPHOSTATISTICAL ANALYSES

The biometric indices H/L and CAD/H were used by Arenillas and others (2007) to delimit three guembelitrid morphospecies in an El Kef Danian sample (KF12.7, ~0.7 m above K-Pg boundary). However, because the morphological and microtextural variability of guembelitrids is greater in the early Danian than in the Maastrichtian, it is doubtful that their results can be extrapolated to the Maastrichtian. Statistical processing of our biometric data shown in Tables 1–3 enabled us to delimit the *Guembelitria* morphospecies of the late Maastrichtian.

The frequency distribution of the H/L index value (univariate analysis), calculated for all measured specimens and represented in a plot histogram of 15 bins (Fig. 3a), suggest three morphogroups of *Guembelitria*: 1) low-spired (low H/L value), medium-spired (middle H/L value), and high-spired (high H/L value). Similar results are obtained with bivariate analysis using H/L and CAD/H values, and plotting them as a scatter diagram with 95% confidence ellipses and convex hulls similarly differentiates the three morphospecies (Fig. 3b).

Low probabilities determined by *t*-Student ($p_t = 1.086 \times 10^{-49}$), Kolmogorov-Smirnov ($p_{KS} = 3.131 \times 10^{-12}$), Mann-Whitney (comparison of medians; $p_{MW} = 1.416 \times 10^{-9}$), and ANOVA (analysis of variance; $p_A = 1.507 \times 10^{-21}$) suggest both low- and medium-spired morphospecies

TABLE 4. Rates of chamber enlargement of *Guembelitria* species. The rate for each species is based on the widths of all chambers (CW) of a representative specimen.

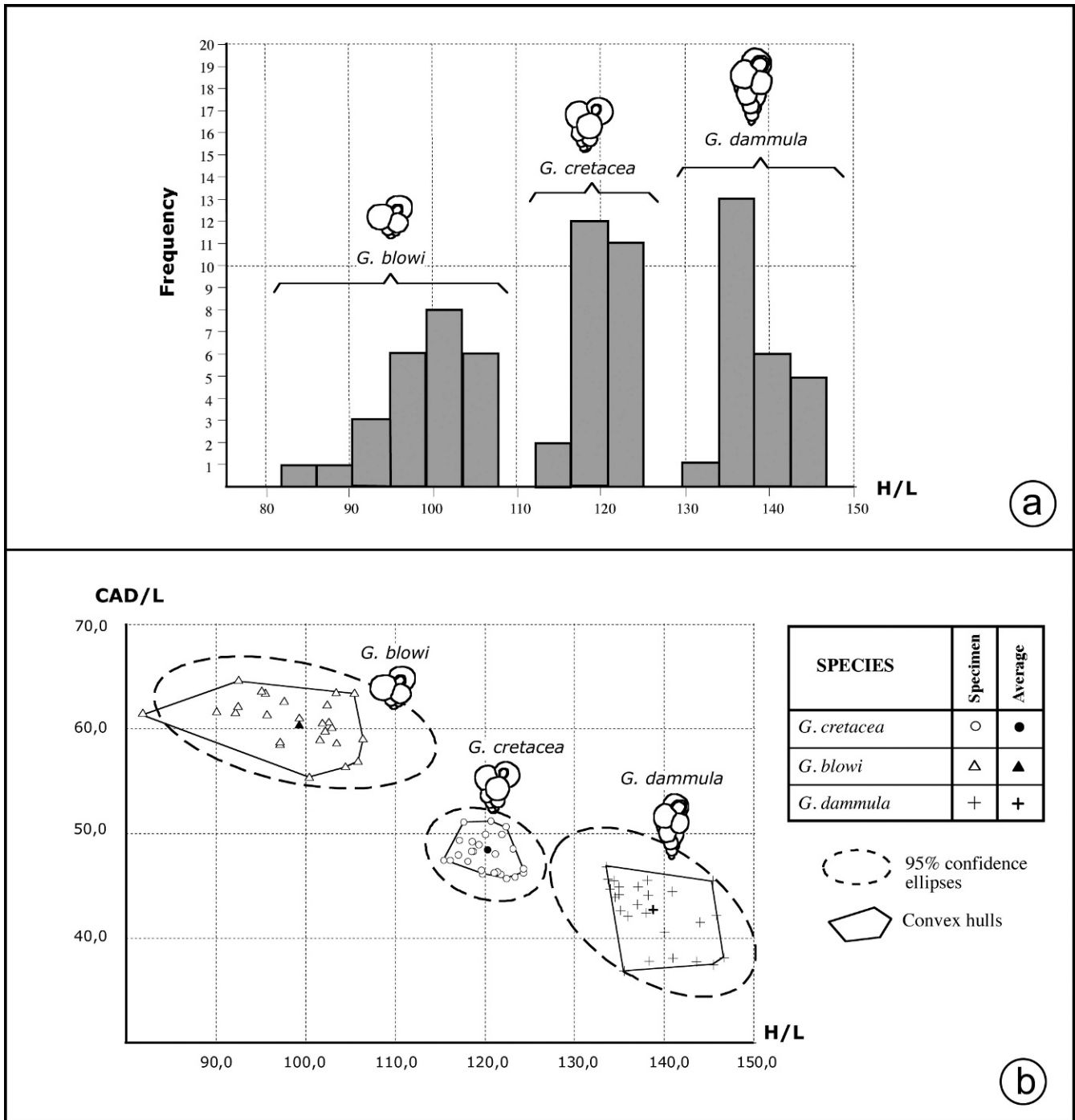| Chamber number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. cretacea* (CW) | 17.5 | 18.5 | 20.5 | 23.4 | 29.7 | 39.7 | 46.8 | 55.6 | 64.9 | 74.8 | | | |
| *G. blowi* (CW) | 18.2 | 18.7 | 22.6 | 29.2 | 36.9 | 44.1 | 60.6 | 77.7 | | | | | |
| *G. dammula* (CW) | 20.1 | 21.4 | 25.2 | 27.1 | 34.0 | 39.0 | 44.1 | 47.9 | 51.6 | 60.1 | 67.4 | 74.3 | 76.8 |

FIGURE 3. Delimitation of guembelitrid species based on **a**, univariate (H/L) and **b**, bivariate (CAD/H, H/L) analyses.

belong to different species. Likewise, the comparison of the medium- and high-spired morphospecies also resulted in low probabilities ($p_t = 1.244 \times 10^{-56}$, $p_{KS} = 3.131 \times 10^{-12}$, $p_{MW} = 1.416 \times 10^{-9}$, and $p_A = 7.563 \times 10^{-21}$). Because all of these values are far below the $< 0.05$ level of significance, it is highly likely that the three morphogroups are different species.

The bivariate H/L and CAD/H (Fig. 4a) and multivariate H/L, CAD/H, CH/H, and H/W (Fig. 4b) cluster analyses, based on Euclidean distance, produced dendrograms with two primary clusters, one grouping high-spired guembeli-

trids and the other grouping low- and medium-spired guembelitrids. The latter group splits into two clusters that differentiate low-spired from medium-spired guembelitrids. The bivariate (Fig. 5a) and multivariate (Fig. 5b) principal component analyses distinguished the three groups, where X and Y are the principal components PC1 and PC2. Convex hulls and 95% confidence ellipses clearly delimit the three morphospecies. The results of the PCA, when compared to those of the cluster analysis, show greater morphological proximity between medium-spired and high-spired populations.
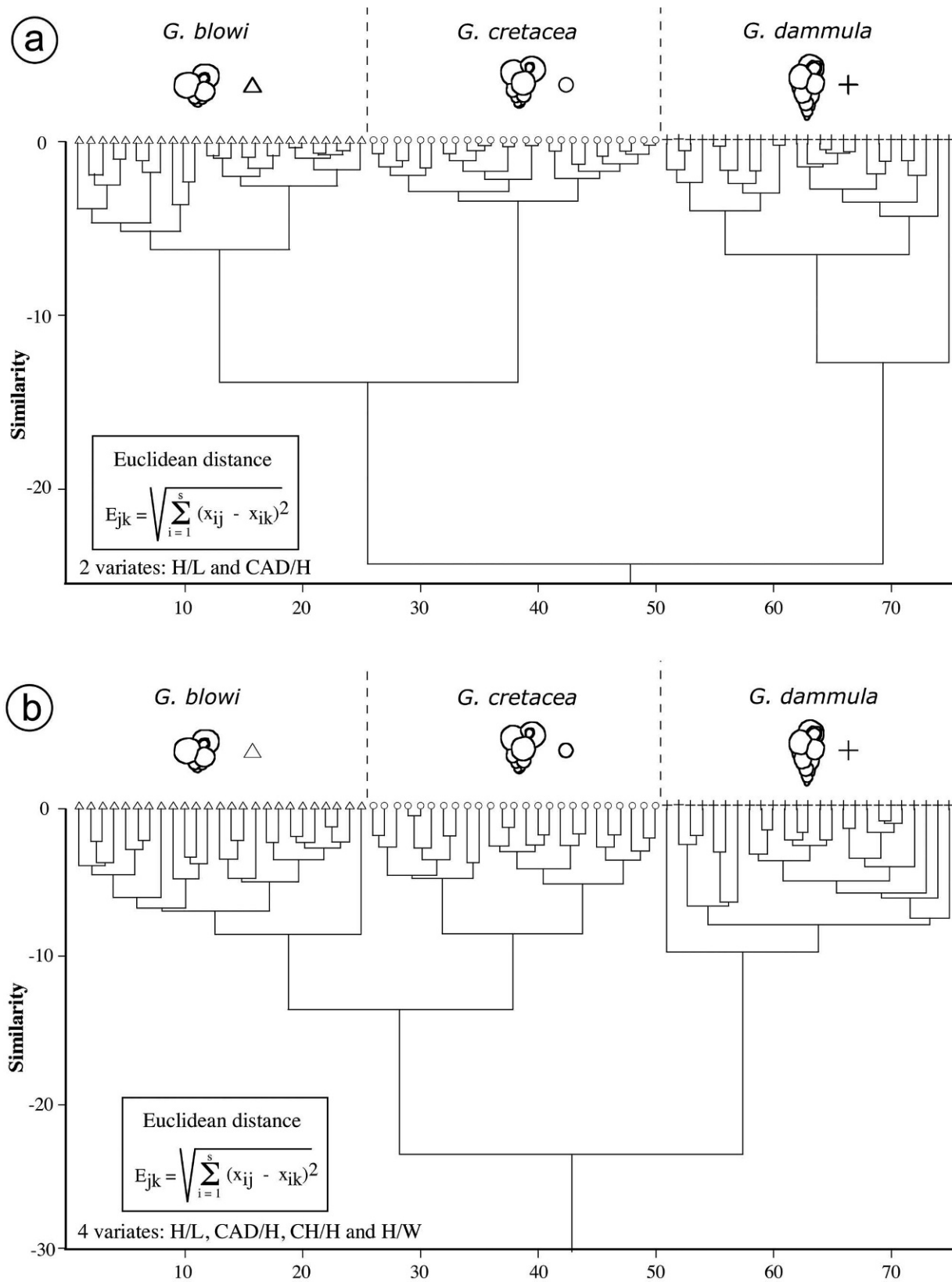
FIGURE 4. Dendrograms produced by **a**, bivariate and **b**, multivariate R-mode cluster analyses of biometric indices for all guembelitrid specimens in this study. $E_{jk}$ = Euclidean distance between specimens j and k; $X_{ij}$ = value of the variable i (biometric index i) of the specimen j; $X_{ik}$ = value of the variable i (biometric index i) of the specimen k.
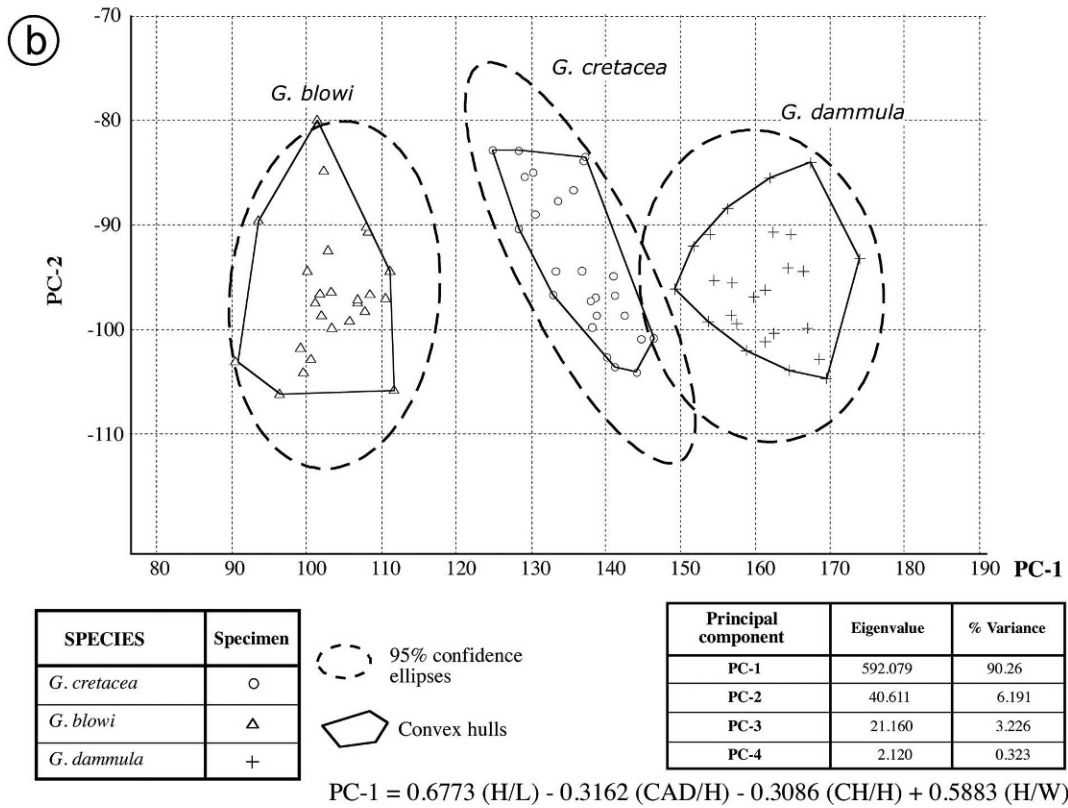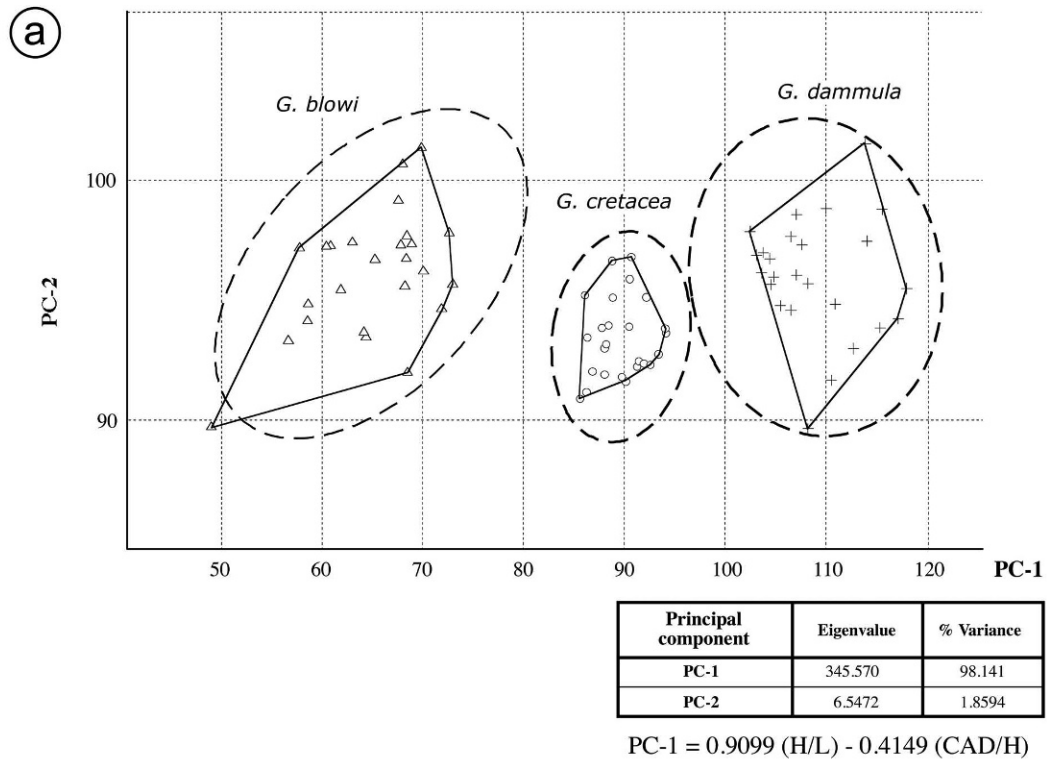
FIGURE 5. Principal component analysis (PCA) applied to **a**, bivariate and **b**, multivariate analyses of the biometric indices for all of guembelitrid specimens in this study.
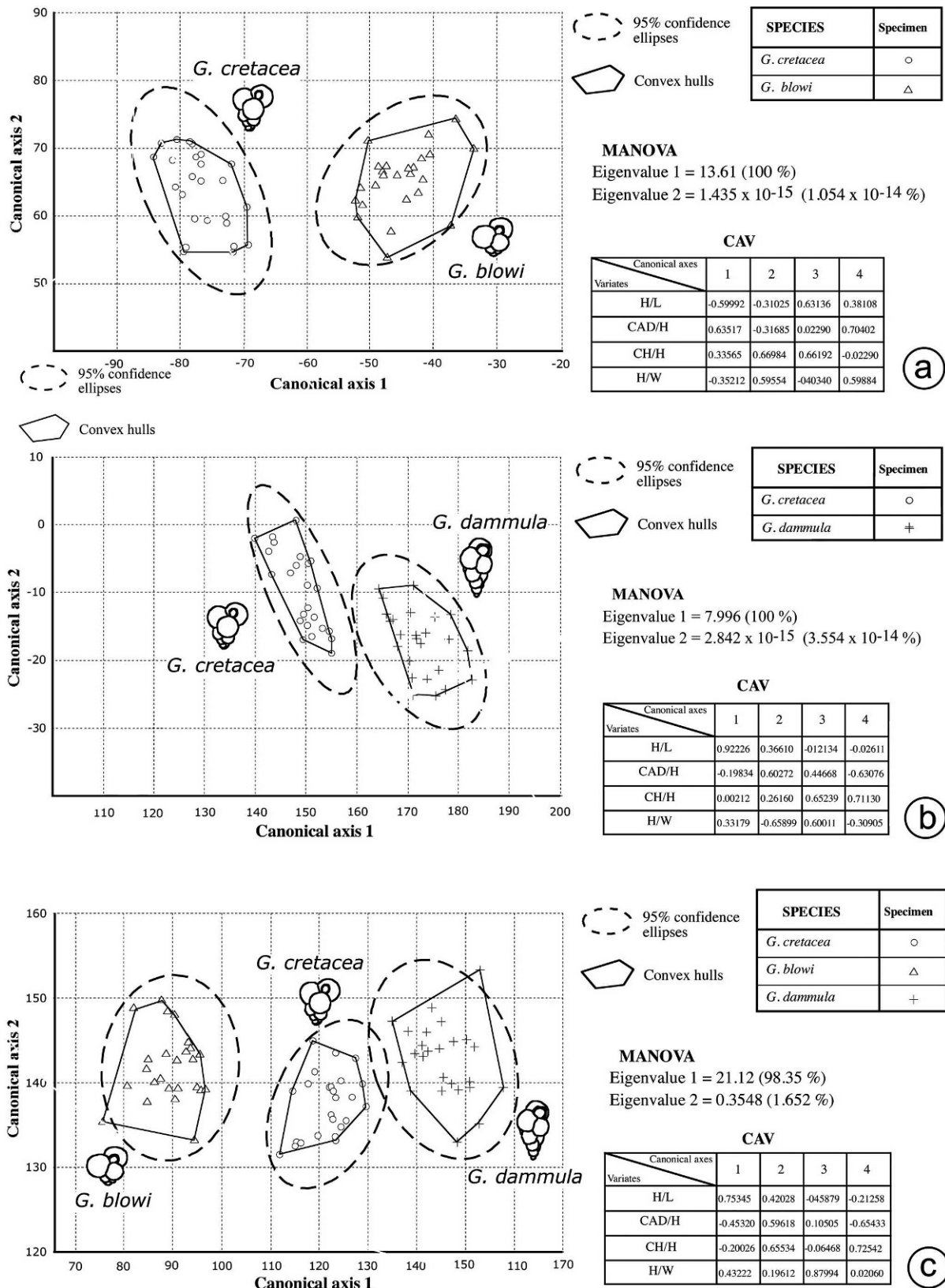
FIGURE 6.    Multivariate analysis of variance (MANOVA) and canonical variates analysis (CVA) applied to **a**, low-spired *Guembelitria blowi*, nov. sp. and middle-spired *G. cretacea* populations; **b**, high-spired *G. dammula* and middle-spired *G. cretacea*) populations; and **c**, the entire data set.
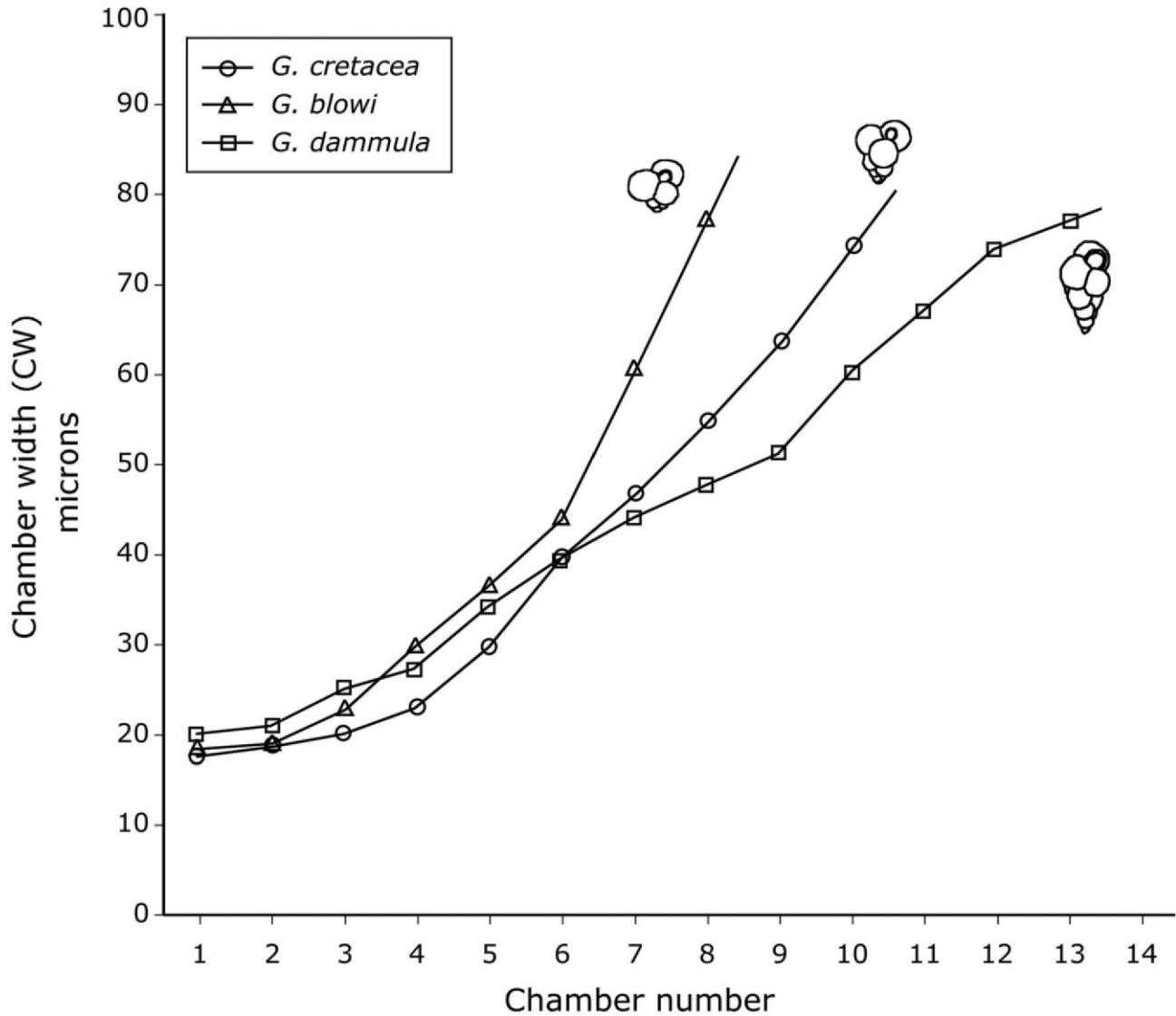
FIGURE 7. Rate of chamber enlargement of guembelitrid species (in microns).

The multivariate analyses of variance (MANOVA) for the pair of low-spired and medium-spired populations (Fig. 6a) yield very low probabilities (Wilk's lambda [$p_{Wl}$] = Pillai trace [$p_{Pt}$] = $1.366 \times 10^{-25}$) that the two populations belong to the same species. The probabilities from MANOVA of the pair of high-spired and medium-spired specimen populations (Fig. 6b) also are very low ($p_{Wl}$ = $2.842 \times 10^{-15}$, Pillai trace $p_{Pt}$ = $3.554 \times 10^{-14}$). The MANOVA on the whole data set (Fig. 6c) gives similar results ($p_{Wl}$ = $2.842 \times 10^{-15}$, $p_{Pt}$ = $3.554 \times 10^{-14}$). The three MANOVA results shown in scatter plots obtained using canonical variates analyses (CVA) reveal groups similar to those given in the PCA (Figs. 6a–c).

The morphostatistical analyses agree with the rate of chamber enlargement throughout the ontogeny of three *Guembelitria* specimens belonging to the three analyzed morphotypes (Fig 7). Given their ontogeny, it is also possible to differentiate three morphospecies: low-spired, medium-spired and high-spired *Guembelitria*, which have a

high, medium and low rate of chamber enlargement respectively.

## DISCUSSION

Traditionally, Maastrichtian guembelitrid morphotypes have been considered as infraspecific variants of *Guembelitria cretacea* Cushman (Smith and Pessagno, 1973; Caron, 1985; Kroon and Nederbragt, 1990; Berggren and Norris, 1997; Olsson and others, 1999). However, some workers claim that *Guembelitria* consists of multiple species distinguished by test height (H), which is linked to spiral height (SH), number of chambers, and rate of chamber enlargement (e.g., MacLeod, 1993; Apellániz and others, 2002; Keller and Pardo, 2004; Arenillas and others, 2007).

Genetic, molecular, and ecological studies on living specimens increasingly suggest that planktic foraminiferal species diversity is considerably higher than inferred from many morphological taxonomies (Darling and others,
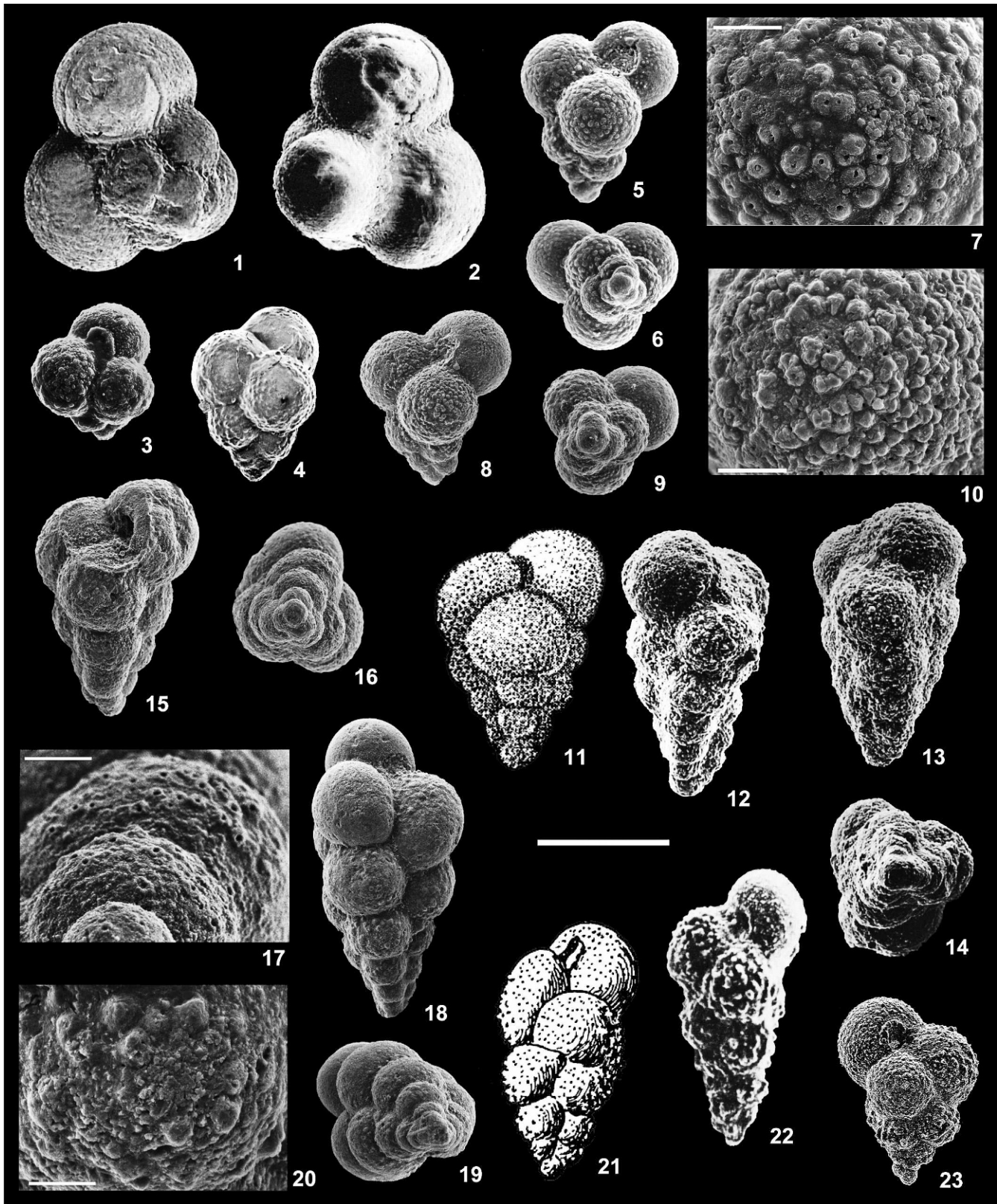
FIGURE 8. Guembelitrid species defined for the Cretaceous–Paleogene transition (scale bars: whole specimens = 100 μm; detailed parts of specimens = 10 μm). **1, 2** *Globigerina* (*Eoglobigerina*) *trifolia* Morozova, holotype, lower Danian, Tarkhankut, Crimea, southern Russia (SEMs from Olsson and others, 1999). **3** *Guembelitria*? *trifolia* (Morozova) sensu Blow (1979), lowest Danian, from DSDP Leg 6, Shatsky Rise, North Pacific. **4** *Guembelitria cretacea* Cushman, holotype, Upper Cretaceous, Guadalupe County, Texas (SEMs from Olsson and others, 1999). **5–7** *Guembelitria cretacea* Cushman, sample KF13.5 (2.5 m above K-Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), lowermost Danian, El Kef, Tunisia. **8–10** *Guembelitria cretacea* Cushman, sample KF11 (1 m below K-Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), upper

2000). The cryptic speciation events caused by paleoceanographic and paleoclimatic changes, modifying the vertical structure and seasonality of the surface pelagic water masses, seem to be more frequent than previously believed (Norris, 2000). It has been shown that the morphospecies *Orbulina universa* d'Orbigny, widely regarded as a single species, includes at least three cryptic species (de Vargas and others, 1999). Similarly, genetic analyses have demonstrated the existence of several cryptic species in some extant morphospecies such as *Globigerinella siphonifera* (d'Orbigny), *Globigerina bulloides* d'Orbigny, and *Globigerinoides ruber* (d'Orbigny) among others (Kucera and Darling, 2002; Darling and Wade, 2008). Morphologically, some of these species can be recognized only by small differences in porosity, as in *O. universa* and *G. siphonifera*. Therefore, a considerable part of planktonic foraminiferal diversity has possibly been attributed to ecophenotypy or infraspecific variability by "lumper" morphological taxonomies.

Based on biometric measures and morphostatitiscal analyses on the late Maastrichtian guembelitrid specimen populations, we have been able to delimit at least three morphospecies according to the test height (H) and the rate of chamber enlargement: *Guembelitria cretacea* Cushman, 1933, *Guembelitria dammula* Voloshina, 1961, and *Guembelitria blowi* nov. sp., corresponding respectively to medium-spired, high-spired, and low-spired *Guembelitria*. In Neogene planktonic foraminiferal taxonomies (e.g., *Zeaglobigerina* Kennett and Srinivasan, 1983; *Globigerinoides* Cushman, 1927), it is usual to delimit morphospecies using diagnostic criteria such as the number of chambers or the spiral height (SH), similar to those used to delimit morphospecies in *Guembelitria* in the present paper. According to genetic analyses, morphospecies thus defined seems to group several cryptic biological species, only *a posteriori* distinguished as morphospecies (pseudocryptic species). Huber and others (1997) and de Vargas and others (2001) provided evidence that the large morphological variability observed in modern morphospecies might indeed be linked to genetic differences. We consider that the three forms of *Guembelitria* delimited here are of sufficient identity to raise them to the category of species.

The use of the surface texture in planktic foraminiferal taxonomy is widely extended and helps to research the ancestor-descendant relationships at genus and species level (Nederbragt, 1991; Olsson and others, 1999; Georgescu, 2007; Georgescu and others, 2008 among others). The three Maastrichtian morphospecies of *Guembelitria* generally present a surface wall with pore-mounds (sometimes two pores per papilla or mound). Nevertheless, some specimens in each morphospecies exhibit a different wall texture, characterized by imperforate papillae instead of pore-mounds, and pore-murals in the smooth part of the wall

surface (Figs. 8.10, 8.20; and 9.9). Arenillas and others (2007) used the term "papillate" for these two types of wall (i.e., that characterized by the presence of pore-mounds (perforate papillae) or of subconical imperforate mounds (papillae). This difference in the wall texture observed in the same morphotype may have been linked to genetic differences similar to the case of the modern *O. universa*, representing cryptic or pseudocryptic species. Alternatively it might be due to ecophenotypic or ontogenetic factors, such as gametogenic calcification. In any case, the variability in the wall texture of the Maastrichtian guembelitrids raises some doubts about the importance of this character at generic level taxonomy (e.g., between *Guembelitria* and the Danian genus *Chiloguembelitria* Hofker, 1978).

## TAXONOMY

The classification of higher categories follows that of Loeblich and Tappan (1987). Only the species of regular *Guembelitria* that occur in the Maastrichtian are described: *Guembelitria cretacea* Cushman, 1933, *Guembelitria blowi*, nov. sp., and *Guembelitria dammula* Voloshina, 1961. The zones and subzones mentioned in the present paper concern the planktic foraminiferal zonations by Arz and Molina (2002) and Arenillas and others (2004). The ranges of *Guembelitria* and its species proposed here are based on biostratigraphic studies and annotations by Smit (1982), Kroon and Nederbragt (1990), Koutsoukos (1994), Olsson and others (1999), Arz and others (2000), Arz and Molina (2002), Arenillas and others (2000a,b; 2007), Keller and Pardo (2004); among others.

Order FORAMINIFERIDA Eichwald, 1830
Suborder GLOBIGERININA Delage and Hérouard, 1896
Superfamily HETEROHELICACEA Cushman, 1927
Family GUEMBELITRIIDAE Montanaro Gallitelli, 1957

Genus *Guembelitria* Cushman, 1933
Type species: *Guembelitria cretacea* Cushman, 1933

*Gümbelitria* Cushman *in* Cushman, 1933, p. 37.
*Guembelitria* Cushman *in* Blow, 1979, p. 1382–1383.
*Guembelitria* Cushman *in* Loeblich and Tappan, 1987, p. 453.
*Guembelitria* Cushman *in* Kroon and Nederbragt, 1990, p. 33.
*Guembelitria* Cushman *in* Olsson and others, 1999, p. 79.
*Guembelitria* Cushman *in* Arenillas and others, 2007, p. 34–37.

*Original description.* "Test similar to *Gümbelina*, but triserial; wall calcareous, finely perforate; aperture large, at the inner edge of the last-formed chamber."

*Diagnostic description.* Test small or minute, subconical, with triserial arrangement. Chambers spherical or globular. Outline lobate, with incised sutures. Wall calcareous hyaline, microperforate, papillate by pore-mounds (some-

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Maastrichtian, El Kef, Tunisia. **11** *Guembelitria dammula* Voloshina, holotype, Maastrichtian, Volin-Podolsk Plateau (western Russia). **12–14** *Guembelitria dammula* Voloshina, hypotype by Olsson and others (1999), lowermost Danian, from Bjala (Bulgaria). **15–17** *Guembelitria dammula* Voloshina, sample KF11 (1 m below K-Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), upper Maastrichtian, from El Kef, Tunisia. **18–20** *Guembelitria dammula* Voloshina, sample JA 680 (19 cm below K-Pg boundary), equivalent to the *A. mayaroensis* Zone, upper Maastrichtian, from Bajada del Jagüel, Argentina. **21** *Chiloguembelitria danica* Hofker, holotype, middle Danian, from DSDP Leg 6, Shatsky Rise, northern Pacific. **22** *Chiloguembelitria danica* Hofker, topotype, Danian from DSDP Leg 6, Shatsky Rise, North Pacific (SEMs from Loeblich and Tappan, 1987). **23** *Chiloguembelitria danica* Hofker, neotype, Danian from DSDP Leg 6, Shatsky Rise, North Pacific (SEMs from Jenkins and others, 1998).
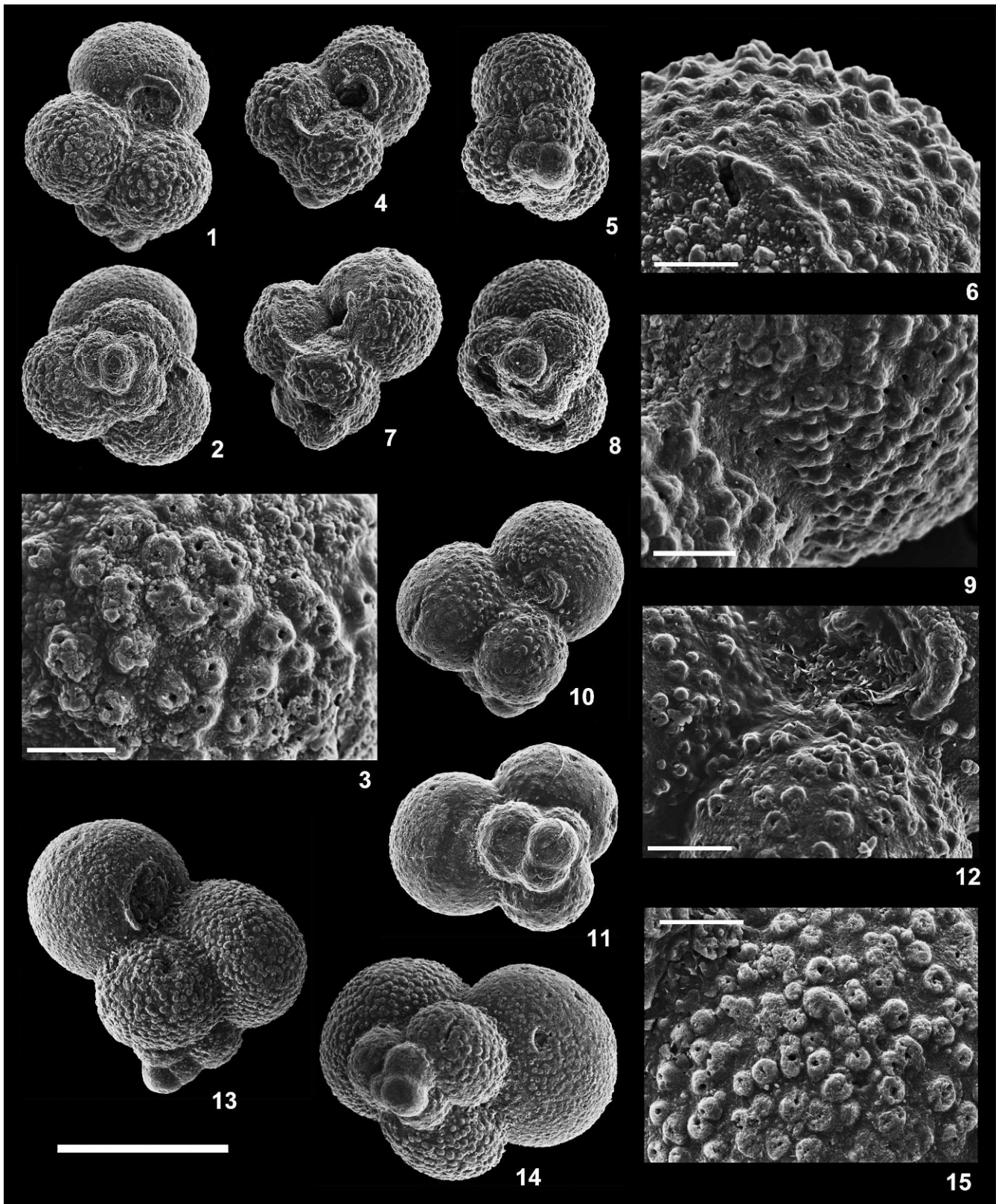
FIGURE 9.     Scanning electron micrographs of the type-specimens of *Guembelitria blowi*, nov. sp. (scale bars: whole test = 100 μm; surface detail = 10 μm). **1–3** Holotype MPZ2009/23, sample KF4.50 (7.5 m below K-Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), upper Maastrichtian, El Kef, Tunisia: 1, axial view; 2, spiral view; 3, surface detail. **4–6** Paratype MPZ2009/24, sample KF11 (1 m below K-Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), upper Maastrichtian, El Kef, Tunisia: 4, axial view; 5, spiral view; 6, surface detail. **7–9** Paratype MPZ2009/25, sample KF11 (1 m below K-Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), upper Maastrichtian, El Kef, Tunisia: 7, axial view; 8, spiral view; 9, surface detail. **10–12** Hypotype MPZ2009/174, sample STWA+20+22 (about 21 cm above K-Pg boundary), *Pv.*

times two pores per papilla) and/or imperforate papillae, irregularly distributed. Aperture interiomarginal, intraumbilical, semicircular, with a thin imperforate lip, often slightly asymmetrical.

*Remarks. Guembelitria* appears in the Aptian (Early Cretaceous) and differs from other genera by its triserial arrangement and presence of well-developed pore-mounds. The diagnostic description is based on the emendations by Blow (1979), Loeblich and Tappan (1987), Olsson and others (1999), and Arenillas and others (2007) who extended the original description and emphasized the presence of pore-mounds in *Guembelitria*. In the original diagnosis only the triserial character was indicated, but the wall type and other characters were not specified. The papillate wall surface by the presence of pore-mounds in *Guembelitria* was recognized and detailed with the advent of the Scanning Electron Microscope.

Hofker (1978) defined a new guembelitrid genus in the early Danian, *Chiloguembelitria*, considering that the aperture of the type-species, *Chiloguembelitria danica* Hofker, is similar to that of the Paleogene genus *Chiloguembelina* Hofker, 1978. Loeblich and Tappan (1987) considered that the main diagnostic trait of *Chiloguembelitria* is the wall surface, indicating that it has blunt pustules (called papillae by Arenillas and others, 2007) instead of pore-mounds (see Fig. 8.22 *C. danica* topotype of Loeblich and Tappan, 1987). D'Hondt (1991) and Olsson and others (1999) suggested that *Chiloguembelitria* is a junior synonymous of *Guembelitria*. Jenkins and others (1998) illustrated topotype specimens of *C. danica*, concluding that they have pore-mounds supporting that both genera are synonymous. However, the wall texture of most of the illustrated topotypes is poorly preserved and might have imperforate papillae, including the neotype of *C. danica* selected by them (Fig. 8.23). Therefore, the presence of pore-mounds in *C. danica* is dubious. Morphologically, *G. dammula* (Fig. 8.11) is very similar to the original illustration of *C. danica* (Fig. 8.21). Since many authors considered that *Guembelitria* and *Chiloguembelitria* are synonymous genera, the Maastrichtian high-spired guembelitrids here assigned to *G. dammula* have sometimes been named *Guembelitria danica* (MacLeod, 1993). However, the neotype selected for *C. danica* has the dimensions of *G. cretacea* and a medium-spired test, thus not reflecting the morphology of the Maastrichtian high-spired specimens. In any case, *G. dammula* was originally defined from Maastrichtian beds and has priority in date of publication over *C. danica*. Additionally, well-preserved Danian specimens from DSDP Site 47.2, Shatsky Rise (North Pacific) that were assigned to *C. danica* exhibit imperforate papillae that are more or less fused into rugosities (Loeblich and Tappan, 1987) not found on Maastrichtian specimens. Therefore, an in-depth study of the morphology and wall surface of Danian guembelitrids is needed to clarify their taxonomy. In this study, we focus on the Maastrichtian guembelitrids.

*Guembelitria cretacea* Cushman, 1933
Figs. 8.4–8.10

*Gümbelitria cretacea* Cushman *in* Cushman, 1933, p. 37, pl. 4, figs. 12a–b.
*Guembelitria cretacea* Cushman *in* Blow, 1979, p. 1383–1384, pl. 258, fig. 11.
*Guembelitria cretacea* Cushman *in* D'Hondt, 1991, pro parte, pl. 1, figs. 2–4; pl. 2, figs. 2–4.
*Guembelitria cretacea* Cushman *in* MacLeod, 1993, pl. 1, figs. 8–10; pl. 2, figs. 1–4, 7–8.
*Guembelitria cretacea* Cushman *in* Olsson and others, 1999, 79–80, pro part, pl. 63, figs. 1, 3–6, 8–9.
*Guembelitria cretacea* Cushman *in* Arenillas and others, 2007, p. 37, figs. 13.2–13.3.

*Original description.* "Test small, triserial; chambers globular, nearly spherical; sutures much depressed; wall smooth, finely perforate; aperture large, semicircular or semielliptical at the inner margin of the last-formed chamber. Length of holotype 0.20 mm; breadth 0.17 mm."

*Diagnostic description.* Test subconical, higher than wide or long. Triserial arrangement, often twisted, with 10–12 spherical chambers distributed in 3–4 spiral whorls, with moderate rate of chamber enlargement. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, intraumbilical, semicircular, with a thin imperforate lip, often slightly asymmetrical. Wall surface microperforate, papillate by blunt pore-mounds (sometimes by imperforate papillae), irregularly distributed. Adult dimensions: height = 110–170 μm, length = 90–135 μm.

*Remarks.* Cushman's (1933) diagnosis of the type specimen (Fig. 8.4) was very brief, but later descriptions have detailed some of the main traits of *G. cretacea*, such as its wall surface and type of pore (Olsson, 1970; Smith and Pessagno, 1973; Loeblich and Tappan, 1987; Kroon and Nederbragt, 1990; D'Hondt, 1991; MacLeod, 1993). According to Kroon and Nederbragt (1990), *G. cretacea* has a global distribution across the Maastrichtian–early Danian, and can also be encountered in the Coniacian–Campanian. The surface wall of *G. cretacea* is papillate, usually by blunt pore-mounds (Figs. 8.5–8.7), such as seen in the holotype of the species (see Jenkins and others, 1998). Nevertheless, the pore-mounds may be sharp at times, and some specimens exhibit imperforated papillae instead of pore-mounds (Figs. 8.8–8.10), developing pore-murals in the smooth part of the wall surface.

*Stratigraphic range.* Coniacian–lower Danian (according to Kroon and Nederbragt, 1990).

*Guembelitria blowi*, nov. sp.
Figs. 9.1–9.15

*Guembelitria? trifolia* (Morozova) *in* Blow, 1979, 1384, pl. 61, fig. 9.
*Guembelitria cretacea* Cushman *in* D'Hondt, 1991, pl. 1, fig. 1.
*Guembelitria trifolia* (Morozova) *in* MacLeod, 1993, pl. 2, figs. 5–6, 9–11.
*Guembelitria cretacea* Cushman *in* Olsson and others, 1999, p. 79–80, pro-part, pl. 63, fig. 7.
*Guembelitria* cf. *trifolia* Cushman *in* Arenillas and others, 2007, p. 37–38, figs. 13.6–13.8.

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*longiapertura* Subzone (*G. cretacea* Zone), lowest Danian, Aïn Settara, Tunisia: 10, axial view; 11, spiral view; 12, surface detail. **13–15** Hypotype SEGEMAR 2893, sample JA 680 (19 cm below K-Pg boundary), equivalent to the *A. mayaroensis* Zone, upper Maastrichtian, Bajada del Jagüel, Argentina: 13, axial view; 14, spiral view; 15, surface detail.

*Description.* Test subconical, often longer than high. Triserial arrangement, often twisted, with 6–8 spherical chambers with high rate of chamber enlargement arranged in 2–2.5 spiral whorls. Outline subtriangular, lobate with incised sutures. Aperture interiomarginal, intraumbilical, semicircular with thin imperforate lip, often slightly asymmetrical. Wall surface microperforate, papillate with blunt pore-mounds or sometimes imperforate papillae, irregularly distributed. Adult size ranges about 85–150 µm in height and 95–160 µm in length.

*Remarks.* Blow (1979) used the "*trifolia*" specific name for the low-spired triserial morphotype (Fig. 8.3). This nomenclatural distinction was maintained by some authors (MacLeod, 1993; Apelláñiz and others, 2002; Abramovich and others, 2003; Keller and Pardo, 2004); even though *Globigerina* (*Eoglobigerina*) *trifolia* Morozova, 1961, is an early Danian trochospiral form (Figs. 8.1, 8.2) that Olsson and others (1999) later considered it as *Globoconusa*. Nevertheless, Arenillas and Arz (2000) and Arenillas and others (2007) identified the low-spired morphospecies as *Guembelitria* cf. *trifolia*, for which we propose *Guembelitria blowi*, nov. sp. As in the case of *G. cretacea*, the surface wall of *G. blowi* is papillate usually with pore-mounds, but some specimens instead have imperforated papillae and pore-murals in their smooth surface (paratype MPZ2009/25; Figs. 9.7–9.9). The source of this variability in texture is unknown; it could be cryptic species, as shown in modern *O. universa* (de Vargas and others, 1999), or infraspecific variability linked to (eco)phenotypy or to gametogenetic calicification during ontogeny.

*Figured specimens.* Holotype MPZ2009/23 (Figs. 9.1–9.3): length = 127.2 µm, width = 116.5 µm, height = 133.2 µm; H/L = 104.6; H/W = 114.3. Paratype MPZ2009/24 (Figs. 9.4–9.6): length = 114.6 µm, width = 88.9 µm, height 107.7 µm; H/L = 94.0, H/W = 121.1. Paratype MPZ2009/25 (Figs. 9.7–9.9): length = 111.4 µm width = 86.9 µm, height = 113.4 µm; H/L = 101.8, H/W = 130.4. Hypotype MPZ2009/174 (Figs. 9.10–9.12): length = 146.5 µm, width = 108.4 µm, height = 127.5 µm; H/L = 87.0, H/W = 117.6. Hypotype SEGEMAR 2893 (Figs. 9.13–9.15): length = 208.2 µm, width = 158.8 µm, height = 211.7 µm; H/L = 101.7, H/W = 133.1. Depository indicated by specimen number prefix: MPZ (Museo Paleontológico of the Universidad de Zaragoza, Aragón Government); SEGEMAR (Micropaleontological collection of the Servicio Geológico Minero Argentino, Buenos Aires, Argentina).

*Etymology.* Dedicated to Walter H. Blow, who was the first to recognize this morphotype at the species level.

*Type locality.* 7.5 m below the K-Pg boundary, El Haria Formation, El Kef section, Tunisia (loc. KF4.50).

*Type level.* *Plummerita hantkeninoides* Subzone of *Abathomphalus mayaroensis* Zone, upper Maastrichtian.

*Stratigraphic range.* Maastrichtian–lower Danian (Arz and Molina, 2002; Arenillas and others, 2007).

<div align="center">

*Guembelitria dammula* Voloshina, 1961
Figs. 8.11–8.20
</div>

*Guembelitria dammula* Voloshina *in* Voloshina, 1961, p. 82–83, pl. 4, fig. 1a.
*Guembelitria cretacea* Cushman *in* D'Hondt, 1991, pro parte, pl. 1, figs. 5–6.

*Guembelitria danica* (Hofker) *in* MacLeod, 1993, pl. 3, figs. 1–5.
*Guembelitria dammula* Voloshina *in* Olsson and others, 1999, pl. 12, figs. 7–9.
*Guembelitria dammula* Voloshina *in* Keller and Pardo, 2004, p. 112, pl. 1, fig. 6.
*Guembelitria danica* Cushman *in* Keller and Pardo, 2004, p. 112, pl. 1, figs. 9–10.

*Original description.* "Triserial test, gradually and regularly widening from the initial end up to the aperture. Initial end pointed, sometimes slightly curved. The rows of the chambers may be twisted with respect to the vertical axis. Each one of these rows is composed of 3–6 chambers that gradually enlarge in size and are added in a compact way. As a consequence of this compact addition of the chambers, three facets in the test can be clearly seen. The facets are separated by extensive blunt and undulating edges. The lateral sides of the initial chambers can be more or less flat, and certain convexity is seen on the edges. The chambers become more and more convex toward the apertural end of the test, the three last chambers having a clear spherical form. The sutures are straight, narrow, and perpendicular to the longitudinal axis of the test or slightly inclined downward. The suture depression is not deep. The aperture has a semi-round or semi-oval shape and is situated in the base of the last chamber. Wall smooth." (Translated from Russian)

*Diagnosis.* Test subconical, much higher than wide or long. Triserial, often twisted, 3.5–6 spiral whorls, 11–18 spherical chambers with moderate to low rate of chamber enlargement. Outline subtriangular, lobate with incised sutures. Aperture interiomarginal, intraumbilical, semicircular, with a thin imperforate lip, often slightly asymmetrical. Wall surface microperforate, papillate with blunt or sharp pore-mounds or imperforate papillae, irregularly distributed. Adult size ranges 120–175 µm in height and 80–125 µm in length.

*Remarks.* Voloshina (1961) defined this species for Maastrichtian elongated guembelitrids from the Volin-Podolsk Plateau of western Russia. He distinguished *G. dammula* from *G. cretacea* by its higher test and more compact chambers. Although its surface was described smooth, re-examination of the holotype is needed to determine the real texture. Rögl and others (1996) recorded a *Guembelitria* sp. with a slender test and appressed globular chambers from the Upper Cretaceous–lower Danian interval of the Bjala section in Bulgaria. A similar but poorly preserved specimen is illustrated as *G. dammula* by Olsson and others (1999; see Figs. 8.12–8.14 in this paper). Abramovich and others (2003) and Keller and Pardo (2004) also ascribed other Maastrichtian specimens with a very high spire and very regular stacking of chambers to *G. dammula*. We have statistically delimited our high-spired specimens as a different morphospecies.

As with the other Maastrichtian guembelitrids, the surface of *G. dammula* is papillate with pore-mounds (Figs. 8.15–8.17), but some specimens have imperforated papillae instead (Figs. 8.18–8.20). Imperforate papillae are more frequent in Argentine populations than in Tunisian ones. Moreover, Argentine tests with imperforate papillae tend to be higher. Abramovich and others (2003) and Keller and Pardo (2004) illustrate very high-spired specimens of *G. dammula* from shelf sections in Madagascar that are

morphologically similar to the Argentine specimen shown in Figs. 8.18–8.20. These data suggest that the two textures are controlled by ecologic or biogeographic factors. Imperforate-papillate morphotypes appear to have been more frequent in neritic or extratropical environments. Taking into account recent genetic studies on living planktic foraminiferal morphospecies, it is conceivable that the *G. dammula* morphotypes are pseudocryptic species.

*Stratigraphic range.* Maastrichtian–lower Danian (Keller and Pardo, 2004).

## CONCLUSIONS

Based on biometric measures and morphostatistical analyses of guembelitrid specimen populations from the El Kef section (Tunisia), it has been possible to recognize three species of late Maastrichtian *Guembelitria*: *G. cretacea* Cushman, 1933, *G. blowi* nov. sp., and *G. dammula* Voloshina, 1961. These morphospecies are distinguished by spiral height and the rate of increase in chamber size. The height of the spire is shortest in *G. blowi*, medium in *G. cretacea*, and tallest in *G. dammula*.

There are two main types of surface texture seen in each of the three Maastrichtian guembelitrid morphospecies: one characterized by pore-mounds, and the other by imperforate papillae with pore pits in the smooth part of the surface. These textural differences might be linked to gametogenetic calcification during ontogeny or (eco)phenotypic expressions of infraspecific variability, but the presence of cryptic or pseudocryptic species cannot be ruled out.

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