On the evolution of the Hedbergellidae from the Praehedbergellidae

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ABSTRACT – In order to establish the relationship between the smooth, microperforate praehebergellid 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 praehebergellid 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 toptotypes and near-toptotype 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 infraestacea* (Glaessner) *occidentalis* BouDagher *et al.* (1996). Early Aptian, North Sea Well 20/2-2, 8300'. Paratypes: fig. 1, spiral side, ×285; figs 2, 3, umbilical views showing clearly the thin porticus as in *B. praetrocoidea*, ×215. This paratype showing development of incipient perforation mounds on the early chambers of the last whorl emphasizing the relationship of this form to *infraestacea* 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, ×213. Paratype 3: figs 7-9, ×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.
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Figs 1–10. Blefuscuiana praeticoidea (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), ×213. Paratype 1: Figs 5, 6, peripheral and umbilical views, ×213; 7, enlargement of the last chamber showing a finely perforated wall lacking muricae, ×1700; figs 8, 9, umbilical and spiral views, ×213; fig. 10, enlargement of the last chamber showing a finely perforated wall, ×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, ×164; figs 2, 5, enlargement of the last chambers, ×819; figs 3, 6, further enlargement of the surface of the penultimate chamber showing a macroperforated wall, ×1700. Department of Palaeontology, Moscow State University Collection. Figs 7–9, Early Albian of Tunisia: Beauvoir III, sample SS170, fig. 7, spiral view, ×150; sample 114, fig. 8, umbilical view, ×177; Djebel Danamers, sample 403, fig. 9, umbilical view showing the large umbilicus, ×160. BMNH PF 53067-53069, respectively.
a flatter dorsal side and the ventral sides of the latest chambers strongly overhang the umbilicus. B. praetrocoida 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. praetrocoida 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 lornei ana* (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); Brønnimann & 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 (toptotypes).

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); 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); 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 *Blefusciuana praetrocoida* 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 *Blefusciuana aptiana* (Bartenstein) s.l., *B. aptica* (Agalarova) and *B. infracretacea* (Gläsner) s.l., the chamber shape and coiling method remain constant in the evolution of *Blefusciuana* 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 lornei ana 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. *Blefusciuana praetrocoida* 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 *Blefusciuana* 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. praetrocoida* 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
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 nannofossil 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 nannoconoids 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 trooidea stems from praetrocoidae in the Aptian. We go further in suggesting that Blefuscuiana praetrocoidae (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 trooidea (see Pl. 3, figs 1–9) (Late Aptian to Early Albian; ?Middle Albian) was the immediate ancestor of Ticinella roberti (Gandolli) (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 Crimean, 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 muricace in H. trooidea, 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. trooidea (with its synonym P. rohri Bolli) are worldwide, while the ancestor, B. praetrocoidae, is known only from an isolated area of northern Tethys in its eastern flank (the Pennine Geosyncline of Hsi, 1977).

Alexander (pers. comm.) studied the cytoplasm and pseudopodia of many living benthic foraminifera and noted that the umbilicus became an extrathalamous digestive zone for ingested nutrient particles; he noted that the characters of the umbilical cytoplasm differed from those of the intrathalamous 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 trooidea–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 muricace. Certainly the evolution of the macroperforate (and muricate) test led immediately to the occupation of the oceans worldwide.

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| Table 1. The comparative morphocharacters of the taxa |
|-----------------------------------------------|
| **Blefuscuiana infracretacea occidentalis** | **Blefuscuiana praetrocoidae** | **Hedbergella trooidea** | **Ticinella roberti** |
| 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 | present interportically |
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