

THE EVOLUTIONARY INTERPRETATION OF THE FORAMINIFERIDA *ARENOBULIMINA*, *GAVELINELLA*, AND *HEDBERGELLA* IN THE ALBIAN OF NORTH-WEST EUROPE

by R. J. PRICE

ABSTRACT. *Arenobulimina macfadyeni* Cushman is suggested as the parent stock from which *A. chapmani* Cushman arose, probably around the Middle-Upper Albian boundary. *A. chapmani* gave rise to *A. franki* Cushman in the *varicosum* Subzone, which in turn gave rise to *A. truncata* (Reuss) in the *auritus* Subzone. *A. sabulosa* (Chapman) also appears in the *auritus* Subzone. *A. franki*, not *A. sabulosa*, is suggested as the parent stock from which *Flourensina intermedia* Ten Dam evolved in the upper *Stoliczkaia dispar* Zone, whilst the extinction of *A. chapmani* at this level is followed by the appearance of *A. advena* (Cushman).

The variations in test morphology of *Gavelinella intermedia* (Berthelin) are discussed. This species is suggested as the parent from which *G. rudis* (Reuss) and *G. cf. baltica* Brotzen arose in the Middle Albian. Both *G. cenomanica* (Brotzen) and *G. baltica* Brotzen arose from *G. intermedia* in the *varicosum* Subzone and *S. dispar* Zone respectively.

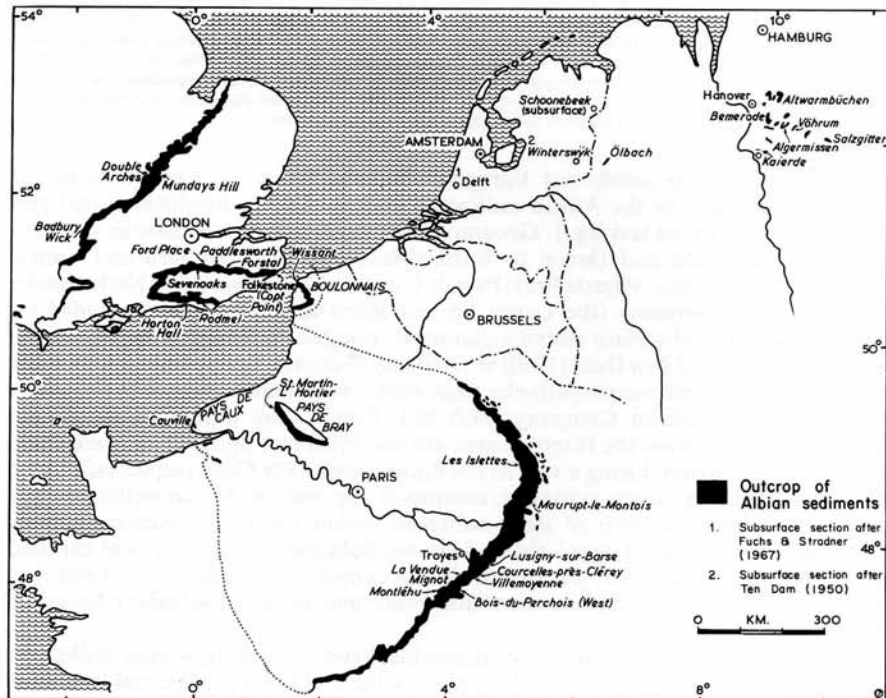
Hedbergella infracretacea (Glaessner) is suggested as the primitive Lower Cretaceous species from which *H. delrioensis* (Carsey) and *H. planispira* (Tappan) arose probably in the Aptian. Their intergradation in the Lower Albian is discussed. *H. infracretacea*, which became extinct around the *rostratum-perinflatum* Subzone boundary, possibly gave rise to *H. brittonensis* Loeblich and Tappan in the *auritus* Subzone.

THE area defined as north-west Europe is outlined below with reference to the geographical extent of the Albian sediments studied. Sample localities visited and collected are shown on text-fig. 1. Geographically the area is defined here as southern England (the Weald and Devon to Bedfordshire outcrop), northern and central France (the Boulonnais, Pays de Bray, Pays de Caux, and Paris Basin), the Netherlands, and north-west Germany (the Lower Saxony Basin and Hils). Also included on text-fig. 1 are the subsurface sections examined from the Netherlands by Fuchs and Stradner (1967), and Ten Dam (1950) at Delft and Winterswýk respectively; together with the Schoonebeek section, samples from which were made available to the writer by the Shell Petroleum Company (N.A.M.). Finally, the numerous subsurface sections examined from the Hanover area are shown on text-fig. 2. These were made available to the writer during a visit to the Bundesanstalt für Geowissenschaften und Rohstoffe. Thus an almost complete, composite sequence of Albian sediments was studied with the exception of three subzones within the Lower Albian, namely *milletooides* (*acuticostata*), *regularis*, and *kitchini* Subzones, which were not exposed during sample collection or penetrated during subsurface investigation. Table 1 is included to show the complete ammonite zonal and subzonal scheme referred to within the text.

The extremely good ammonite stratigraphical control during sample collection enabled species ranges to be defined, largely for the first time, to subzonal level over a wide geographical area, and together with population percentage variation was used to show horizons of acme and extinction. The subzonal ranges of species are

given only from those samples studied personally. Where other workers have recorded older or younger occurrences note is made of this.

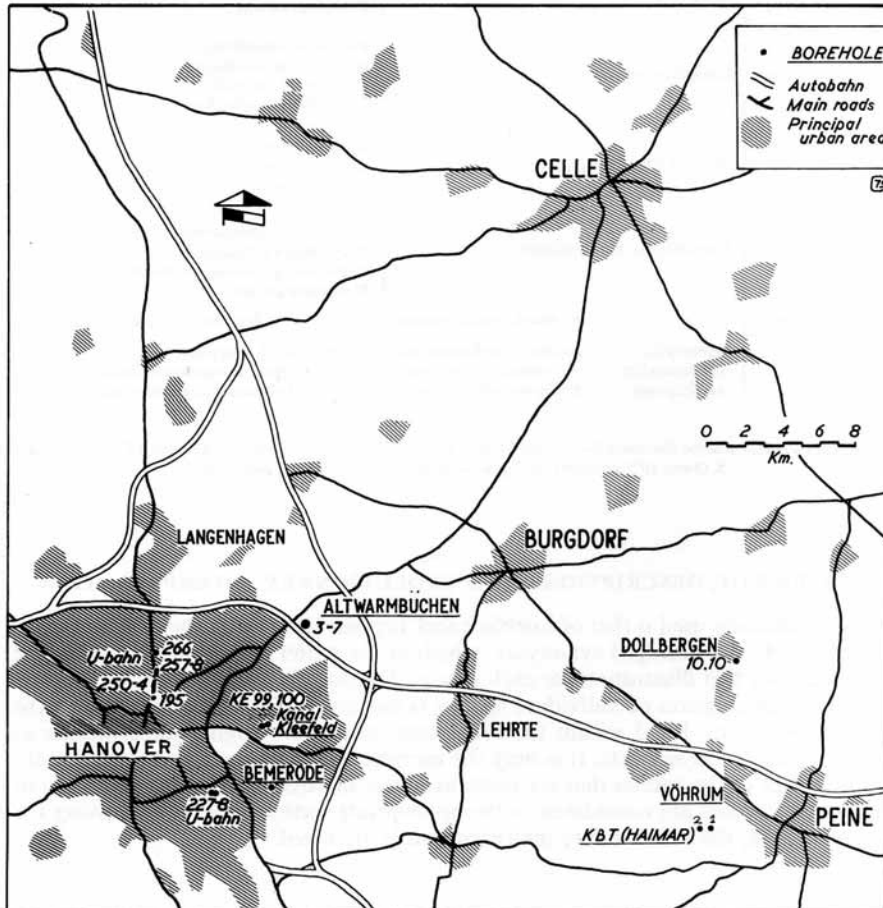
The sudden diversification of foraminiferid species, and their rapid evolution is a product of the Upper Albian only. This high diversity is particularly marked within the *S. dispar* Zone, which was an horizon of rapid radiation of species whose ancestors range from the Lower and Middle Albian. Their radiation at this level is probably related to environmental changes in the Upper Albian as discussed by the writer (in press (a)). Thus the *S. dispar* Zone illustrates examples of evolutionary development which have aided both stratigraphical zonation, especially in the Upper Albian, together with the opportunity to study the morphological variation of species to subzonal level. In all cases the morphological changes in test outline have been used to establish an evolutionary sequence with note made of microspheric and megalospheric generations as discussed by other workers. However, the exact stratigraphical position of species within the uppermost *S. dispar* Zone cannot always be correlated with ammonite subzone, as the macro-fauna at this level is sometimes very rare. Also samples were often obtained from borehole sections without ammonite control.



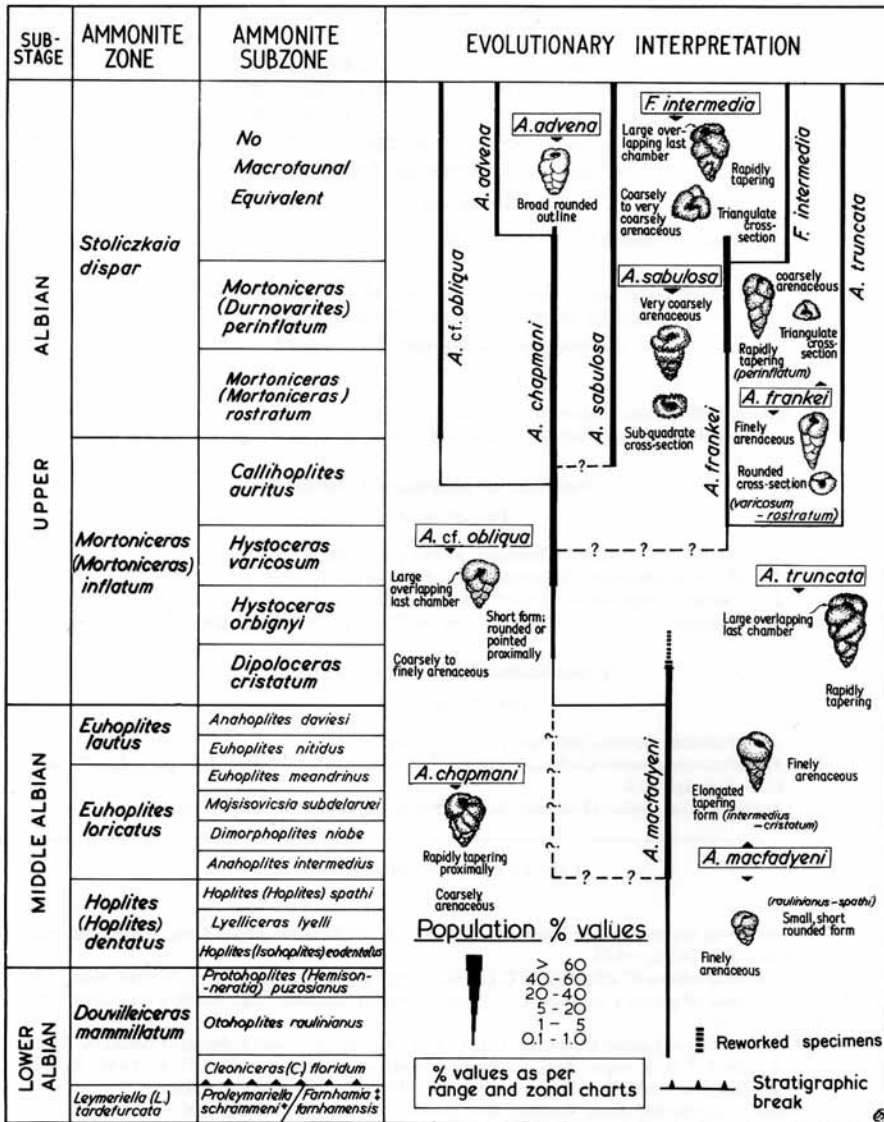
TEXT-FIG. 1. Sample localities and outcrop of the Albian strata in north-west Europe.

Nevertheless, the very useful stratigraphical index foraminifera within the *S. dispar* Zone have enabled the writer to establish a refined zonation scheme for this horizon (in press (b)).

The percentage abundance of individual species within the foraminiferal assemblage is shown on text-fig. 3. All other figures are referable to this. The methods and calculations used in assemblage analyses have been discussed by the writer elsewhere (1975). All the illustrated specimens have been deposited in the collections of the Department of Geology (Micropalaeontology), University College, London, and bear the numbers given in the explanations of the plates.



TEXT-FIG. 2. Borehole localities studied in the Lower Saxony Basin (north-west Germany).



TEXT-FIG. 3. Evolutionary interpretation of the genus *Arenobulimina* (and *Flourensina*) in the Albian of north-west Europe.

FLOURENSINA and ARENOBULIMINA
 Suborder TEXTULARIINA Delage and Hérouard, 1896
 Superfamily LITUOLACEA de Blainville, 1825
 Family ATAXOPHRAGMIIDAE Schwager, 1877
 Subfamily VERNEULININAE Cushman, 1911
 Genus FLOURENSINA Marie, 1938
Flourensina intermedia Ten Dam

Plate 59, figs. 1, 2

1950 *Flourensina intermedia* Ten Dam, pl. 1, fig. 16a-c.

Subfamily GLOBOTEXTULARIINAE Cushman, 1927
 Genus ARENOBULIMINA Cushman, 1927
Arenobulimina advena (Cushman)

Plate 59, fig. 3

1936 *Hagenowella advena* Cushman, p. 43, pl. 6, fig. 21.

1969 *Arenobulimina advena* Cushman; Gawor-Biedowa, p. 86, pl. 8, figs. 1-4; text-figs. 7, 8.

Arenobulimina chapmani Cushman

Plate 59, fig. 4

1892 *Bulimina presli* non Reuss; Chapman, p. 755, pl. 12, fig. 4.

1936 *Arenobulimina chapmani* Cushman, p. 26, pl. 4, fig. 7a, b.

1965 *Arenobulimina chapmani* Cushman; Neagu, p. 10, pl. 2, fig. 9.

1967 *Arenobulimina preslii* (non Reuss); Fuchs (*in* Fuchs and Stradner), pp. 272-273, pl. 4, fig. 3.

Arenobulimina frankei Cushman

Plate 59, figs. 5, 6, 9

1936 *Arenobulimina frankei* Cushman, p. 27, pl. 4, fig. 5a, b.

1969 *Arenobulimina frankei* Cushman; Gawor-Biedowa, p. 84, pl. 5, figs. 4, 5; pl. 7, figs. 6, 7a, b, 8a, b; text-figs. 5, 6.

non 1964 *Arenobulimina frankei* (Brotzen); Loeblich and Tappan, C. 273, figs. 183, 4a-c.

EXPLANATION OF PLATE 59

S.E.M. photographs.

Figs. 1, 2. *Flourensina intermedia* Ten Dam, U.C.L. 129-130, *Stoliczkaia dispar* Zone, Bemerode, north-west Germany. 1, $\times 70$; 2, $\times 150$.

Fig. 3. *Arenobulimina advena* (Cushman), U.C.L. 142, *S. dispar* Zone, Schoonebeek, Netherlands, $\times 80$.

Fig. 4. *Arenobulimina chapmani* Cushman, U.C.L. 143, *orbigny* Subzone, Copt Point, Folkestone, south-east England, $\times 80$.

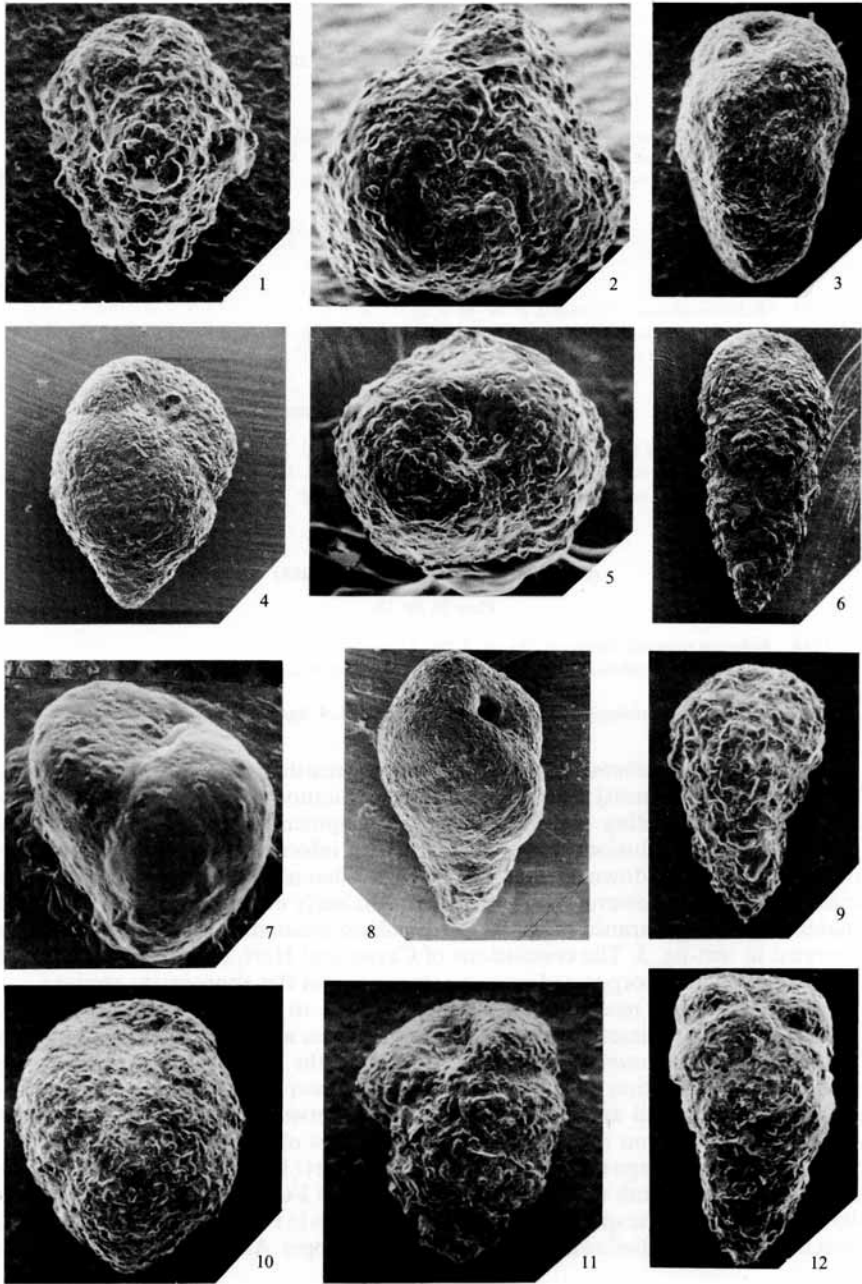
Figs. 5, 6, 9. *Arenobulimina frankei* Cushman, U.C.L. 144-146. 6, *varicosum* Subzone, Forstal, Aylesford, south-east England. 5, 9, *S. dispar* Zone, Bemerode, north-west Germany. 6, $\times 60$; 5, $\times 150$; 9, $\times 70$.

Figs. 7, 8. *Arenobulimina macfadyeni* Cushman, U.C.L. 147-148. 7, *raulianus* Subzone, Villemoyenne, Aube, France. 8, *nitidus* Subzone, Wissant, Bouloonnais, France. 7, $\times 140$; 8, $\times 90$.

Fig. 10. *Arenobulimina* cf. *obliqua* (d'Orbigny), U.C.L. 149, *S. dispar* Zone, Schoonebeek, Netherlands, $\times 75$.

Fig. 11. *Arenobulimina sabulosa* (Chapman), U.C.L. 151, *auritus* Subzone, Forstal, Aylesford, south-east England, $\times 70$.

Fig. 12. *Arenobulimina truncata* (Reuss), U.C.L. 152, *S. dispar* Zone, Schoonebeek, Netherlands, $\times 55$.



PRICE, *Flourensina* and *Arenobulimina*

Arenobulimina macfadyeni Cushman

Plate 59, figs. 7, 8

- 1892 *Bulimina orbigny* non Reuss; Chapman, p. 754, pl. 12, fig. 2.
 1936 *Arenobulimina macfadyeni* Cushman, p. 26, pl. 4, fig. 6a, b.
 1965 *Arenobulimina macfadyeni* Cushman; Neagu, p. 10, pl. 2, figs. 7, 8.

Arenobulimina cf. *obliqua* (d'Orbigny)

Plate 59, fig. 10

- 1840 ?*Bulimina obliqua* d'Orbigny, p. 40, pl. 4, figs. 7, 8.
 1892 *Bulimina obliqua* d'Orbigny; Chapman, p. 754, pl. 12, fig. 3.
 1937 ?*Arenobulimina obliqua* (d'Orbigny); Cushman, pp. 41-42, pl. 4, figs. 18-20.

Arenobulimina sabulosa (Chapman)

- 1892 *Bulimina preslii* Reuss var. *sabulosa* Chapman, p. 755, pl. 12, fig. 5.
 1937 *Arenobulimina sabulosa* (Chapman); Cushman, p. 36, pl. 3, figs. 29, 30.
 non 1969 *Arenobulimina sabulosa* (Chapman); Gawor-Biedowa, p. 77, pl. 5, fig. 3; pl. 7, fig. 3a, b; text-figs. 1, 2.

Arenobulimina truncata (Reuss)

Plate 59, fig. 12

- 1844 *Bulimina truncata* Reuss, p. 215, pl. 8, fig. 73.
 1969 *Arenobulimina sabulosa* (non Chapman); Gawor-Biedowa, p. 77, pl. 5, fig. 3; pl. 7, fig. 3a, b; text-figs. 1, 2.
 1937 *Arenobulimina truncata* (Reuss); Cushman, p. 40, pl. 4, figs. 15, 16.

The genus *Arenobulimina* has received much attention from previous workers. Carter and Hart (in press) have formulated an evolutionary scheme for the arenobuliminids, concentrating mainly on their development in the Cenomanian and Turonian. Their conclusions are based largely on information obtained from sub-surface sections put down during the English Channel tunnel site investigation project. The writer, however, concentrates on the early evolution of this genus and equates the first appearance of species with Albian ammonite subzone horizons, as illustrated in text-fig. 3. The conclusions of Carter and Hart, together with those of other workers, are incorporated into this discussion in the appropriate sections.

A. macfadyeni was recorded from the *raulianus* to lower *crisatum* Subzones, although derived specimens often showing signs of test abrasion were found in beds of *orbigny* and *varicosum* Subzonal age, following the reworking of pre-*crisatum* sediments. The extinction of the species within the lower *crisatum* Subzone is stratigraphically very useful and marks the boundary between the Middle and Upper Albian. This conclusion is supported by the findings of Magneiz-Jannin (1975) in the Aube, France; Neagu (1965) in Romania; and Hart (1973a) at Folkestone, south-east England. Also, both Gawor-Biedowa (1972) and Fuchs, in Fuchs and Stradner (1967), do not record the species in the Albian sequences in Poland and the Netherlands respectively. Gawor-Biedowa (1972) assigned an Upper Albian age for the Polish

sequence, whereas Fuchs, *in* Fuchs and Stradner (1967), recorded a late Middle Albian age for the Dutch section. The writer has now revised the latter and suggests an *orbigny* Subzonal age for this section (*in press (b)*).

A. macfadyeni shows a gradual change in test outline through Albian time. Its first appearance within the studied area is recorded from the Lower Albian clays of the Paris Basin. These clays contain large amounts of fine angular quartz and glauconite. In this environment the species is typically small and rounded in outline (Pl. 59, fig. 7). This form is found in sediments of *raulianus* to *spathi* Subzonal age. However, from the *intermedius* to *cristatum* Subzones it becomes distinctly elongate (Pl. 59, fig. 8) and also more common. *A. macfadyeni* is quite distinct in that it has the most finely agglutinated test of all the Albian arenobuliminids. It shows no relationship to the surrounding detrital grains as regards incorporation of material into its test wall. This factor has been suggested to account for levels of abundance of some species, but has not been found to apply to any of the Albian forms examined.

The extinction of *A. macfadyeni* in the *cristatum* Subzone is followed by the sudden appearance in abundance of *A. chapmani* during the upper *cristatum* and *orbigny* Subzones, although the writer recorded extremely rare individuals and therefore possible contaminants from the *intermedius* Subzone onwards in southern England. However, the possible coeval existence of *A. macfadyeni* and *A. chapmani* in the Middle Albian could be indicative of gradually changing environmental conditions favouring the latter's development. Its sudden appearance in large numbers may be related to the regional erosive horizon within the *cristatum* Subzone.

Both Cushman (1937) and Gawor-Biedowa (1969) have made extensive studies and illustrations of *Arenobulimina* in the Cretaceous. However, neither worker has suggested an evolutionary sequence for this genus. With reference to the Albian, Gawor-Biedowa (1969) concludes that *A. chapmani* has three different generations, i.e. is trimorphic, based on observations of proloculus size and development, stating, however, that the over-all test outline in all generations does not vary except for its size and number of chambers. In the light of this suggestion, it is possible that many Upper Cretaceous species of *Arenobulimina* identified by Cushman (1937) may be synonymous with one another and therefore in need of review. *A. chapmani* itself has a distinctive outline being very wide distally but rapidly tapering and pointed proximally. The test wall is coarsely agglutinated although again not related to surrounding detrital grain size. Although both *A. chapmani* and *A. sabulosa* are common in the sandy environment of the Upper Greensand, as recorded by Hart (1973*b*), they were also found in abundance by the writer in the *auritus* Subzone, in predominantly clastic free residues. Also at Wissant, Boulonnais, the large influx of *A. chapmani* within the basal *varicosum* Subzone is associated with a phosphatic nodule horizon, as it is in the *cristatum* Subzone at Folkestone, south-east England. Thus the abundance of this species is probably related to environmental control namely shallowing rather than detrital abundance. Evidence for shallowing is indicated by the presence of phosphate nodules within the *cristatum* and basal *varicosum* Subzones as suggested by Owen (1971*a*, 1972), and by small numbers of planktonic foraminifera in an otherwise abundant assemblage, as shown by the writer (*in press (b)*).

During and following the *varicosum* Subzone, many species radiated from the *A. chapmani* parent stock. The triserial *A. frankei* appears during the upper *varicosum*

Subzone. This species had a distinctly elongate, tapering test with a round cross-section throughout its length in the *varicosum* to *auritus* Subzones (Pl. 59, fig. 6). Its early development resembles Middle Albian forms of *A. macfadyeni*, however its test is more coarsely agglutinated. Morphologically it could have evolved from *A. macfadyeni* but the stratigraphical break between the occurrence of these species would suggest otherwise. Within the *rostratum* and *perinflatum* Subzones, *A. frankei* develops a distinctly triangulate cross-section in the proximal portion of its test whilst distally it remains rounded (Pl. 59, figs. 5, 9).

In the upper *S. dispar* Zone, the first occurrence of *F. intermedia* is recorded. Hart (1973a) has suggested that *A. sabulosa*, discussed below, evolved into *F. intermedia*. The writer, however, disagrees with this, as *A. sabulosa* is quadriserial and subquadrate in cross-section. Its evolution into a triserial and triangulate cross-sectioned *F. intermedia* does not seem likely when the respective localized and ubiquitous occurrences of *A. sabulosa* and *F. intermedia* are considered. The writer therefore suggests that *F. intermedia* arose from the triserial and triangulate cross-sectioned *A. frankei* through the gradual morphological changes discussed later. *A. frankei* disappears in the upper *S. dispar* Zone within the studied area. Hart (1973b) also records the disappearance of a form *Arenobulima* sp. cf. *A. frankei* in the Upper Albian. *F. intermedia* has been considered indicative of Cenomanian age. However, it is recorded in the Upper Albian by Ten Dam (1950), by Hart (1973a, b) in the Upper Albian and Cenomanian respectively, and by the present writer in the upper *S. dispar* Zone. It is of interest to note that Gawor-Biedowa (1972) does not record this species or indeed genus in the Upper Albian or Cenomanian in Poland, but records *A. frankei* ranging into the Cenomanian. Also Cushman (1936, 1937) records *A. frankei* ranging into the Cenomanian but makes no mention of the genus *Flourensina*. Cushman, however, states that his specimens of *A. frankei* are from the Cenomanian just east of Hildesheim, Germany and at this level they show a tendency to become uniserial distally, a characteristic development of the species in the *rostratum* to *perinflatum* Subzones. Thus the following evolutionary sequence linking *A. frankei* with *F. intermedia* is suggested. *A. frankei* with a completely rounded triserial test in the *varicosum* and *auritus* Subzones developed an initial triserial, triangulate portion, whilst distally still remaining rounded, during the *rostratum* and lower *perinflatum* Subzones. This triangulate portion extended the entire length of the test in the upper *perinflatum* Subzone onwards leaving only a rounded uniserial chamber distally. The appearance of the latter form is taken as the first occurrence of *F. intermedia* in the upper *S. dispar* Zone, whilst *A. frankei* disappears at this level. Nevertheless, although the present writer has not recorded *A. frankei* ranging into the uppermost *S. dispar* Zone, further research and collection of material from Hildesheim would be needed to ascertain whether or not it extends into the Cenomanian as described by Cushman (1936).

A. cf. obliqua probably originates from *A. chapmani* in the *auritus* Subzone. This species closely resembles the Upper Cretaceous forms described by d'Orbigny (1840) and Cushman (1937), and is tentatively suggested as being synonymous with them. It is rare but distinct, having an extremely flat distal portion with a very large overlapping last chamber, a feature also characteristic of *A. chapmani*. *A. cf. obliqua* most closely resembles Lower Albian forms of *A. macfadyeni*, but is distinctly bigger

and more coarsely agglutinated, and is clearly separated from the latter stratigraphically.

A. sabulosa probably arose from *A. chapmani* in the upper *auritus* Subzone. However, its distribution appears to be confined within north-west Europe to southern England and the southern North Sea. Ten Dam (1950) also does not record *A. sabulosa* in the Netherlands, and it does not range into the Cenomanian, as confirmed by Cushman (1937). The species has an extremely coarse agglutinated test wall and superficially resembles *F. intermedia*, but as suggested above, does not evolve into the latter species.

Within the lower *auritus* Subzone, *A. truncata* first appears. It probably evolved from *A. frankei*. This species is, in the writer's opinion, that form described by Gawor-Biedowa (1969) as *A. sabulosa*. She describes the species as possessing a long, gradually tapering test with rounded cross-section. This is a different form from *A. sabulosa* whose test is subquadrate in cross-section, generally short in length, and often possesses subparallel sides. Both species are, however, very coarsely agglutinated although the sutures on *A. truncata* are clearly visible, unlike those of *A. sabulosa* whose extremely coarse test often obscures them. *A. truncata* is also recognized by Hart (pers. comm.) in the Upper Albian and Cenomanian of England, and has been recorded by the writer from the *auritus* Subzone onwards in southern England, the Netherlands, and north-west Germany.

In north-west Europe, *A. chapmani* is therefore suggested as the parent stock from which nearly all other species of Albian arenobuliminids arose. It is found in large numbers from the *cristatum* to the upper *S. dispar* Zone where it disappears. Its disappearance within the Upper Albian is also suggested by Hart (1973b) from a study of the Cambridge Greensand. However, Gawor-Biedowa (1969) records it ranging into the Cenomanian in Poland, but her illustrated species now possess the characteristic internal radial divisions of *Hagenowina*, Loeblich and Tappan (1961). Gawor-Biedowa (1969) does not generically separate *Arenobulimina* and *Hagenowina* on the appearance of internal radial partitions of the latter. This important evolutionary feature has been recorded by Barnard and Banner (1953) in Cenomanian, '*Arenobulimina*' from southern England. The arguments for and against the recognition of a new genus, i.e. *Hagenowina* have been discussed by Loeblich and Tappan (1964).

A. chapmani in turn gives rise to *A. advena* within the *S. dispar* Zone, as also suggested by Carter and Hart (in press). The latter has a rounded outline in contrast to that of *A. chapmani*. According to Gawor-Biedowa (1969), *A. advena* is also characterized by internal radial partitions. However, she only records this feature in specimens of '*A.*' *advena* from the Cenomanian. The present writer has sectioned many specimens of Albian *A. advena* and has found no internal radial partitions. However, Gawor-Biedowa (1969) also states that the type of preservation or degree of recrystallization of the test wall may destroy the internal structure. The predominantly marl facies of the upper *S. dispar* Zone in north-west Europe readily lends itself to recrystallization which would destroy any delicate internal structures if present. Walters (1958) figures Albian specimens identified as *A. chapmani* but which, from observations by the writer, appear to possess more rounded outlines akin to *A. advena*. His specimens also show evidence of internal partitions in the

absence of recrystallization of the test wall and infilling of the chambers. The recognition of *A. advena* in the Albian by Carter and Hart (in press) is defined on the absence of internal radial partitions. This conclusion is also supported by Barnard (pers. comm.) who suggests that *Arenobulimina* in the Albian lack internal radial partitions and that this feature is characteristic of the Cenomanian. Nevertheless, although the present writer believes radially partitioned forms to be absent from the Albian of north-west Europe, it cannot be stated categorically that this is the case due to the lack of internally well-preserved specimens in the uppermost *S. dispar* Zone.

The rapid radiation of arenobuliminid species within the Upper Albian of north-west Europe is predominantly a product of the Boreal realm. Indeed, the maximum species diversity in the area of study was found within a proposed area of transition between the Boreal and Tethyan realms, as discussed by the writer (in press (a)). Further south the species diversity is proportionately reduced as the truly Tethyan realm is reached. This is shown from illustrations of species by Magniez-Jannin (1975) and Moullade (1966) from the Paris Basin and 'Fosse Vocontienne' respectively.

GAVELINELLA

Suborder ROTALIINA Delage and Hérouard, 1896

Superfamily CASSIDULINACEA d'Orbigny, 1839

Family ANOMALINIDAE Cushman, 1927

Subfamily ANOMALININAE Cushman, 1927

Genus GAVELINELLA Brotzen, 1942

Gavelinella cf. *baltica* Brotzen

Plate 60, figs. 1, 2

1972 *Gavelinella* (*Gavelinella*) *baltica* Brotzen; Gawor-Biedowa, pp. 125-126, pl. 17, fig. 5a-c.

Gavelinella baltica Brotzen

Plate 60, figs. 3, 4

1942 *Gavelinella baltica* Brotzen, p. 50, pl. 1, fig. 7.

1967 *Gavelinella* aff. *baltica* Brotzen; Malapris and Jannin, p. 2, pl. 1, figs. 4-7.

EXPLANATION OF PLATE 60

S.E.M. photographs.

Figs. 1, 2. *Gavelinella* cf. *baltica* Brotzen, U.C.L. 283-284, *auritus* Subzone, Schoonebeek, Netherlands, $\times 90$.

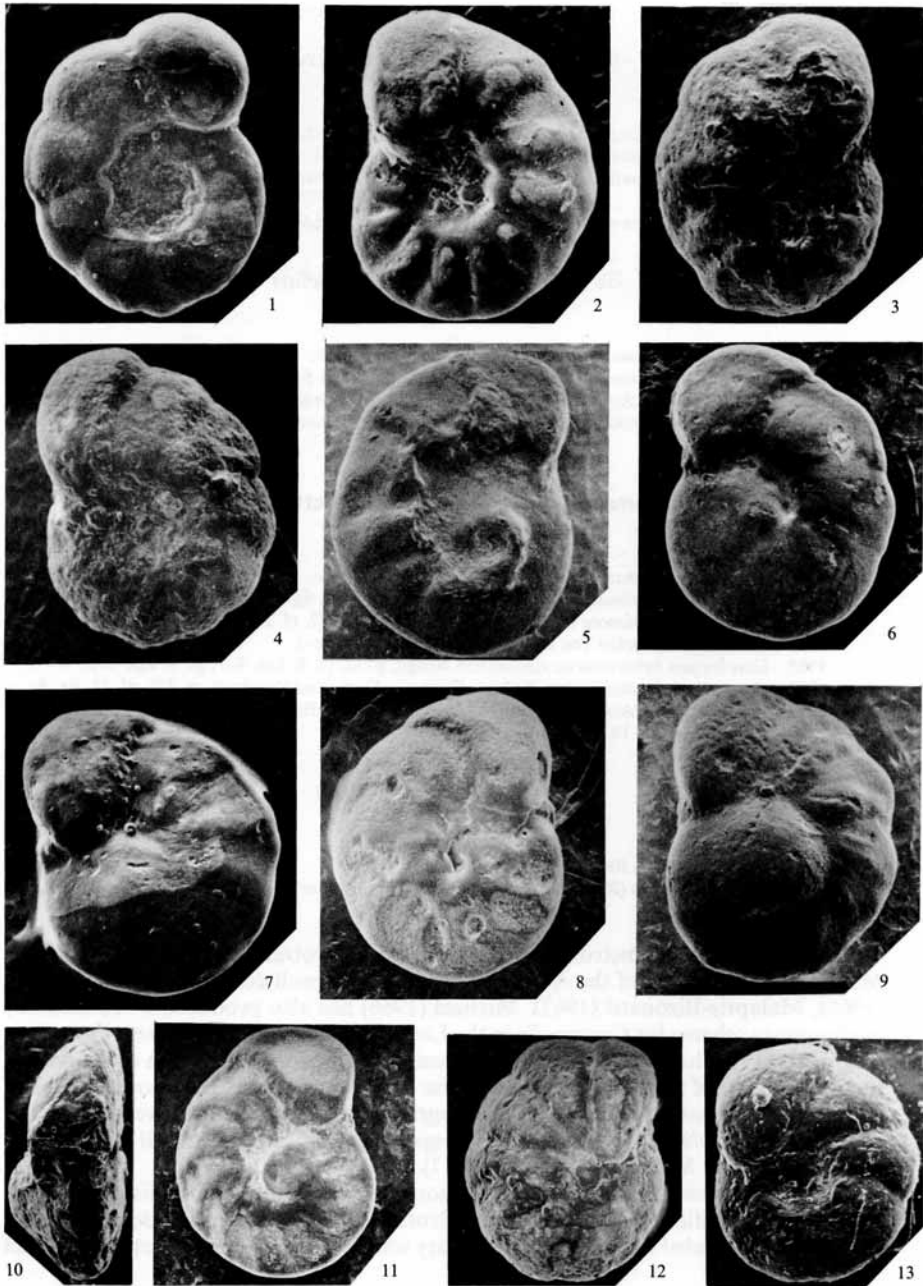
Figs. 3, 4. *Gavelinella baltica* Brotzen, U.C.L. 285-286, *Stoliczkaia dispar* Zone, Bemmerode, north-west Germany, $\times 90$.

Figs. 5, 6. *Gavelinella cenomanica* (Brotzen), U.C.L. 287-288, *varicosum* Subzone, Copt Point, Folkestone, south-east England, $\times 105$.

Figs. 7, 8. *Gavelinella intermedia* (Berthelin), U.C.L. 289-290, *puzosianus* Subzone, St. Martin-l'hortier, Pays de Bray, France, $\times 105$.

Figs. 9-11. *Gavelinella intermedia* var. A (Berthelin), U.C.L. 291-293, *puzosianus* Subzone, St. Martin-l'hortier, Pays de Bray, France. 9, $\times 105$; 10, $\times 80$; 11, $\times 85$.

Figs. 12, 13. *Gavelinella rudis* Reuss, U.C.L. 294-295, *nitidus* Subzone, Salzgitter-Bad (Finkenkuhle), north-west Germany, $\times 80$.



PRICE, *Gavelinella*

Gavelinella cenomanica (Brotzen)

Plate 60, figs. 5, 6

- 1942 *Cibicidoides* (*Cibicides*) *cenomanica* Brotzen, p. 54, pl. 2, fig. 2a-c.
 1966 *Gavelinopsis cenomanica* (Brotzen); Michael, p. 436, pl. 50, figs. 16, 17.
 1972 *Gavelinella* (*Gavelinella*) *cenomanica* (Brotzen); Gawor-Biedowa, pp. 126-128, pl. 17, fig. 4a-c.
 1973(a) *Gavelinella cenomanica* (Brotzen); Hart, p. 278, text-fig. 3.

Gavelinella intermedia (Berthelin)

Plate 60, figs. 7, 8

- 1880 *Anomalina intermedia* Berthelin, p. 67, pl. 4, fig. 14a, b.
 1942 *Gavelinella intermedia* (Berthelin); Brotzen, p. 52, text-fig. 18.
 1965 *Gavelinella* (*Berthelina*) *intermedia* (Berthelin); Malapris, pp. 138-139, pls. 1, 2, 5.
 1972 *Gavelinella* (*Berthelina*) *intermedia* (Berthelin); Gawor-Biedowa, pp. 120-122, pl. 15, figs. 7-9(a-c).

Gavelinella intermedia var. A (Berthelin)

Plate 60, figs. 9-11

- 1863 *Rosalina complanata* Reuss var. Reuss, pl. 11, fig. 3a-c.
 1880 *Anomalina complanata* (Reuss); Berthelin, p. 66, pl. 4, figs. 12, 13.
 1950 *Anomalina complanata* (Reuss) var. *reussi* Khan, p. 277, pl. 2, figs. 17, 18.
 1950 *Anomalina berthelini* Ten Dam, pp. 56-57, pl. 4, fig. 9a-c.
 1965 *Gavelinopsis infracretacea simionescui* Neagu, p. 32, pl. 8, figs. 4-7; pl. 9, figs. 1-2.
 1967 *Gavelinopsis berthelini* (non Keller); Fuchs (*in* Fuchs and Stradner), p. 336, pl. 18, fig. 8a-c.
 1972 *Gavelinella* (*Berthelina*) *belorussica* (Akimez); Gawor-Biedowa, pp. 116-118, pl. 16, figs. 5, 6 (a-c); text-fig. 10.

Gavelinella rudis (Reuss)

Plate 60, figs. 12, 13

- 1863 *Anomalina rudis* Reuss, p. 87, pl. 11, fig. 7.
 1967 *Gavelinella rudis* (Reuss); Fuchs (*in* Fuchs and Stradner), p. 335, pl. 19, fig. 2a-c.

The stratigraphical distribution of *Gavelinella* Brotzen and *Lingulogavelinella* Malapris in the Albian of the Aube, France, has been well documented by Malapris (1965), Malapris-Bizouard (1967). Michael (1966) has also produced a rudimentary evolutionary scheme for *Gavelinella* in the Lower Cretaceous of north-west Germany. Also Hart (1970) has proposed an evolutionary scheme for both genera in the Albian to Cenomanian of south-west England. The writer reinterprets the above in light of additional information from the larger geographical area studied. However, only the evolution of *Gavelinella* is discussed, as *Lingulogavelinella* has been well documented and described by Malapris-Bizouard (1967).

Text-fig. 4 shows the suggested evolutionary interpretation for this genus. The evolutionary position of *G. tormarpensis* Brotzen (1942) is difficult to determine and has not been included within the evolutionary scheme. The species possesses a distinct

'star-like' pattern to the sutures on its ventral side, a characteristic of *Lingulogavelinella*; but it also has an umbilicus, this feature being absent in that genus. It ranges throughout the Albian whereas *Lingulogavelinella* is endemic to the Paris Basin in Lower Albian times and was not found by the writer below the *raulinianus* Subzone. It is possible that *G. tormarpensis* is the ancestral species from which the *Lingulogavelinella* plexus evolved, although this suggestion is only tentative and requires the further investigation of pre-Albian sediments.

G. intermedia, which ranges throughout the Albian, is suggested as the parent stock from which other Albian species arose. In the Lower Albian it is abundant in beds of *raulinianus* to *eodentatus* Subzonal age. At these horizons and throughout the Middle Albian, it is the single most abundant benthic species. In the *puzosianus* Subzone the form *G. intermedia* var. A (nov. com.) is found in association with it. Morphologically both *G. intermedia* and *G. intermedia* var. A are extremely similar, except that in certain specimens of the latter a distinct boss is developed on its spiral side. However, both forms are completely intergradational. Khan (1950) adopts the name *Anomalina complanata* var. *reussi* to differentiate *G. intermedia* var. A from *G. intermedia*. However, the writer agrees with the suggestion of Malapris (1965) in that it is merely a variety of *G. intermedia* and does not warrant a new specific name. She also erects the new subgenus *Berthelina* whilst placing *A. complanata* (Reuss) and *A. intermedia* Berthelin in synonymy. The significance of subgeneric erection is discussed by Malapris (1965), but is not considered here. Thus *G. intermedia* var. A is only given variety status which serves as an observation that high boss development on the spiral side of the species frequently occurs. In any Albian population, however, total gradation may be found. This is particularly well illustrated in the Lower and Middle Albian where from the *puzosianus* Subzone onwards both forms are very common. Within the upper *auritus* Subzone *G. intermedia* decreases in abundance.

Further confusion within the literature has also arisen because *G. intermedia* var. A has been placed in synonymy of *G. berthelini* (Keller, 1935) as described by Ten Dam (1950), Michael (1966), and Fuchs, in Fuchs and Stradner (1967). However, *G. berthelini* is of Cenomanian and Turonian age as illustrated by Keller (1935) and Gawor-Biedowa (1972) respectively, and discussed by Hart (oral comm.), who all correctly refer back to the quite different species originally termed *Anomalina berthelini* by Keller (1935). The possible difference between these species was also tentatively suggested by Ellis and Messina (1951).

During the *spathi* Subzone, the first appearance of *G. rudis* is recorded. This species is suggested as ancestor to *G. baltica*, as discussed below. However, its evolutionary relationship with *G. intermedia* is not clear. The rounded periphery of *G. rudis* and its involute form is in marked contrast to the sharp periphery and evolute appearance of *G. intermedia*.

Within the *subdelaruei* Subzone a form similar to *G. baltica* is found, although very rarely. It has been named here *G. cf. baltica*. In the writer's opinion the form identified as *G. (G.) baltica* by Gawor-Biedowa (1972) in the Upper Albian in Poland is this form. Its common occurrence at this level is recorded by Gawor-Biedowa and the writer. The species possesses raised sutures in the initial part of the last whorl and is biumbilicate. Both umbilici are wide and deep. The former whorls are often,

but not always, visible on the spiral side of this predominantly evolute, planispiral form. However, it does not possess raised sutures in the distal portion of its last whorl, or the very wide last whorl of the involute *G. baltica*. It probably evolved from *G. intermedia* rather than *G. rudis*, and possibly merits a new species name.

Within the basal *varicosum* Subzone, the distinct species *G. cenomanica* appears, although recorded by Hart (1973a) as ranging from the *cristatum* Subzone. It closely resembles *G. intermedia* in outline, from which it probably evolved. However, it possesses a clearly visible spiral ridge. It is common from the *auritus* Subzone onwards. However, Hart (pers. comm.) now suggests that *G. cenomanica* s.s. is a Cenomanian species, with which the writer disagrees.

During the *perinflatum* Subzone, *G. baltica* appears, probably arising from *G. rudis* which disappears in the upper *S. dispar* Zone. The globular last chamber of *G. baltica* is a feature of the species which serves to relate it to *G. rudis* or possibly *G. cf. baltica* in the Upper Albian. The extension of the stratigraphical range of *G. baltica* downwards into the upper *S. dispar* Zone is proposed here. It was originally recorded by Brotzen (1942) in the Cenomanian. However, both Hart (1973b) and Malapris and Jannin (1967) have tentatively recorded it within the Upper Albian.

HEDBERGELLA

Suborder ROTALINA Delage and Hérouard, 1896

Superfamily GLOBIGERINACEA Carpenter, Parker, and Jones, 1862

Family HEDBERGELLINAE Loeblich and Tappan, 1974 (emend. Rotaliporidae Sigal 1958)

Subfamily HEDBERGELLINAE Loeblich and Tappan, 1961

Genus HEDBERGELLA Brönnimann and Brown, 1958

Hedbergella brittonensis Loeblich and Tappan

Plate 61, figs. 1-3

- 1961 *Hedbergella brittonensis* Loeblich and Tappan, pp. 274-275, pl. 4, figs. 1-8.
 1967 *Hedbergella brittonensis* Loeblich and Tappan; Fuchs (*in* Fuchs and Stradner), p. 331, pl. 18, fig. 1a-c.
 1972 *Hedbergella brittonensis* Loeblich and Tappan; Gawor-Biedowa, pp. 67-68, pl. 7, figs. 1, 2(a-c).

Hedbergella delrioensis (Carsey)

Plate 61, figs. 4-6

- 1926 *Globigerina cretacea* d'Orbigny var. *delrioensis* Carsey, p. 43.
 1959 *Praeglobotruncana* (*Hedbergella*) *delrioensis* (Carsey); Banner and Blow, p. 8.
 1961 *Hedbergella delrioensis* (Carsey); Loeblich and Tappan, p. 275, pl. 2, figs. 11-13.
 1972 *Hedbergella infracretacea* (non Glaessner); Gawor-Biedowa, pp. 69-70, pl. 6, fig. 8a-c.
 1973 *Hedbergella infracretacea* (non Glaessner); Damotte and Magneiz-Jannin, p. 40, pl. 4, figs. 26-30.
 1974 *Hedbergella delrioensis* (Carsey); Longoria, pp. 54-55, pl. 10, figs. 7-9; pl. 26, fig. 11.

Hedbergella infracretacea (Glaessner)

Plate 61, figs. 7-9

- 1890 *Globigerina cretacea* non d'Orbigny; Burrows, Sherborn, and Bailey, p. 566, pl. 11, fig. 18.
 1937 *Globigerina infracretacea* Glaessner, p. 28, text-fig. 1.

- 1962 *Globigerina infracretacea* Glaessner; Bartenstein and Bettenstaedt, pp. 280-281, pl. 39, fig. 15a, b.
 1966 *Hedbergella infracretacea* (Glaessner); Glaessner, pl. 1, figs. 1-3.
 1967 *Hedbergella infracretacea* (Glaessner); Fuchs (*in* Fuchs and Stradner), p. 331, pl. 17, fig. 13a-c.
 non 1972 *Hedbergella infracretacea* (Glaessner); Gawor-Biedowa, pp. 69-70, pl. 6, fig. 8a-c.
 1973 *Hedbergella infracretacea* (Glaessner); Damotte and Magniez-Jannin, p. 40, pl. 4, figs. 31-34.
 1974 *Hedbergella delrioensis* (non Carsey); Longoria, pp. 54-55, pl. 10, figs. 1-6, 10-12.
 1974 *Hedbergella infracretacea* (Glaessner); Longoria, pp. 59-60, pl. 13, fig. 9.

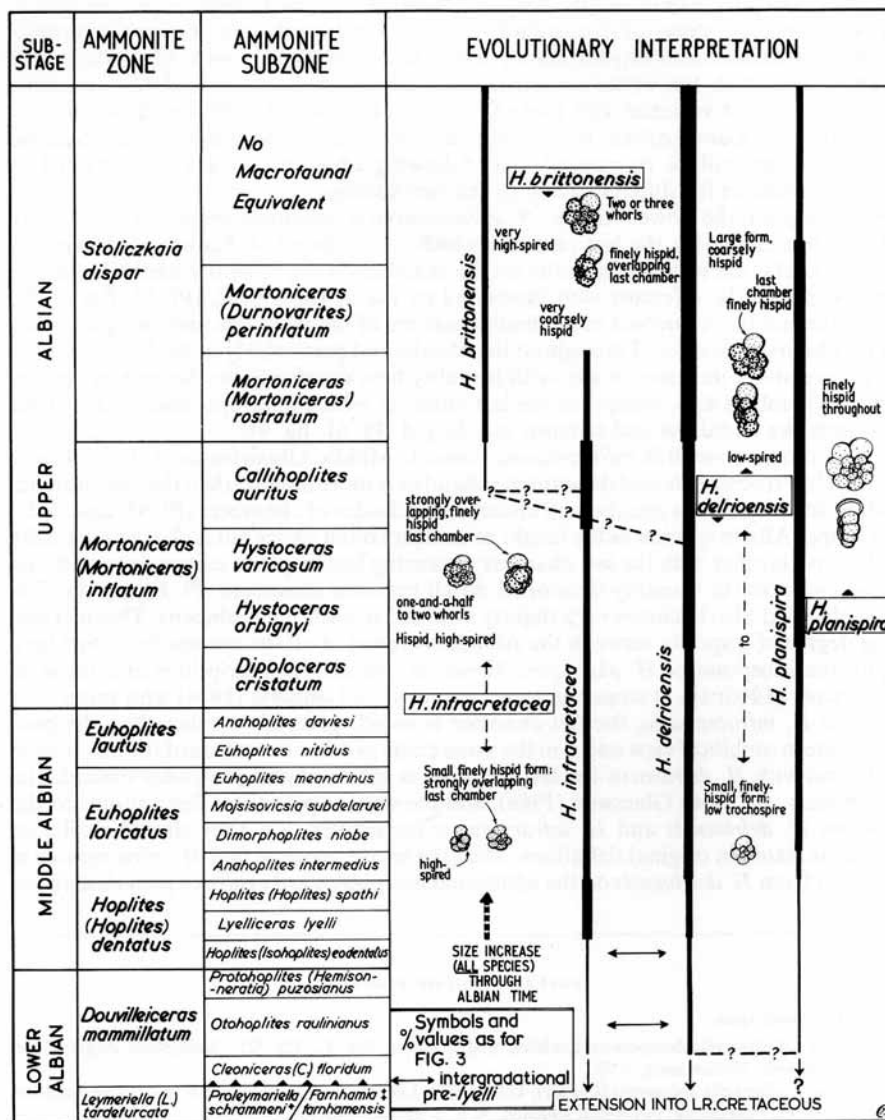
Hedbergella planispira (Tappan)

Plate 61, figs. 10-12

- 1940 *Globigerina planispira* Tappan, p. 122, pl. 19, fig. 12.
 1957 *Praeglobotruncana planispira* (Tappan); Bolli, Loeblich, and Tappan, p. 40, pl. 9, fig. 3.
 1961 *Hedbergella planispira* (Tappan); Loeblich and Tappan, pp. 267-268, pl. 5, figs. 4-11.
 1974 *Hedbergella planispira* (Tappan); Longoria, pp. 64-65, pl. 11, figs. 4-6; pl. 23, figs. 1-7, 17-18; pl. 24, fig. 10.

A general feature in the development of this genus throughout the Albian is the gradual size increase in all species within successively younger beds. Text-fig. 5 shows the suggested evolutionary interpretation for the genus. The first occurrence of *Hedbergella* within the Albian was recorded in the *raulinianus* Subzone. Its appearance here is, however, probably environmentally controlled as both *H. delrioensis* and *H. infracretacea* occur in older beds as recorded by other workers and discussed below.

The greatest problem in establishing an early hedbergellid evolutionary sequence has been the tendency to group forms into a single species, namely *H. (Globigerina) infracretacea* (Glaessner). From the synonymy list given above, it is the writer's opinion that this 'species' also includes *H. delrioensis*. Bartenstein and Bettendstaedt (1962) figure *H. infracretacea* s.s. as ranging from the Lower Barremian, but they do not record *H. delrioensis* within the Lower Cretaceous. Damotte and Magneiz-Jannin (1973) have recorded *H. infracretacea* in the Lower Aptian of the Aube, France. However, in the writer's opinion, their figured specimens include both *H. infracretacea* and *H. delrioensis*. Both these species have been considered possibly synonymous by Loeblich and Tappan (1961), but they state that the typically small *H. infracretacea* has not been examined by them. Glaessner (1966, p. 181) in reply states that his subsequent study suggested that *H. infracretacea* is distinguishable by small size, moderately elevated rather than depressed early coil, and absence of a large spatulate lip which flares slightly at its umbilical end, the presence of such features being characteristic of *H. delrioensis*. Glaessner further states that Hofker's study (1961) suggests the possibility of evolutionary trends which would link *H. infracretacea* with younger and more advanced forms, some of which may possess the characters of *H. delrioensis*; and also that *H. infracretacea* may therefore be given the status of a chronosubspecies of *H. delrioensis* rather than that of a species. However, he adds that the placing of *H. infracretacea* in synonymy of *H. delrioensis* which was done by Maslakova (1963) without qualifications or stated reasons cannot be accepted.



TEXT-FIG. 5. Evolutionary interpretation of the genus *Hedbergella* in the Albian of north-west Europe.

Finally, Longoria (1974) states that '... *H. infracretacea* (Glaessner) has served as a "waste basket" name for almost thirty-five years and nearly every Lower Cretaceous species of unknown affinity has been referred to this species...' with which the writer agrees. However, the writer's interpretation of *H. infracretacea* and *H. delrioensis* appears to be at variance with that of Longoria (1974) and is discussed below.

Within the Lower Albian both species are intergradational, although distinct end members can still be recognized. The following observations are put forward as further evidence for differentiation of the two species.

Throughout the Lower Albian, *H. infracretacea* is extremely small and has a finely hispid test except for the last chamber which is not hispid. A feature of the species at this level is the very fine hispidity on the chambers being more markedly developed on its spiral side, a feature well illustrated by use of the S.E.M. (Pl. 61, figs. 7, 8). Also the last two chambers in the final whorl are of the same size and the species has a very high trochospire. Throughout the Middle and particularly in the Upper Albian it progressively increases in size with hispidity now developed on the ventral surface of the chambers also, except for the last chamber which in all specimens is incurved towards the umbilicus and remains non-hispid (Pl. 61, fig. 9).

In comparison with *H. infracretacea*, Lower to Middle Albian forms of *H. delrioensis* have a low trochospire and the ultimate chamber is more inflated than the penultimate, while fine hispidity is equal on all chambers and sides of chambers (Pl. 61, figs. 4, 5). In Upper Albian specimens the height of the spire often varies but is characteristically a low trochospire with the last chamber appearing less hispid in comparison with the now more coarse hispidity developed on all previous chambers (Pl. 61, fig. 6). The last chamber also becomes very slightly inturred toward the umbilicus. This increasing degree of hispidity through the Albian is typical of all the species described here with the exception of *H. planispira*. However, the above descriptions and those of Glaessner (1966) are at some variance with those of Longoria (1974) who states that '... in *H. infracretacea*, the last chamber is ovoid, generally smaller than the penultimate in umbilical view and is in the same plane as other chambers of the last whorl; whereas with *H. delrioensis* the last chamber is spherical and protrudes towards the umbilicus...'. Both Glaessner (1966), and the writer apply these descriptions to the species *H. delrioensis* and *H. infracretacea* respectively, i.e. they should read vice versa as stated in original definition. Thus the writer suggests that *H. infracretacea* is distinct from *H. delrioensis* on the additional morphological evidence provided above

EXPLANATION OF PLATE 61

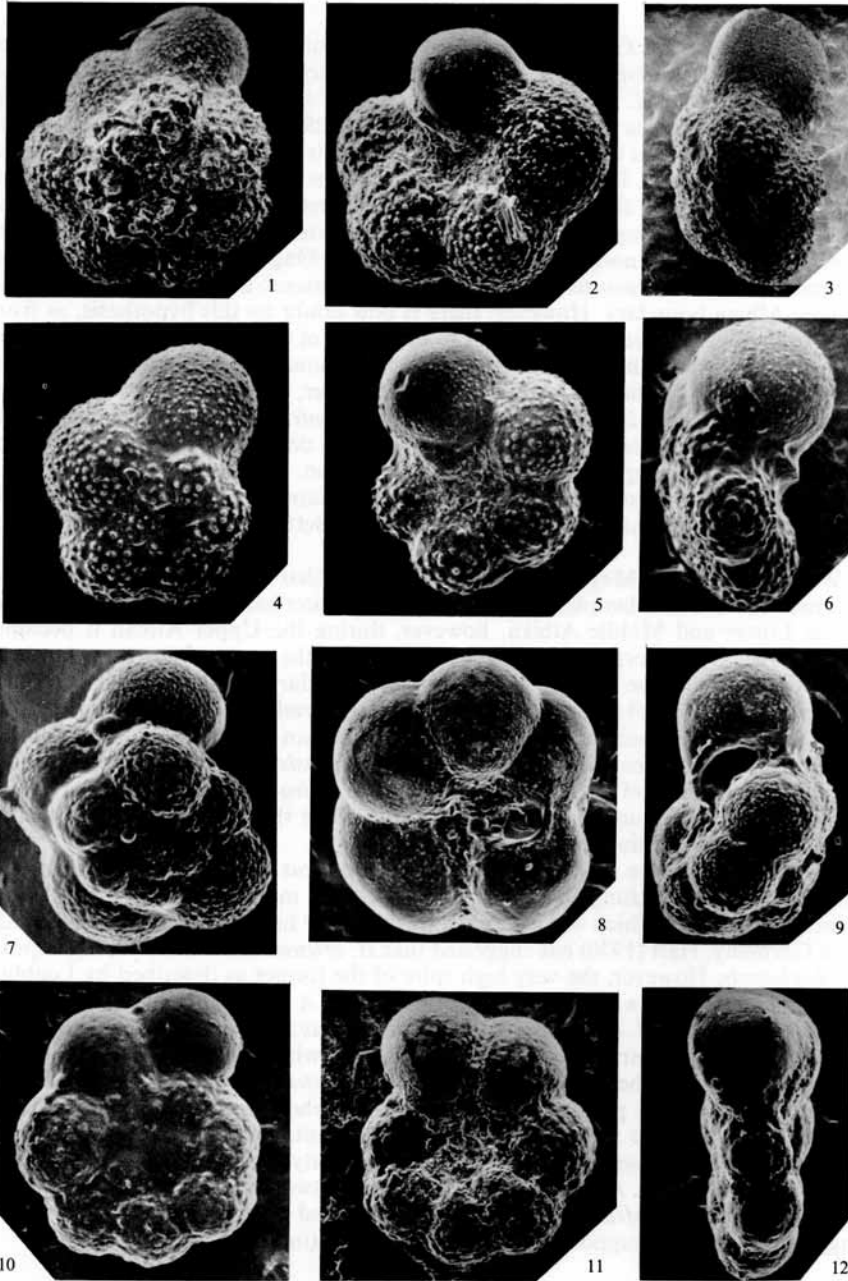
S.E.M. photographs.

Figs. 1-3. *Hedbergella brittonensis* Loeblich and Tappan, U.C.L. 325-327, *Stoliczkaia dispar* Zone, Schoonebeek, Netherlands, $\times 70$.

Figs. 4-6. *Hedbergella delrioensis* (Carsey), U.C.L. 328-330. 4, 5, *niobe* Subzone. 6, *varicosum* Subzone, Copt Point, Folkestone, south-east England. 4, 5, $\times 105$; 6, $\times 85$.

Figs. 7-9. *Hedbergella infracretacea* (Glaessner), U.C.L. 331-333. 7, 8, *niobe* Subzone. 9, *varicosum* Subzone, Copt Point, Folkestone, south-east England. 7, 8, $\times 120$; 9, $\times 90$.

Figs. 10-12. *Hedbergella planispira* (Tappan), U.C.L. 334-336, *orbigny* Subzone, Copt Point, Folkestone, south-east England, $\times 150$.



PRICE, *Hedbergella*

and corroborated by Glaessner (1966). Also the former species is not a chronosubspecies of *H. delrioensis*, but formed the root stock and primitive hedbergellid parent from which *H. delrioensis* arose. Longoria (1974) records '*H. delrioensis*' stratigraphically earlier than '*H. infracretacea*' in the Aptian, and it is therefore possible that the latter arose from the former at this level, i.e. *H. delrioensis* arose from *H. infracretacea*. Unfortunately, Longoria illustrates *H. infracretacea* s.s. with only one view, namely that of its umbilical side. Therefore other specimens identified as *H. delrioensis* by Longoria but possessing characteristic features of *H. infracretacea* have been placed in synonymy of the latter as given. Magniez-Jannin (1975) has also suggested that *H. delrioensis* arose from *H. infracretacea*, but around the Lower to Middle Albian boundary. However, there is now doubt on this hypothesis, as from her work with Damotte (1973) on the Lower Aptian of the Aube, France, they figure both forms all nevertheless identified as *H. infracretacea* but listed by the present writer separately in the synonymies above. However, the writer would agree with Magniez-Jannin that *H. delrioensis* arose from *H. infracretacea* although probably in the Aptian as 'suggested' by Longoria (1974). The derivation and first appearance of early hedbergellid species is outside this discussion. However, an examination of this genus from its first appearance in the Upper Hauterivian, see Longoria (1974) or within the Lower Barremian, see Bartenstein and Bettenstaedt (1962), is the subject of current research.

Within the Albian, Magniez-Jannin (1975) states that *H. infracretacea* is not very common relative to other planktonic species. The writer has found this to be the case in the Lower and Middle Albian, however, during the Upper Albian it becomes common at certain horizons and reaches its acme in the *auritus* Subzone prior to its extinction around the *rostratum-perinflatum* boundary. Both Hart (1973a) and Magniez-Jannin (1975) agree on its extinction of this level. However, Gawor-Biedowa (1972) records the species ranging into the Cenomanian of Poland, but examination of her figured specimens show them to be *H. delrioensis*, as listed in synonymy. The gradual size increase of both *H. delrioensis* and *H. infracretacea* through the Albian is a well-marked feature of their development, whilst the abundance of the former species increases within the Cenomanian.

The first occurrence of *H. brittonensis* in the *auritus* Subzone is coincident with *H. infracretacea* reaching its acme. This species is more common in the Lower Cenomanian chalk, which was examined by the writer in the Netherlands and north-west Germany. Hart (1970) has suggested that *H. brittonensis* is merely a high-spired *H. delrioensis*. However, the very high spire of the former as described by Loeblich and Tappan (1961) is a major feature of this species, it being much higher than high-spired specimens of *H. delrioensis*. Also, *H. delrioensis* although showing a gradation in height of trochospire still possesses a wide last whorl with a globular to ovoid ultimate chamber. The writer suggests that *H. brittonensis* possibly evolved from *H. infracretacea* as it possesses all the major morphological features of the latter species with regard to its Upper Albian development. The major difference which characterizes *H. brittonensis* is its very coarse hispidity and large size in comparison with *H. infracretacea*. Also it normally has two or two and a half visible whorls as compared with *H. infracretacea* which has one and a half visible whorls. These suggestions are now supported by Carter and Hart (in press).

The stratigraphical level at which *H. planispira* evolved in the Lower Cretaceous is difficult to determine due to the very small number of specimens recorded from horizons within the Aptian and Lower Albian. It does not occur in large numbers until the Middle Albian. Longoria (1974) records the species from the Lower Aptian, while the writer has recorded it in the Lower Albian. At these levels it shows a close affinity with early forms of *H. delrioensis*, and therefore it is probable that *H. planispira* arose from *H. delrioensis* within the Aptian, although the exact stratigraphical horizon at which it first appears is unknown. The species is quite distinct in that it possesses a planispiral or very low trochospiral coil and is the smallest Albian hedbergellid species. However, it shows a slight size increase from the Middle Albian onwards and becomes extremely abundant in the Upper Albian, where very rarely large individuals are found in an otherwise small-sized population. Its small size is in marked contrast to the now larger *H. delrioensis*, *H. infracretacea*, and *H. brittonensis*. In the upper *S. dispar* Zone the species, however, decreases in abundance.

In conclusion to the discussion of hedbergellid evolution within the Albian the problematic evolutionary position of '*Hedbergella*' *washitensis* (Carsey, 1926) has not been included within the suggested evolutionary scheme. This is for two reasons. First, the species is a tethyan warm-water form that is only found at periods of hiatus, notably the Middle to Upper Albian, and Lower to Middle Cenomanian boundaries, over north-west Europe. Thus its evolutionary position is uncertain. Secondly, its elevation to new generic status, namely *Favusella washitensis* by Longoria (1974) and adopted by van Hinte (1976) would seem to strengthen its exclusion from any evolutionary interpretation involving the hedbergellids. This new generic status is, however, still problematic and not discussed here.

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R. J. PRICE

Robertson Research (North America) Ltd.
501 Cleveland Crescent
S.E. Calgary, Alberta T2G 4R8
Canada

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