

On the evolution of the Hedbergellidae from the Praehedbergellidae

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ABSTRACT – In order to establish the relationship between the smooth, microperforate praehedbergellid forms of the genus *Blefuscuiana* with the younger, macroperforate and muricate forms typical of *Hedbergella*, two similar taxa but with the different characters of the two genera, are studied here: *Blefuscuiana praetrocoidea* (Kretchmar & Gorbachik) and its descendant *Hedbergella trocoidea* (Gandolfi), the type species of *Hedbergella*, and which typifies the Hedbergellidae.

B. praetrocoidea was only found in the Early Aptian in the North Tethys. *H. trocoidea* ranges from the Late Aptian to Early Albian (?M. Albian) and is a cosmopolitan species. It evolves into *Ticinella roberti* (Gandolfi), a Late Aptian–Albian species with fused portici. The evolution of the Praehedbergellidae into the Hedbergellidae appears to be related to a relative sea-level rise in the Late Aptian and Albian (and the opening of the Proto-Atlantic) which provided a number of deep-water niches which the Hedbergellidae occupied. *J. Micropalaeontol.* 17(2): 97–103, December 1998

INTRODUCTION

We consider that the probable earliest known member of the lineage of *Blefuscuiana* taxa which evolved into *Hedbergella* was *B. infracretacea occidentalis* BouDagher *et al.* (1996). Its probable descendant *Blefuscuiana praetrocoidea* (Kretchmar & Gorbachik) from SW Crimea is studied here and illustrated in order to compare it with younger specimens similar in shape, but clearly macroperforate and muricate, from the same area and from Tunisia. These are *Hedbergella trocoidea* (Gandolfi). The relationship between these two taxa shows a derivation, in the Aptian, from small, smooth, microperforate praehedbergellid forms to larger, true hedbergellid taxa with larger perforations surrounded by muricae (see Plate 3).

There is ongoing debate concerning the subdivision of the Aptian. In this paper we recognize an Early Aptian time interval, equivalent to the Bedoulian Stage, and a Late Aptian which includes the Gargasian Stage and begins with the *Leupoldina cabri* Zone. With this terminology, the 'Middle Aptian' of authors is included in the Late Aptian.

SYSTEMATICS

Superfamily **Globigerinacea** Carpenter, Parker & Jones, 1862

Family **Praehedbergellidae** Banner & Desai, 1988

Genus ***Blefuscuiana*** Banner & Desai, 1988

Blefuscuiana praetrocoidea (Kretchmar & Gorbachik, 1986)
emended

(Pl. 1, figs 4–9; Pl. 2, figs 1–10)

1986 *Hedbergella praetrocoidea* Kretchmar & Gorbachik (*in* Gorbachik): 95, pl. 16, figs 3–5.

?1993 *Hedbergella praetrochoidea* Gorbachik (*sic*); Shahin: pl. 6, fig. 4.

Emended diagnosis. *Blefuscuiana praetrocoidea* has a medium-sized test, about 0.17–0.25 mm at its maximum diameter, with six to seven chambers in the last whorl, increasing gradually in size; early chambers spherical in peripheral view, final chamber ovoid; umbilicus narrow, circular. The aperture is a narrow slit, extending from the umbilicus to the periphery of the last whorl, and is furnished with a thin porticus. The surface of the test is smooth and non-muricate and it is uniformly microperforate.

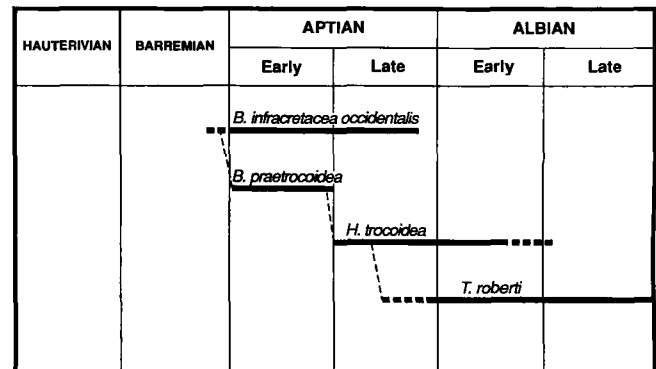


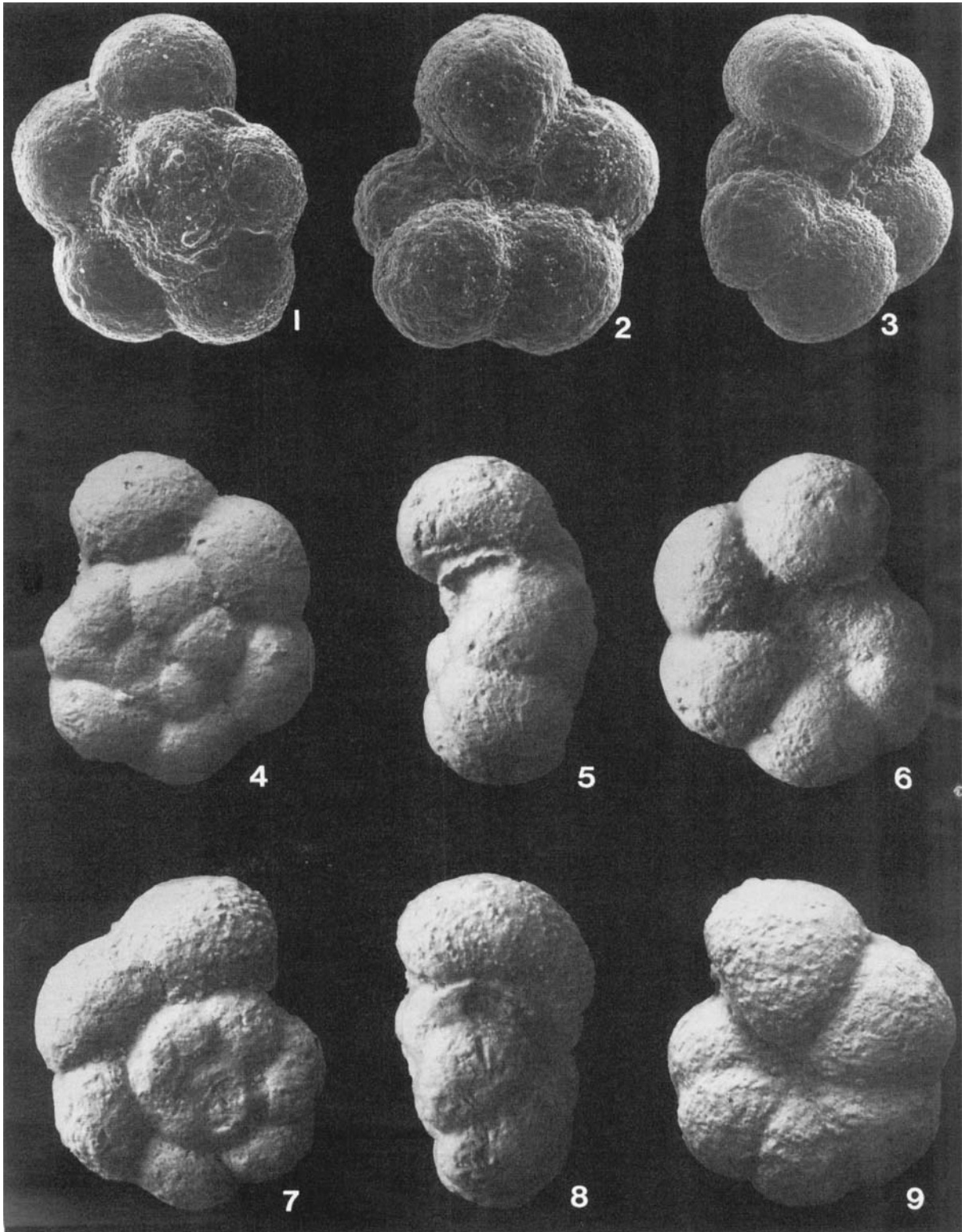
Fig. 1. The stratigraphic relationship between *Blefuscuiana infracretacea occidentalis*, *B. praetrocoidea*, *Hedbergella trocoidea* and *Ticinella roberti*.

Figured specimens. In the collections of the Department of Palaeontology, Moscow State University.

Remarks. *Blefuscuiana praetrocoidea* occurs in the Early Aptian of SW Crimea (Fig. 1). It has not until now been confidently recorded from anywhere else. However, Shahin (1993) illustrated a specimen under the name of *B. praetrocoidea* from the Late Aptian of Northern Sinai. This record is not yet confirmed, because Shahin's picture is not clear and the specimen is probably deformed. Therefore, more information is needed to prove its presence in this part of Tethys.

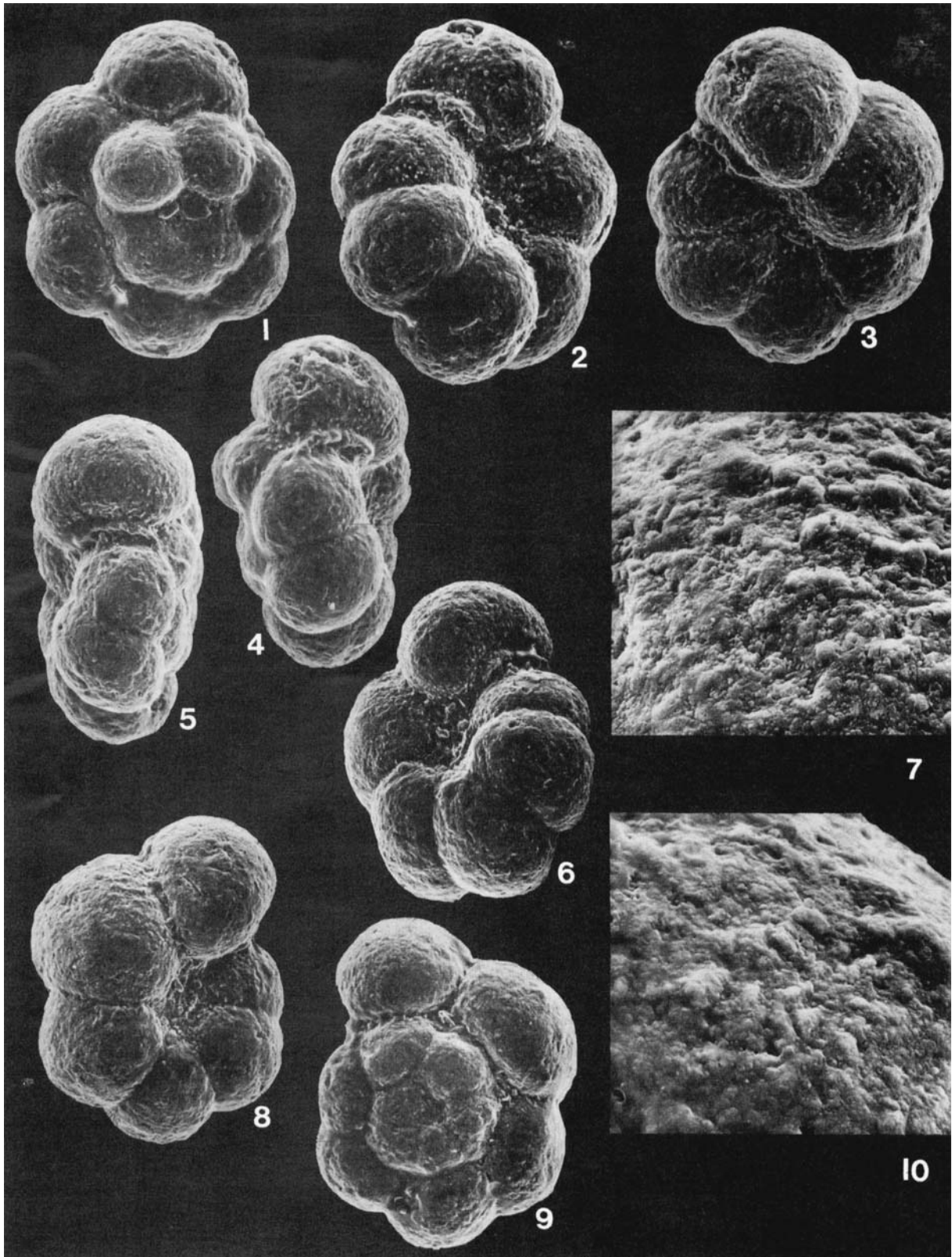
Kretchmar & Gorbachik (*in* Gorbachik, 1986) illustrated only one specimen (the holotype) of *B. praetrocoidea*; we now have many topotypes and near-topotype specimens, with their identity confirmed by the original co-author (T.N.G.). These are metatypes, which allow a fuller description of the species.

It differs from *B. infracretacea* (Glaessner) *occidentalis* BouDagher-Fadel *et al.* (1996) in having more chambers in a whorl, and a larger umbilicus (Pl. 1, figs 2, 3). It is very close morphologically and probably a descendant of *B. infracretacea occidentalis* in the easternmost Vardar geosyncline of Tethys (for palaeoceanography, see Hsü, 1977). *B. hispaniae* (Longoria) has



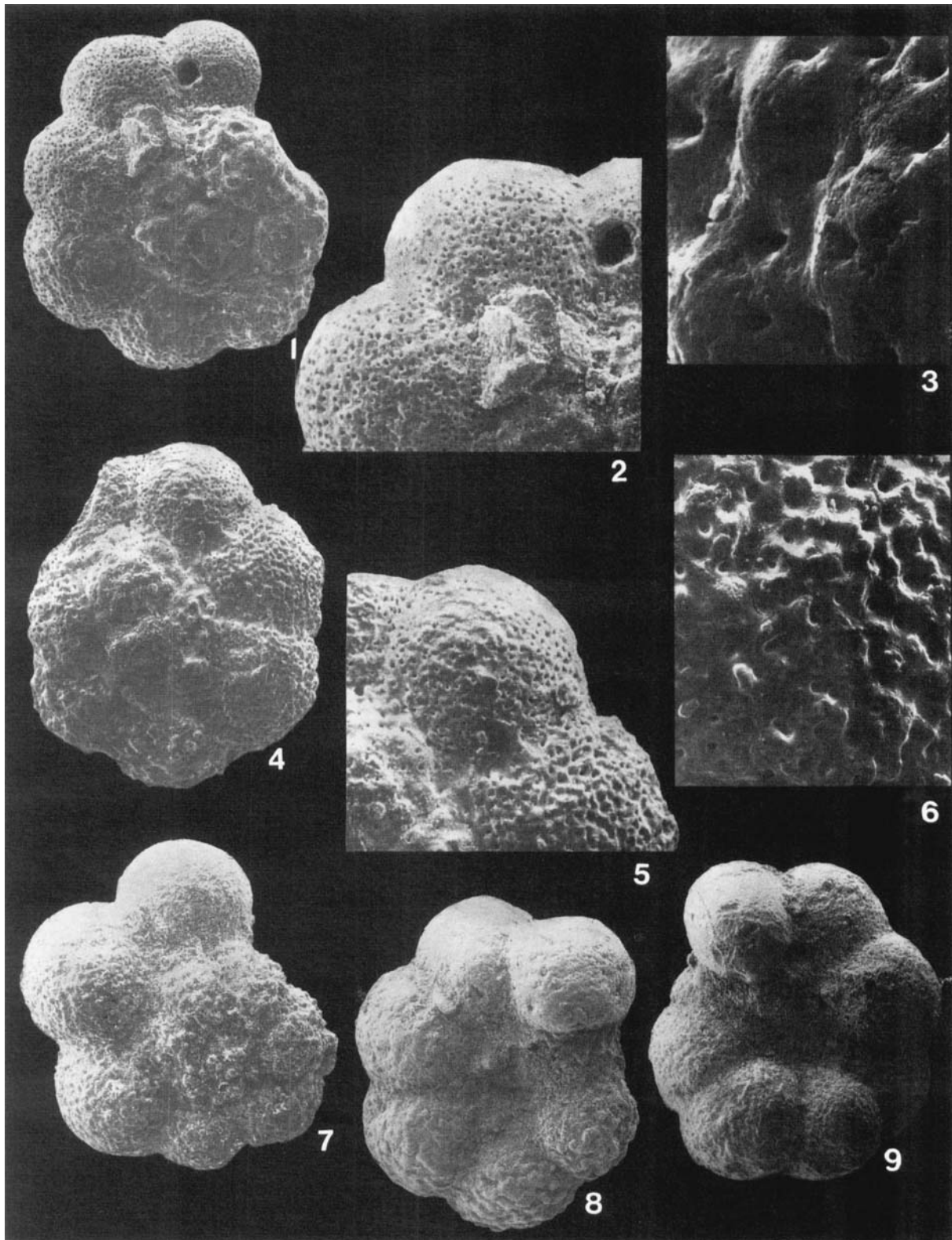
Explanation of Plate 1

Figs 1–3. *Blefuscuiana infracretacea* (Glaessner) *occidentalis* BouDagher *et al.* (1996). Early Aptian, North Sea Well 20/2-2, 8300'. Paratypes: fig. 1, spiral side, $\times 285$; figs 2, 3, umbilical views showing clearly the thin porticus as in *B. praetrocoidea*, $\times 215$. This paratype showing development of incipient perforation mounds on the early chambers of the last whorl emphasizing the relationship of this form to *infracretacea* s.s. BMNH P 52098. P52099. **Figs 4–9.** *Blefuscuiana praetrocoidea* (Kretchmar & Gorbachik). SEM taken in the Environmental Chamber (without coating) of paratypes from the Early Aptian of the Kacha River, SW Crimea. Paratype 4 and 3, respectively: figs 7–9, $\times 213$. Paratype 3: figs 7–9, $\times 213$. 4, 7, spiral views; 5, 8, peripheral views showing clearly the thin porticus; 6, 9, umbilical views showing the narrow umbilicus. Department of Palaeontology, Moscow State University Collection.



Explanation of Plate 2

Figs 1–10. *Blafuscuiana praetrocoidea* (Kretchmar & Gorbachik). Paratypes from the Early Aptian of the Kacha River, SW Crimea. Paratype 2: Figs 1–4, spiral, oblique-umbilical, umbilical and peripheral view (showing clearly the thin porticus), $\times 213$. Paratype 1: Figs 5, 6, peripheral and umbilical views, $\times 213$; 7, enlargement of the last chamber showing a finely perforated wall lacking muricae, $\times 1700$; figs 8, 9, umbilical and spiral views, $\times 213$; fig. 10, enlargement of the last chamber showing a finely perforated wall, $\times 1700$. Department of Palaeontology, Moscow State University Collection.



Explanation of Plate 3

Hedbergella trocoidea (Gandolfi). Figs 1–9, Late Aptian of Crimea, Simferopol: Figs 1, 4, spiral views, $\times 164$; figs 2, 5, enlargement of the last chambers, $\times 819$; figs 3, 6, further enlargement of the surface of the penultimate chamber showing a macroperforated wall, $\times 1700$. Department of Palaeontology, Moscow State University Collection. Figs 7–9, Early Albian of Tunisia: Beauvoir III, sample SS170, fig. 7, spiral view, $\times 150$; sample 114, fig. 8, umbilical view, $\times 177$; Djebel Danamers, sample 403, fig. 9, umbilical view showing the large umbilicus, $\times 160$. BMNH PF 53067-53069, respectively.

a flatter dorsal side and the ventral sides of the latest chambers strongly overhang the umbilicus. *B. praetrocoidea* differs from *Hedbergella trocoidea* (Gandolfi) in being microperforate with a smooth wall, instead of being clearly macroperforate with muricae on the early whorls (see Plate 2). In all other respects the morphological resemblance between *B. praetrocoidea* and *H. trocoidea* is so great that the evolution of the latter from the former is clearly indicated.

***Hedbergella trocoidea* (Gandolfi, 1942)**

(Pl. 3, figs 1–9)

1942 *Anomalina lorneiana* (d'Orbigny) var. *trocoidea* Gandolfi: 99, pl. 2, figs 1a–c; pl. 4, figs. 2, 3; pl. 13, figs 2a, b, 5a, b.

1948 *Globigerina almadenensis* Cushman & Todd: 95, 96, pl. 16, figs 18, 19.

1958 *Hedbergella trocoidea* (Gandolfi); Brönnimann & Brown: 16, 17, text-figs 1a–c.

1959 *Praeglobotruncana rohri* Bolli: 267, pl. 22, figs 5–7.

1965 *Hedbergella planispira* (Tappan); Neagu: 36, pl. 10, figs 1, 2, 4.

1966 *Hedbergella (Hedbergella) trocoidea* (Gandolfi); Moullade: 90–93, pl. 7, fig. 26.

1971 *Hedbergella trocoidea* (Gandolfi); Risch: 47, pl. 4, figs 20–22.

1974 *Hedbergella trocoidea* (Gandolfi); Longoria: 69–72, pl. 17, figs 1–16; pl. 18, figs 3–5.

1977 *Globigerina trocoidea* (Gandolfi); Masters: 475, pl. 25, figs 1–3 (topotypes).

1980 *Hedbergella trocoidea* (Gandolfi); Salaj: 51, 63, figs 11, 13, 18, 19, 20, 23, 57.

1981 *Hedbergella trocoidea* (Gandolfi); Bellier & Chitta: 44, pl. 4, figs 31–33.

1985 *Hedbergella trocoidea* (Gandolfi); Caron: 60, figs 25, 17, 18.

1986 *Hedbergella trocoidea* (Gandolfi); Gorbachik: 93–95, pl. 17, figs 1–5.

1987 *Hedbergella trochoidea* (Gandolfi)(*sic*); Ben Haj Ali: 83, pl. 2, figs 1–3, 9–11.

1991 *Hedbergella trocoidea* (Gandolfi); Altiner: 170, pl. 15, figs 7–12.

1993 *Hedbergella trochoidea* (Gandolfi)(*sic*); Shahin: 423.

Figured specimens. The specimens illustrated in this paper are deposited in the collections of the Department of Palaeontology, Moscow State University and the Department of Palaeontology, The Natural History Museum, London [BMNM], nos PF 53067–53069.

Remarks. *Hedbergella trocoidea* has a large test of about 0.31–0.40 mm. It was described and studied intensively from many different places. The list of synonymic references could be greatly expanded, if need be. Those which we have included are important taxonomically, palaeogeographically or stratigraphically. It is probable that this species has derived from *Blefuscuiana praetrocoidea* in the Late Aptian (Fig. 1) by acquiring muricae over the early whorls and macroperforations all over the test. As in other lineages of the Praehedbergellidae (see M. BouDagher-Fadel *et al.*, 1996) concerning *Blefuscuiana aptiana* (Bartenstein) *s.l.*, *B. aptica* (Agalarova) and *B. infracretacea* (Glaessner) *s.l.*, the chamber shape and coiling method remain constant in the evolution of *Blefuscuiana* into

Hedbergella. The test evolved with an increase of its size, of its perforations (from microperforations to clear macroperforations) and with the appearance of the muricae on an otherwise smooth test.

H. trocoidea also has a cosmopolitan distribution. It ranges from the Late Aptian into the Early Albian (Fig. 1); it may persist locally into the Middle Albian. It was originally described from the Breggia River section of Switzerland by Gandolfi, 1942 (as *Anomalina lorneiana trocoidea*). It has been reported from the probable Lower Cretaceous of California (Cushman & Todd, 1948, as *G. almadenensis*); the Albian of the Maridale Formation of Trinidad (Bolli, 1959, as *Praeglobotruncana rohri*); the Albian of Romania (Neagu, 1965, as *Hedbergella planispira*); from the Late Gargasian to Middle Albian of France (Moullade, 1966); from the uppermost Aptian to Middle Albian of the Bavarian calcareous Alps (Risch, 1971); from the Upper Aptian to the Lower Albian in northern Mexico (Longoria, 1974); from the Late Aptian to earliest Albian (Caron, 1985); from the Aptian and Early Albian of Tunisia (Salaj, 1980; Bellier & Chitta, 1981; Ben Haj Ali, 1987); from the Late Aptian into the Early Albian of Crimea (Gorbachik, 1986); from the Late Aptian of Turkey (Altiner, 1991), and from the Late Aptian of northern Sinai, Egypt (Shahin, 1993). The specimens figured in this study are from the Late Aptian of Crimea and the Early Albian of Tunisia.

CONCLUSIONS

Our studies of early planktonic foraminifera (BouDagher-Fadel *et al.*, 1996) demonstrates that certain taxa are endemic whilst others have different stratigraphical ranges in different basins. *Blefuscuiana praetrocoidea* is only known from the former Soviet Union; *H. trocoidea*, on the other hand, is a cosmopolitan species.

It was postulated (Banner & Desai, 1988) that the small, microperforate smooth species of *Blefuscuiana* lived very near the surface of the ocean, and that their evolution into the larger, macroperforate, muricate species of *Hedbergella* was accompanied by an adaptation to feeding in deeper, subsurface waters. The evolution of the geographically restricted *B. praetrocoidea* to the almost cosmopolitan *H. trocoidea* indicates the occurrence of deeper environments in the Late Aptian–Early Albian, which allowed it to become much more widespread.

Haq *et al.* (1988) indicate that the Aptian–Early Albian was a time of significant eustatic sea-level change. According to their eustatic sea-level chart, major sea-level rises occur at the base of the *Leupoldina cabri* Zone and at the Aptian/Albian boundary. An overall pattern of moderately falling eustatic sea-level in the Aptian is replaced by a pattern of rising sea-level in the Albian, initiated by the transgressive event at the Aptian/Albian boundary. This eventually culminates in the mid-Cretaceous sea-level maxima. The Albian rising sea-level pattern described by Haq *et al.* (1988) may correspond with the spread of deeper environments created by the broadening and deepening of the Proto-Atlantic we postulate to account for the wide distribution of *H. trocoidea*. The radiation and geographic dispersal of true *Hedbergella* may also be related to the cessation of the Aptian oceanic anoxic events documented by Bralower *et al.* (1994). An anoxic or dysoxic water column in the many parts of the World

	<i>Blefuscuiana infracretacea occidentalis</i>	<i>Blefuscuiana praetrocoidea</i>	<i>Hedbergella trocoidea</i>	<i>Ticinella roberti</i>
Maximum diameter (in mm)	0.16–0.20	0.17–0.25	0.31–0.40	0.33–0.50
Number of chambers in last whorl	5–6	6–7	7–8	8–9
Type of perforations	micro	micro	macro	macro
Ratio of umbilical breadth to test diameter	0.11	0.17	0.23	0.25
Accessory apertures	absent	absent	absent	present interportically

Table 1. The comparative morphocharacters of the taxa

Ocean would have prevented the dispersal of hedbergellids and also prevented their preservation.

The Late Aptian is also a time of turnover in the calcareous nanofossil record. Erba (1994) has observed a marked turnover in nannoconid species at the Early Aptian/Late Aptian boundary which she terms the 'nannoconid crisis'. Large nannoconids become extinct and are replaced by new, deeper-water dwelling species. This may relate to the same events noted above which we cite as being responsible for turnover in the planktonic foraminiferal record.

In this paper we follow Gorbachik (1986) in considering the evolution of *Hedbergella trocoidea* stems from *praetrocoidea* in the Aptian. We go further in suggesting that *Blefuscuiana praetrocoidea* (Pl. 1, figs 4–9; Pl. 2, figs 1–10) evolved from *Blefuscuiana infracretacea occidentalis* BouDagher-Fadel *et al.* (see Pl. 1, figs 1–3) (?latest Barremian; Early to within the Late Aptian) and that *Hedbergella trocoidea* (see Pl. 3, figs 1–9) (Late Aptian to Early Albian; ?Middle Albian) was the immediate ancestor of *Ticinella roberti* (Gandolfi) (Late Aptian to latest Albian), the type species of *Ticinella* Reichel (see Fig. 1). This evolutionary trend is best observed in the Early Cretaceous sediments of the Crimea, where all the taxa concerned are present. It is marked by a gradual increase of the size of the test, an increase in the number of chambers in the whorl, an evolution of macroperforations and muricae in *H. trocoidea*, a widening of the umbilicus which reaches its maximum in *T. roberti* where the portici are distally fused forming umbilical accessory apertures (see Table 1). Concomitant with this evolution is an increase in palaeogeographic distribution, so that *T. roberti* and *H. trocoidea* (with its synonym *P. rohri* Bolli) are worldwide, while the ancestor, *B. praetrocoidea*, is known only from an isolated area of northern Tethys in its eastern flank (the Pennine Geosyncline of Hsü, 1977).

Alexander (pers. comm.) studied the cytoplasm and pseudopodia of many living benthic foraminifera and noted that the umbilicus became an extrathalamic digestive zone for ingested nutrient particles; he noted that the characters of the umbilical cytoplasm differed from those of the intrathalamic cytoplasm and pseudopodia, and that the latter had a sharper differentiation when the umbilicus was partly covered by the skeletal structure of broad apertural lips or umbilical plates. Banner & Desai (1988) correlated these interesting findings with the development of umbilical structures in the Globigerinacea, and from this it can be suggested that the broadening of the portici and their subsequent fusion in the *Hedbergella trocoidea*–*Ticinella roberti* evolution results from a skeletally more concealed and bigger digestive zone in the organism's cytoplasm.

This could follow from the ingestion of food particles larger than those ingested by the ancestral *Blefuscuiana* and this would be followed (as suggested in general terms by Banner & Desai, 1988) by the ability of *Hedbergella* and *Ticinella* to thrive in waters deeper than those inhabited by the surface-dwelling *Blefuscuiana*. The increase in depth and probable decrease in the partial pressure of dissolved oxygen could lead to an increase in the size of the test perforations, while the large size of particles demanded their disaggregation by muricae. Certainly the evolution of the macroperforate (and muricate) test led immediately to the occupation of the oceans worldwide.

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