

## The evolution of Early Cretaceous Dorothiinae (Foraminiferida)

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**ABSTRACT**—*Dorothia* and *Marssonella* are ataxophragmiacean genera typically possessing canaliculate walls. They are believed to have evolved independently from noncanaliculate *Praedorothia* gen. nov. and *Protomarssonella* 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 canalication.

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 noncanaliculate species are here referred to the new genera *Praedorothia* 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 Verneuulinacea Cushman, Ataxophragmiacea Schwager and Textulariacea Ehrenberg cannot be maintained. Loeblich & Tappan (*op. cit.*) defined all of the Verneuulinacea (including 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 uniserial canaliculate genera (e.g. *Clavulinoides* and *Clavulinopsis*) evolved independently within the Verneuulinacea, 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 *Verneuulina* but which is canaliculate. This is the earliest evolution of canaliculation in the Verneuulinidae yet known to us (compare Banner & Desai, 1985, p. 87–89) and the species predates solid walled true *Verneuulina* 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* Verneuulinacea: essentially triserial, sometimes becoming biserial or even uniserial with growth. To include the families Verneuulinidae 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 canaliculate; 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 (occasionally 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, Pseudoboliviniidae and Nouriiidae.

#### 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).

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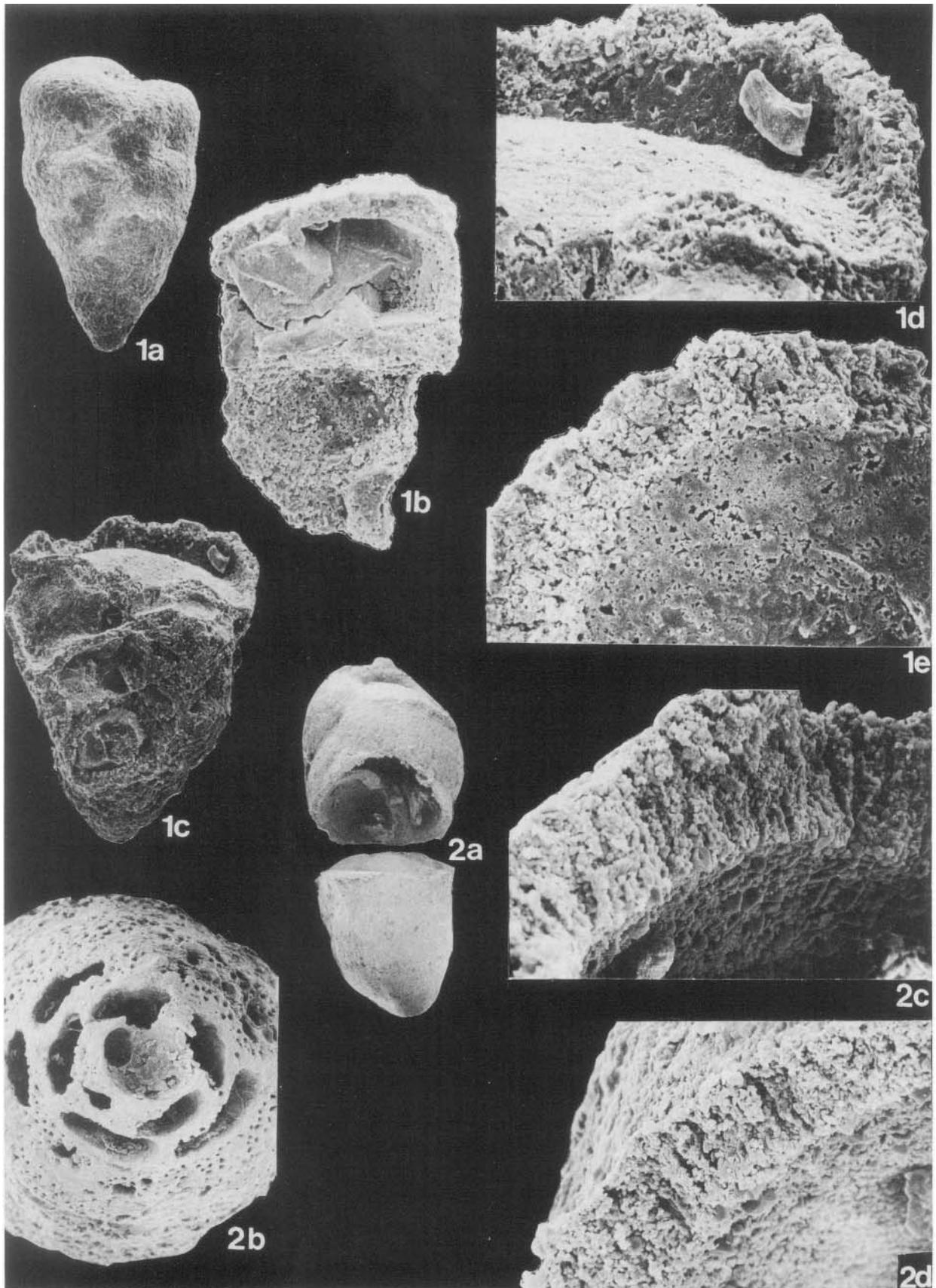
#### Explanation of Plate 1

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

Fig. 1a, holotype ( $\times 115$ ); 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 ( $\times 265$ ); fig. 1d, enlargement ( $\times 665$ ), 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 ( $\times 665$ ). 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. 2a, 2b, *Dorothia pupa depressa* Barnard & Banner from Harford Bridges, Norwich (Rowe 161); fig. 2a, whole syntype broken to show convex septa ( $\times 45$ ); fig. 2b, initial end, acid stripped showing coiling, canaliculate walls, solid septa ( $\times 120$ ); figs. 2c, 2d, *D. pupa sensu stricto* from Council's pit, Newmarket Road (Rowe 158); broken chambers showing canaliculate walls ( $\times 625$  and  $\times 750$  respectively).



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 Dorothisidae Balakhmatova, 1972

Subfamily Dorothisinae 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

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### Explanation of Plate 2

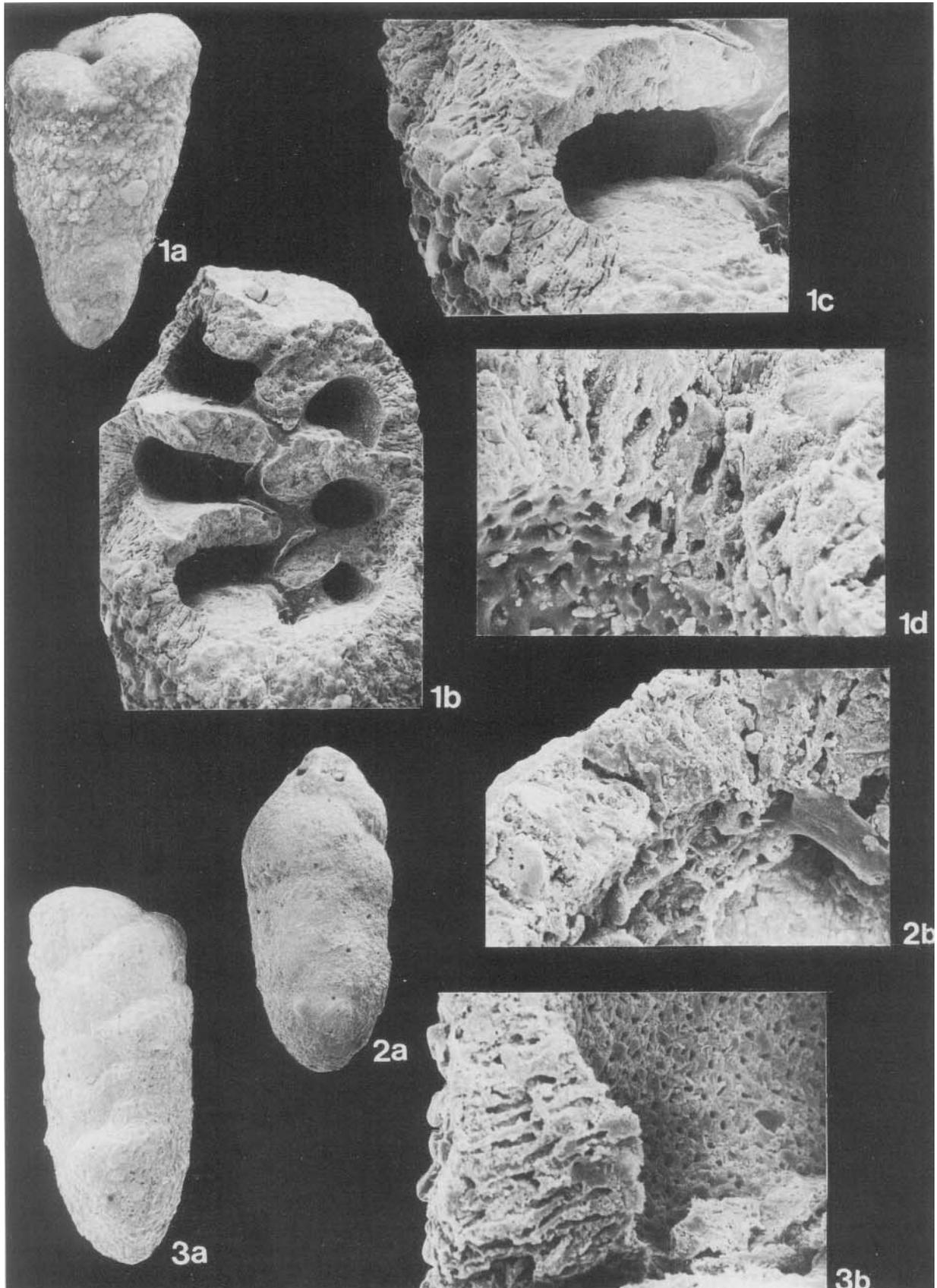
Modern species of *Dorothia* from Recent sediments of the Caribbean Sea. (All specimens by courtesy of the British Museum, Natural History). All specimens have been dissected and their destruction has precluded their subsequent curation.

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).



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 0.46 mm, width 0.15 mm.

**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.

#### Genus *Praedorothia* nov.

**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 ?*Dorothia 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).

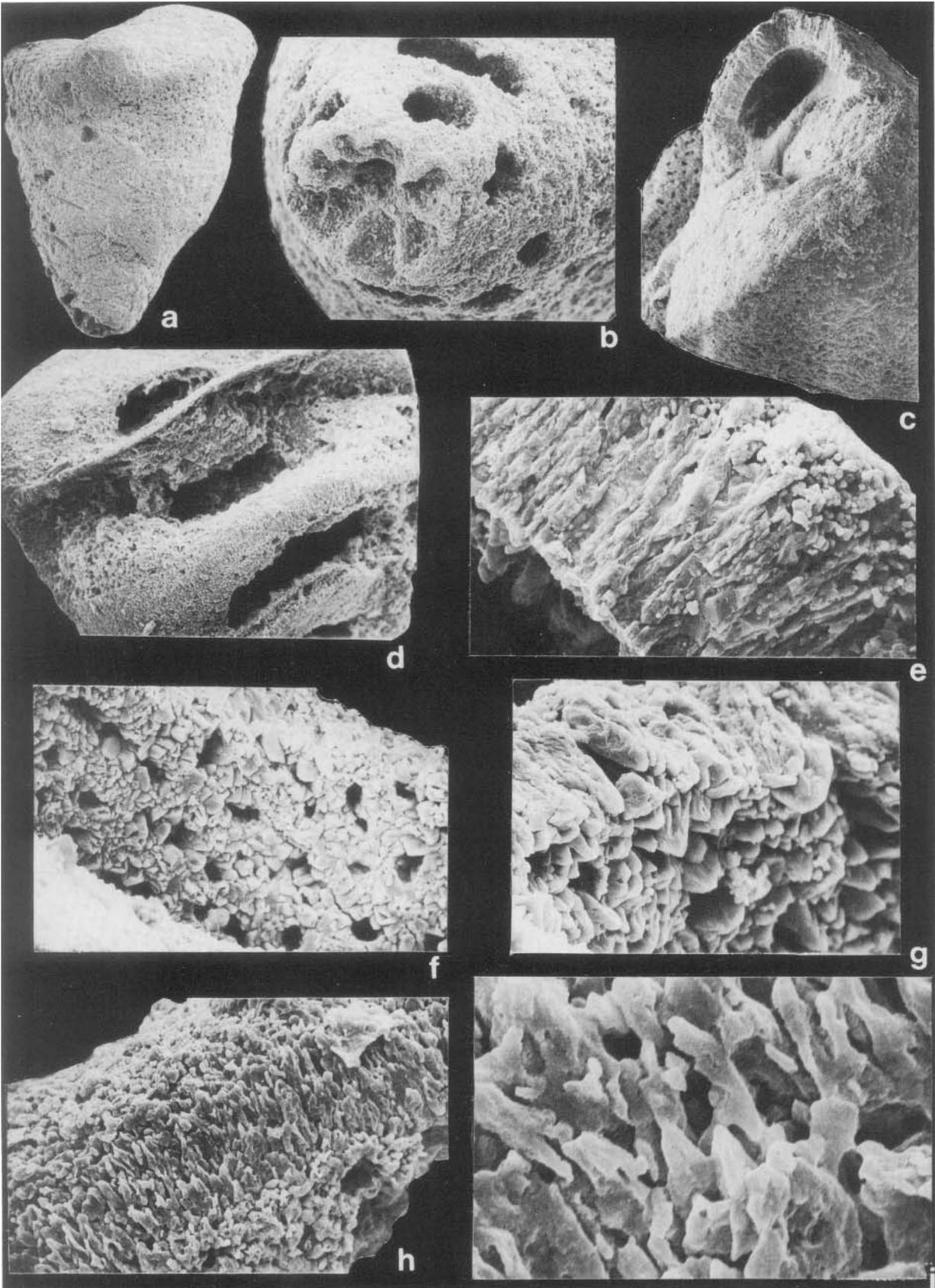
**Distribution.** This very cylindrical *Praedorothia* dominates the pre-Hauterivian dorothiid assemblage. The figured specimens (Pl. 4, figs. 2a–d) were obtained from the type locality (Orosei, Sardinia) and are dated as Late Valanginian (Dieni & Massari, 1966). Moullade (1984) and Luterbacher (1972) 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*.

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#### Explanation of Plate 3

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

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



*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.

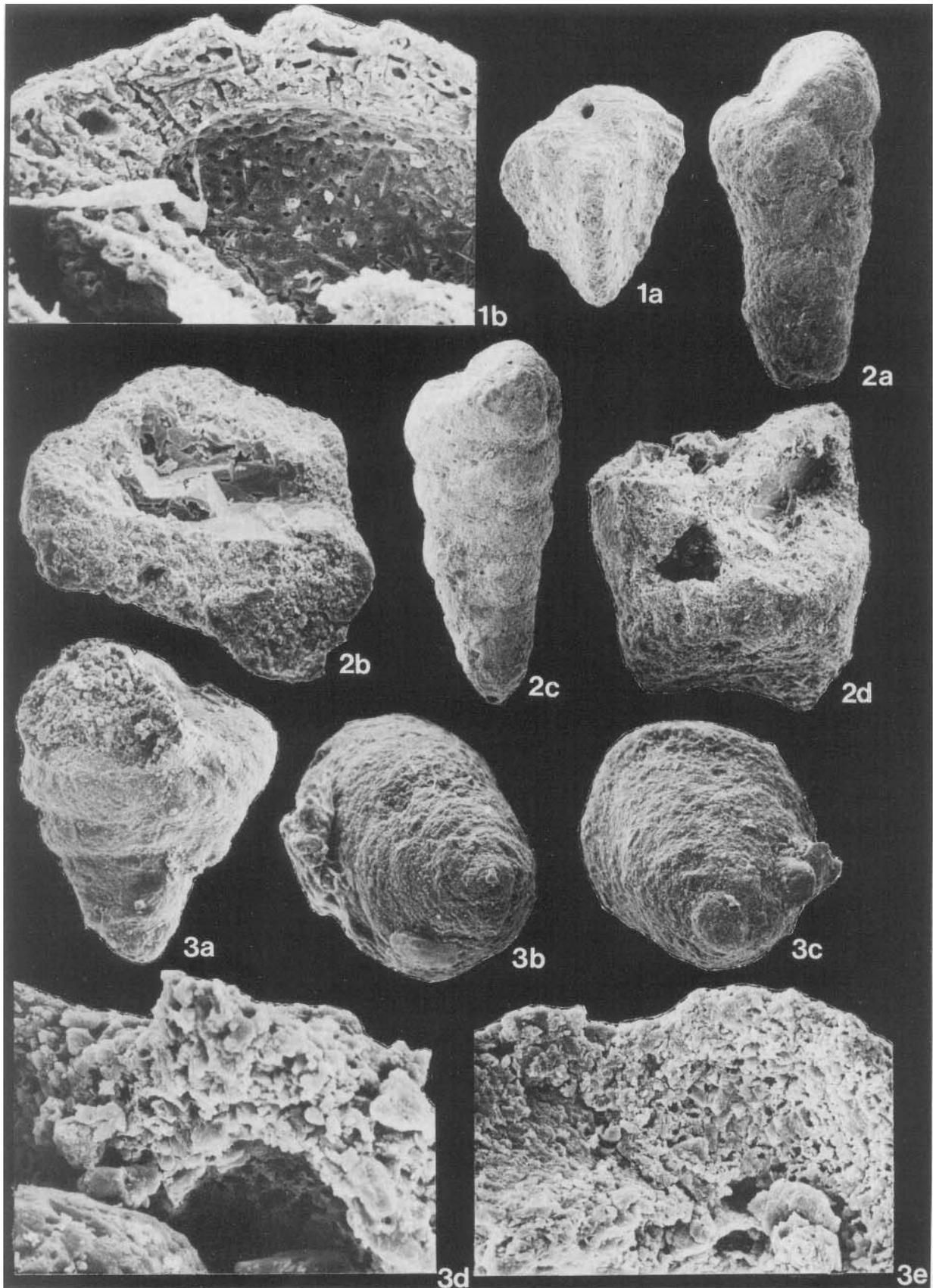
**Emended Diagnosis.** Early stage trochospiral, with four or more chambers to a whorl, later stage reduced to

#### Explanation of Plate 4

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

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

Figs. 3a–3e. *Praedorothia praeoxycona* (Moullade), sample SC6831, Hauterivian (Bed C4, *gottschei* zone of Rawson, 1971): fig. 3a, lateral view (last chamber damaged) ( $\times 175$ ); figs. 3b, 3c, initial ends (3b, microspheric? 3c, megalospheric?) (both  $\times 233$ ); figs. 3d–e, broken specimens showing coarsely agglutinated, solid walls ( $\times 1,166$  and  $\times 875$  respectively).



biserial; wall agglutinated, may be of calcareous particles; aperture an interior marginal slit; septa flat or concave; wall canaliculate.

**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, Cenomanian and Upper Gault. As we show in this paper that there are significant structural differences in the Dorotheidae 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 Drensteinfurt (about 30 km south-south east of Münster, Westphalia, 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 *Dorothea* or *Praedorothea*. 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 exteriorly 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 canaliculi; confinement of the canaliculi to the lateral chamber walls is common in Verneulinids 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. altisuturalis* Poag, from the Alabama, appears to be triserial throughout.

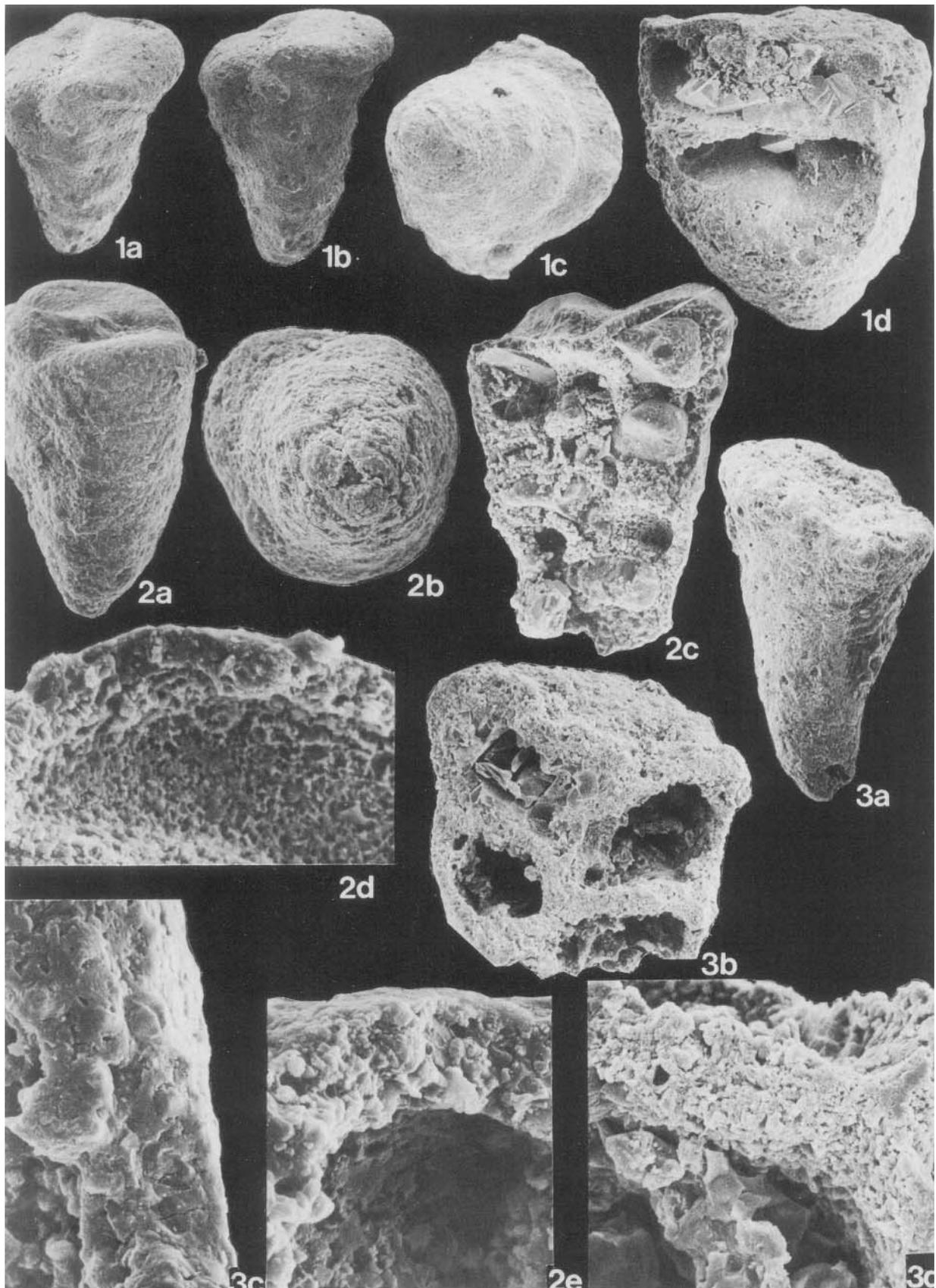
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#### Explanation of Plate 5

Figs. 1a–1d. *Praedorothea zedlerae* (Moullade) *luterbacheri* subsp. nov. All from D.S.D.P.398, Core 104–2, Late Aptian: figs. 1a, b, whole specimens ( $\times 50$ ); fig. 1c, initial end ( $\times 75$ ); 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 ( $\times 175$ ); fig. 2b, initial stage ( $\times 375$ ); figs. 2c–e, cut specimens showing wall structure: fig. 2c, longitudinal cut ( $\times 315$ ); fig. 2d, empty chamber and its solid, pitted but imperforate wall ( $\times 875$ ); fig. 2e, enlargement showing the agglutinated, solid, noncanaliculate wall ( $\times 2,190$ ).

Figs. 3a–3d. *Protomarssonella hechti* (Dieni & Massari), topotypes, Orosei, Sardinia, Late Valanginian: fig. 3a, whole specimen ( $\times 175$ ); figs. 3b–3d, cut specimens showing wall structure: fig. 3b longitudinal cut ( $\times 265$ ); fig. 3c, detail of solid, noncanaliculate wall ( $\times 2,044$ ); fig. 3d, solid, agglutinated wall and septum ( $\times 875$ ).



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 canaliculate.

**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 & Kaefer, 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 & Kaefer (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.

*Protomarssonella kummi* (Zedler)  
(Pl. 5, figs. 2a–2e)

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 "Mündung 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



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## 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 *Praealveolina*-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).

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