The evolution of Early Cretaceous Dorothiinae (Foraminiferida)

DAMINI DESAI & F. T. BANNER
Department of Geological Sciences, University College London,
Gower Street, London WC1E 6BT

ABSTRACT—Dorothia and Marssonella are ataxophragmiacean genera typically possessing canaliculate walls. They are believed to have evolved independently from noncanaliculate Praedorothia gen. nov. and Protiomarssonella gen. nov. of Early Cretaceous time.

INTRODUCTION
High spired Ataxophragmiacea have long been considered to possess agglutinated, noncanaliculate walls (e.g. Loeblich & Tappan, 1984, p. 14). However, it has more recently been shown (Banner & Desai, 1985) that initially triserial genera (Clavulinoides Cushman, Valvulina d’Orbigny, Clavulinopsis Banner & Desai etc.) independently develop canaliculate walls in their evolution from noncanaliculate ancestors, during or at the end of the Late Cretaceous. Gaudryina bulletta Carsey was designated by Plummer (1931) as the type species of her new genus Dorothia, the main point of distinction being that Dorothia contains “more than three” chambers in the initial part of the test. This multiserial group is studied, in this paper, for its canaliculation.

Topotypes of D. bulletta were figured by Loeblich & Tappan (1964) from Texas (Onion Creek, Texas). Hofker (1969) studied specimens of D. bulletta from the type level (Navarro); his figures (1969, p. 31, fig. 69) show clearly that the agglutinated walls are distinctly canaliculate. Loeblich & Tappan (1985, p. 201–202, pl. 12) again showed that Dorothia Plummer exhibits a finely canaliculate wall. Hofker (1969) also observed the canaliculate nature of the wall in D. pupoides (Reuss) from the Santonian. We are able to confirm this canaliculate structure in Dorothia pupa (Reuss), from the Campanian chalk of Norfolk. D. pupa depressa (Barnard & Banner) and D. pupa s.s. both show (Pl. 1. figs. 2a–d) tightly packed, subparallel canaliculi regularly developed in the wall of all chambers from the first whorl to the last (Pl. 1. fig. 2b).

Hofker (1976) showed that Recent D. curta (Cushman) and D. scabra (Brady) were also canaliculate (1976, p. 184–87, figs. 51–52). Again, we are able to confirm the canaliculate nature of Recent species of Dorothia. Plate 2 illustrates essentially similar developments of canaliculi in the walls of three different species from Recent Caribbean sediments deposited from the upper slope to the bathyal.

Gaudryina oxycona was designated as the type species of his new genus Marssonella by Cushman in 1933. Many authors (e.g. Trujillo, 1960; Loeblich & Tappan, 1964) believed that Marssonella Cushman and Dorothia Plummer are synonyms and Marssonella, being the junior synonym, should be disused. However, for the reasons given by Barnard & Banner (1980, p. 391, 392) and by Bartenstein et al. (1971, p. 131). Marssonella should be distinguished from Dorothia at generic level. All of the group of species which can be referred to Marssonella have concave or flat septa, and have an evolution into Pseudotextulariella in the Early Cretaceous (to Cenomanian). In contrast, the group of species which relate to Dorothia have convex septa and persist to the Recent, not being internally complex until the Campanian (Mantanzia). Specimens of Marssonella oxycona (Pl. 3. figs. a–i) are here shown to possess walls which are canaliculate with a very distinctive “keriothecal” structure (Pl. 5. figs. g–i). This is the first time this pronounced structure has been observed in the Ataxophragmiacea, and is quite different from the wall structure seen in species of Dorothia, be they obtained from the Late Cretaceous (Pl. 1) or from the Recent (Pl. 2).

We are now able to show, however, that not all species which have been referred to the genera Dorothia or Marssonella possess canaliculate walls. Species described below, from the Early Cretaceous, may have solid walls, with no trace of canaliculations. These are worthy of distinction at generic level, although we would not go so far as to separate them into a distinct family. When Loeblich & Tappan (1985) reviewed the systematic position of Dorothia, they referred the genus (and the subfamily Dorothiinae) to the family Eggerellidae because of the canaliculate wall in the type species of both Dorothia and Eggerella. However, the fact that canaliculate walls develop independently in different lineages (Banner & Desai, 1985) and the fact that it may be difficult to recognise
the early evolutionary development of such walls, indicate that it is unwise in practise and improper in
taxonomy to separate canaliculate and noncanaliculate
genera (which are otherwise similar) into different,
high-category, suprageneric groups. The noncanalicu-
late species are here referred to the new genera
*Pradedorothia* and *Protomarssonella*, which are defined,
described and discussed below. We believe them to be
directly ancestral to the respective canaliculate
*Dorothia* and *Marssonella* of younger sediments.

The diagnosis given by Loeblich & Tappan (1984) to
distinguish between the superfamilies *Verneuilinacea*
Cushman, *Ataxophragmiacea* Schwager and *Textulari-
iaea* Ehrenberg cannot be maintained. Loeblich &
Tappan (*op. cit.*) defined all of the *Verneuilinacea* (includ-
ing the family *Textulariopsidae*), as well as all of the
*Ataxophragmiacea* (including the *Dorothiidae*), as
being noncanaliculate, distinguishing them on this
supposedly primary character from the canaliculate
*Textulariacea* (including the biserial *Textulariidae* and
the initially triserial *Valvulinidae*). Not only have
terminally uniseria
canalicate genera (e.g. *Clavulinoides* and *Clavulinopsis*) evolved independently within
the *Verneuilinacea*, wholly triserial forms may also
have become canaliculate. An example of this last
situation is a species obtained from the Early Aptian of
D.S.D.P. site 398 (Pl. 4, figs. 1a–1b) which is
externally a *Verneulinina* but which is canaliculate.
This is the earliest evolution of canaliculation in the
*Verneuilinidae* yet known to us (compare Banner & Desai,
1985, p. 87–89) and the species predates solid walled
true *Verneulina* of the Late Cretaceous. This confirms
that wall canaliculation has evolved independently at
different times in several generic groups and cannot be
taken to be a primary phyletic character.

Therefore, it is proposed that the superfamilies
discussed here should be redefined as follows:

**Superfamily Verneuilinacea:** essentially triserial, some-
times becoming biserial or even uniserial with growth.
To include the families *Verneuilinidae* Cushman (1911)
(wall solid or canaliculate or both; aperture single with
no distal tooth), *Valvulinidae* Berthelin (1880) (wall
canaliculate, with distal tooth and toothplate) and
*Chrysalidinidae* Neagu (1968) (wall solid or canalicu-
late; aperture areal and multiple; with internal pillars).

**Superfamily Ataxophragmiacea:** essentially polyserial
(four or more chambers initially) sometimes reducing to
biseriality or uniseriality; wall solid or canaliculate;
aperture sometimes with a lateral tooth but not with a
distal tooth or internal toothplate. To include the
families *Ataxophragmiidae* Schwager (1877),
*Dorothiidae* Balakhmatova (1972) and *Eggerellidae*
Cushman (1937).

**Superfamily Textulariacea:** essentially biserial (occas-
ionally with a third chamber in the very first whorl);
wall canaliculate (as in the *Textulariidae*) or solid (as in the
*Textulariopsidae*). Also here can be accommodated
the families *Plectorecurvoididae*, *Pseudobolivinidae*
and *Nouriidae*.

**MATERIALS**

For the purposes of this paper we have used material
which has been collected from the following localities:-
1. Speeton, North Yorkshire, England; the Speeton
Clay outcrop is on the coast of the southern part of
Filey Bay, where Cretaceous beds from Berriasian
to Aptian age are exposed in the cliff and on the
foreshore. The section was collected on three
occasions (once under the guidance of Dr. P. F.
Rawson) using the stratigraphy described by Kay
(1964), Rawson (1971), Rawson and Mutterlose
(1983), Fletcher (1969) and Neale (1960, 1962).

---

**Explanation of Plate 1**

Figs. 1a–1e. *Dorothia moorbergensis* sp. nov. All samples MO.17, Early Hauterivian.

*Fig. 1a*, holotype (×115); figs. 1b–1e, cut specimens showing structure: fig. 1b, longitudinal cut, chambers
partly empty, partly calcite infilled, showing inner perforations of the chamber walls, but solid septa; fig. 1c,
longitudinal cut showing convex septa (×265); fig. 1d, enlargement (×665), showing canaliculate, internally
perforate chamber walls; fig. 1e, internal view of an empty chamber showing canaliculate walls and inner
calcareous lining, internally sealing some of the perforations (×665). BM(NH) Holotype: P 52036, Paratype:
P 52037.

Figs. 2a–d. *Dorothia pupa* (Reuss) *sensu lato*. All from the Campanian (*Belemnitella mucronata* zone Chalk),
Norwich. These are the same specimens used by Barnard & Banner, 1953, p. 191.

Figs. 2, 2b, *Dorothia pupa depressa* Barnard & Banner from Harford Bridges, Norwich (Rowe 161); fig. 2a,
whole syntype broken to show convex septa (×45); fig. 2b, initial end, acid stripped showing coiling,
canalicate walls, solid septa (×120); figs. 2c, 2d, *D. pupa sensu stricto* from Council's pit, Newmarket Road
(Rowe 158); broken chambers showing canalicate walls (×625 and ×750 respectively).
Evolution of Early Cretaceous Dorothiinae
2. Moorberg near Sarstedt, N.W. Germany. The locality, lithostratigraphy and cephalopod zonation of this exposure has been described by Mutterlose (1984, p. 40–44). The samples were collected by Dr. J. A. Crux and Dr. M. Partington (British Petroleum Company) under the guidance of Dr. J. Mutterlose.

3. Orosei, Sardinia. The Valanginian exposure of Badde Funtana Morta (Orosei) has been described by Dieni and Massari (1985, p. 207–211) and was collected under the guidance of Dr. I. Dieni.

4. The Cretaceous Chalk of Norfolk as collected by A. W. Rowe. Rowe collected the zones of the Norfolk Chalk during 1903–11, and although much of his work remains unpublished his localities have been used for outcrop stratigraphy (Peake & Hancock, 1961) and his irreplaceable collection was made available by Prof. T. Barnard (see Barnard & Banner, 1953, p. 210–211).

5. The Recent sediments of the Caribbean Sea: samples in the curation of the British Museum (Natural History) kindly made available by Dr. C. G. Adams.

6. Core subsamples from D. S. D. P. site 398 (Leg 47b) Vigo Seamount off the west coast of Portugal (see Sibuet et al., 1979).

SYSTEMATIC DESCRIPTIONS
Superfamily Ataxophragmiacea Schwager, 1877
Family Dorothiidae Balakhmatova, 1972
Subfamily Dorothiinae Balakhmatova, 1972

Genus Dorothia Plummer, 1931 emend.

Type species: Gaudryina bulletta Carsey, 1926.

Emended Diagnosis. Early stage trochospiral, with 4 or more chambers to a whorl, later stage reduced to biserial; wall agglutinated, may be of calcareous particles; aperture an interiomarginal slit; septa convex throughout; chamber walls (and sometimes the septa) canaliculate.

Dorothia moorbergensis sp. nov. (Pl. 1, figs. 1a–1e)

Description. This species has a finely agglutinated wall with calcareous cement, smooth both exteriorly and interiorly but penetrated by fine canaliculi which open into the interior of the chambers but which are sealed exteriorly by a very thin imperforate granular layer (approximately equal in thickness to the lining of the chamber interiors). The septa appear to be partly or wholly noncanaliculate. The initial trochospiral part of the test has about four chambers in the earliest whorls, rapidly reducing to three per whorl; it is circular in cross-section and relatively rapidly tapering (apical angle about 50°). The biserial part tapers much more slowly (angle of taper about 15°) and contains chambers which are almost as high as they are broad; as in the holotype, three pairs of biserial chambers comprise about 2/3 of the total test length. The apertural and

Explanation of Plate 2

Modern species of Dorothia from Recent sediments of the Caribbean Sea. (All specimens by courtesy of the British Museum, Natural History). All specimens have been dissected and their destruction has precluded their subsequent curation.

These three species all possess the convex septa of Dorothia (compare Pl. 1, fig. 2a) but include the closest gross homeomorphs of Marssonella available for study from Recent material.

Figs. 1a–c. Dorothia pseudoturris (Cushman) from 2,050 fathoms, 21°17’N, 83°06’W: fig. 1a, whole specimen (×40); fig. 1b, longitudinal cut of biserial portion (same specimen) showing convex solid septa and canaliculate walls partly covered by an external agglutinated crust (×65); fig. 1c, detail of 1b enlarged (×120).

Figs. 2a–b. Dorothia caribaea Cushman from 190 fathoms, 22°12’N, 81°10’W: fig. 2a, whole specimen (×45); fig. 2b, same specimen broken to show irregularly canaliculate wall (×130).

Figs. 3a–b. Dorothia bradyana Cushman from 300 fathoms, 23°21’N, 79°58’W: fig. 3a, whole specimen (×38); fig. 3b, same specimen, broken to show densely canaliculate wall and internal perforations (×325).
Evolution of Early Cretaceous Doro thiinae
terminal faces (like the septa) are convex: the terminal face meets the chamber sides at a bluntly rounded obtuse angle. The interio-marginal aperture is a low, narrow, opening, which can become laterally constricted and subrounded.

**Type locality.** Bed 86 (of Mutterlose, 1984). Early Hauterivian, *regale* zone, Moorberg (Sample Mo-17).

**Holotype.** BM(NH) no. P 52036 (Pl. 1, fig. 1a). Length 0.46mm, width 0.15mm.

**Comparative diagnosis.** *Dorothia moorbergensis* possesses distinctly convex septa throughout growth and is therefore distinguishable from all species of *Protomarssonella* and *Marssonella*. It possesses a canaliculate wall which distinguishes it from all species of *Praedorothia*. *D. moorbergensis* is readily distinguished from *D. bulletta*, *D. pupa* and *D. pupoides* but its very high biserial chambers (almost as high as broad) compared with the much lower chambers of the biserial portion of the Late Cretaceous species.

**Remarks.** This appears to be the geologically oldest known species of true, canaliculate *Dorothia* Plummer. It has probably descended from *Praedorothia* sp. but its ancestry is not yet fully known.

**Distribution.** This species is found from the mid-Early Hauterivian the late-Early Hauterivian beds of Moorberg (N.W. Germany). *D. moorbergensis* is found in bed 97 (*noricum* zone) of Mutterlose (1984) as well as in the holotype horizon where the specimens become abundant.

**Type species.** *Dorothia praehauteriviana* Dieni & Massari, 1966, here designated.

**Diagnosis.** The chamber arrangement, septal form and apertures are similar to *Dorothia* as here emended, but the agglutinated wall is solid, not canaliculate.

**Praedorothia praehauteriviana** (Dieni & Massari) (Pl. 4, figs. 2a–2d)

1966 *Dorothia praehauteriviana* Dieni & Massari: 108, pl. 2, figs. 23a–24b; pl. 10, figs. 9–13.

1972 *Dorothia praehauteriviana* Dieni & Massari; Luterbacher: 562, pl. 1, figs. 20, 24; pl. 5, figs. 7, 8.

1984 *Dorothia praehauteriviana* Dieni & Massari; Moullade: 450, pl. 7, figs. 12–13, 16–18.

1985 *Praedorothia praehauteriviana* Dieni & Massari; Kuznetsova & Gorbachik: 88, pl. 5, figs. 1–1b.

**Remarks.** Moullade (1984) reviewed the published references to "D. praehauterivian" and excluded the citations by Neagu (1972) and Sliter (1980) (their figures were reproduced in Moullade, 1984, pl. 7 figs. 11, 12–13, respectively); in the taxonomy employed in this paper, those references would be to *Protomarssonella*, and not even to *Praedorothia*, because of their flat to concave septa. The specimens figured here, in this paper, are virtual topotypes and are included to enable reliable comparison to be made with the other species recorded. The wall is solid (Pl. 4, fig. 2b, d).

**Distribution.** This very cylindrical *Praedorothia* dominates the pre-Hauterivian dorothiid assemblage. The figured specimens (Pl. 4, figs. 2a–d) were obtained from the type locality (Orosei, Sardinia) and are dated as Late Valanginian (Dieni & Massari, 1966). Moullade (1984) and Luterbacher (1972) confirm the Early Valanginian to Late Valanginian occurrence of this species from various DSDP cores. Kuznetsova & Gorbachik (1985) recorded "D. praehauteriviana" from the Tithonian of the Crimea; without study of their specimens it is difficult to assess this identification but their drawing suggests that they have misidentified a species of a *Protomarssonella*.

---

**Explanation of Plate 3**

Figs. a–i. *Marssonella oxyconu* (Reuss); type species of *Marssonella* Cushman; all specimens from the Campanian (*Belemnitella mucronata* Chalk), Burgh, Norfolk, England (Rowe locality 163).

Fig. a, whole specimen (×90), with outer crust partly eroded from later chambers, revealing the canaliculate wall; fig. b, initial end acid stripped (×230), showing solid septa; fig. c, broken biserial stage showing canaliculate wall and fibrous structure of the septa (×210); fig. e, detail of the fibrous wall (note the thin outer "crust", top right) (×1,333); fig. f, enlargement of fig. c, showing inner chamber surface with internal perforations and the inner end of the fibrous units (×625); fig. g, enlargement of the broken wall and inner chamber surface, showing the longitudinal fibrous structure (×1,135); fig. h, the "keriothecal" structure of the canaliculate fibrous wall (×1,025); fig. i, enlargement of fig. h (×5,625).
Praedorothia praeoxycona (Moullade)  
(Pl. 4, figs. 3a–e)

Dorothia praeoxycona Moullade, 1966, p. 30, pl. 3, figs. 8–11, pl. 10, figs. 7–9.  
Dorothia praeoxycona Moullade; Gorbachik, 1971, p. 138, pl. 3 (23), fig. 1.  
Dorothia praeoxycona Moullade; Luterbacher, 1975, p. 716, pl. 4, figs. 10–14.  
Marssonella praeoxycona (Moullade); Bartenstein & Bolli, 1977, p. 548, pl. 1, figs. 25–26.  
Marssonella praeoxycona (Moullade); Bartenstein & Kovatcheva, 1982, p. 631, pl. 1, figs. 20–21.  
Dorothia praeoxycona Moullade; Moullade, 1984, p. 460, pl. 9, figs. 12–15, pl. 10, figs. 14–15 (Holotype and paratypes refigured).  

Remarks. Scanning micrographs (Pl. 4, figs. 3d–e) can confirm the noncanaliculate character of the walls of this species. This species is characterised by the exaggerated inflation of the chambers of the last two whorls, which is clearly shown in our specimens.

Distribution. Moullade (1984) reviewed some of the published records of "D". praeoxycona and supposed that this species evolved from and replaced "D". hauteriviana at the base of the Barremian. Our specimens were obtained from well dated Hauterivian (Speeton, bed C4, gottschei zone of Rawson, 1971) so this evolution, if it happened, must have occurred before Barremian time. Luterbacher (1975, p. 707) recorded "D". praeoxycona from a horizon referred to either Barremian or Hauterivian.

Praedorothia zedlerae (Moullade) luterbacheri  
subsp. nov.

1966 aff. Dorothia zedlerae Moullade: 2, pl. 2, figs. 9–11.

1975 Dorothia zedlerae Moullade; Luterbacher: 715, pl. 4, figs. 15–16.  
1975 Dorothia zedlerae Moullade; Neagu (In Moullade 1984, p. 458, pl. 8, figs. 15, 16).  
1984 Dorothia zedlerae Moullade; Salaj: 593, pl. 1, fig. 10.

Diagnosis. The test of Praedorothia zedlerae luterbacheri n. subsp. is similar to that of P. zedlerae (Moullade) s.s. but the biserial chambers are lower, being markedly broader than high, especially towards the apertural end of the test, and are strongly overlapping. The septa and the terminal faces are less convex and are sometimes somewhat flattened near the apertural face, which is lower and less steep than in P. zedlerae s.s.

Remarks. The morphological difference between P. zedlerae s.s. and P. zedlerae luterbacheri parallels that between Dorothia pupa (Reuss) and D. pupa depressa Barnard & Banner (1953, p. 191, pl. 8, figs. 3, 4, text fig. 4b–4c) from the Campanian of Europe. The holotype and paratypes of P. zedlerae luterbacheri were obtained from DSDP, site 398, core 104–2, at an horizon dated by Sigal (1979) as Late Aptian. Luterbacher (1975) obtained his figured specimen from DSDP site 306, core 19, dated by him as Barremian or Early Aptian (on very limited planktonic foraminiferal evidence). Salaj (1984) obtained his figured specimen from outcrop of Djebel Oust, Tunisia, dated by him as Early Hauterivian. This may contrast with the known range of P. zedlerae s.s., which has been stated to be Late Valanginian to Early Barremian (Luterbacher, 1975).

Genus Marssonella Cushman, 1933 emend.

Type species. Gaudryina oxycona Reuss, 1860.

Emended Diagnosis. Early stage trochospiral, with four or more chambers to a whorl, later stage reduced to

Explanation of Plate 4

Figs. 1a–b. “Verneuilina” sp. A, D.S.D.P. 398, Core 104–2 Late Aptian; fig. 1a, whole specimen (× 100); fig. 1b, broken wall of another specimen showing canaliculi and internal perforations (× 665).

Figs. 2a–2d. Praedorothia praehauteriviana (Dieni & Massari), Orosee, Sardinia, Late Valanginian: figs. 2a, 2b, whole specimens (initial end of 2a is missing) (× 100 and × 375 respectively); figs. 2cm 2d, broken specimens showing solid, noncanaliculate wall and septa (× 75 and × 375 respectively).

Figs. 3a–3e. Praedorothia praeoxycona (Moullade), sample SC6831, Hauterivian (Bed C4, gottschei zone of Rawson, 1971): fig. 3a, lateral view (last chamber damaged) (× 175); figs. 3b, 3c, initial ends (3b, microspheric? 3c, megalospheric?) (both × 233); figs. 3d–e, broken specimens showing coarsely agglutinated, solid walls (× 1,166 and × 875 respectively).
biserial; wall agglutinated, may be of calcareous particles; aperture an interiomarginal slit; septa flat or concave; wall canalicate.

Remarks. Reuss (1860, p. 229) described *Gaudryina oxycona* but designated no holotype or type locality for his species. In consequence, the species name has been loosely used for forms of *Marssonella* which have been retrieved from Cretaceous strata over the whole age-range of the outcrops from which Reuss obtained his collections. These outcrops included “Hilgenberg bei Hamm und Drensteinfurth” (*mucronata* chalk, Campanian) and others in the Early Senonian, Turonian, Carnian and Upper Gault. As we show in this paper that there are significant structural differences in the Dorothiidae between stages of the Cretaceous, it is necessary to restrict the concept of *Marssonella oxycona* (Reuss). The original collections made by Reuss from the Westphalia Chalk prior to 1860 cannot be located and must be presumed to be lost. We here designate the type locality as Hilgenberg, between Hamm and Drensteinfurth (about 30 km south-east of Münster, Westphalia, German Federal Republic of Germany). This designation is in full accord with the opinion expressed by Cushman (1937, p. 57) that this may be taken as the type locality. The age of the *mucronata*-chalk at this locality is Campanian and is very close to that of the *mucronata* chalk of the area of Norwich (Norfolk, England) from which we have obtained our comparative material.

The specimens of *M. oxycona* from the *mucronata* chalk of Burgh, Norfolk, which have been studied for this research, show that the calcium carbonate of the chamber lateral walls is morphologically a set of elongate grains rigorously arranged perpendicularly to the inner chamber surface (Pl. 3, figs. c and e), externally coated by a crust of equidimensional, randomly arranged grains. This is a structure similar to that previously observed in *Verneuilina tricarinata* d’Orbigny (Banner & Desai, 1985, pl. 3) but as yet unknown in either *Dorothyia* or *Praedorothia*. However, in *Marssonella oxycona* (but not observed in *V. tricarinata*), canaliculi are regularly developed between the aligned carbonate columns of the chamber walls (Pl. 3, figs. c, f and g). The canaliculi are closed externally by the outer crust, but open into the chamber lumen over the whole of the inner surface of the lateral chamber walls. Where the crust is abraded, the caniculi become exposed to the exterior (Pl. 3, fig. a). The terminal face and septa are as fibrous as the lateral chamber walls (Pl. 3, figs. d and h) but do not possess canalici; confinement of the canaliculi to the lateral chamber walls is common in Verneuilinids and Valvulinids (e.g. Banner & Desai, 1985, pl. 1, fig. 9; Banner & Pereira, 1981) but this structure is newly described for the genus *Marssonella*.

We report below on the structures of species from the Early Cretaceous which possess the test form, coiling mode and chamber shape of *Marssonella* but which have solid walls, lack both grain alignment and canaliculi, and which we here distinguish as *Protomarssonella* n. gen.

The genus *Marssonella* Cushman ranges from the Late Cretaceous to Paleocene or Early Eocene; e.g. *M. oxycona floridana* Applin & Jordan was first recorded from the Velasco Formation (Late Paleocene) and *M. lodoensis* Israelsky has its type horizon in the Lodo Formation of California, which may be as young as Early Eocene. Other species which are stratigraphically younger may not be referable to *Marssonella*, e.g., *M. keijzeri* van Bellen, from the Middle Eocene of the Netherlands, has a broad valvuline-like tooth and *M. alisauralis* Poag, from the Alabama, appears to be triserial throughout.

---

**Explanation of Plate 5**

Figs. 1a–1d. *Praedorothia zedlerae* (Moullade) *luterbachi*eri subsp. nov. All from D.S.D.P.398, Core 104–2, Late Aptian: figs. 1a, b, whole specimens (×50); fig. 1c, initial end (×75); fig. 1d, broken specimen showing initial stage and solid, noncanaliculate walls and septa. Fig. 1a is holotype (BM(NH) P 52038).

Figs. 2a–2e. *Protomarssonella kummi* (Zedler). All from sample SC6831, Hauterivian (Bed C4, *gottschei* zone of Rawson 1971): fig. 2a, whole specimen (×175); fig. 2b, initial stage (×375); figs. 2c–e, cut specimens showing wall structure: fig. 2c, longitudinal cut (×315); fig. 2d, empty chamber and its solid, pitted but imperforate wall (×875); fig. 2e, enlargement showing the agglutinated, solid, noncanaliculate wall (×2,190).

Figs. 3a–3d. *Protomarssonella hechti* (Dieni & Massari), topotypes, Orosei, Sardinia, Late Valanginian: fig. 3a, whole specimen (×175); figs. 3b–3d, cut specimens showing wall structure: fig. 3b longitudinal cut (×265); fig. 3c, detail of solid, noncanaliculate wall (×2.044); fig. 3d, solid, agglutinated wall and septum (×875).
Genus **Protomarssonella** nov.

**Type species.** *Protomarssonella hechti* = *Dorothia hechti* Dieni & Massari, 1966, here designated.

**Diagnosis.** Coiling mode, septa and apertures as in *Marssonella* Cushman here emended, but the agglutinated wall is solid, not canalicate.

**Remarks.** This genus differs from *Marssonella* just as *Praedorothia* differs from *Dorothia*. Each of these genera contains a distinct group of species and each characterises a distinct stratigraphical interval. For the reasons noted above (in the Introduction), the differences in wall structure are not regarded as of suprageneric significance.

*Protomarssonella* may occur in beds as old as Late Jurassic (e.g., *“Marssonella” donesiana* Dain, as figured by Luterbacher, 1972 (Pl. 1, figs. 16, 17); the specimens called *“Dorothia praehauteriviana”* Diena and Massari”, obtained by Kuznetsova & Gorbachik, 1985, from the Early Tithonian, are, as noted above, also referable to a (new) species of *Protomarssonella*, and is shown below to be well established in Early Cretaceous time.

*Protomarssonella hechti* (Dieni & Massari)  
(Pl. 5, figs. 3a–3d)

1966 *Dorothia hechti* Dieni & Massari: 106, pl. 52 (2), figs. 17a–22b.

1971 cf. *Marssonella kummi* Zedler; Bartenstein, Beltenstaedt & Kovatcheva: 130–131, pl. 1, fig. 2. cf. *Marssonella kummi* Zedler; Bartenstein & Kaever, 1973, pl. 6, fig. 105.

1984 cf. *Dorothia kummi* (Zedler); Moullade: pl. 8, figs. 2–3 (after Sliter, 1980), figs 7–8 (after Neagu, 1975).

1984 *Dorothia cf. kummi* (Zedler); Moullade: pl. 8, figs. 5–6.

**Remarks.** Topotype specimens of this species, obtained from the Late Valanginian of Orosei, Sardinia, show it to possess solid, noncanaliculate, agglutinating walls.

*P. hechti* differs from *P. kummi* in its regularly tapering, conical test, very weakly depressed or flush sutures, and more depressed chambers.

**Distribution.** The primary types of this species, like the topotypes figured here, are from the Late Valanginian of Sardinia. Bartenstein & Kaever (1973) and Bartenstein et al. (1971) recorded “*M. kummi*” from the Valanginian to Middle Barremian; they included specimens referable to *P. hechti* in this identification and the specimen figured by Bartenstein et al. (1971) (correctly identifiable as *P. hechti*), was obtained from the Barremian of Bulgaria, confirming that range for this species.

1946 *Gaudryina oxycona* Reuss; ten Dam: 572, pl. 87, figs. 9a, b (*non* Reuss, 1860).

1961 *Marssonella kummi* Zedler: 31, pl. 7, fig. 1.

1966 *Dorothia kummi* (Zedler); Dieni & Massari: 107, pl. 2, fig. 16 (not fig. 15).

1977 *Marssonella kummi* Zedler; Bartenstein & Bolli: 548, pl. 1, figs. 23–24.

1984 *Dorothia kummi* (Zedler); Moullade: pl. 7, figs. 19–20 (after Zedler, 1961), figs. 23–24, NOT figs. 21–22 (after Dieni & Massari, 1966).

1986 *Marssonella kummi* Zedler; Lott, Fletcher & Wilkinson: fig. 4R.

**Remarks.** In her original diagnosis of *Marssonella kummi*, from the Early Hauterivian of Germany, Zedler (1961, p. 32) particularly noted the “Miindung feld konkav”, proving this species to be marssonellid and not dorothiid. Dieni & Massari (1966) figured two specimens from the Valanginian of Sardinia; although both were placed in the synonymy of *M. kummi* by Moullade (1984, p. 448), only one of these (1984, pl. 2, fig. 16) has the characteristically concave apertural face of a marssonellid. The other specimen (Dieni & Massari, 1966, pl. 2, fig. 15) has the convex apertural and terminal face of a *Praedorothia* sp. It is an example of the lack of distinction between dorothiid and marssonellid forms which has led to much confusion in the taxonomy of this group.

*Protomarssonella kummi* has the solid walls characteristic of this new genus. This is observed in specimens from the Hauterivian of the Speeton Clay. *P. kummi* possesses a narrowly and slowly tapering, subconical test with very weakly depressed sutures. *P. hechti* (described above) differs in its more broadly conical, more rapidly and regularly tapering test and more depressed chambers.

**Distribution.** The primary types of *P. kummi* were obtained by Zedler from Late Valanginian to Early Hauterivian of Germany; Dieni & Massari’s specimens came from the Late Valanginian of Sardinia. The specimens figured here were obtained from the Hauterivian of Speeton as were the specimens obtained by Lott et al. (1986).

**DISCUSSION**

New evidence has been presented here to modify previously published opinions about the Early Cretaceous evolution of the Dorothiinae; e.g., Moullade (1984) suggested a phylogeny very different from that proposed here (Fig. 1). This paper distinguishes marssonellid from dorothiid tests and recognises the development of canaliculations in the walls of both of
Evolution of Early Cretaceous Dorothiinae

The stratigraphic succession suggests that *Protomarssonella kummi* either descended from *P. hechti* or that they both had a common ancestor in the Berriasian or E. Valanginian. The succession of species of *Praedorothia* suggests the evolutionary sequence *P. praehauteriviana* to *P. praexoxycona* to *P. zedlerae*, as depicted on figure 1. *Dorothia moorbergensis* n. sp. is now the oldest known true *Dorothia*, and its Early-Middle Hauterivian occurrence suggests its descent from *P. praehauteriviana*. *D. moorbergensis* n. sp. is not yet known above the Hauterivian and would therefore seem to be phylogenetically unrelated to *Dorothia* spp. of the Late Cretaceous and younger beds; *Dorothia* is probably polyphylectic and it seems as though canalicular evolution evolved independently at least twice in this stock. This hypothesis is in accord with that already published for the repeated evolution of the canalicate wall in Late Cretaceous – Paleocene Verneuilinidae and Valvulinidae (Banner & Desai, 1985). It is likely that *Praedorothia* and *Protomarssonella* had a common ancestor in the Late Jurassic. Because ataxophragmoids, dorothiids, verneuilinids and valvulinids of Late Cretaceous and younger strata are well known to show repeated evolution involving reduction of the number of chambers per whorl (e.g. to develop a biseriality and even uniseriarity), it may be supposed that the ancestor to the Dorothiinae possessed more chambers per whorl than did *Protomarssonella* or *Praedorothia*. It is possible that the ancestor was a Tethyan species. A suitable candidate is *Riyadhella* Redmond (see also Barnard & Banner, 1980, p. 391, 400), which is a high trochospire, initially with four to six chambers in the whorl reducing to three or four (*Pseudomarssonella* possesses a broad apertural flap and is therefore unlikely to be the ancestor). Further reduction, during terminal growth, to ultimate biseriarity, would produce *Protomarssonella* and *Praedorothia*. *Protomarssonella* arose in the Tithonian, probably giving rise both to *Pseudotextulariella* (see Barnard & Banner, 1980) in the Berriasian/Valanginian and, quite separately, to *Praedorothia*, at least by Valanginian time. *Dorothia* first evolved, from *Praedorothia*, in the Hauterivian, and then, again in the Aptian (Barnard & Banner, 1980, op. cit., p. 392), supplanting *Praedorothia* by the Late Cretaceous and persisting into Recent Seas. *Marssonella* is not known to have evolved from *Protomarssonella* until the Late Cretaceous and seems to have become extinct in the Eocene. The evolutionary history of the two principal lineage-stocks seems to have been distinct since the beginning of Cretaceous time.

| LATE JURA | BERR. | VAL. | HAU. | BARREM. | APT. | POST-APTIAN |
|-----------|-------|------|------|---------|------|-------------|
|           |       |      |      |         |      |             |

---

Fig. 1. Possible phylogeny of species of the *Dorothiinae.*
ACKNOWLEDGEMENTS

We acknowledge the financial support supplied by the British Petroleum Company plc. and appreciate the permission to publish granted by the B.P. Research Centre, Sunbury-on-Thames, Middlesex; particularly, we wish to thank Dr. J. A. Crux and Dr. M. Partington, both of the Stratigraphy Branch, B.P. Research Centre, for their collaboration with the samples from N.W. Germany. We are grateful to Dr. A. R. Lord and Dr. P. F. Rawson, Department of Geological Sciences, University College London, for their support, and the latter for his guidance in the field at Speeton. We thank the curators of the Deep Sea Drilling Project Sample Depository, Lamont-Doherty Geological Observatory for supplying us for some of the materials used in the study. We are grateful also to Drs. C. G. Adams, and J. E. Whittaker and Mr. R. L. Hodgkinson, British Museum (Natural History), for their help and advice.

POSTSCRIPT

In an attempt to relate the findings of this study to practical biostratigraphy, the wall structure of marssonellids was observed in random thin sections of many hundreds of limestone samples from the Barremian-Earliest Albian and Cenomanian of the Middle East. The Early Cretaceous samples were obtained from subsurface cores and the Cenomanian from outcrop, and both were studied through the collaboration of BP Exploration Co. Ltd. at BP RCS, Sunbury-on-Thames. The marssonellid walls through the Barremian-Aptian-Earliest Albian sections were found consistently to be granular, imperforate and noncanaliculate, and the specimens are all to be referred to Protomarssonella. In contrast, the marssonellids seen in sections of Cenomanian Praevalveolina-limestones are distinctly canaliculate and are referable to Marssonella. The transition from Protomarssonella to Marssonella in central Tethys occurred, therefore, somewhere within the Early Albian to top Albian/basal Cenomanian interval (possibly at the beginning of Cenomanian time).

Our thanks are due to the British Petroleum Co, Plc. for permission to publish this postscript.

REFERENCES

Balakhmatova, V. T. 1972. K sistematike sievestva Ataxophragmiidae Schwager, 1877. (On the systematics of the family Ataxophragmiidae Schwager, 1877). Vop. Mikropaleont., Moscow, 15, 70–74 [In Russian].

Banner, F. T. & Desai, D. 1985. The genus Clavulinoiides. Cushman emended and the new Cretaceous genus Clavulinopsis. J. foramin. Res., Washington, D.C., 15, 79–90.

Banner, F. T. & Pereira, C. P. G. 1981. Some biserial and triserial agglutinated smaller foraminifera: their wall structure and its significance. J. foramin. Res., Washington, D.C., 11, 85–117.

Barnard, T. & Banner, F. T. 1953. Arenaceous foraminifera from the Upper Cretaceous of England. Q. Jl geol. Soc. Lond., 109, 173–216.

Barnard, T. & Banner, F. T. 1980. The Ataxophragmiidae of England: Part 1. Albian-Cenomanian, Arenobulimina and Crenaverneuclina. Revta exp. Micropealeont., Madrid, 12, 383–430.

Bartenstein, H., Bettenstaedt, F. & Kovatcheva, T. 1971. Foraminiferen des Bulgarsichen Barreme. Neues Js. Geol. Paläont. Abh., Stuttgart, 139, 125–162.

Bartenstein, H. & Bolli, H. M. 1977. The foraminifera in the Lower Cretaceous of Trinidad, West Indies, Part 4: Cuche formation, upper part. Ecol. geol. Helv., Basel, 70, 543–573.

Bartenstein, H. & Kaever, M. 1973. Die Unterkreide von Helgoland und ihre mikropaläontologische Gliederung. Senckenberg. leth., Frankfurt a.M., 54, 207–264.

Bartenstein, H. & Kovatcheva, T. 1982. A comparison of Aptian Foraminifera in Bulgaria and N.W. Germany. Ecol. geol. Helv., Basel, 75, 621–667.

Berthelin, G. 1880. Mémoire sur les foraminifères fossiles de l’étage Albian de Montceley (Doubles) Méém. Soc. géol. Fr., Paris, (3), 1 (5), 1–84.

Carsey, D. O. 1926. Foraminifera of the Cretaceous of central Texas: Univ. Tex. Bull., Austin, 2612, 1–56.

Cushman, J. A. 1911. A monograph of the foraminifera of the North Pacific Ocean. Part 2, Textulariidae. Bull. U.S. natn. Mus., Washington, D.C., 71 (2), 1–108.

Cushman, J. A. 1933. Some new foraminiferal genera. Contr. Cushman Lab. foramin. Res., Sharon, Mass., 9, 32–38.

Cushman, J. A. 1937. A monograph of the foraminifer family Valvulinidae. Spec. Publs Cushman Lab., Sharon, Mass., 8, 1–210.

Dam, ten, A. 1946. Arenaceous Foraminifera and Lagenidae from the Neocomian (Lower Cretaceous) of the Netherlands. J. Paleont., Ithaca, 20, 570–577.

Dieni, I. & Massari, F. 1966. I Foraminiferi del Valanginiano superiore di Orosei (Sardegna). Palaeontogr., Pisa, 61, 75–86.

Dieni, I. & Massari, F. 1985. Valanginian of Badde Funtana Morta (Orosei). In Cherchi, A. (Ed.). 19th European Micropaleontological Colloquium Guidebook. pp. 207–211. Agip, Cagliari.

Fletcher, B. N. 1969. A lithological subdivision of the Speeton Clay C Beds (Hauterivian), East Yorkshire. Proc. Yorks. geol. Soc., Leeds, 37, 323–327.

Gorbachik, T. N. 1971. On Early Cretaceous foraminifera of the Crimea. Vop. Mikropaleont., Moscow, 14, 125–139 [In Russian].

Hofker, J. 1969. Recent Foraminifera from Barbados. Stud. Fauna Curacao., The Hague, 31, 1–158.

Manuscript received February 1987
Revised manuscript accepted March 1987
Hofker, J. 1976. Further studies on Caribbean Foraminifera. Stud. Fauna Curacao, The Hague, 49, 1–256.
Kaye, P. 1964. Observations on the Speeton Clay (Lower Cretaceous). Geol. Mag., London, 101, 340–356.
Kuznetsova, K. I. & Gorbachik, T. N. 1985. Upper Jurassic and Lower Cretaceous stratigraphy and foraminifers of the Crimea. Trudy geol. Inst., Moscow, 395, 1–126.
Loeblich, A. R. & Tappan, H. 1964. Sarcodina, chiefly “Thecamoebians” and Foraminifera. In Moore, R. C. (Ed.). Treatise on Invertebrate Paleontology, Protiota, 2, Part C, 900 pp., Kansas University Press.
Loeblich, A. R. & Tappan, H. 1984. Suprageneric classification of the Foraminifera (Protozoa). Micropaleontology, New York, 30, 1–70.
Loeblich, A. R. & Tappan, H. 1985. Some new and redefined genera and families of agglutinated foraminifera. II. J. foramin. Res., Washington, D.C., 15, 175–217.
Lott, G. K., Fletcher, B. N. & Wilkinson, I. P. 1986. The stratigraphy of the Lower Cretaceous Speeton Clay formation from a cored borehole off the coast of N.E. England. Proc. Yorks. geol. Soc., Leeds, 46, 39–56.
Luterbacher, H. 1972. Foraminifera from the Lower Cretaceous and Upper Jurassic of the North-western Atlantic. Init. Repts. Deep Sea Drilling Project, Washington, D.C., 11, 561–593.
Luterbacher, H. P. 1975. Early Cretaceous foraminifera from the North-western Pacific. Init. Repts. Deep Sea Drilling Project, Washington, D.C., 32, 703–718.
Moullade, M. 1966. Etude stratigraphique et micropaléontologique du Cretacé inférieur de la “fosse Vocontienne”. Documents Lab. Géol. Fac. Sci. Lyon, 15, 1–369.
Moullade, M. 1984. The value of “deep” benthic foraminifera in the biostratigraphy and analysis of Mesozoic oceanic paleoenvironments. In: Oertli, H. J. (Ed.). Benthos ’83 2nd International Symposium on Benthic Foraminifera (Pau, April 1983), pp. 429–464, Elf Aquitaine, Esso REP & Total CFP, Pau & Bordeaux. [In French].
Mutterlose, J. 1984. Die Unterkreide-Aufschlüsse (Valangin-Alb) im Raum Hannover-Braunschweig. Mitt. geol. Inst. tech. Univ. Hannover, 24, 1–62.
Neagu, T. 1968. *Andersenia rumana* n. gen., n. sp., and some nmonic observations on the subfamily Valvulininae. Contr. Cushman Fdn foramin. Res., Sharon, Mass., 19, 120–122.
Neagu, T. 1972. The Eo-Cretaceous foraminiferal fauna from the area between the Ialomitza and Prahova valleys (Eastern Carpathians). Revta esp. Micropaleont., Madrid, 4, 181–224.
Neagu, T. Monographie de la faune des Foraminifères éocératiques du couloir de Dimbovcioarca, de Codlea et des Monte Persani (Couches de Carhaga). Mém. Inst. Géol. Geophys. Bucarest 25, 1–141.
Neale, J. W. 1960. The subdivision of the Upper D Beds of the Speeton Clay of Speeton, East Yorkshire. Geol. Mag., London, 97, 353–362.
Neale, J. W. 1962. Ammonioidea from the Lower D Beds (Berriasian) of the Speeton Clay. *Paleontology*, London, 5, 272–296.
Oak, N. B. & Hancock, J. M. 1961. The Upper Cretaceous of Norfolk. Trans. Norfolk Norwich Nat. Soc., Norwich, 19, 293–339.
Plummer, H. J. 1931. Some Cretaceous Foraminifera in Texas. Univ. Tex. Bull., Austin, 3101, 109–203.
Rawson, P. F. 1971. Lower Cretaceous ammonites from north-east England: the Haute Riverian genus Simberskites. Bull. Br. Mus. nat. Hist., London (Geol.), 20, 25–86.
Rawson, P. F. & Mutterlose, J. 1983. Stratigraphy of Lower B and basal cement Beds (Barremian) of the Speeton Clay, Yorkshire, England. Proc. Geol. Ass., London, 94, 133–46.
Reuss, A. E. 1860. Die foraminiferen der Westphalischen kreideformation. Sber. Akad. Wiss. Wien, 40, 147–238.
Salaj, J. 1984. Foraminifers and detailed microbiostratigraphy of the Boundary beds of the Lower Cretaceous stages in the Tunisian Atlas. Geol. Sb., Bratisl., 35, 583–599.
Schwager, C. 1877. Quadro del proposito sistema de classificazione del foraminifera con guscio. Boll. R. Com. geol. Ital., Florence, 7, 475–485.
Sibuet, J.-C., Ryan, W. B. F. et al. 1979. Leg 47, Part 2 of the Cruises of the Drilling Vessel Glomar Challenger, Vigo, Spain to Brest, France. April-May 1976. Init. Repts Deep Sea Drilling Project. Washington, D.C., 47(2), 1–772.
Sigal, J. 1979. Chronostratigraphy and Ecosтратigraphy of Cretaceous formations recovered on D.S.D.P., Leg 47B, Site 398. Init. Repts Deep Sea Drilling Project, Washington, D.C., 47, 287–327.
Sitter, W. V. 1980. Mesozoic foraminifera and deep sea benthic environments from Deep Sea Drilling Project Sites 415 and 416, eastern North Atlantic. Init. Repts Deep Sea Drilling Project. Washington, D.C., 50, 353–427.
Trujillo, E. F. 1960. Upper Cretaceous Foraminifera from near Redding, Shasta County, California. *J. Paleont.*, Ithaca, 34, 290–346.
Zedler, B. 1961. Striatigraphische Vebreitungen und phylogenie von foraminiferen des nordwestdeutschen Oberhautevi- vian. *Palaeont. Z.*, Stuttgart. 35, 28–61.