

## On *Everticyclammina* Redmond (Foraminifera), especially *E. kelleri* (Henson).

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**ABSTRACT** – *Everticyclammina kelleri* (Henson) (= *E. eccentrica* Redmond and *E. elegans* Redmond), a Berriasian-Valanginian index in the Middle East, is descended from the Late Jurassic Tethyan *E. praekelleri* sp. nov, a species which probably had its ancestry in Late Jurassic *Ammobaculites* sp. From this ancestor also evolved *E. virguliana*, and, in the Middle East, its Early Cretaceous descendants *E. hensoni* Redmond, *E. contorta* Redmond and *E. greigi* (Henson), which themselves formed the ancestry of the Albian *Hemicyclammina whitei* (Henson) and the Tethyan Albian - Cenomanian index *H. sigali* (Maync). Another, independent lineage from *Ammobaculites*, *Buccicrenata hedbergi* (Maync) (= *B. libyca* Gohrbandt) to *B. subgoodlandensis* (Vanderpool), transglobal in the Barremian - Cenomanian, is distinguished.

### INTRODUCTION

#### The type specimens of *Everticyclammina kelleri* (Henson)

In his review of the Mesozoic litiolids distinguished by the Iraq Petroleum Co., its Chief Palaeontologist, F.R.S. Henson, described the new species *Pseudocyclammina kelleri* (Henson, 1948, p. 16, pl. 9, figs. 4, 5 and 7), illustrating three of the 'many hundreds' of syntypes used by the company to define the species. All of the syntypes were random thin-sections, in limestone drilled by the British Oil Development Co. (later assimilated into the Mosul Petroleum Co., which was associated with I.P.C.) at 4726-4741 ft depth in the Awasil No. 5 Well, about 38 km west of Ramadi (and about 140 km west of Baghdad), Iraq. Henson (1948) originally believed that this limestone was of Argovian-Calloviaian age, but this age-determination was later revised. The beds in Awasil No. 5 which contained *P. kelleri* were firmly referred, by Wetzel and Dunnington, to the upper part of the Chia Gara formation, Berriasian, correlatable with the uppermost six beds of the stratotype Chia Gara of Kurdistan, the outcrop south of Amadia, north Iraq, which also contain *P. kelleri* (Dunnington *et al.*, 1959, pp. 72-77). The rich ammonite faunas of the type Chia Gara show that this formation straddles the Jurassic-Cretaceous boundary, ranging in age from Middle Tithonian to Berriasian; the appearance and frequency of record of *P. kelleri* in the Berriasian part of the formation (*loc. cit.*) would suggest that potentially it is a basal Cretaceous index species. "It is now believed that this foraminifer is limited to rocks of Berriasian and very early Valanginian age in northern Iraq" (*op. cit.*, p. 76) and subsequent records, discussed below, confirm that this is true for at least 200 km to the south-east, to Saudi Arabia (Redmond, 1964) and adjacent areas.

This is in spite of the fact that the original description of *P. kelleri* given by Henson (1948) was very limited by modern standards. All that was written was

*"Test thick-walled, arenaceous, with much cement; sub-epidermal layer largely obscured; labyrinthic layer pronounced, with scattered sand grains; the spiral part of the*

*test is involute, lenticular with two whorls and with twelve to thirteen chambers in the last whorl; the serial part of the test is somewhat elliptical in section with up to four chambers."*

The three syntypes which were photographed (Henson, 1948, pl. 9) consisted of one-near equatorial section (pl. 9, fig. 5) of what may now be regarded probably as a microspheric specimen, one subaxial section of an uncoiling (and possibly also microspheric) specimen (pl. 9, fig. 4), and one slightly oblique, axial section of a megalospheric specimen (pl. 9, fig. 7). The thin-sections of limestone in which these figured syntypes occur (registered in the British Museum (Natural History), numbers P. 35968, P. 35967 and P. 35969 respectively) contain many other syntypic specimens, including equatorial sections of megalospheric examples, which are figured here (Plate 1, figs. 1, 2) for the first time. Almost all these syntypes (including those originally figured) are pyritised. In many, the wall-structure is not clear; the 'labyrinthic layer' may be particularly obscure. Some of the specimens do not possess a "labyrinthic" wall at all, and may belong to the genera *Ammobaculites*, *Lituola* or similar forms. Others, like the syntypes figured by Henson (1948), have narrowly alveolar walls; these and others have been photographed (Plates 1, 2) and from them a lectotype is chosen (below). This restudy of the syntypes has enabled revision of the taxonomy and diagnosis, so that the species may more readily and confidently be identified as a basal Cretaceous biostratigraphic index.

Although it was not mentioned by Henson (1948), it was clear from two of his figures (pl. 9, figs. 4, 5) that the syntypes showed that the species possessed a single, large areal aperture in each septum, not many small ones (comparable in size to the primary alveolae of the wall, as shown for *Alveosepta* in Plate 5, figs. 1, 2, and as seen in *Pseudocyclammina lituus* (Yokoyama), even as figured by Henson himself, pl. 9., fig. 6). This single, areal aperture can also be seen to be characteristic of all species of *Everticyclammina* photographed by Redmond (1964), in his original descriptions of the members

of this, his new genus; it was suggested by Redmond (1964, p. 408), and accepted by Maync (1965, p. 39), that "*P.*" *kelleri* Henson should be included in *Everticyclammina*. As noted below, *E. eccentrica* Redmond (1964, p. 408, pl. 1, figs. 16-18, pl. 2, figs. 12-13), from the Saudi Arabian upper Yamama formation (Redmond, 1964, 1965), and *E. elegans* Redmond (1964, p. 408, pl. 1, figs. 19-21, pl. 2, figs. 14-16) from the lower Yamama, both parts of the formation together covering the Valanginian stage (Powers, 1968, pp. 159-162; Hughes Clarke, 1988, p. 13), are undoubtedly conspecific with *E. kelleri* (Henson).

### The species of *Everticyclammina* Redmond

The genus *Everticyclammina* was proposed primarily to accommodate a group of species which had been used by the micropalaeontologists of the Arabian American Oil Company (Aramco) in their stratigraphy of the Early Cretaceous of Saudi Arabia, and which could not satisfactorily be referred to *Pseudocyclammina*. However, the original description of the genus *Everticyclammina* given by Redmond (1964, pp. 407-8) was, and is, difficult to comprehend precisely. It was interpreted by Maync (1965) to "include all those transitional forms of 'pseudocyclamminid' *Ammobaculites*" in which the septa were "simple, not pierced", but he did not clarify the nature of the aperture, although this has become one of the premier diagnostic characters of the genus.

The originally designated type species of *Everticyclammina* was *E. hensoni* Redmond, 1964; the sectioned paratypes of this species (Redmond, 1964, pl. 1, figs. 22-25) show that it possessed a narrowly but regularly alveolar chamber wall but solid, non-alveolar septa, and that its aperture was simple, single, areal and "ammobaculitid". The primary types came from the Buwaib Formation drilled in Aramco well Damam-16, Saudi Arabia (Redmond, 1964, p. 409), which was dated by Aramco as of Hauterivian age (Powers, 1968, p. 53) although it contains no fossils other than benthic foraminifera and is overlain by the totally unfossiliferous Biyadh Sandstone (Powers, *loc.cit.*). The Buwaib Formation is currently regarded as being of Late Hauterivian to Early Barremian age, the Early Hauterivian being missing in its disconformity with the underlying, Valanginian Yamama Formation (Hughes Clarke, 1988). The type specimens of *E. hensoni* must also be considered to have belonged to the Late Hauterivian or Early Barremian or both.

The sectioned paratypes of *E. hensoni* (Redmond, 1964), also show that it is congeneric with "*Cyclammina*" *greigi* Henson, 1948. The sectioned paratypes of this latter species (Henson, 1948, pl. 13, figs. 9, 11; BM (NH) P. 35795-6) were drawn by Banner (1966, pl. 2, figs. 2, 3; 1970, pl. 9, figs. 2, 3) and were reinterpreted as possessing a single, simple, areal aperture throughout ontogeny, an alveolar chamber wall, but solid, non-alveolar septa (Banner, 1966, pp. 206, 212; 1970, p. 272; see also Plate 5, fig. 4). The genus *Mayncella* was proposed by Banner (1966), with *C. greigi* as its type species, to be distinguished from *Everticyclammina* Redmond by the separation of the lower parts of the septa of *E. hensoni*, which

meet the spiral suture almost perpendicularly (see Redmond, 1964, pl. 1, figs. 22-25) compared to the tangential approach to the spiral suture and their thickening and coalescence into a continuous, "basal layer" in *C. greigi*. These are specific, not generic differences, for they grade, with geological time, from species to species, and *Mayncella* must be regarded as a junior synonym of *Everticyclammina*, as noted by Hottinger (1967, p. 87).

The primary types of *E. greigi* were obtained from I.P.C. well Dukhan-2, Qatar, "just above the horizon of *Pseudocyclammina lituus*" (Henson, 1948, p. 13) in the Early Cretaceous beds which were almost certainly of Barremian age, being above the equivalent of the beds with the *P. lituus* illustrated by Banner (1966, pl. 4, fig. 3, and pl. 5, fig. 1-4; 1970, pl. 6, figs. 1-4) which are now believed to be Hauterivian.

The late Hauterivian/Early Barremian Buwaib Formation, drilled in the Aramco Saudi Arabian well Abqaiq-62, yielded the primary types of *E. contorta* Redmond (1964, pl. 1, figs. 12-15). Hottinger (1967) illustrated equatorially-sectioned topotypes (1967, pl. 9, figs. 17-18), which he believed to be synonymous with *E. greigi*. However, this species is clearly distinguishable from the contemporaneous *E. hensoni* and the younger *E. greigi*, using the equatorial sections of all of them. In *E. hensoni* (Plate 3, fig. 6), not only are the lower parts of the septa separated, meeting the preceding spiral suture nearly perpendicularly, but the upper part of the septa meet the chamber-peripheries also almost at right-angles; consequently, in equatorial section the adult chambers are of quadrilateral shape, almost parallelograms. In *E. contorta* (Plate 3, fig. 3), the lower parts of the septa, while still separated, meet the preceding spiral suture at about 45° and the chamber peripheries at a similar angle; the chambers are reniform in equatorial section. In *E. greigi*, as noted above, the lower parts of the septa are coalescent, being thickened on meeting the preceding spiral suture tangentially, while the upper parts of the septa meet the chamber-peripheries obliquely (Plate 5, fig. 4, as in *E. contorta*).

The stratigraphic range of this group of species of *Everticyclammina*, in this area of the Mid-East Gulf, is now believed to be from the Berriasian-Valanginian (Upper Chia Gara and Yamama Formations and their equivalents), through Hauterivian and Barremian (Simmons & Hart, 1987, pp. 189-190) to probable Aptian (Banner, 1970). There is a clear stratigraphical succession in this plexus of forms which, when separated taxonomically, can be used both biostratigraphically and phylogenetically. For the former, it should be remembered that the taxa were originally employed stratigraphically, by both Iraq Petroleum and its associated companies and by Aramco; as Redmond wrote (1965, p. 185), they "were selected for publication because of their importance in a zonation set up over a more than fifteen year period of work in Saudi Arabia." To regard them as wholly conspecific, as was done by Brun and Rey (1975), has no justification.

Brun and Rey (1975) considered all the taxa noted above, including *E. kelleri* (Henson), to be junior synonyms of the

European, Kimmeridgian species *Pseudocyclammina virguliana* Koechlin (1942), which they re-designated as the new type species of *Everticyclammina*. This is not allowable by the ICZN code (Ride, *et al.*, 1985, Articles 67, 68) but it is also not helpful in understanding the phylogeny involved. Maync (1965, p. 39) had already noted that he intended to propose the new genus *Pseudobaculites* for *Pseudocyclammina virguliana*, which also has an alveolar chamber wall but non-alveolar septa and single, areal "ammobaculitid" septal and terminal apertures, but this name was not only junior to *Everticyclammina*, it was also a junior homonym (of *Pseudobaculites* Cobban, 1952 *teste* Loeblich and Tappan, 1988, p. 99). Nevertheless, *Everticyclammina virguliana* (Koechlin), a binomen already suggested by Redmond (1964), is the stratigraphically oldest named species of this genus. Koechlin (1942, pl. 6) figured six sectioned, Middle Kimmeridgian, type specimens from the Berner Jura, and Maync (1953a, pl. 16) reproduced three of them. Hottinger (1967, text-fig. 43 and pl. 9, figs. 10-16) excellently illustrated equatorial sections of this species as found in the Kimmeridgian of east Morocco, representing the A<sub>1</sub> and A<sub>2</sub> and B generations (Koechlin's published photomicrographs showed only dimorphism). In all its generations, *E. virguliana* has adult septa which are very similar indeed to those of *E. contorta*, except that in some specimens (Plate 2, fig. 5) the septa are anteriorly protruberant; the chambers are, in equatorial section, just as reniform. However, the megalospheric forms of *E. virguliana* may have more chambers in the adult whorls (up to 9, as on Plate 2, fig. 5) and the microspheric (B) forms also have more chambers in the adult whorl (8-12, compared to 6-7 in *E. contorta*). The alveoles of the test-wall of *E. virguliana* are simple (at their most advanced, in the "Portlandian", irregularly and distally bifurcating, as SEM imaged by Bellier *et al.*, 1979, pl. 2, figs. 1-2; at their simplest, in the Kimmeridgian, beautifully drawn by Hottinger, 1967, p. 19, and 1978, p. 209), not regularly or closely bifurcating as they are in *E. contorta* (as shown by Hottinger, 1967, p. 87, pl. 9, figs. 17, 18) and *E. greigi* (see Banner, 1970, pl. 9).

### The phylogeny of *Everticyclammina*

The species *Everticyclammina virguliana* (Koechlin), *E. kelleri* (Henson), *E. hensoni* Redmond, *E. contorta* Redmond and *E. greigi* (Henson) are not only congeneric, they represent stages in a phylogenetic plexus of evolving communities bridging the Kimmeridgian to Aptian interval. The story of the evolution, shown on text-figure 1, may be outlined as follows.

In the Middle/Late Jurassic (probably Callovian/Oxfordian), a descendant of a species of *Ammobaculites* developed an alveolar wall. This was the first representative of the new genus *Everticyclammina*.

In conglomeratic, sparitic limestone outcropping at Broumana (about 20 miles east of Beirut), Lebanon, are abundant specimens of *Everticyclammina* with coarsely alveolar and irregularly labyrinthic, thick hypodermis. This deposit, of an inner neritic palaeoenvironment, is probably of

Kimmeridgian-Tithonian age, for this, heavily block-faulted area is mapped (Dubertret, 1963) as exposing thin limestone beds of this age and the succeeding Neocomian sandstones, lignites and contemporary basalts (Dubertret, 1963, pp. 38-45, 71-77). This species, here regarded as the new species *Everticyclammina praekelleri* (it was regarded by Henson, 1948, p. 17, as an untypical form of "*Pseudocyclammina kelleri*") differs from all other known forms of *Everticyclammina* by the large size and coarseness of both the alveolae and the dividing wall-elements of its thick hypodermis. The broad alveolae were closed in the latero-posterior parts of chamber walls, as the hypodermis there fused to the epidermis of the wall of the preceding chamber (Plate 3, fig. 5.) On the innermost surfaces of the posterior parts of the hypodermis, this produced very large alveolae, of irregular size and (polygonal) shape, with ramifying walls (Plate 1, fig. 1).

Its Kimmeridgian deeper water contemporary, with narrow alveolae and a regularly labyrinthic hypodermis, *E. virguliana*, ranged from Portugal (where its oldest occurrence may be at the summit of the Oxfordian, see Ramalho, 1985), through north Africa and southern Europe to the Middle East. *E. virguliana* ranged from Kimmeridgian to "Portlandian" (Tithonian) and occupied a deeper-water palaeoenvironment (outer neritic to bathyal) even than the contemporaneous *Alveosepta* (outer to inner neritic) (see Pélissié *et al.*, 1984) and one which was much deeper than that occupied by the shallow-neritic *E. praekelleri*. *E. virguliana* was axially biconcave, with depressions at each umbilical area, and (like *E. praekelleri*) in equatorial section it had reniform chambers, with solid septa which met the chamber periphery and the inner spiral suture obliquely. The wall had alveoles which in the Kimmeridgian were simple, not bifurcating, and relatively broad, but by the end of the Jurassic ("Portlandian" or Tithonian equivalent) had narrowed and had begun to bifurcate. The posterior hypodermal alveoles of *E. virguliana* were larger than the rest, and formed a distinctive row of subcircular spaces in the latero-posterior walls of each chamber (Koechlin, pl. 1, fig. 7; Plate 3, fig. 4), smaller and more regularly formed than those of *E. praekelleri*. The microspheric generation of *E. virguliana* had 8 to 12 chambers in an adult whorl, while the megalospheric had 6 to 9 (Plate 2, fig. 5), more than in *E. praekelleri* (Plate 1, fig. 1).

In the earliest Cretaceous (Berriasian - Valanginian), the Iraqi-Arabian area saw the evolution of *Everticyclammina kelleri*, which, in equatorial section, was virtually indistinguishable from *E. virguliana*, and which had much finer and regularly formed alveolae than its ancestral *E. praekelleri*. The latter had a coarsely labyrinthic hypodermis; the new *E. kelleri* had a smooth, regularly structured hypodermis. In axial section, *E. kelleri* had no trace of umbilical biconcavity; the umbilical areas were now very convex, and axially the test was diamond-shaped when in section (Plate 1, figs. 4-6; Plate 2, figs. 2, 4). The latero-posterior alveolae of the hypodermis of the chamber-walls were very large compared to those of *E. virguliana*, but smaller and more regularly formed than those

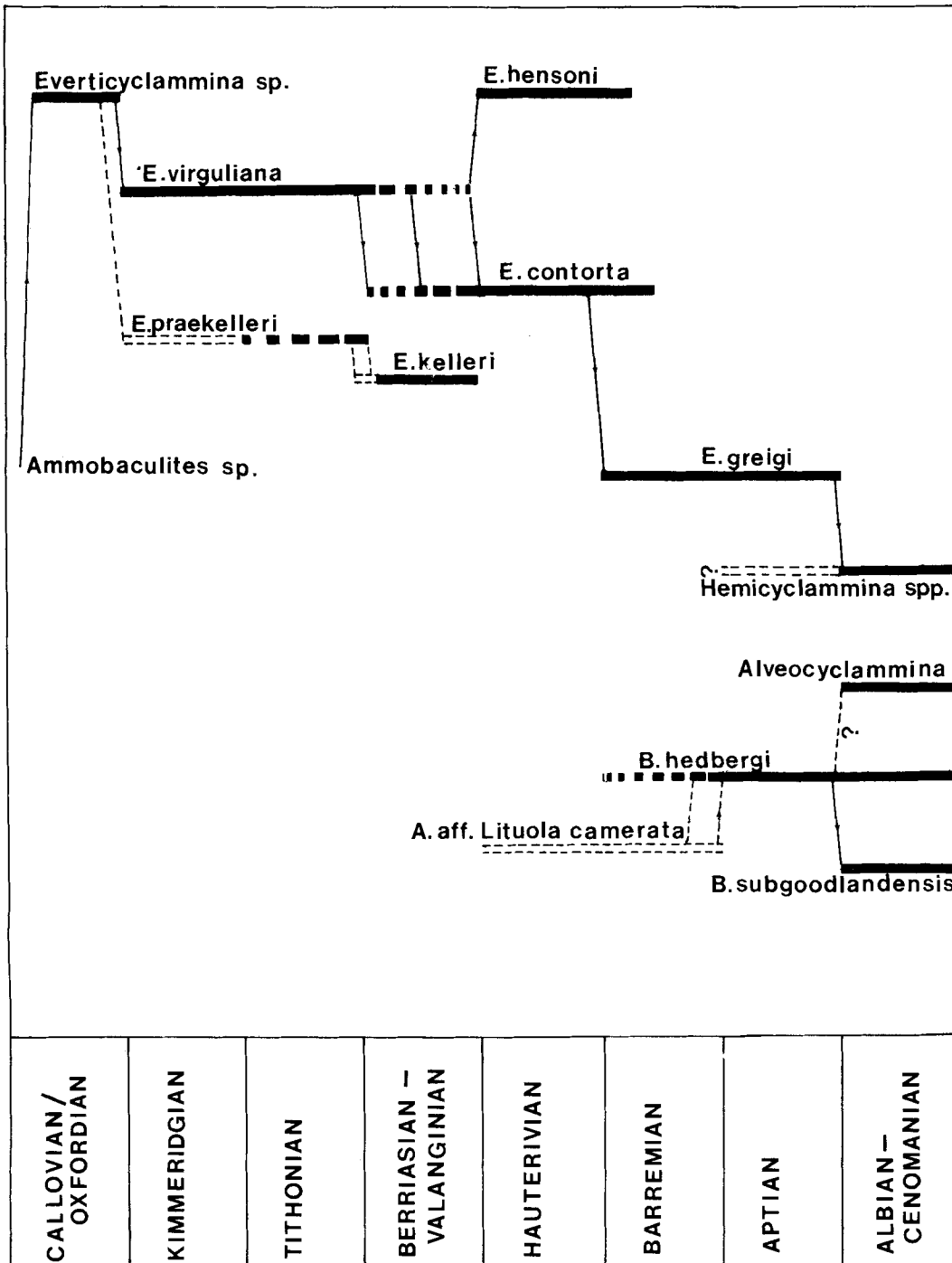


Fig. 1. The phylogeny of *Everticyclammina*.

#### Explanation of Plate 1

- Fig. 1. *Everticyclammina praekelleri* n.sp., holotype, x 38.6; equatorial section in slide P 52255, Kimmeridgian-Tithonian limestone exposed at Broumana, near Beirut, Lebanon.
- Figs. 2-6. *E. kelleri* (Henson); all from well Awasil -5, Iraq, in Berriasian-Valanginian limestones. Figs. 2a, 2b. paralectotype, equatorial section in slide P. 35968; fig. 2a, x 45; fig. 2b, enlargement of part of same specimen, showing hypodermal alveolae, x 177.
- Figs. 3a, 3b, lectotype, near-centred axial section of probable microspheric form, in slide P. 35967; fig. 3a, x 37; fig. 3b, enlargement x 93. Figs. 4-6, axial sections of megalospheric paralectotypes; fig. 4, in slide P. 35969, x 43; fig. 5, in slide P. 52256, x 44.5; fig. 6, on slide P. 52256, x 54.



of the ancestral *E. praekelleri*, and lacked undulating, rami-fying margins; they formed a distinctive row of subcircular to subquadrilateral spaces at the base of each chamber, when they were cut tangentially in axial (Plate 1, figs. 3a, 3b) or oblique-equatorial sections (Plate 2, figs. 3a, 3b; Plate 3, figs. 1, 2). Some Valanginian representatives of this species (from the basal Yamama formation and called *E. elegans* by Redmond, 1964, 1965) often were relatively small (Plate 2, fig. 4), but the later Arabian representatives (from the top of the Yamama, and called *E. eccentrica* by Redmond, 1964) were nearly double this size (Plate 2, fig. 2) and were similar to the Iraqi Berriasian syntypes of *E. kelleri* (Plate 1, figs. 4-6). Like *E. virguliana*, the microspheric *E. kelleri* had 9-12 chambers in adult whorls (Plate 2, fig. 1a), while the megalospheric had about 6 (Plate 1, figs. 1, 2a; Plate 2, fig. 3a). However, *E. kelleri* became extinct at the end of the Valanginian, and left no descendants.

The other Early Cretaceous species formed part of a continuous lineage. *E. contorta* (Plate 3, fig. 3), from the Hauterivian/Early Barremian, closely resembled ancestral *E. virguliana* but had reduced the number of chambers in its microspheric adult whorls to 7-8 per whorl and the alveolae were regularly and tightly bifurcating: the latero-posterior alveolae of each chamber hypodermis were no longer relatively enlarged. It is clearly intermediate between *E. virguliana* and its descendant, the Barremian-Aptian *E. greigi*, a species in which the lower parts of the adult septa become oblique, then tangential, to the spiral suture, and thicken and coalesce to form an imperforate "basal layer" to the chambers (Plate 5, fig. 4). The reduction of the distinct, lower parts of the septa, and the smoothing out of the "basal layer", produced the Albian - Cenomanian genus *Hemicyclammina*, in which the upper parts of the septa are thinned and meet the test periphery almost at right-angles, so that the chambers become almost quadrangular in equatorial section (as in *H. whitei*, Plate 5, fig. 3). There was an earlier attempt to develop such quadrangular chambers but without the development of a "basal layer"; here, in the Hauterivian/Early Barremian, the septa meet both the chamber periphery and the spiral suture almost perpendicularly. This was in *E. hensoni* (Plate 3, fig. 6), the type species of *Everticyclammina*, which apparently also left no direct descendants.

#### SYSTEMATIC PALAEOONTOLOGY

Suborder Textulariina Delage & Hérouard, 1896  
Superfamily Loftusiacea Brady, 1884

Family Cyclamminidae Marie, 1941  
Subfamily Buccicrenatinae Loeblich & Tappan, 1985  
Genus *Everticyclammina* Redmond, 1964  
*Everticyclammina kelleri* (Henson, 1948), emended  
(Pl. 1, figs. 2-6; Pl. 2, figs. 1-4; Pl. 3, figs. 1-2)

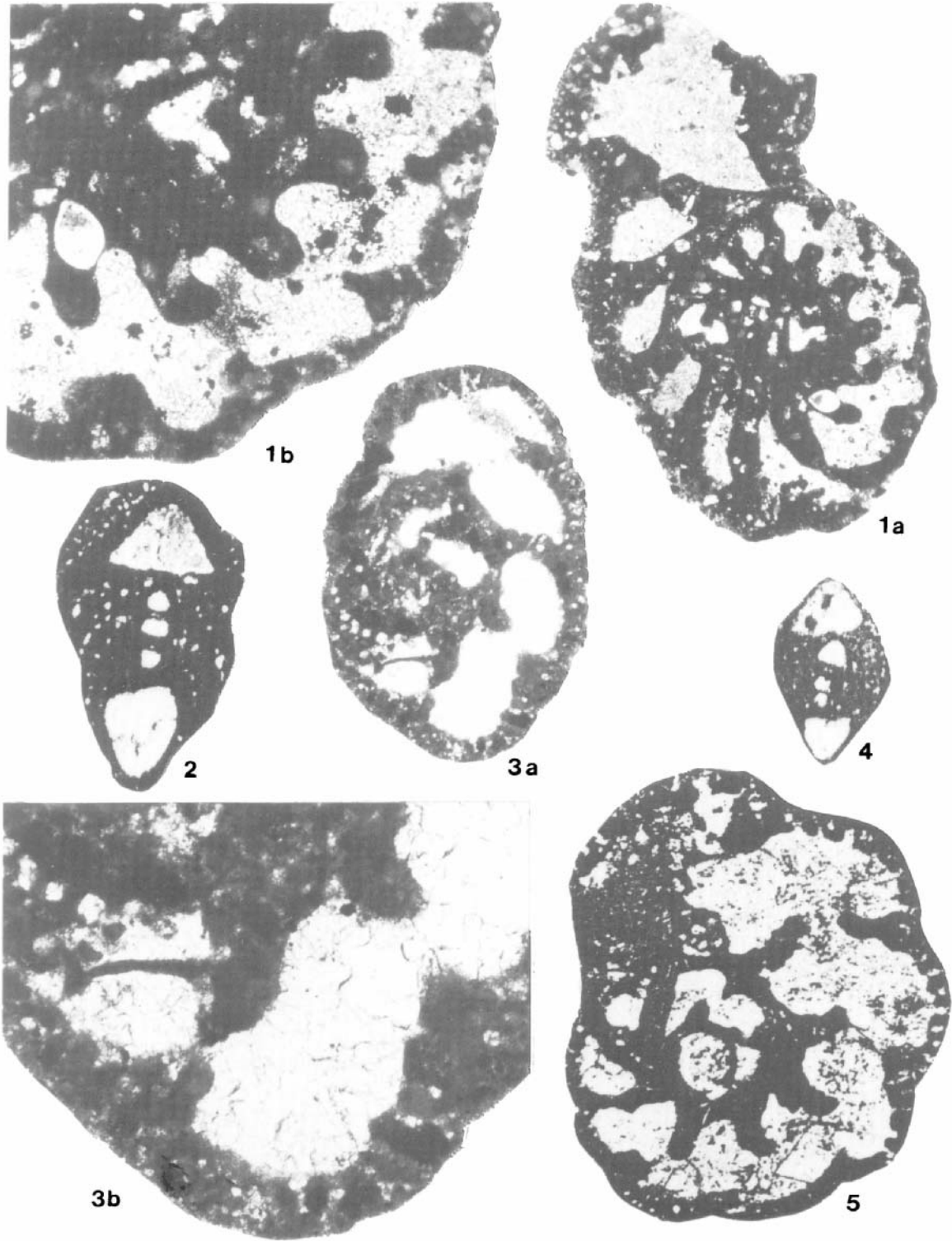
- 1948 *Pseudocyclammina kelleri* Henson, pp. 16-17; pl. 9, figs. 4,5,7.  
1964 *Everticyclammina eccentrica* Redmond, p. 408; pl. 1, figs. 16-18; pl. 2, figs. 12-13.  
1964 *Everticyclammina elegans* Redmond, pp. 408-409; pl. 1, figs. 19-21; pl. 2, figs. 14-16.

**Type Specimens** The specimen registered in the British Museum (Natural History) in slide P. 35967, which was originally figured by Henson (1948, pl. 9, fig. 4) and which is here rephotographed (Plate 1, figs. 3a, 3b), is here designated as lectotype; the other specimens figured by Henson and rephotographed here, plus the other specimens from slides P. 35968 and P. 35969 figured here (Plates 1-3, as noted above) are paralectotypes. All are from subsurface, well Awasil No. 5, Iraq, from the stratotype Zangura Formation (Dunnington *et al.*, 1959, pp. 305-6), at levels thought to be correlatable with the Upper Chia Gara Formation, and therefore Berriasian-Valanginian in age. All are random thin sections in micritic limestone.

**Description** Test made of microgranular, imperforate calcite with agglutinated, scattered, fine-silt size, quartz and other exotic grains; planispirally coiled, involute, with umbilical overlap of successive chamber-walls, so that the umbilical areas become thickened and convex and the test becomes subrhombic in axial section; megalospheric tests may consist of about 2 whorls of chambers and the microspheric tests of about 3, and the last few (up to 3 or 4) chambers may uncoil and become oval in cross-section and rectilinear in microspheric forms; megalospheric tests have 6 to 7 chambers in each adult whorl, while microspheric tests have up to about 12 or 13 before uncoiling starts; in thickness, the chamber walls are about one-quarter of the total chamber height when the test is seen in equatorial thin section; the walls of the chambers of the first whorls may be solid, but in subsequent whorls the chamber walls have an alveolar hypodermis, with antero-peripheral areas containing bifurcating alveoles, each in total about three times as long as broad and spaced apart at distances approximately equal to their diameters, but with postero-lateral areas with broadening alveoles which cease to

#### Explanation of Plate 2

- Figs. 1a, 1b, and 3a, 3b. *Everticyclammina kelleri* (Henson), paralectotypes, in slide P. 35968, Berriasian-Valanginian limestone cored in well Awasil-5, Iraq. Figs. 1a, 1b, equatorial section of microspheric specimen; fig. 1a, x 42.5; fig. 1b, enlargement x 92.5. Figs. 3a, 3b, oblique equatorial section of megalospheric section; fig. 3a, x 44.7; fig. 3b, enlargement, x 100.  
Figs. 2,4, axial sections enlarged from Redmond (1964, pl. 1). Fig. 2, "*E. eccentrica*" Redmond, paratype, x 38, from Aramco well Dammam-16, 3485-90 ft, (upper?) Yamama Formation, Saudi Arabia, Valanginian. Fig. 4, "*E. elegans*" Redmond, paratype, x 38, from Aramco well Ain Dar-60, 4980-82 ft, (lower?) Yamama Formation, Saudi Arabia, Valanginian. Both are synonyms of *E. kelleri* (Henson).  
Fig. 5. *E. virguliana* (Koechlin), enlarged from Hottinger (1967, pl. 9), equatorial section of megalospheric hypotype, x 63; from Mechra Klila, east Morocco, Late Jurassic.



bifurcate, which increase their diameters by 4 to 5 times, yet which are still separated by thin hypodermal walls (approximately as thick as those which separate the antero-peripheral alveoles); the alveolar hypodermis is covered by a very thin, imperforate epidermis, which seals the hypodermal alveoles; the septa are curved, meeting both the chamber peripheral walls and the inner spiral suture obliquely; the septa are solid, non-alveolar, and are each pierced medially by a single, areal, suboval or slit-like aperture; in thickness, the septa may be about equal to the chamber walls, but the upper part of some septa may be thinned relative to both the adjacent chamber walls and the inner (lower) parts of the same septa.

**Remarks.** The lectotype (like the paralectotype illustrated in Plate 2, figs. 3a, 3b) contains flecks of iron pyrites in its test wall; the other figured paralectotypes are more heavily pyritised.

The lectotype, which is an off-centred, axial, microspheric specimen, shows (Plate 1, fig. 3b) the solid wall of the first whorl and the alveolar walls of subsequent whorls, plus (Plate 1, figs. 3a, 3b) the marked and progressive broadening of the postero-lateral alveoles of the hypodermis. These broader alveoles are also seen in the axial sections of Plate 1, fig. 4, and Plate 2, fig. 2 (which is a paratype of "*E. eccentrica* Redmond"); in equatorial and oblique-equatorial sections, they may be clearly seen on Plate 2, figs. 3a, 3b and Plate 3, figs 2 and 2. The thick-walled spaces on the left of the umbilical area of the subaxial section of Plate 1, fig. 6, are parts of chambers of the last whorl (compare the thin-walled, broadened alveolae of Plate 1, fig. 3b); the umbilical overlap of such chambers produced the biconvex, subrhombic or "diamond-shaped" axial section, which, with the greatly broadened postero-lateral hypodermal alveolae, enable this species to be readily distinguished from all other known species of *Everticyclammina*.

The occasional presence of an apparently many-holed aperture ("a narrow slit or a series of pores along the bottom of a long narrow depression") noted by Redmond (1964, pp. 408-9) must be due to its partial infilling with matrix in the extracted specimen; no axial, equatorial or oblique thin section is known which shows anything other than the single, areal, "ammobaculitid" aperture now generally agreed (e.g. Brun & Rey, 1975; Loeblich & Tappan, 1988) to be charac-

teristic of *Everticyclammina*. However, the "retral-process-like parallel ridges crossing sutures" noted by Redmond (*loc. cit.*) may be external, epidermal covers for the enlarged postero-lateral alveoles of the hypodermis, which are largest adjacent to the posterior intercameral sutures; only re-examination of extracted specimens can resolve this.

*Everticyclammina praekelleri* sp.nov.  
(Pl. 1, fig. 1; Pl. 3, fig. 5; Pl. 4, figs. 1-11)

**Derivation of Name.** From its stratigraphically earlier occurrence than *E. kelleri*.

**Diagnosis.** A species of *Everticyclammina* with enlarged postero-lateral alveolae and irregularly alveolate wall.

**Type Specimens.** The holotype is that specimen figured here as Plate 1, fig. 1; all the other specimens figured here (Plate 3, fig. 5; Plate 4, figs. 1-11) are paratypes. All are random sections in a thin-section of limestone, registered in the British Museum (Natural History) as P. 52255.

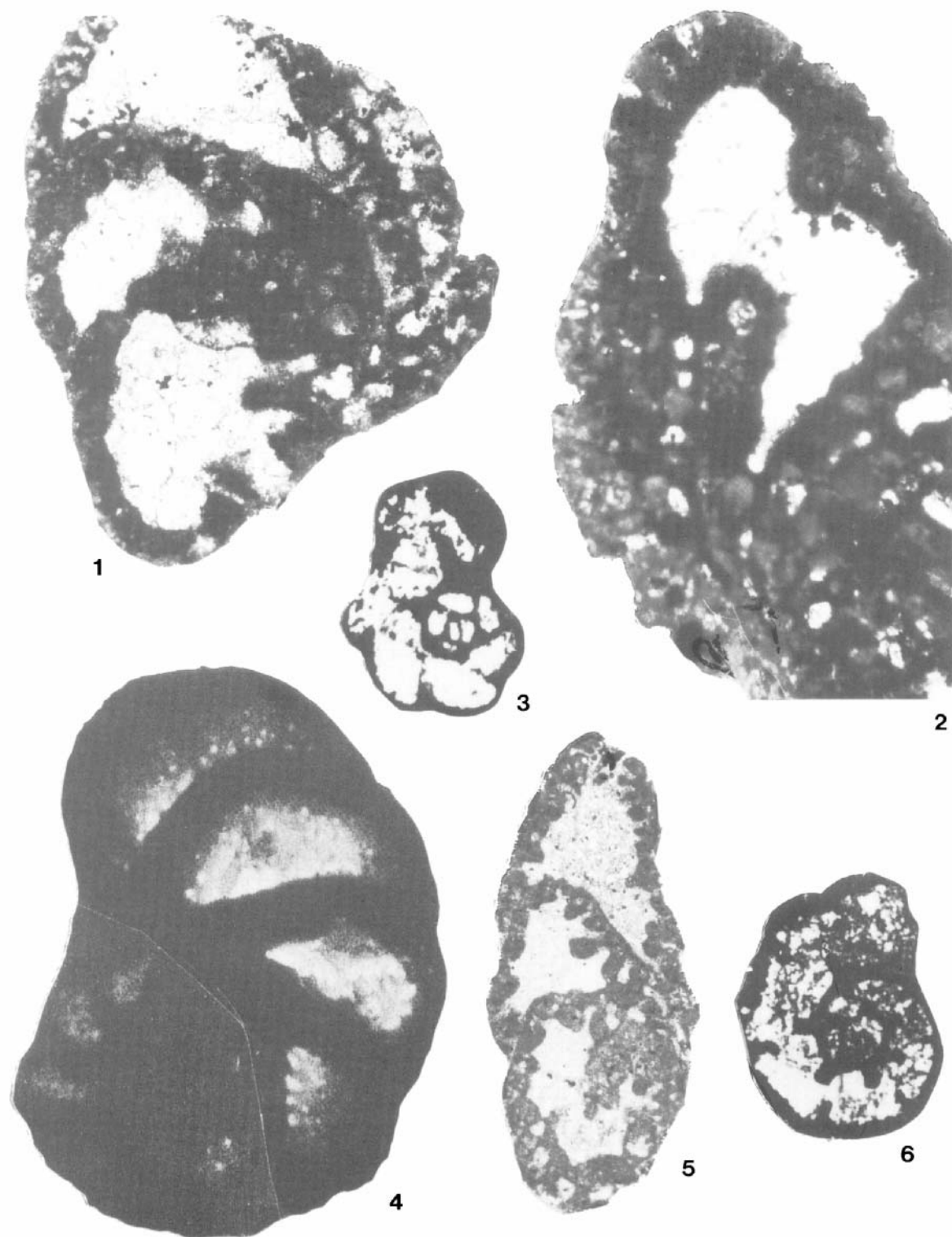
**Locality and Horizon.** The rock-sample was collected from Broumana, near Beirut, Lebanon, from an outcrop on the road to Mar Mousa, between Baabdat and Bhannès, near a spring (Henson, 1948, p. 17), from limestones judged by macrofossils to be Kimmeridgian-Tithonian in age (Dubertret, 1963)

**Description.** Test made of microgranular, micritic, imperforate calcite; planispirally coiled, involute, chambers touching or minimally overlapping in the umbilical regions, so that the umbilical areas are flattened or slightly convex; megalospheric tests may consist of about one to two whorls of chambers with about six in the final whorl; in thickness, the chamber walls are about one-quarter of the total chamber height when seen in equatorial section, but they appear to vary from about one-third to one-sixth depending on preservation and angle of cut; the walls of the chambers of the first whorl may be solid, but in the last whorl coarse alveolae develop irregularly in the hypodermis; in the antero-peripheral areas of the chamber walls, the alveoles may be about as broad, or about half as broad as long, simple (not bifurcating along their length) and spaced irregularly but at distances equal to or greater than their breadth; in the postero-lateral areas of the hypodermis, the irregular alveoles become much broader and closely spaced, so that (when sectioned in the plane of the innermost

### Explanation of Plate 3

- Figs. 1, 2. *Everticyclammina kelleri* (Henson), paralectotypes from Iraq, well Awasil-5, 4728 ft., core of Berriasian-Valanginian limestone; oblique-equatorial sections showing postero-lateral hypodermal enlarged alveolae. Fig. 1, in slide P. 52257, x 95. Fig. 2, in slide P. 35969, x 98.
- Fig. 3. *E. contorta* Redmond, equatorially sectioned, megalospheric paratype, enlarged from Redmond, 1964, (pl. 1, fig. 12), x 38; from Aramco well Abqaiq-62, core at 5263 ft., Buwaib Formation (Late Hauterivian/Early Barremian), Saudi Arabia.
- Fig. 4. *E. virguliana* (Koechlin), syntype x 61, enlarged from Koechlin, 1942 (pl. 6, fig. 7) from *Virgula*-Mergel, la Chaux, Switzerland, Upper Kimmeridgian; the enlarged postero-lateral alveolae of the hypodermis are particularly well seen in the chamber which is fourth from the last.
- Fig. 5. *E. praekelleri* sp.nov., obliquely off-centred paratype x 41; in slide P 52255, limestone from Broumana, near Beirut, Lebanon; showing large, irregular hypodermal alveolae, and their enlargement in the postero-lateral region with their fusion in this region to the preceding epidermis.
- Fig. 6. *E. hensoni* Redmond, equatorially sectioned, megalospheric paratype, enlarged from Redmond, 1964 (pl. 1, fig. 22), x 37.5; from Aramco well Dammam-16, ditch sample at 3315-20 ft., Buwaib Formation (Late Hauterivian/Early Barremian), Saudi Arabia.





surface of the hypodermis) they possess thinner and irregularly ramifying walls (when sectioned in an outer plane, just below the epidermis, the alveolus-walls are thicker, and can be seen to fuse against the epidermis of the preceding chamber); when cut equatorially, the large, postero-lateral alveoles are subpolygonal in shape; when cut obliquely, they give the appearance of ridge-like, ramifying but subparallel structures, but when cut axially these alveoles are irregularly subquadrilateral in shape; the hypodermis is covered by an imperforate epidermis of variable thickness, which externally seals the hypodermal alveoles; the septa are curved, meeting both the chamber peripheral walls and the inner spiral suture obliquely; the septa are solid and non-alveolar, and each is pierced medially by a single, area, suboval aperture; the septa are about as thick as the chamber walls.

**Remarks.** *Everticyclammina praekelleri* differs from *E. kelleri* because of its

(a) less regularly structured wall, with a hypodermis which varies in thickness even within one chamber (Plate 4, figs. 3, 9, 11), and in which the inner surface may undulate as the microgranular walls (of the alveolae) grow thicker or thinner (Plate 3, fig. 5; Plate 4, figs. 3, 4, 9, 11).

(b) broader, wider antero-peripheral hypodermal alveoles, which are less regularly and more widely spaced (as in all figures),

(c) bigger and more irregular postero-lateral hypodermal alveoles, which may be very variable in size and in subpolygonal shape in equatorial section (Plate 1, fig. 1), and which adopt a subparallel, elongate appearance when sectioned obliquely (Plate 4, figs. 3, 4). These enlarged posterior alveoles clearly arise by their fusion on to the preceding epidermis (Plate 3, fig. 5; Plate 4, fig. 11) and do not form a discrete, isolated posterior alveolae row, but are part of an irregular series of enlarged postero-lateral alveoles (Plate 1, fig. 1; Plate 4, figs. 1, 3, 4),

(d) less convex umbilical areas,

(e) broader, less slit-like aperture.

The microspheric form has not been seen in equatorial section, but two subaxial sections (Plate 4, figs. 1, 10) show more whorls than are known in megalospheric specimens and have short, uncoiling terminal growth stages; they may be sections of microspheric specimens and are strictly comparable to the lectotype of *E. kelleri* (Plate 1, fig. 3a, 3b).

*Everticyclammina praekelleri* is believed to be the Late Jurassic (Tithonian and possible Kimmeridgian) immediate ancestor of the earliest Cretaceous (Berriasian-Valanginian) *E. kelleri*. *E. praekelleri* is not yet known from the Iraqi-Arabian region, but, in those areas, the Hiith and Gotnia anhydrites (and associated dolomitisation) make preservation

of Late Kimmeridgian-Tithonian foraminifera very rare (Dunnington *et al.*, 1959).

The very enlarged postero-lateral alveolae and the irregularly alveolate wall (together with the tendency towards fewer chambers per whorl) distinguish *E. praekelleri* from members of the lineage of *E. virguliana* - *E. greigi*.

## COMPARISON WITH THE LINEAGE OF BUCCICRENATA

In the evolution of *Everticyclammina*, the early species of the main lineage (Text-figure 1) ranged from Iberia to the Middle East (see, e.g., *E. contorta*, as figured by Brun & Rey, 1975, pl. 2, figs. 1, 2, 7, 8 and pl. 3, figs. 1-5, from the Hauterivian of Portugal), while the younger and the side-shoot members (*E. greigi*, *E. kelleri*, *E. hensoni*) are, as yet, known only from the Iraq - Arabia - Oman area. With the final straightening of the upper parts of the septa and total loss of the lower parts, the evolution of the new, (Aptian?) - Albian - Cenomanian genus *Hemicyclammina* saw not only new species confined to the Middle East (like *H. whitei*, Plate 5, fig. 3) but also the appearance of western to central Tethyan species (*H. sigali* Maync, 1953b). No member of this phylogeny has yet been recorded from the Americas.

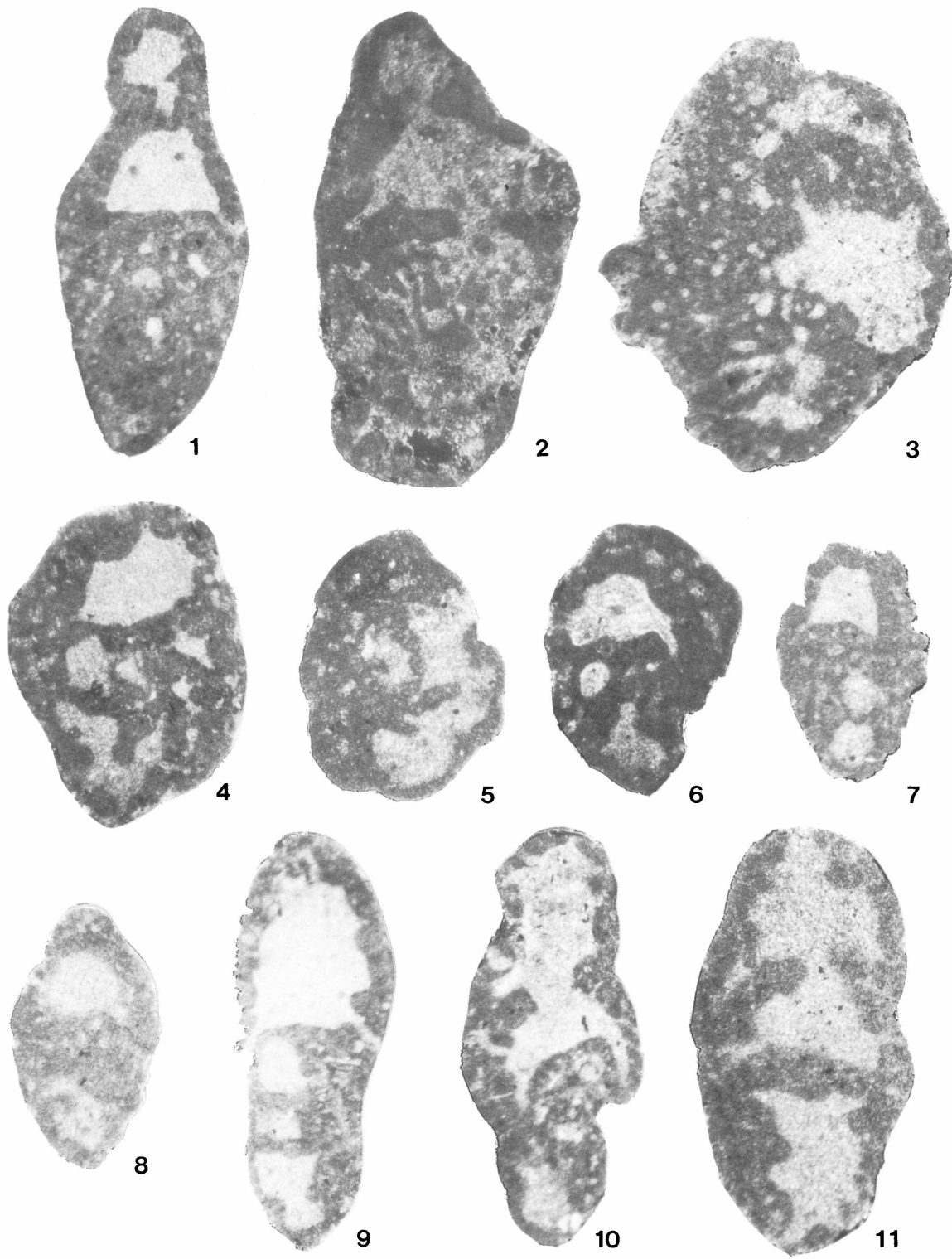
In contrast, the shorter (?Barremian - Aptian - Cenomanian) phylogeny of taxa which can be related to the genus *Buccicrenata* Loeblich & Tappan (1949; emended 1985, p. 100) seems to have either ranged from America to the Middle Easter (*Buccicrenata* itself) or to be confined to central America (*Alveocyclammina* Hillebrandt, 1971). Like *Everticyclammina*, *Buccicrenata* has an alveolar hypodermis and a single, areal, "ammobaculitid" septal/terminal aperture; unlike *Everticyclammina*, the septa are also alveolar and are extensions of the lateral chamber walls.

Like *Hemicyclammina*, the descendant *Alveocyclammina* has lost the lower part of its septa, so that the apertures are now basal, and no longer areal.

The oldest known and named species of *Buccicrenata* is *B. hedbergi* (*Pseudocyclammina hedbergi* Maync, 1953), with its type specimens described from the Early Aptian to Middle Albian of Venezuela but with other records from Florida (Maync, 1953, pp. 95, 101). It has four to five, long, reniform chambers per whorl, with a distinctively thick hypodermis (which, in equatorial section, may occupy one-third of the total chamber height), with distinct alveoles (often three times as long as thick) which irregularly bifurcate. The few, long, reniform chambers, alveolar septa and thick hypodermis readily afford a distinction from *Everticyclammina virguliana*, and all the specimens beautifully photographed by Gušić (1975, pls. 6-9), from the uppermost Aptian-lowermost Al-

## Explanation of Plate 4

Figs. 1-11. *Everticyclammina praekelleri* sp. nov., paratypes; thin sections in Kimmeridgian/Tithonian limestone from Broumana, near Beirut, Lebanon, in slide P. 52255. Figs. 1, x 49; fig. 2, x 53; fig. 3, x 46; fig. 4, x 49; fig. 5, x 56; figs. 6-7, x 50; fig. 8, x 55; fig. 9, x 47.5; fig. 10, x 52; fig. 11, x 54. Specimens in figs. 1, 2 and 10 are probably microspheric and show trends towards terminal rectilinearity; all the other specimens are probably megalospheric. The enlarged postero-lateral hypodermal alveolae are seen in figs. 1, 2, 3, 6, 9, 11. No specimens show the tight, regular, antero-peripheral alveolae of *E. kelleri*.



bian of Yugoslavia, although originally called "*E. virguliana*", are typical *B. hedbergi*. Other, younger Tethyan records have gone under another name; *B. lybica* Gohrbandt, originally described from the Cenomanian Jefren Marl, Ain Tobi Formation, Mobil Oil Libya Ltd collection (Gohrbandt, 1966), and other Cenomanian specimens from the British Petroleum Exploration Company's collections from Libya (called "*Pseudocyclammina cf hedbergi*" by Banner, 1966, pl. 3, figs. 3 a-c, and 1970, pl. 5, fig. 4) are indistinguishable from typical *B. hedbergi* (Maync). They are the same as other "*P. group hedbergi*" specimens figured from the Barremian and Aptian of the Mid-East Gulf by Banner (1966, pl. 3, figs. 1, 2, 4, and 1970, pl. 5, figs. 5, 6).

However, the specimens called "*Pseudocyclammina aff hedbergi*" by Banner (1966, pl. 3, figs. 5a-5b, and 1970, pl. 5, figs. 7, 7a), which were obtained from Mid-East Gulf beds called "Cenomanian" (but which the recorded association with *Hemicyclammina sigali* and *Favusella washitensis* shows to have been Late Albian or Early Cenomanian), are undoubtedly conspecific with *Buccicrenata subgoodlandensis* (Vanderpool), so that species is also known from America to the Middle East.

#### ACKNOWLEDGEMENTS

We wish to thank our colleagues John E. Whittaker and Richard L. Hodgkinson for their constructive criticisms. The support of BP International Ltd and microphotographic help by the Stratigraphy Branch, BP Research Centre, is gratefully acknowledged.

Manuscript received December 1988

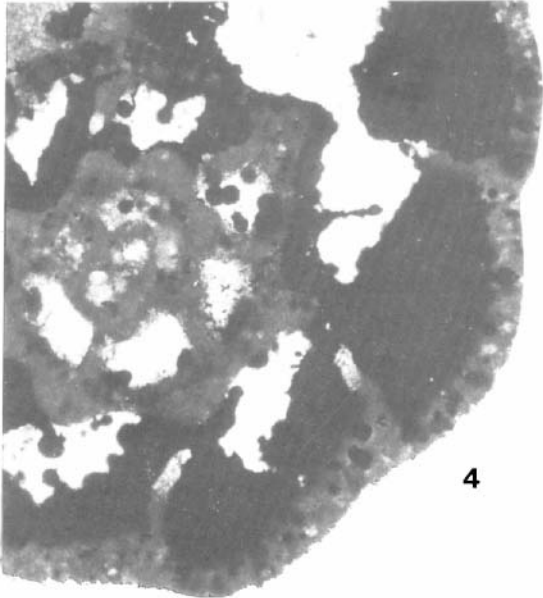
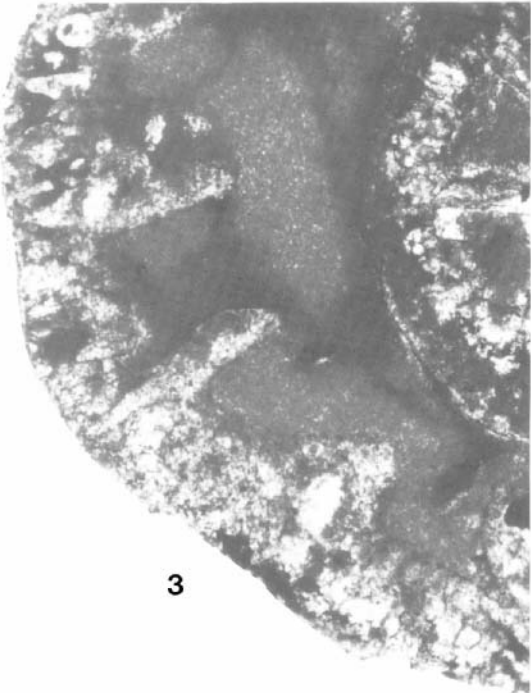
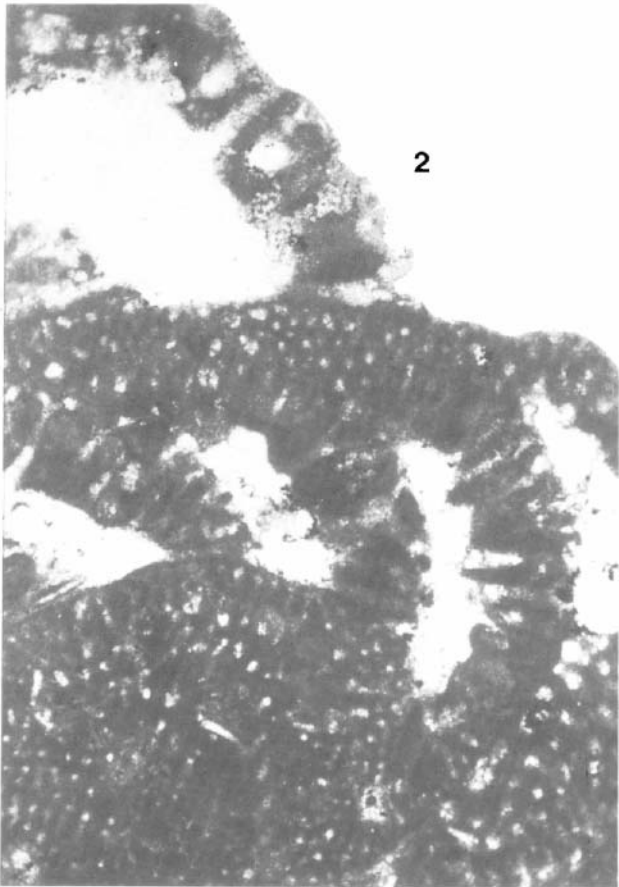
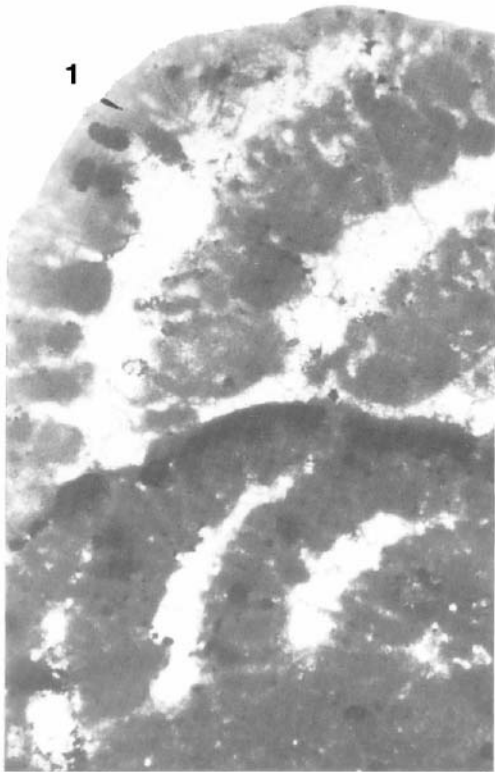
Revised manuscript accepted August 1989

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#### Explanation of Plate 5

- Figs. 1, 2. *Alveosepta sequana* (Tobler) (synonym of *A. jaccardi* (Schrodt)), topotypes from the Late Jurassic (Kimmeridgian), "Sequanian" of Blauen, near Bâle, Switzerland, showing narrow, abundant hypodermal alveolae and their continuation from the chamber walls into the septa, where they become enlarge anteriorly to form areal, multiple apertures; fig. 1, P. 52258, x 83; fig. 2, P. 52259, x 113.
- Fig. 3. *Hemicyclammina whitei* (Henson), paratype, from well Dukhan-3, Qatar, ?Albian/Early Cenomanian, P. 35797, x 100; showing tightly packed, bifurcating hypodermal alveoles distinct from the solid, imperforate septa, which meet the chamber-periphery perpendicularly.
- Fig. 4. *Everticyclammina greigi* (Henson), paratype, from well Dukhan-2, Qatar, Barremian/Aptian, P. 35796, x 108; showing thin hypodermis with packed, bifurcating alveoles, and distinct, solid septa which obliquely meet the chamber periphery and the spiral suture (where they coalesce to form an undulating basal layer).



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