ON THE PHYLOGENY OF THE LATE ALBIAN GENUS *PLANOMALINA*

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ABSTRACT

The ancestor-descendant relationships of the late Albian *Planomalina* lineage have been reconstructed using morphologic observations obtained from the Scanning Electron Microscope and supported by morphometric analysis using X-ray images of the shell ontogeny. Both techniques are key to resolving questions on phylogeny and taxonomy, as they allowed us to propose that the trochospiral species *Hedbergella wondersi* is the ancestor of the genus *Planomalina*, and to document the *Hedbergella wondersi* - *Globigerinelloides pulchellus* - *Planomalina praebuxtorfi* - *Planomalina buxtorfi* evolutionary lineage.

INTRODUCTION

The evolution of planktonic foraminifera in the late Albian (Leckie and others, 2002) is characterized by a high rate of turnover (extinction plus speciation) and by a high rate of diversification (speciation minus extinction). The accelerated speciation rate resulted in the appearance of new genera such as *Biticinella*, *Rotalipora*, *Planomalina* and *Praeglobotruncana*. Among these genera the planispiral and keeled *Planomalina* displays the shortest stratigraphic range, which is totally contained within uppermost Albian sediments.

Based on the morphology of the end member of the lineage, *Planomalina buxtorfi*, *Planomalina* is thought to have originated during the late Albian from the planispiral genus *Globigerinelloides* through acquisition of a peripheral keel (Moullade, 1966; Pessagno, 1967; Longoria, 1974; Wonders, 1975; Leckie, 1984). Alternatively, Randrianasolo and Anglada (1989) suggested that the trochospiral species *Hedbergella wondersi* was the ancestral species of *Planomalina*.

The aim of this paper is to present an investigation of the ancestor-descendant relationships of the *Planomalina* lineage based on morphometric comparison of key morphological characters in order to more reliably differentiate the members of this lineage. The taxonomic characters used in the classification of foraminifera are traditionally based on the external morphology of the adult shell such as (among other features) the mode of coiling of the test (e.g., trochospiral, planispiral), wall texture (smooth, totally or partially muricate) and pore size (<1 µm = microperforate, 1–2.5 µm = finely perforate, >2.5 µm = macroperforate). However, observation of the internal shell morphology, including ontogenetic changes in chamber size and shape, provides a considerably more complete understanding of the shell morphology and, thus, improves understanding of the phylogenetic relationships within similar species (e.g., Huber, 1994; Huber and Boersma, 1994; Huber and others,

1997). For this reason we investigate the *Planomalina* lineage by using comparative external and internal morphologic observations of well-preserved specimens using the Scanning Electron Microscope (SEM) images and by performing morphometric analysis of X-ray images.

MATERIALS AND METHODS

To perform this study we analyzed uppermost Albian specimens recovered from ODP Sites 1050 and 1052, which were drilled on the margin of Blake Plateau off northeastern Florida (Fig. 1). The generally excellent preservation of the planktonic foraminiferal assemblages allows recognition of morphocharacters that are essential for determination of phylogenetic relationships between taxa, as well as clarification of taxonomic assignments and stratigraphic ranges of some species that have been previously overlooked or misidentified. High-resolution planktonic foraminiferal biostratigraphic study of these samples, together with study of coeval material drilled at DSDP Site 547 (Moroccan margin) on the opposite side of the North Atlantic Ocean (Petrizzo and Huber, 2006), has permitted development of a detailed bio- and chronostratigraphic framework for the North Atlantic region that shows good agreement with the stratigraphic distribution of standard Tethyan planktonic foraminifer biomarker species.

Samples of about 10 cc were processed following procedures described in Petrizzo and Huber (2006). Specimens were examined under a light microscope before SEM images were obtained. X-ray images of specimens mounted in axial view were obtained using methods outlined by Huber (1994). Metrics obtained from the X-ray images include chamber expansion rate, chamber number in the final whorl, and total chamber number.

Taxonomic descriptions of all species discussed in this work are included in Petrizzo and Huber (2006), along with comments on the distinguishing characters among species.
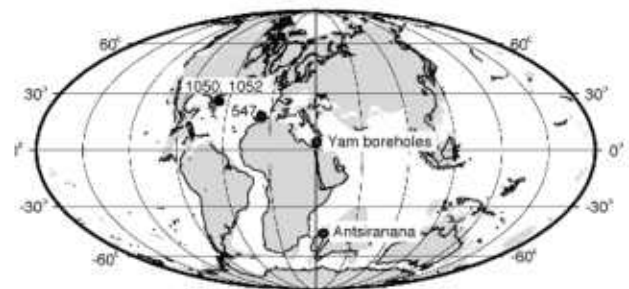

FIGURE 1. Paleogeographic reconstruction for the late Albian (101 Ma) according to Hay and others (1999), showing the localities mentioned in this study: ODP Sites 1050 and 1052 (Blake Nose), DSDP Site 547 (Moroccan margin), Yam boreholes (offshore of Israel), and the Antsiranana region (northern Madagascar).

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TABLE 1. External morphologic characters of the species discussed in this study.

	MODE OF COILING	WALL TEXTURE	PORE SIZE	PERIPHERAL MARGIN	SUTURES	CHAMBERS
Globigerinelloides bentonensis	planispiral	smooth	macroperforate (pore size > 2.5μm)	rounded	strongly depressed, curving backward as on either side of the periphery	inflated
Hedbergella wondersi	low trochospiral	randomly distributed muricae on the first chambers of the final whorl	macroperforate (pore size > 2.5μm)	rounded	straight and depressed on both side	inflated
Globigerinelloides pulchellus	planispiral	heavily muricate on the early part of the final whorl, becoming smooth on the final 2 or 3 chambers	macroperforate (pore size > 2.5μm)	rounded-subrounded without keel	straight to slightly curved and depressed on both side	inflated
Planomalina praebuxtorfi	planispiral	randomly distributed and fused muricae on the first chambers, becoming smooth on the last chambers	macroperforate (pore size > 2.5μm)	subacute to acute, peripheral keel only on the earlier chambers of the final whorl resulting from concentration of muricae	curved and depressed with those between the earlier chambers bordered by moderately developed muricae giving the impression of raised sutures	compressed
Planomalina buxtorfi	planispiral	smooth	macroperforate (pore size > 2.5μm)	acute with a distinctive peripheral keel	strongly raised and curved backwards	compressed

PREVIOUS STUDIES ON THE ORIGIN OF *PLANOMALINA*

There has been a general consensus among most authors that the late Albian *Planomalina* lineage was derived from the genus *Globigerinelloides* (Moullade, 1966; Pessagno, 1967; Longoria, 1974; Wonders, 1975; Leckie, 1984). However, opinions have varied regarding what the ancestral species was. Citing morphological similarities such as the planispiral coiling mode and the acquisition of a keel and raised sutures, Moullade (1966) and Wonders (1975) concluded that *Globigerinelloides caseyi* (=*G. eaglefordensis* in Moullade's study) is the ancestral species of the *Planomalina* lineage through the evolutionary series *G. caseyi* - *P. praebuxtorfi* - *P. buxtorfi*. Later, Moullade and others (2002) inferred that *Globigerinelloides bentonensis* gave rise to the planomalinids by progressive development of a peripheral keel and raised sutures through coalescence of muricae. The conclusions of Moullade and others (2002) are based on their studies of topotypes of *G. caseyi* (the 'boreal' species) from the Gault of England and specimens of *G. bentonensis* (the 'Tethyan' species) from various upper Albian levels of ODP Site 1050. These authors believe that the two species are distinct, with the former characterized by a smooth, probably microperforate wall texture that is totally devoid of muricae, whereas *G. bentonensis* has a macroperforate wall with moderately developed muricae that are mostly confined to the first chambers of the last whorl.

Our re-examination of the primary type specimens of *Globigerinelloides caseyi* (=*Planomalina caseyi*, USNM 4869) and *Globigerinelloides bentonensis* (*Anomalina bento-*

nensis, USNM 65381) deposited at the Smithsonian Museum of Natural History (Washington, D. C.) reveal that both species have a smooth and macroperforate surface texture and an identical external morphology. For this reason the two species are considered synonymous, and *G. bentonensis* is designated as the senior synonym because of priority, as was observed previously by Leckie (1984).

A different origin for the *Planomalina* lineages was proposed by Randrianasolo and Anglada (1989). These authors considered a trochospiral form, *Hedbergella wondersi*, as the ancestor of the genus *Planomalina* through the evolutionary series *Hedbergella wondersi* - *Globigerinelloides praebuxtorfi* - *Planomalina pulchella* - *Planomalina buxtorfi*. However, Randrianasolo and Anglada (1989) mistook *G. praebuxtorfi* (a species restricted by their emendation to planispiral forms with globular chambers, and therefore assigned to the genus *Globigerinelloides*) for *P. pulchella*, based on different concepts of both holotypes (see also discussion in Moullade and others, 2002).

RESULTS

MORPHOLOGIC OBSERVATIONS

The hypothesis that a planispiral test may have originated from trochospiral forms is discussed using evidence obtained from morphologic observations (Table 1) together with the observed species' stratigraphic ranges (Fig. 2).

Hedbergella wondersi, which first occurs in the lowermost part of the *Rotalipora ticinensis* Zone, was first described by Randrianasolo and Anglada (1989) from upper Albian sediments in the Antsiranana (Diego-Suarez) region of
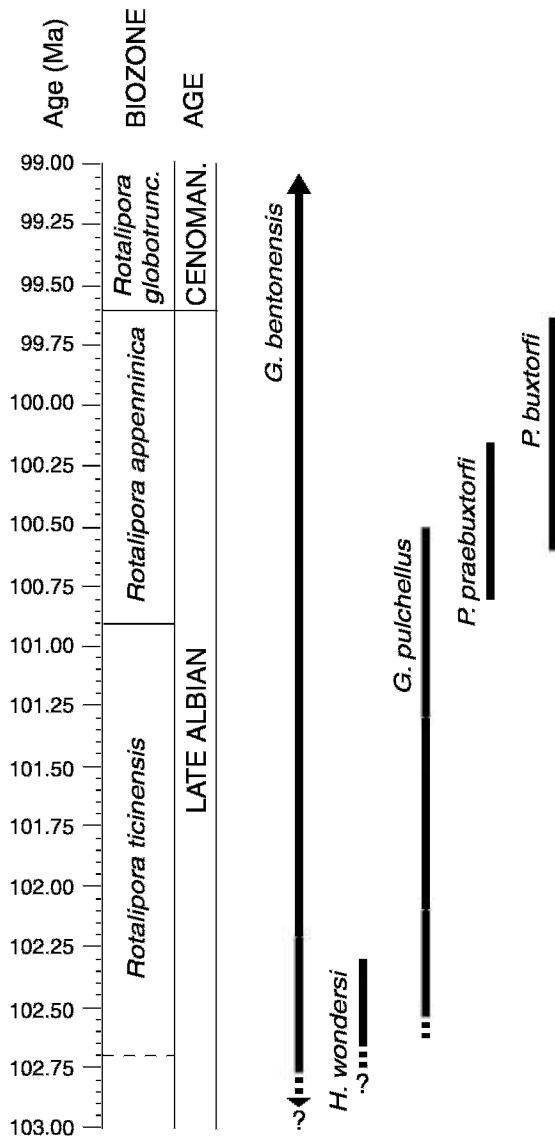
FIGURE 2. Stratigraphic ranges of the late Albian species discussed in this study. Biostratigraphic distribution and planktonic foraminiferal zonation after Petrizzo and Huber (2006); time scale according to Gradstein and others (2004).

northern Madagascar. It is distinguished by its low trochospiral coiling and macroperforate wall, with well developed, randomly distributed muricae on the first chambers of the final whorl (Pl. 1, Figs. 1–3).

In the lower part of the *R. ticinensis* Zone, *H. wondersi* gives rise to *Globigerinelloides pulchellus* (=*Planomalina pulchella*, emended by Petrizzo and Huber, 2006) through a decrease in spire height and a change from a trochospiral to planispiral coiling mode. Intermediate morphologies between *H. wondersi* and *G. pulchellus* co-occur just below the level where *H. wondersi* disappears and just above the lowest occurrence of *G. pulchellus*.

Globigerinelloides pulchellus is distinguished by having a planispiral, macroperforate wall with randomly distributed and fused muricae on the first chambers, and by lacking development of a peripheral keel. This species was first described by Todd and Low (1964) from a dredge haul

taken on the north slope of the Puerto Rico Trench, in an assemblage including *Rotalipora appenninica*.

In the lowermost part of the *R. appenninica* Zone, *G. pulchellus* (Pl. 1, Figs. 4–7) gave rise to *Planomalina praebuxtorfi* (Pl. 2, Figs. 1–3) through: (1) the development of a peripheral keel limited to the earlier chambers of the final whorl and resulting from concentration of muricae; and (2) the acquisition of curved sutures bordered by moderately developed muricae, giving the impression of raised sutures at least on the earlier chambers of the final whorl. Several intermediate specimens between the two morphotypes have been observed in the Blake Nose sediments within a short stratigraphic interval slightly below the extinction level of *G. pulchellus*.

The evolution from *P. praebuxtorfi* to *P. buxtorfi* (Pl. 2, Figs. 4–6, 8) in the lower part of the *R. appenninica* Zone is characterized by the development of a very distinctive peripheral keel on all the chambers of the final whorl and by the acquisition of raised sutures that are curved backwards. Intermediate forms between *P. praebuxtorfi* and *P. buxtorfi* commonly occur and are characterized by the absence of a peripheral keel and presence of depressed sutures on the last chamber (Pl. 2, Fig. 7). In *P. buxtorfi*, the end member of this lineage, the peripheral keel and raised sutures are very distinctive. Generally, its test size and the density of ornamentation increase following the extinction of *P. praebuxtorfi*. Specimens of *P. buxtorfi* with double keels and/or a tendency to uncoil occur in rare abundance in the intervals bearing the largest-sized specimens. For this reason we do not consider these double-keeled morphotypes to be reliable biomarkers.

ONTOGENETIC MORPHOMETRICS

The *Hedbergella wondersi – Planomalina buxtorfi* ancestor-descendant relationship is interpreted from the comparative morphologic observations discussed above and is supported by ontogenetic morphometric analysis. By comparing X-ray images taken from the umbilical views, it is clear that the internal morphology is extremely useful in characterizing population variability, especially in planispirally coiled forms, which show chamber shape and coiling arrangement throughout the shell ontogeny.

Measurements of the rate of chamber-size increase provide important information for comparison of ontogenetic growth trajectories. This metric is log-linear for all species of the *H. wondersi – P. buxtorfi* lineage (Fig. 3a). *Hedbergella wondersi, G. pulchellus, P. praebuxtorfi* and *P. buxtorfi* all share a similar logarithmic curve, but offsets in the rate of chamber-size increase reveal distinct and diagnostic differences. The similarity of the best-fit exponential regression curves (slope value: *H. wondersi*, 0.118; *G. pulchellus*, 0.121; *P. praebuxtorfi*, 0.126; and *P. buxtorfi*, 0.128) indicates that these species follow very close ontogenetic growth paths (Fig. 3b). Greater variability in the mean size of the last chamber is an artifact of differences in the total number of chambers measured for each species (Table 2).

The later portion of the ontogenetic growth-rate curve measured from specimens of *G. bentonensis* is offset relative to those from species of the *H. wondersi – P. buxtorfi*
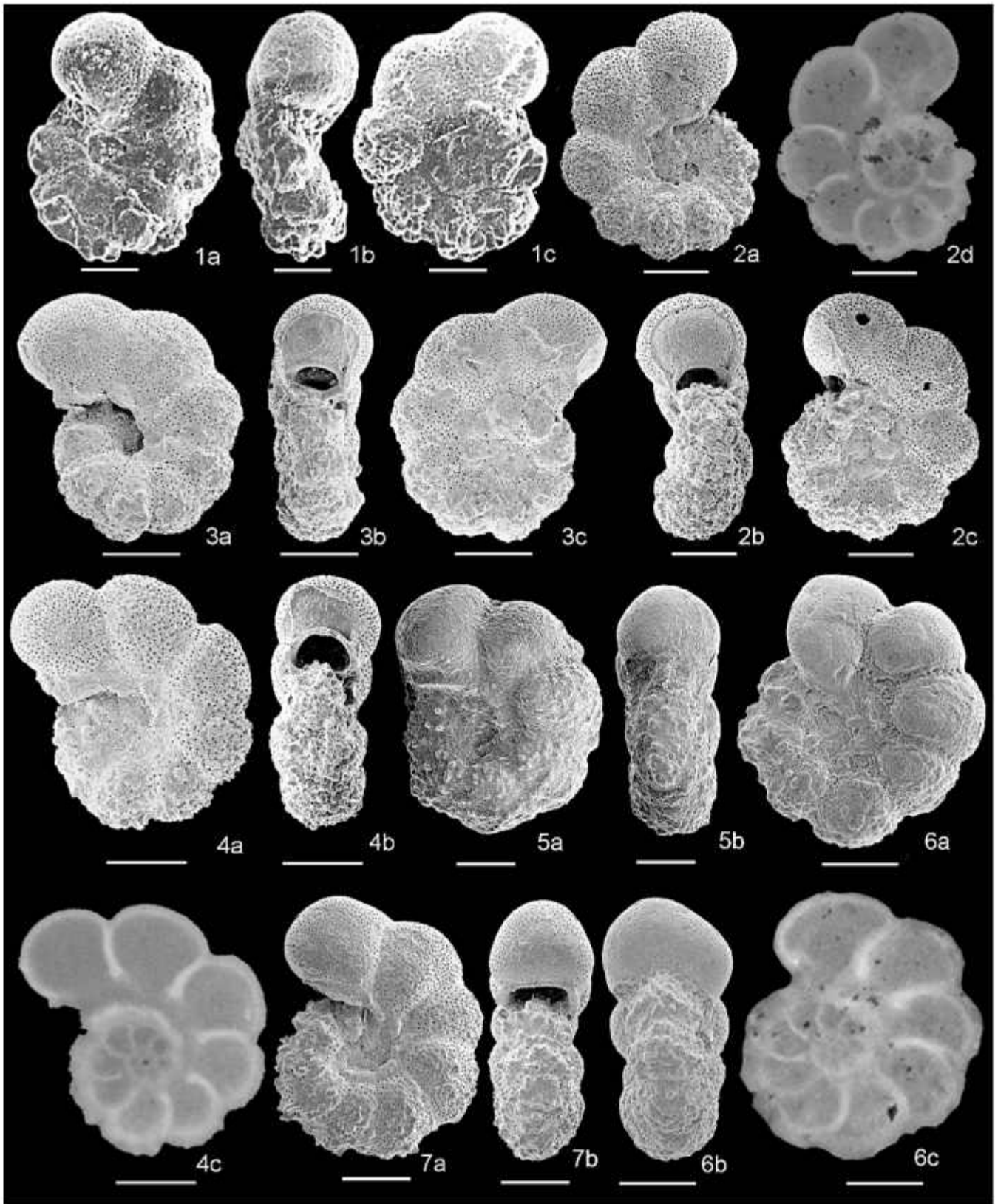
PLATE 1

1a–c. *H. wondersi* holotype. 2a–d. *H. wondersi* Sample 1050C- 31R-6, 88–91 cm. 3a–c. *H. wondersi* Sample 1050C- 31R-6, 88–91 cm. 4a–c. *G. pulchellus* Sample 1050C- 31R-6, 88–91cm. 5a–b. *G. pulchellus* holotype. 6a–c. *G. pulchellus* Sample 1052E-43R-1, 68–70 cm. 7a–b. *G. pulchellus* Sample 1050C-27R-4, 134–136 cm. Scale bars: 100 μm.
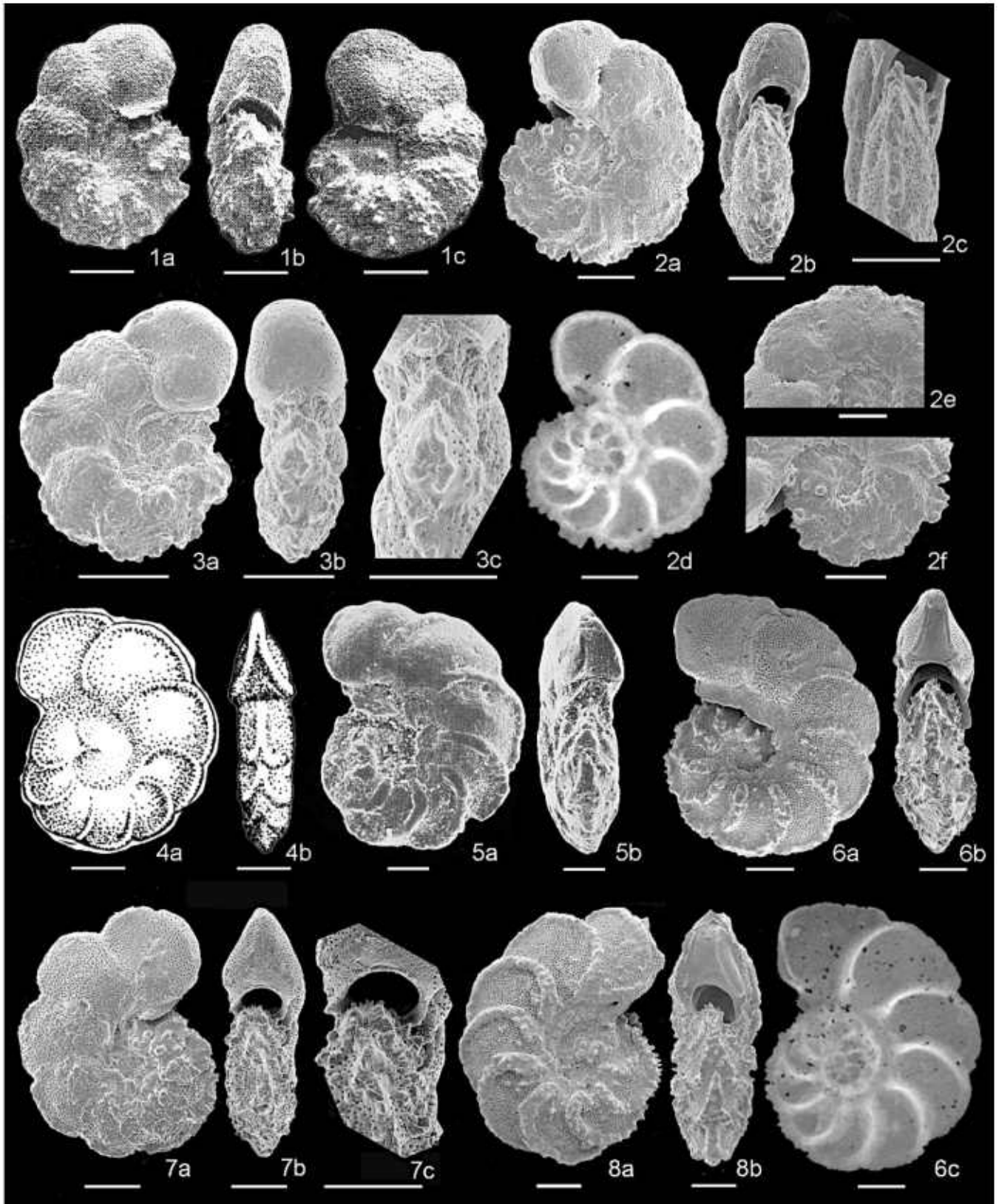
PLATE 2

1a–c. *P. praebuxtorfi* holotype. 2a–f. *P. praebuxtorfi* Sample 1052E- 42R-5, 146.5–148.5 cm. 3a–c. *P. praebuxtorfi* Sample 1052E-42R-5, 31.5–33.5 cm. 4a–b. *P. buxtorfi* holotype. 5a–b *P. buxtorfi* paratype. 6a–c *P. buxtorfi* Sample 1052E-40R-1, 127–130 cm. 7a–c. intermediate *P. praebuxtorfi*- *P. buxtorfi* Sample1052E-5, 146.5–148.5 cm. 8a–b. *P. buxtorfi* Sample 1052E-42R-1, 43–46 cm. Scale bars 100 μm.
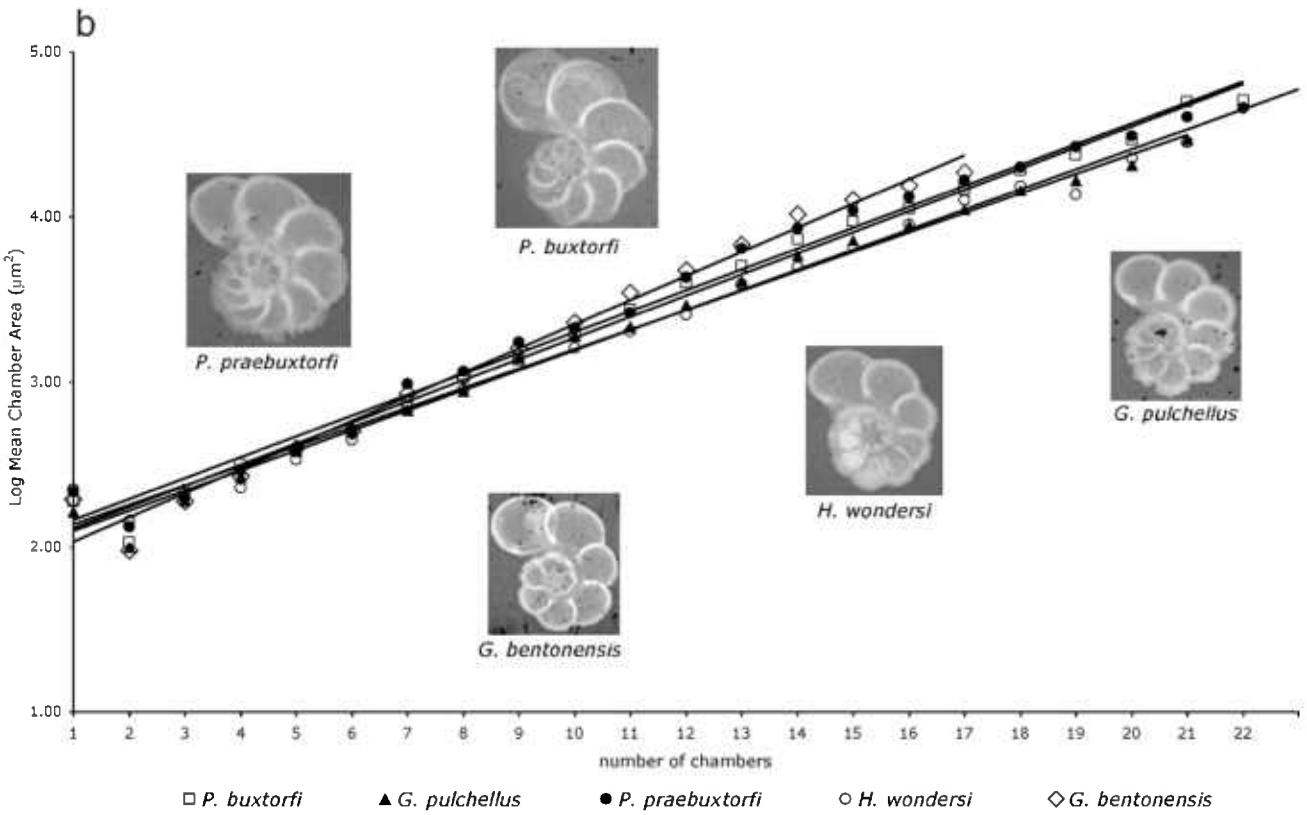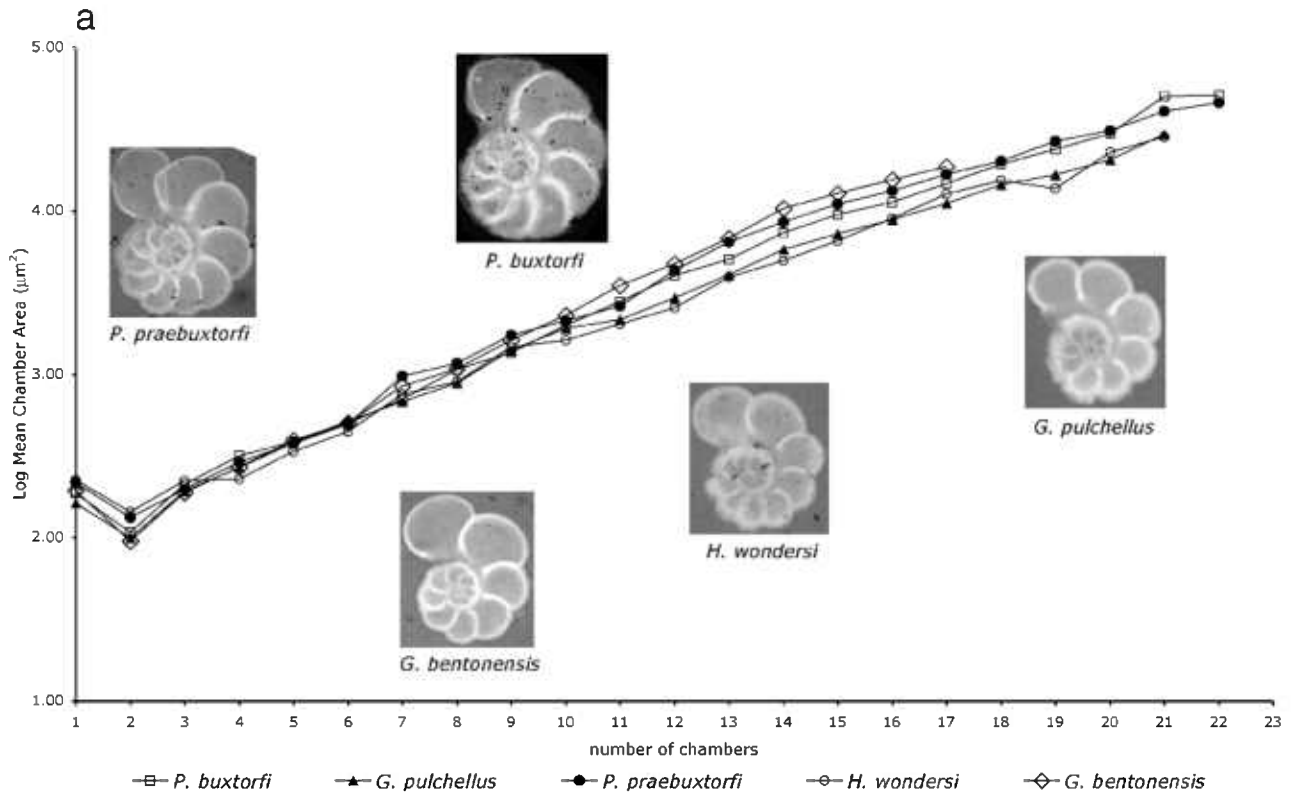
FIGURE 3.   a) Logarithmic plots of the chamber-by-chamber increase in chamber area (μm^2), and b) linear regression curve calculated from the mean rate of increase in chamber size of *G. bentonensis*, *H. wondersi*, *G. pulchellus*, *P. praebuxtorfi* and *P. buxtorfi*.
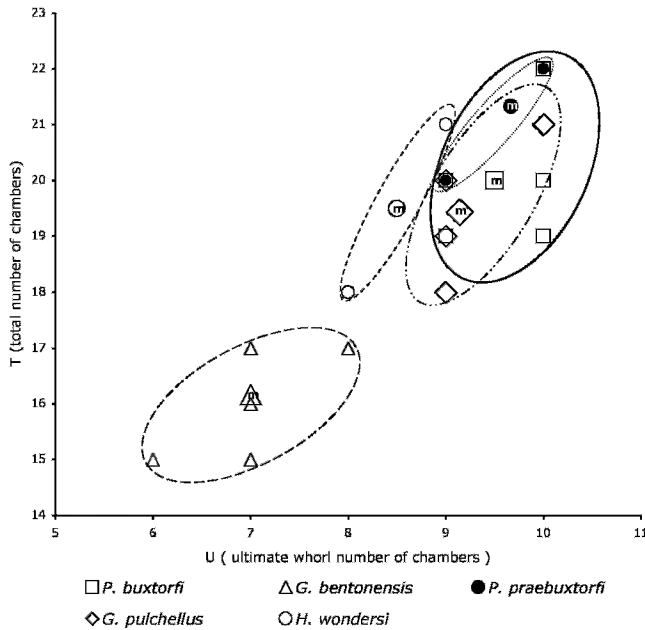
FIGURE 4. Total number of chambers (T) vs. the number of chambers in the ultimate whorl (U) of *G. bentonensis*, *H. wondersi*, *G. pulchellus*, *P. praebuxtorfi* and *P. buxtorfi*; when two or three data points have the same value they overplot each other; m = mean value for each species (see Table 2).

TABLE 2. Measurements of the total number of chambers (= T) and the number of chambers in the ultimate whorl (= U) counted from X-ray images of specimens. These data are presented in Figure 4.

	T	U
P. buxtorfi		
171-1052E-41R-2, 53-55	20	9
171-1052E-40R-4, 57-59	19	10
171-1052E-41R-4, 20-22	20	10
171-1052E-41R-7, 25-26	20	9
171-1052E-41R-7, 99-100	19	9
171-1052E-42R-1, 43-46	22	10
mean	20.00	9.50
P. praebuxtorfi		
171-1052E-43R-2, 9-11	22	10
171-1050C-27R-4, 5-7	20	9
171-1052E-42R-5, 146.5-148.5	22	10
mean	21.33	9.67
G. pulchellus		
171-1052E-43R-2, 50-52	21	10
171-1052E-44R-1, 8-10.5	18	9
171-1050C-27R-2, 3-5	20	9
171-1050C-27R-3, 8-10	19	9
171-1050C-27R-3, 57-59	18	9
171-1052E-43R-1, 68-70	20	9
171-1050C-27R-4, 134-136	20	9
mean	19.43	9.14
H. wondersi		
171-1050C-31R-6, 88-91	21	9
171-1050C-31R-6, 88-91	18	8
mean	19.50	8.50
G. bentonensis		
171-1052E-41R-4, 29-31	15	7
171-1052E-41R-4, 99-100	16	7
171-1052E-42R-3, 48-50	17	7
171-1052E-42R-4, 119-121	17	7
171-1052E-43R-5, 78-81	17	8
171-1050C-27R, CC	15	6
mean	16.17	7.00

lineage. From the first through tenth chambers, the plot of mean chamber area for *G. bentonensis* shows a log-linear increase that is very similar and overlaps the curves of *H. wondersi*, *G. pulchellus*, *P. praebuxtorfi* and *P. buxtorfi* (Fig. 3a). However, in the last whorl (typically from the tenth chamber on) *G. bentonensis* is clearly distinguished by having fewer chambers that are larger in size within the final whorl, as is shown in Figures 3a, 3b and 4. This is also demonstrated by the significantly higher (0.146) slope of the best-fit regression curve for this species, reflecting a faster rate of chamber-size increase particularly in later ontogenetic series.

CONCLUSIONS

By using comparative observations of the exterior and interior shell morphology, we have investigated two proposed phylogenetic hypotheses for the derivation of the *Planomalina* lineage: (1) the derivation from a trochospiral ancestor (*Hedbergella wondersi*), as suggested by Randrianasolo and Anglada (1989), and (2) derivation from *Globigerinelloides bentonensis* (=*G. caseyi*), which has traditionally been regarded as the *Planomalina* ancestor species (Moullade, 1966; Pessagno, 1967; Longoria, 1974; Wonders, 1975; Leckie, 1984; Moullade and others, 2002).

According to Moullade and others (2002), *G. bentonensis* evolved from *H. wondersi* (regarded by them as a possible junior synonym of *H. almadenensis*) through progressive transformation from a trochospiral to planispiral coiling mode, and gave rise to *P. buxtorfi* by progressive development of a peripheral keel. In our opinion, *G. bentonensis* cannot have evolved from *H. wondersi* and cannot be the planomalinid ancestor for the following

reasons: (1) it possesses a smooth wall texture, (2) its ontogenetic growth trajectory differs from that of *H. wondersi* (=*H. almadenensis* of Moullade and others, 2002), and (3) it has fewer chambers in the final whorl and fewer chambers in the test. Inferences from the phylogenetic hypothesis suggested by Moullade and others (2002) are complicated by their species and/or genus concepts, as they illustrate specimens of *Globigerinelloides bentonensis* with moderately developed muricae on the first chambers of the last whorl (see Moullade and others, 2002, *Planohedbergella*? *bentonensis*, fig. 5, F-M). We believe these specimens resemble *Globigerinelloides pulchellus*.

Our studies strongly suggest that a macroperforate trochospiral form, *Hedbergella wondersi*, gave rise to the macroperforate planispiral genus *Planomalina*, and we document the *Hedbergella wondersi* - *Globigerinelloides pulchellus* - *Planomalina praebuxtorfi* - *Planomalina buxtorfi* evolutionary series. The *H. wondersi* - *P. buxtorfi* lineage

spans the upper Albian interval from the *R. ticinensis* Zone to the top of the *R. appenninica* Zone (Fig. 2) and is well recorded in the central Atlantic Ocean (Blake Nose, ODP Sites 1050 and 1052, and Moroccan margin DSDP Site 547) and northern Madagascar (Antsiranana region). Specimens of *H. wondersi* and *G. pulchellus* were also reported from late Albian sediments (Yam boreholes) drilled offshore of Israel (Lipson-Benitah and Almogi-Labin, 2000; Fig. 1). The occurrence of *H. wondersi* and *G. pulchellus* in other Tethyan locations has not yet been verified. At Blake Nose and Moroccan deep-sea sites, *H. wondersi* first occurs within the *R. ticinensis* Zone, whereas its first occurrence in northern Madagascar was reported in the middle Albian *Ticinella primula* Zone by Randrianasolo and Anglada (1989). Based on our data from the Atlantic region, the duration of the *H. wondersi* – *P. buxtorfi* lineage is estimated as ca. 4 m.y.

ACKNOWLEDGMENTS

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