Evolution and Geological Significance of Larger Benthic Foraminifera

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Chapter 4

The Mesozoic Larger Benthic Foraminifera: The Jurassic

4.1 Introduction

The mass extinction in the marine realm at the end of the Triassic affected all groups of the larger benthic foraminifera that had previously survived the end Palaeozoic. Most notable was the total extinction of the Endothyrida. Having survived the much greater extinction event at the end of the Permian, small Triassic endothyrids persisted but with a steadily declining diversity through the Triassic, until their final demise, in the European realm, at the end of the Triassic. This fate was also shared by most other benthic foraminifera, except for a few small forms from the Textulariida, Involuitinida and Milolida orders. Of the different orders of foraminifera with large representatives present in the Jurassic, however, only the agglutinated textulariides exhibited important evolutionary developments; becoming large, complicated and forming many lineages. The aragonitic/calcareous microgranular walls of their Palaeozoic ancestors were by now replaced by calcareous walls bonded by organic cement. The early Jurassic witnessed the steady evolution of the agglutinated forms from being small and simple to being internally complicated, which became abundant from the Pliensbachian onwards, thereby giving the carbonate facies of the Jurassic a characteristic appearance that is recognizable throughout Tethys (Fig. 4.1).

In contrast to the Triassic benthic foraminifera, the Jurassic larger benthic foraminifera have been systematically studied on a regional scale by a number of authors. Early Jurassic Hettangian-Sinemurian foraminifera from the present-day Mediterranean region were studied by Septfontaine (1981), BouDagher-Fadel (2000), Fugagnoli (2000), BouDagher-Fadel et al. (2001), Noujaim Clark and BouDagher-Fadel (2001, 2004, 2005), BouDagher-Fadel et al. (2001), BouDagher-Fadel and Lord (2002), Scherreiks et al. (2006, 2010, 2016), BouDagher-Fadel and Bosence (2007), and by BouDagher-Fadel (2016). These authors have proposed standard Jurassic biozonations for the Mesozoic realm on the basis of foraminiferal generic ranges and assemblages. Benthic forms in comparable facies have also been illustrated and described from the Early Jurassic of north Italy (Sartoni and Crescenti, 1962; Bosellini and Broglio Loriga, 1971; Castellarin, 1972), and south and central Italy (e.g. Chiocchini et al., 1994; Barattolo and Bigozzi, 1996). Jurassic larger benthic foraminifera have also been studied from Saudi Arabia (e.g. Redmond, 1964, 1965; Banner and Whittaker, 1991; Wyn and Hughes, 2004), Morocco (Hottinger, 1967; Septfontaine, 1984), the southern Tethyan realm (Sartorio and Venturini, 1988), from the ‘vast carbonate platform’ (e.g. García-Hernández et al., 1978; Vera, 1988; Rey, 1997) that included the external zones of the Betic Cordillera of southern Iberia (e.g. González-Donoso et al., 1974; Braga et al., 1981), Gibraltar (BouDagher-Fadel et al., 2001), and the Western Mediterranean (BouDagher-Fadel and Bosence, 2007).
In this chapter, a review and revision of the taxonomy of the main genera of the Jurassic larger foraminifera is presented, and their evolutionary lineages and phylogenetic relationships are discussed. Finally, revised and updated biostratigraphic ages, palaeogeographic and palaeoenvironmental interpretations are presented.

4.2 Morphology and Taxonomy of Jurassic Larger Benthic Foraminifera

The dominant larger foraminifera of the Jurassic were the agglutinated Textulariida. The Involutinida persisted throughout, while the Miliolida were present but were mainly composed of morphologically small genera, and it was not before the Cenomanian that larger miliolides played an important role in the benthic assemblages of carbonate platforms. The Lagenida were small and simple in the Jurassic and will not be discussed in this chapter, which will instead focus on the three orders:

- Involutinida
- Textulariida
- Miliolida
The development and evolution of the major superfamilies of these orders is schematically shown in Fig. 4.2.

**Order Involutinida Hohenegger and Piller, 1977**
An order including all forms with an enrolled second chamber. They have walls that are aragonitic, but commonly they are recrystallised to give a homogenous microgranular structure. They show an umbilical region with pillar-like structures on one or both sides of the test. They range from Triassic to Late Cretaceous (Cenomanian).

**Superfamily Involutinoidea Bötschli, 1880**
Forms consisting of a first chamber followed by a planispiral to trochospiral enrolled tubular second chamber. Triassic to Late Cretaceous (Cenomanian).
Family Involutinidae Bütschli, 1880
The globular proloculus is followed by a trochospiral, coiled tubular second chamber. Secondary lamellar thickenings on one or both umbilical regions. The aperture is at the open end of the tube. Late Triassic (Norian) to Late Cretaceous (Cenomanian).

- **Andersenolina** Neagu, 1994 (Type species: *Andersenolina perconigi* Neagu, 1994). The test maybe lenticular, and conical in shape. The spherical proloculus is followed by a tubular, trochospiral second chamber. The umbilical side is covered by perforated lamellae added with each whorl and surrounded by small rounded “collarette” margins. A primary aperture is absent. It differs from *Trocholina* (Fig. 4.3) and *Auloconus* (see Chapter 3) by the presence of a perforated umbilical plate relative to the former, and from the latter by the substitution of the primary aperture by pores and the absence of external lamellae. Middle Jurassic to Early Cretaceous (Bathonian to Aptian) (Plate 4.1, figs 4-5; Fig. 4.8).

- **Involutina** Terquem, 1862 (Type species: *Involutina jonesi* Terquem and Piette, in Terquem, 1862). Both umbilical regions are filled with lamellar deposits (Figs 4.4; 4.5). Late Triassic to Late Cretaceous (Norian to Cenomanian) (see Chapter 3; Plate 4.1, fig. 1; Fig. 4.8).

- **Neotrocholina** Reichel, 1956 (Type species: *Involutina conica* Schlumberger, 1898). Loeblich and Tappan (1988, p. 300) considered *Neotrocholina* Reichel as a synonym of *Trocholina* Paalzow. However, the two forms are different and should be separated. The outer wall of *Neotrocholina* is thick (approximately as thick as the spiral septum), perforate and the umbilicus is deeply fissured. On the other hand, the outer wall of *Trocholina* (= *Coscinocmus alpinus* Leupold) is thin (usually much thinner than the spiral septum, and often eroded), imperforate, and the test lacks the deeply fissured, canaliculated umbilical structure of *Neotrocholina* (Fig. 4.6). Late Middle Jurassic to Cretaceous (Bathonian to Cenomanian) (Plate 4.1, figs 2-3; Fig. 4.8).

<table>
<thead>
<tr>
<th>Primary Characteristic</th>
<th>Specific Characteristic</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biconvex test</strong></td>
<td>Apical angle 130 - 150 degrees; pustulate / weakly pilled on both sides</td>
<td>Neotrocholina lenticularis (Cenomanian)</td>
</tr>
<tr>
<td><strong>Base convex</strong></td>
<td>Base robust; apical angle ca. 80 degrees; base pustular</td>
<td><em>Andersenolina alpina</em> (Bathonian - Barremian)</td>
</tr>
<tr>
<td><strong>Conical tests</strong></td>
<td>Base flat</td>
<td><em>T. arctica</em> (Cenomanian)</td>
</tr>
<tr>
<td></td>
<td>Smaller more delicate; apical angle obtuse</td>
<td><em>T. conica</em> (Bajocian - Oxfordian) (Plate 4.1, fig. 6)</td>
</tr>
<tr>
<td></td>
<td>Small, delicate; spiral chamber &lt;0.1mm high</td>
<td><em>T. multispira</em> (Late Triassic) (Plate 3.1, figs 6-7)</td>
</tr>
<tr>
<td><strong>High cones tending to be parallel sided</strong></td>
<td>Large robust; spiral chamber</td>
<td><em>A. elongata</em> (Bathonian - Barremian) (Plate 4.1, fig. 4)</td>
</tr>
<tr>
<td></td>
<td>&gt;0.1 mm high</td>
<td><em>T. allispira</em> (Cenomanian)</td>
</tr>
</tbody>
</table>

**Fig. 4.3.** Key to main species of *Trocholina* (*T.*) and *Andersenolina* (*A.*).
**Septatrocholina** BouDagher-Fadel 2016 (Type species: *Septatrocholina banneri* BouDagher-Fadel and Banner 2008, type species designated in BouDagher-Fadel, 2016). The test is conical, consisting of a globular proloculus followed by a trochospirally enrolled, divided tubular second chamber with rudimentary septa around a solid core of pillars, filling the umbilical area. Secondary lamellar thickenings are on one or both umbilical regions. The aperture is terminal at the open end of the tube. This species is distinguished from other involutinides by the solid core of pillars filling the umbilicus and the rudimentary septa. Rigaud et al. 2013 included the genus *Septatrocholina* within the synonyms of *Coscinoconus* Leupold in Leupold and Bigler 1936, on the basis that *Coscinoconus* has “possibly slightly constricted endoskeletal structures or wall thickenings” similar to the rudimentary septa of *Septatrocholina*. However, the septa in the latter are almost non-existent, while those of *Coscinoconus* are complete (see Rigaud et al. 2013, Figs 7–11, new illustrations of syntypes of *Coscinoconus chouberti*). In addition, *Septatrocholina* lacks the complex canal system which form polygonal nodes at the umbilical surface of *Coscinoconus*. Jurassic (Callovian to Oxfordian) (Plate 4.2, figs 1-4; Plate 4.3, figs 1-6; Fig. 4.8).

**Trocholina** Paalzow, 1922 (Type species: *Involutina conica* Schlumberger, 1898). *Trocholina* may be conical, plano-convex or lenticular in shape. It consists of a globular proloculus followed by a trochospirally enrolled undivided tubular second chamber around a solid core of pillars, filling the umbilical area. The aperture is at the end of a tubular chamber. *Trocholina* is distinguished from *Neotrocholina* by having a thinner, imperforate wall, and in lacking the deeply fissured, canaliculated umbilical structure of the latter (Fig. 4.6). Late Triassic to Late Cretaceous (Norian to Cenomanian) (Plate 3.1, figs 6-7; Plate 4.1, figs 6-9; Plate 4.4, fig. 1).

<table>
<thead>
<tr>
<th>Primary Characteristics</th>
<th>Specific Characteristics</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Streptospiral coiling (chamber - plane oscillates through ca. 45 degrees)</td>
<td></td>
<td><em>Aulotortus</em> Wenschenk (Middle Triassic to Middle Jurassic)</td>
</tr>
<tr>
<td>Planispiral coiling</td>
<td>umbilici pillared incised</td>
<td><em>Involutina</em> Terquem (Upper Triassic to Cenomanian)</td>
</tr>
<tr>
<td></td>
<td>umbilici umbonate, smooth</td>
<td><em>Vidalina</em> Schlumberger (Cenomanian to Santonian)</td>
</tr>
<tr>
<td>Trochospiral coiling</td>
<td>Outer wall thick, perforate; umbilicus deeply fissured</td>
<td><em>Neotrocholina</em> (Jurassic - Cretaceous)</td>
</tr>
<tr>
<td></td>
<td>Outer wall thin, imperforate</td>
<td><em>Trocholina</em> (Upper Triassic to Cenomanian)</td>
</tr>
</tbody>
</table>

*Fig. 4.4.* Key to main involutinides genera.
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Fig. 4.5. *Involutina liassica* (Jones), Early Jurassic, Italy, axial section, scale bar = 0.5 mm.

Fig. 4.6. A) *Trocholina conica* (Schlumberger) Umm Shaif, core 3883 ft, Bajocian; B) *Trocholina* sp. sketch; C-E) *Neotrocholina friburgensis* Guillaume and Reichel, type figures, late Barremian – early Aptian, west-central Switzerland.
Family Ventrolaminidae Weynschenck, 1950
Members of this superfamily have a lenticular test, which is planispiral to low trochospiral with numerous chambers in a rapidly enlarging whorl. The wall is calcareous with two layers, an inner microgranular one and an outer hyaline radial layer. Middle Jurassic to Early Cretaceous (late Bajocian to Berriasian).

• *Protopeneroplis* Weynschenck, 1950 (Type species: *Peneroplis senoniensis* Hofker, 1949). The test is enrolled in about two rapidly enlarging and loosely coiled whorls. The final whorl has twelve to sixteen chambers, and is involute with a rounded to angular periphery. The aperture is areal, in the early part of the test and slightly protruding. Middle Jurassic to Early Cretaceous (Berriasian) (Plate 4.5, fig. 7; Fig. 4.8).

Order Textulariida Delage and Hérouard, 1896
The tests of these agglutinated foraminifera are made of foreign particles bound by organic cement. They range from Early Cambrian to Holocene.

Superfamily Verneuilinoidea Cushman, 1911
Members of this family have a trochospiral early stage that is triserial or biserial, which later may be uniserial. Walls are non-canaliculate. Late Carboniferous to Holocene.

Family Verneuilinidae Cushman, 1911
Members of this family have biserial tests, at least in early stages. Chambers are globular with a terminal aperture.

• *Duotaxis* Kristan, 1957 (Type species: *Duotaxis metula* Kristan, 1957). Originally regarded as a member of the Tetrataxidae, *Duotaxis* differs in having an agglutinated rather than a two-layered microgranular calcareous wall, so it was reassigned to the Family Verneuilinidae by Loeblich and Tappan (1988). The genus had earlier (Loeblich and Tappan 1964) been considered a synonym of *Valvulina*, but differs by not having an early triangular stage and in lacking a truly valvular tooth (Loeblich and Tappan 1988). Triassic to Early Jurassic (?Ladinian-Rhaetian to Pliensbachian) (Plate 3.4, figs 1-2; Plate 3.8, fig. 5; Plate 4.6, fig. 1).

Superfamily Pfenderinoidea Smout and Sugden, 1962
Members of this superfamily (see Fig. 4.7) have a trochospiral test throughout, or one that may become uncoiled. Some forms have a siphonal canal, others develop a central composite columella, with pillars between apertural plates and septa. Early Jurassic (Hettangian) to Cretaceous.

Family Pfenderinidae Smout and Sugden, 1962
Members of this family have a loose trochospiral conical test with siphonal canals that connect successive apertures in primitive forms. Some forms develop a central composite columella composed of thickened innermost septal ends (“septal buttons”) with or without additional pillars and a spiral canal between the columella and the thickened inner parts of the adjacent septa. A subcameral tunnel (simple or multiple) is present in advanced forms. The chamber interior of advanced taxa is subdivided by vertical
or horizontal (or both) exoskeletal partitions, resulting in a reticulate subepidermal layer. In the trochospires, the spiral and intracamerial septa are strongly oblique to the long (coiling) axis (resembling Arenobulimina), but rectilinear, uniserial developments (if present) produce peneropliform, conical (“coskinoliniform”) or lituoliform tests. The aperture is always cribrate, areal. Early Jurassic to Late Cretaceous (Sinemurian to Maastrichtian).

Subfamily *Pseudopfenderininae* Septfontaine, 1988

The test is trochospirally coiled throughout with no subcameral tunnel. The middle of the test has a siphonal canal, or is filled in with a columella made by interseptal pillars and calcitic filled material. No peripheral partitions or chamberlets are present. Early Jurassic (Hettangian) to Late Cretaceous.

- *Pseudopfenderina* Hottinger, 1967 (Type species: *Pfenderina butterlini* Brun, 1962). The test is a high trochospiral with numerous chambers. The umbilical part of the chamber interior is filled with numerous pillars that are continuous from chamber to chamber. Early Jurassic (Sinemurian to Bathonian) (Plate 4.6, figs 10-16).
- *Siphovalvulina* Septfontaine, 1988 (Type species: *Siphovalvulina variabilis* Septfontaine, 1988). The test is trochospirally coiled (high or low) in general with three chambers per whorl; the test wall is canaliculate, but rarely visible as such; the interiors of the chambers are free; a twisted siphonal canal connects successive apertures; the aperture is unique, interiomarginal, but may become cribrate in the last chambers of advanced forms. Early Jurassic (Hettangian) to Early Cretaceous to Late Cretaceous? (Plate 4.6, figs 2B, 3-8, 9A).

Subfamily *Paleopfenderininae* Septfontaine, 1988

The adult chambers of this subfamily may be uncoiled with various shapes. A simple or multiple spiral subcameral canal may be present. There are pillars between apertural plates and septa have calcitic fillings, giving the appearance of a columella. No peripheral partitions or chamberlets are present. The aperture is terminal and multiple in the apertural plate. Jurassic (Bajocian to early Oxfordian).

- *Conicopfenderina* Septfontaine, 1988 (Type species: *Lituonella mesojurassica* Maync, 1972). The genus includes conical forms, with a trochospiral early part followed by a rectilinear uniserial part with separated irregular pillars filling the centres of the chambers. The marginal zone of the chambers is not subdivided. *Conicopfenderina* differs from *Parurgonina* Cuvillier, Foury and Pignatti Morano, 1968, by the uniserial arrangement of its chambers, which in the latter is trochospiral. Apertures occur multiply. Middle Jurassic (Bajocian to Callovian) (Plate 4.7, figs 8-11).
- *Chablaisia* Septfontaine, 1978 (Type species: *Pfenderina? chablaisensis* Septfontaine, 1977). This genus differs from other pfenderinoids in having a low trochospiral test and by the presence of a spiral canal and calcitic fillings (septal knobs) in the chambers. Jurassic (late Bathonian to early Oxfordian) (Plate 4.7, figs 12-13).
- *Palaeopfenderina* Septfontaine, 1988 (Type species: *Pfenderina salernitana* Sarton and Crescenti, 1962). This genus includes forms with tight trochospiral coiling, which increase in diameter with spiral height, with a central microgranular
columella twisted along the coiling direction. The apertures are multiple and crib-rate. *Palaeopfenderina* differs from *Pfenderina* Henson, 1948 (Plate 4.6, figs 6-7) by the superficial position of the tunnel, as a groove at the surface of the columella, and by the filling of the inter-pillar spaces with calcitic material. In *Pfenderina* the filling is less developed and the pillars are clearly visible. Jurassic (Bathonian to Callovian) (Fig. 4.7).

- *Pseudoeggerella* Septfontaine, 1988 (Type species: *Pseudoeggerella elongata* Septfontaine, 1988). This genus includes forms with high trochospiral coiling and a narrow columella in the axis of the test. The stalagmitic protuberance is deeply incised against the columella. This genus lacks the subcamierral tunnel of *Palaeopfenderina* and differs from *Pseudopfenderina* by the presence of calcitic protuberances in the chambers. Jurassic (Bathonian) (Plate 4.7, fig. 14).

- *Sanderella* Redmond 1964 (Type species: *Sanderella laynei* Redmond, 1964). The test has long and narrow chambers without secondary septa. The initial portion of the test is a low trochospire with a single subcamierral tunnel. The later portion of the test becomes discoid, with multiple subcamierral tunnels. Jurassic (Bathonian to Oxfordian) (Plate 4.7, fig. 17).

- *Satorina* Fourcade and Chorowicz, 1980 (Type species: *Satorina apuliensis* Fourcade and Chorowicz, 1980). This genus differs from *Conicopfenderina* by possessing radial pillars at the margin of the central mass formed by interseptal pillars. Jurassic (late Bathonian to early Oxfordian) (Plate 4.7, figs 15-16).

- *Steinekella* Redmond, 1964 (Type species: *Steinekella steinekei* Redmond, 1964). This form is a pfenderinine with a massive, central, continuous columella of fused or coalescent pillars, as in *Pfenderina*, not the discontinuous end skeletons of thickened septal buttons, as in *Kurnubia*. It has a high trochospiral test with very long and narrow chambers. Multiple subcamierral tunnels combined with strong transverse partitions and very fine and weak subepidermal structure are present throughout the test. Jurassic (late Callovian to Oxfordian) (Plate 4.7, figs 18-20).

**Subfamily Pfenderininae Smout and Sudgen, 1962**

Members of this subfamily have a test with a single subcamierral tunnel that is always buried in the columella, which is formed by pillars and calcitic deposits. No peripheral partitions or chamberlets are present. The aperture is multiple, crib-rate, and on the apertural plate. Early Cretaceous (Valanginian to Barremian or?Aptian).

- *Pfenderella* Redmond, 1964 (Type species: *Pfenderella arabica* Redmond, 1964). The test is an elongate cone consisting of a trochoid spiral of relatively short chambers arranged around the axis of coiling in such a manner that each chamber overlaps approximately one-half of its predecessor. Successive chambers are indirectly connected by a tunnel. Secondary septa are absent. The test is, without a solid core. *Pfenderella* differs from *Kurnubia*, *Praekurnubia* and *Steinekella* (Plate 4.7, figs 18-20) by lacking secondary partitions in the chambers. It differs from *Pfenderina* in not having a solid central core, and its chambers are also broader in proportion to their length than are those of *Pfenderina*. Jurassic (Bajocian to Callovian) (Plate 4.7, figs 21-24).
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Pfenderinoidea

Fig. 4.7. The phylogenetic development of the Pfenderinoidea through the Jurassic.
The Mesozoic Larger Benthic Foraminifera: The Jurassic

- **Pfenderina** Henson, 1948 (Type species: *Eorupertia neocomiensis* Pfender, 1938). This genus differs from *Pfenderella* in having long narrow chambers communicating with each other, and with the exterior of the test, by means of a spiral subcameral tunnel which lies mostly beneath the surface of a solid core. Jurassic (Bajocian to Valanginian) (Plate 4.7, figs 6-7).

**Subfamily Kurnubiinae Redmond, 1964**
Members of this subfamily have a test with no subcameral tunnel or tunnels, and may or may not have a solid core. The peripheral zone is divided by radial partitions.

- **Conicokurnubia** Septfontaine, 1988 (Type species: *Conicokurnubia orbitoliniformis* Septfontaine, 1988). The test is conical. Vertical partitions join the centre of the chambers and coalesce with the pillars. The apertures are multiple, cribrate. It differs from *Dictyoconus* Blanckenhorn, 1900 (see Chapter 5) by having a less complicated marginal zone of the chambers. Jurassic (late Bathonian to Kimmeridgian) (Plate 4.8, figs 1-2).

- **Kurnubia** Henson, 1948 (Type species: *Kurnubia palastiniensis* Henson, 1948). The test is conical, cylindrical or elongate fusiform, consisting of chambers arranged in an elongate trochoid spiral. The inner surfaces of individual chambers are divided into chamberlets by several sets of inward-projecting transverse and longitudinal secondary partitions. The aperture is represented by a number of closely-set pores on the base of the test. Jurassic (Bajocian to early Tithonian) (Plate 4.8, figs 3-21; Plate 4.9, fig. 13C).

- **Praekurnubia** Redmond, 1964 (Type species: *Praekurnubia crusei* Redmond, 1964). This differs from *Kurnubia* in having transverse partitions only. Jurassic (Bathonian to early Oxfordian) (Plate 4.8, figs 22-24).

**Family Valvulinidae Berthelin, 1880**
The test is trochospirally coiled, and generally triserial in the early stage. The wall is microgranular, and may be alveolar. The interior of chambers is simple. The aperture is interiomarginal, with a large valvular tooth (simple or complicated). The Valvulinidae show the first known example of a crosswise-oblique stolons system (the marginoporiform structure of Hottinger and Caus (1982)) among the Pfenderinoidea. This disposition of stolons appears as a morphological convergence in different groups of lituoloids: the valvulinids (trochospirally coiled), the orbitolinids (trocho- to uniserial) and the reniform-discoidal lituoloids (planispiral to uniserial).

**Subfamily Valvulininae Berthelin, 1880**
This subfamily includes forms with a simple or complicated valvular tooth plate. Aperture: simple or cribrate. Jurassic (Pliensbachian) to Holocene

- **Kilianina** Pfender, 1933 (Type species: *Kilianina blancheti* Pfender, 1933). This form is distinguished by its conical test, where the central zone septa thicken and coalesce into an almost solid mass (hummocks). In some forms the latter half of the test is formed by thin irregular plates intergrown by finer broadly-spaced pillars. The early chambers are trochospiral. They coil along a vertical axis and occupy almost half
the test, later they become rectilinear, with the outer parts of chamberlets subdivided by numerous pillars. Jurassic (Bathonian to Kimmeridgian) (Plate 4.4, fig. 3; Plate 4.6, fig. 9B; Plate 4.10, figs 12, 14).

- **Valvulina** d’Orbigny, 1826 (Type species: Valvulina triangularis d’Orbigny, 1826). The test is trochosiral throughout, and triserial. The valvular tooth plate is simple or perforated by supplementary apertures. The primary aperture is a basal slit. Jurassic (Pliensbachian) to Holocene (Plate 4.11, fig. 15).

**Subfamily Parurgonininae Septfontaine, 1988**
This subfamily includes genera with eight or more chambers per whorl. The valvular tooth plate is complicated by pillars. The apertures are multiple, with a crosswise-oblique stolons system. Late Jurassic.

- **Parurgonina** Cuvillier, Foury and Pignatti Morano, 1968 (Type species: Urgonina (Parurgonina) caelinensis Cuvillier et al., 1968). This genus has a highly conical test with numerous chamberlets, separated by curved septal extensions of the outer wall in a low trochosiral. The septa break in the umbilical region to form sub-conical pillars. Jurassic (late Oxfordian to Tithonian) (Plate 4.10, figs 17-18).
- **Neokilianina** Septfontaine, 1988 (Type species: Paravalvulina complicata Septfontaine 1988). This genus differs from Kilianina in having a higher number of chambers per whorl in the adult stage (25 instead of 8), and a more pronounced development of pillars in the central part of the test. Jurassic (early Kimmeridgian) (Plate 4.10, figs 13, 15-16).

**Superfamily Lituoloidea de Blainville, 1825**
Members of this superfamily have conical, multilocular, rectilinear and uniserial tests. The early stage has plani- (strepto-) or trochosiral coiling. The periphery of the chambers has radial partitions; but centrally they are with or without scattered, separated pillars. The septa are arched into hummocks (almost solid mass) between the apertures. The bases of the arches can be fused to the hummocks of previous septum, with the apertures then opening at the suture. The alignment of the apertures and thickening of the hummock walls produces the appearance of a series of “gutters”. No true pillars are formed. The walls are solid, non-alveolar, non-canaliculate. The aperture is simple, with no internal tooth-plates, areal or multiple, cribrate. Late Triassic (Carnian) to Holocene.

**Family Hauraniidae Septfontaine, 1988**
The test is uncoiled, uniserial or planispirally coiled. The wall is microgranular with a hypodermic network. The septa are simple or with complicated microstructures. The interior of the chambers is simple or with pillars. The aperture is multiple. Jurassic (late Sinemurian) to Cretaceous.

**Subfamily Hauraniinae Septfontaine, 1988**
The test is uncoiled, uniserial or planispirally coiled. The septa are simple or with complicated microstructures, and the interior of the chambers have fine pillars in the central zone. Jurassic (late Sinemurian to Bathonian).
• *Ataxella* Bassoullet and Lorenz, 1988 (*Paracoskinolina occitanica* Peybernès, 1974). The test is conical to cylindrical with an early streptospiral stage followed by a rectilinear, uniserial stage. The marginal zone is divided by alternating radial partitions. The central zones is full with pillars which are often coalescent. Middle Jurassic (Bathonian) (Plate 4.4, fig. 10).

• *Cymbriaella* Fugagnoli, 1999 (Type species: *Cymbriaella lorigae* Fugagnoli, 1999). The test is coarsely agglutinated with a coarse irregular subepidermal polygonal network, locally appearing as bifurcated alveolar cavities with a blind ending of polygonal outline below a thin epidermis. Megalospheric forms possessing a complex embryonic apparatus represented by a spherical proloculus enveloped by a subspherical deutoconch, which is characterized by having short beams (exoskeletal partitions of the chamber lumen perpendicular to the septa) perpendicular to the wall. *Cymbriaella* is the oldest representative of the Hauraniidae that developed a complex megalospheric form. It differs from *Amijiella* by being larger, and having a more irregular, coarser subepidermal network. Jurassic (Hettangian to Pliensbachian) (Plate 4.11, fig. 14).

• *Gutnicella* Moullade, Haman and Huddleston, 1981 (Type species: *Coskinolina (Meyendorffina) minoricensis* Bourrouilh and Moullade, 1964). *Gutnicella* is a new name for *Lucasella* Gutnic and Moullade, 1967. The test is highly conical with a large spherical proloculus, enclosed in an early planispiral and involute coil, that is later briefly trochospiral, followed by being uniserial and rectilinear. Chambers are subdivided in the outer part by many short radial vertical partitions, creating a narrow peripheral zone of quadrate chamberlets; one row to each chamber. The broad central zone is filled with irregular scattered separated pillars of different sizes. Jurassic (Pliensbachian to Callovian) (Plate 4.11, figs 16-17; Plate 4.12, figs 7-9).

• *Haurania* Henson, 1948 (Type species: *Haurania deserta* Henson, 1948). The radial partitions are delicate, often bifurcating vertically to form a partial tier of peripheral chamberlets. Jurassic (late Sinemurian to Bathonian) (Plate 4.11, figs 18-20; Plate 4.12, figs 1-4).

• *Meyendorffina* Aurouze and Bizon, 1958 (Type species: *Meyendorffina bathonica* Aurouze and Bizon, 1958). The test is initially enrolled planispirally with a low, long initial trochospire, later becoming uniserial. Chambers are subdivided by vertical pillars that project a short distance inward from the outer wall, but lack horizontal rafters (exoskeletal partitions of the chamber lumen parallel to the septa and perpendicular to the beams and the lateral chamber wall, see Hottinger (2006)). Central zone filled with pillars. Jurassic (Bathonian to early Oxfordian) (Plate 4.8, fig. 23B; Plate 4.12, figs 5-6, 19).

• *Platyhaurania* Bassoullet and Boutakiout, 1996 (Type species: type species *Haurania (Platyhaurania) subcompressa* Bassoullet and Boutakiout, 1996). This form differs from *Haurania* in possessing cylindrical chambers in the uncoiled part. Jurassic (late Sinemurian to Toarcian) (Plate 4.12, fig. 12).

• *Robustoconus* Schlagintweit, Velić and Sokač 2013 (Type species: *Robustoconus tisljari* Schlagintweit et al., 2013). The test is conical with an early planispiral stage. Chambers are subdivided into a marginal zone formed of radial and intercalary beams with rafters or horizontal partitions forming a network of chamberlets. The
central zone is large and complex, consisting of anastomising septal excrescences (with constrictions and swellings). Middle Jurassic (early Bajocian) (Plate 4.4, fig.12).

- **Socotraina** Banner, Whittaker, BouDagher-Fadel and Samuel, 1997 (Type species: *Socotraina serpentina* Banner et al., 1997). Tests are non-canaliculate, septate, initially coiled planispirally or in a low trochospire. Uniserial chambers are filled with near-vertical, subradial partitions with a sinuous serpentine form. In the central areas of the chambers the partitions fuse laterally. The aperture consists of many small pores between the partitions and is situated subterminally. Jurassic (Pliensbachian to Toarcian) (Plate 4.4, fig. 6; Plate 4.12, figs 10-11).

- **Timidonella** Bassoullet, Chabrier and Fourcade, 1974 (Type species: *Timidonella sarda* Bassoullet et al., 1974). Chambers have a subepidermal network of horizontal and vertical pillars connecting consecutive septa. This network is followed by a zone of quadrangular chamberlets formed by the pillars, an undivided zone termed the annular canal, and a zone of interseptal pillars. *Timidonella* differs from *Orbitopsella* in its alveolar hypodermis, which compare with the Cretaceous *Loftusia* (see Chapter 5). Jurassic (Aalenian to early Bathonian) (Plate 4.12, figs 13-16).

- **Trochamijiella** Athersuch, Banner and Simmons, 1992 (Type species: *Trochamijiella gollesstanehi* Athersuch, et al., 1992). This genus is similar to *Socotraina*, *Haurania* and *Platyhaurania*, but has an initial trochospiral coil. Late Jurassic (Bajocian to Callovian) (Plate 4.12, fig. 17).

**Subfamily Amijiellinae Septfontaine, 1988**

Members of this subfamily have an uncoiled or planispirally coiled test. The septa are simple or have a complicated microstructure. The interior of the chambers is simple, however, some genera may develop pillars. Walls may have alveoles. The apertures are multiple. Jurassic (late Sinemurian) to Cretaceous.

- **Alzonella** Banner and Neumann, 1970 (Type species: *Alzonella cuvillieri* Bernier and Neumann, 1970). A planispiral test with a hypodermis consisting of a coarse lattice of beams and rafters. Jurassic (Bathonian to Callovian) (Plate 4.13, figs 6-8).

- **Alzonorbitopsella** BouDagher-Fadel, 2008 (Type species: *Alzonorbitopsella arabia* BouDagher-Fadel, 2008, genus and species validated in BouDagher-Fadel, 2016). A planispiral, annular and discoidal test with no septulae. Any subepidermal reticulate mesh is absent in septa, which are thickened around cribrate apertures, but lacking the true pillars linking septum to septum as in *Orbitopsella*. There is a delicate reticulate hypodermis of beams and rafters as in *Alzonella*, but there is a lack of continuation of this structure on to the septa. Chambers are annular, immediately following the large megalospheric proloculus, as in *Cyclorbitopsella*, but not in the megalospheric *Alzonella*. The alveolar hypodermis and septa, and the annular A-form differentiate *Alzonorbitopsella* from *Orbitopsella* with no (hypodermal) network, and from *Timidonella* with subepidermal network and partitions. The absence of medial pillars and the presence of subepidermal beams and rafters differentiate *Alzonorbitopsella* from *Cyclorbitopsella*. Jurassic (late Bathonian) (Plate 4.2, figs 5-10; Plate 4.14, figs 1-6).
• *Amijiella* Loeblich and Tappan, 1985 (Type species: *Haurania amiji* Henson, 1948). The test is straight and uniserial or planispiral, to uniserial in megalospheric generations. The chambers have no pillars in the central zone. The radial partitions are strong, tending to become thickened towards the central zone. They bifurcate vertically to form a few, scattered chamberlets. Jurassic (late Sinemurian to Bathonian or? Callovian) (Plate 4.15, figs 2-4).

• *Anchispirocyclina* Jordan and Applin, 1952 (Type species: *Anchispirocyclina henbesti* Jordan and Applin, 1952). Tests are compressed and peneropliform. The central zone is filled by a complex reticulum of densely spaced pillars. Jurassic to Early Cretaceous (Oxfordian to early Campanian) (Plate 4.15, figs 6-7, 8-9).

• *Bostia* Bassoullet, 1998 (Type species: *Bostia irregularis* Bassoullet, 1998). A dimorphic test with clearly distinct microspheric and megalospheric generations. It is characterized by a complicated embryonic apparatus and a lack of pillars in the central zone. Walls have a subepidermal network formed by irregular radial and transverse partitions that constitute a superficial extension of the chambers. It is similar to the unpillared *Amijiella* and *Alzonella*, but differs in possessing an ammobaculoid test morphology in both generations. It has a wall structure similar to *Spiraloconulus*, but differs by having an orbitoliniform test. Jurassic (Bathonian) (Plate 4.15, figs 10-11).

• *Dhrumella* Redmond, 1965 (Type species: *Dhrumella evoluta* Redmond, 1965). The initial part of the test is a low concavo-convex trochoid spiral, with chambers that are completely involute on the convex side and moderately evolute on the concave side. The later chambers become strongly evolute, becoming flattened and uniserial. Chambers are subdivided into chamberlets by prominent transverse partitions that generally alternate in position from chamber to chamber. Jurassic (Bajocian to Bathonian) (Plate 4.5, fig. 4).

• *Ijdranella* Bassoullet, Boutakiout and Echarfaoui, 1999 (Type species: *Ijdranella atlasic* Bassoullet, et al., 1999). An hauraniid with a compressed peneropliform uncoiled stage and an exoskeleton containing long radial pillars superficially united by a coarse network. *Ijdranella* differs from *Amijiella* in its compressed test and from *Trochamijiella* in its trochospiral initial coiling and canaliculated wall. Jurassic (Pliensbachian) (Plate 4.12, fig. 18).

• *Kastamonina* Sirel, 1993 (Type species: *Kastamonina abanica* Sirel, 1993). Tests are elongated to conical, morphologically similar to *Amijiella*, but with a much reduced initial coiled portion and a more complex internal structure. The marginal zone of each chamber is subdivided by an irregular polygonal subepidermal network, consisting of vertical partitions (beams) and horizontal partitions (rafters), forming numerous irregular alveolar compartments. This genus differs from *Haurania* by the absence of a planispiral part and by lacking endoskeletal pillars in the centre of the test. It differs from *Rectocyclammina* (Plate 4.12, fig. 18) in its early chambers and cribrate aperture. Jurassic (Kimmeridgian to Tithonian) (Plate 4.10, fig. 1).

• *Pseudospirocyclina* Hottinger, 1967 (Type species: *Pseudospirocyclina maynci* Hottinger, 1967). Tests are planispiral, then rectilinear or flabelliform with an alveolar hypodermis. There are thick septa with equally thick, scattered irregular pillars. Jurassic (Bajocian to Tithonian) (Plate 4.5, figs 9-15).
• *Spiraloconulus* Allemann and Schroeder, 1980 (Type species: *Spiroconulus percnonigi* Allemann and Schroeder, 1972). The test is planispiral to low trochospiral, then uncoiling to become thick and conical, with a coarsely reticulate hypodermis. Thin septa, linked by thick heavy pillars, are irregularly and widely spaced. The central zone possesses endoskeletons of pillars from septum to septum. The septa are not alveolar. *Spiraloconulus* differs from *Pseudospirocyclina* by its thick, flat initial spire and its thick, conical rectilinear stage, by its reticulate hypodermis of “*Alzonella*-like” structure, and its thin, non-alveolar septa. *Spiraloconulus* differs from *Robustoconus* by its exoskeleton, which consist of a narrow marginal zone of thin-walled chamberlets and the large central zone with septa typically agglutinating large grains (Schlagintweit et al., 2013). Jurassic (Bajocian to Callovian) (Plate 4.10, fig. 11).

• *Streptocyclammina* Hottinger, 1967 (Type species: *Pseudocyclammina (Streptocyclammina) parvula* Hottinger, 1967). A peneropliform, low streptospiral test with an empty central zone, lacking pillars. It differs from *Pseudocyclammina* only in its streptospirality. Jurassic (Pliensbachian to Kimmeridgian) (Plate 4.16, fig. 7).

**Family Lituolidae de Blainville, 1827**

The early stages of the tests are enrolled, but later they may become rectilinear. Walls are made from agglutinating foreign particles. Few chambers (less than 10) per whorl. Carboniferous to Holocene.

**Subfamily Ammomarginulininae Podobina, 1978**

Tests in the early stage are coiled, but later show uncoiling. Aperture are single. Carboniferous (Early Mississippian) to Holocene.

• *Ammobaculites* Cushman, 1910 (Type species: *Spirolina agglutinans* d’Orbigny, 1846). The test is simple, not compressed and uncoils in the adult. Apertures are single and areal. Carboniferous (Mississippian) to Holocene (Plate 5.6, fig. 18).

**Subfamily Lituolinae de Blainville, 1827**

Members differs from the Ammomarginulininae in having a multiple aperture. Late Triassic to Holocene.

• *Lituola* Lamarck, 1804 (Type species: *Lituolites nautiloidea* Lamarck, 1804). These forms have no internal partitions and a multiple cribrate aperture. Late Triassic to Holocene (Plate 5.9, fig. 14; Plate 5.10, fig. 9).

**Superfamily Loftusioidea Bradey, 1884**

The test is planispiral, but may uncoil in later stage. The wall is agglutinated with differentiated outer and inner alveolar layers. Late Triassic (Carnian) to Holocene.

**Family Choffatellidae Maync, 1958**

This family is characterised by having hypodermal alveoles. The test is planispiral, but the early part may be streptospiral, lacking continuously developed endoskeletal pillars. Early Jurassic (Pliensbachian) to Late Cretaceous (Coniacian).
• *Alveosepta* Hottinger, 1967  (Type species: *Cyclammina jaccardi* Schrod, 1894). A planispiral test, that may have a streptospiral early stage. The wall is finely and complexly alveolar. The chambers are low with curved septa, perforated fine apertures and often have a clear line and/or median lamella (or pillars) only in equatorial plane. Jurassic (Oxfordian to Kimmeridgian) (Plate 4.12, fig. 20; Plate 4.13, figs 1-3).

• *Choffatella* Schlumberger, 1905 (Type species: *Choffatella decipiens* Schlumberger, 1905). A planispiral test, with a wall that is finely and complexly alveolar. The septa have many fine apertures in the median line and are as complex and thick as the hypodermis of the wall. The chambers are high with the central zone being empty with no pillars. Late Jurassic to Late Cretaceous (Oxfordian to Santonian) (Plate 4.5, figs 1-2; Plate 5.5, Figs. 8–9; Fig. 5.3).

• *Feurtillia* Maync, 1958 (Type species: *Feurtillia frequens* Maync, 1958). The test is planispiral with an involute early stage and a rectilinear later stage with no basal layer. The chamber walls are with narrow, shallow alveoles surmounted by an *Alzonella*-like (Plate 4.12, figs 6-8) reticulum of beams and rafters. The septa are weakly alveolar with single areal aperture possessing a thickened, invaginated rim. Early Jurassic to Late Cretaceous (Tithonian to Valanginian) (Plate 5.3, fig. 8).

• *Palaeocyclammina* Bassoullet, Boutakiout and Echarfaoui, 1999 (Type species: *Palaeocyclammina complanata* Bassoullet et al., 1999). The test is planispiral, compressed and involute with long low chambers. It differs from *Pseudocyclammina* in having a reticulate subepidermal skeleton comprised of an irregular superficial network, made of short radial blades perpendicular to the septa. Early Jurassic (Pliensbachian) (Plate 4.15, fig. 1).

• *Pseudocyclammina* Yabe and Hanzawa, 1926 (Type species: *Cyclammina lituus* Yokoyama, 1890). A planispiral nautiliform test, sometimes becoming uncoiled. The central zone of the test lacks the continuous endoskeletal pillars (discontinuous, columnar partitions on the inner surface of the chamber wall, see Hottinger (2006) for definition). Walls are coarsely alveolar and labyrinthic. Apertures are spread over the apertural face. Early Jurassic to Cretaceous (Pliensbachian to early Maastrichtian) (Plate 4.10, figs 3-10).

• *Redmondellina* Banner and Whittaker, 1991 (Type species: *Pseudocyclammina powersi* Redmond, 1964). This form has a compressed test and differs from *Alveosepta* in having pillar-like hypodermal extensions linking the septal hypodermis to the anterior of the epidermis of each preceding septum. The division of the hypodermal alveoles distally produces finer and finer alveoles, as they bifurcate or trifurcate on approaching the epidermis. The pillars are present only in the median, equatorial plane, and are not spread throughout the chamber space as in *Pseudospirocyclina*. Late Jurassic (late Oxfordian to Kimmeridgian) (Plate 4.9, fig. 13A; Plate 4.13, figs 4-5).

• *Torinosuella* Maync, 1959 (Type species: *Choffatella peneropliformis* Yabe and Hanzawa, 1926). The test is flabelliform, with simplified, thin septa. Late Jurassic to Early Cretaceous (Oxfordian to Barremian) (Plate 4.15, fig. 5).

**Family Everticyclamminidae Septfontaine, 1988**
Tests are streptospiral or planispiral in early stages, but uncoiled in the adult or uniserial throughout. Walls are microgranular with an alveolar microstructure. Interiors
of chambers are simple. Apertures are unique and terminal. Early Jurassic to Early Cretaceous (Sinemurian to Aptian).

- **Everticyclammina** Redmond, 1964 (Type species: *Everticyclammina hensoni* Redmond, 1964). A planispiral test with an alveolar wall. The septal aperture is single, and the initial coil is very short and missing in most random sections, which only show the elongate uniseri al part. Loeblich and Tappan (1988) assigned *Everticyclammina* to the Family Cyclamminidae, but Septfontaine (1988) assigned it to his new, monogen eric Family Everticyclamminidae. This proposal, seemingly overlooked by Banner and Highton (1990), when revising the genus to accommodate five named species other than the type, is adopted by Fugagnoli (2000) and herein. Fugagnoli’s amended phylogeny and BouDagher-Fadel et al. (2001) illustrate a known origin of the genus *Everticyclammina* from *E. praevirguliana* (Plate 4.16, fig. 3) in the Early Jurassic (late Sinemurian) rather than from species of the Middle or Late Jurassic (Callovian or Oxfordian) as generally accepted by previous authors, with a supposed ancestry in near coeval *Ammobaculites*. Therefore, the earliest known *Everticyclammina* is of middle Sinemurian age, and this suggests that by this time the genus was more widely dispersed in the Tethyan realm than recorded hitherto. Jurassic to Cretaceous (mid Sinemurian to Aptian) (Plate 4.4, fig. 11; Plate 4.16, figs 3-6).

- **Buccicrenata** Loeblich and Tappan, 1949 (Type species: *Ammobaculites subgoodlandensis* Vanderpool, 1933). *Buccicrenata* was erected by Loeblich and Tappan, 1949 with *Ammobaculites subgoodlandensis* Vanderpool, 1933 as its type species. Loeblich and Tappan (1985, p.100; 1988, p.99) redefined the genus *Buccicrenata* to include an alveolar wall, which was first illustrated for *B. libyca* Gohrbandt (1966, p.67, pl.1, fig.11). However, they denied the presence of alveoles in the septum of *Buccicrenata*. Nevertheless, in examining numerous randomly thin sectioned specimens of *Buccicrenata* from different localities, some of them hypotypes of both *B. subgoodlandensis* and *B. hedbergi*, the alveoles are clearly seen to be present, and were used by Banner and Highton (1990) to distinguish this genus from *Everticyclammina*. Subsequently BouDagher-Fadel (2001) reviewed these forms and traced their evolution from a primitive form, *B. primitiva*, from the Kimmeridgian of Lebanon. It is characterized by a planispiral test with septa that are a continuation of chamber walls, but with alveoles reduced and with no basal layer. Jurassic to Cretaceous (Kimmeridgian to Cenomanian) (Plate 4.5, fig. 8; Plate 5.6, fig.16).

- **Rectocyclammina** Hottinger, 1967 (Type species: *Rectocyclammina chouberti* Hottinger, 1967). The test is elongate, the early stage is planispiral, later uncoiling and becoming rectilinear. The septa are thick, and the aperture is terminal and circular in the centre of the apertural face. Jurassic to Early Cretaceous (Pliensbachian to early Berriasian) (Plate 4.12, fig. 18).

**Family Mesoendothyridae Voloshinova, 1958**

Members of this family have a strepto- or planispirally coiled test, that has involute initial chambers, and later is uncoiled. Adult chambers are cylindrical or flattened, falciform to cyclical. They are simple, with radial partitions or with pillars. The wall may have alveoles or a hypodermic network. Early Jurassic (Sinemurian) to Holocene.
Subfamily *Mesoendothyrinae* Voloshinova, 1956

Tests are biumbilicate, or very compressed, strepto- or planispirally coiled, but later they are uncoiled to various degrees. Chambers increase rapidly in height with monolamellar septa. Adult chambers are cylindrical or flattened. Walls are microgranular to agglutinated, imperforate or alveolar, simple or with radial partitions, with or without pillars. Apertures are a single slit or made of numerous pores. Jurassic (Sinemurian) to Cretaceous.

- *Mesoendothyra* Dain, 1958 (Type species: *Mesoendothyra izjumiana* Dain, 1958). The test is involute, globose, and twisted in a tight streptospire. The wall has an outer imperforate layer and an inner alveolar layer. The aperture is a basal slit. Middle Triassic to Jurassic (Ladinian to Kimmeridgian) (Plate 4.5, figs 5-6).

Subfamily *Orbitopsellinae* Hottinger and Caus, 1982

Tests have an early planispiral coil followed by a uniserial part in the adult, becoming cylindrical, or falciform to cyclical. The wall has an alveolar microstructure. The interior of the chambers are divided by vertical radial partitions, with pillars in the central zone. Early Jurassic (late Sinemurian to Toarcian).

- *Cyclorbitopsella* Cherchi, Schroeder and Zhang, 1984 (Type species: *Cyclorbitopsella tibetica* Cherchi et al., 1984). An orbitopsellinine with adult chambers becoming annular. It has medial pillars in the central zone, but no subepidermal beams and rafters, in contrast to *Alzonorbitopsella*. Apertures are cribrate. Early Jurassic (late Sinemurian to Toarcian) (Plate 4.17, figs 8-9).

- *Lituosepta* Cati, 1959 (Type species: *Lituosepta recoarensis* Cati, 1959). This species is characterized by having a simple proloculus followed by a planispiral stage, and a well-developed uncoiled part, which becomes fan shaped particularly in the microspheric forms. The test possesses multiple cribrate apertures. The apertural openings between the pillars penetrate the height of the chamber space. Peripheral partitions are seen in transverse sections. The flaring flabelliform test and the canaliculated wall distinguishes it from *Labyrinthina*. Early Jurassic (late Sinemurian to Aalenian) (Plate 4.16, figs 8-9).

- *Orbitopsella* Munier-Chalmas, 1902 (Type species: *Orbitulites praecursor* Gümbl, 1872). An orbitopsellinine with a discoidal test, the first stage being planispiral followed by a flaring, flabelliform stage with 35 to 40 annular chambers. The wall has simple endoskeletal and exoskeletal pillars. Early Jurassic (late Sinemurian to Toarcian) (Plate 4.16, fig.10; Plate 4.17, figs 1-6).

Subfamily *Planiseptinae* Septfontaine, 1988

Tests are planispiral, compressed laterally and involute. Walls are microgranular with an alveolar microstructure. Interior of chambers are simple, or with vertical partitions and pillars in the median layer. Apertures are multiple. Early Jurassic (late Sinemurian to Pliensbachian).

- *Planiseta* Septfontaine, 1988 (Type species: *Lituola compressa* Hottinger, 1967). Tests have vertical radial partitions and pillars. Early Jurassic (Pliensbachian) (Plate 4.9, figs 1-3).
• *Palaeomayncina* Septfontaine, 1988 (Type species: *Mayncina termieri* Hottinger, 1967). Differs from *Planisepta* by the absence of the pillars and partitions. Septfontaine (1988) named *Mayncina termieri* Hottinger, 1967 as the type species and proposed that this new genus is closely related to *Lituolipora* (Plate 4.11, fig. 7). Early Jurassic (Late Sinemurian-Pliensbachian) (Plate 4.10, fig. 2).

**Subfamily Labyrinthininae** Septfontaine, 1988
Tests are planispirally coiled in early stages, but uncoiled in the adult. Walls are thick and may have alveoles. Interior of chambers are subdivided by vertical, radial partitions. Pillars may be present in the central zone. Late Jurassic.

• *Labyrinthina* Wenschenk, 1951 (Type species: *Labyrinthina mirabilis* Wenschenk, 1951). A labyrinthine with multiple apertures, with internal radial partitions and pillars. Late Jurassic (Plate 4.9, figs 4-5).
• *Orbitammina* Berthelin (Type species: *Orbicula elliptica* d’Archiac, 1843). The test is compressed, with a planispiral early stage. The early chambers are narrow and elongate, increasing rapidly in size to produce a reniform test. The aperture is cribrate and radially aligned. The peripheral margin lack the thickness of *Orbitopsella*, while the internal structure is similar as in *Orbitopsella* but with finer pillars. Hottinger (1967) and Septfontaine (1981) believe *O. elliptica* to be the microspheric form, and the senior synonym of *Meyendorffina bathonica* s.s. but no comparable B-form is known to match *M. bathonica* (Plate 4.11, figs 5-6). Also *O. elliptica* is known in late Bajocian, while *M. bathonica* is widely regarded as being Bathonian only. Middle Jurassic (late Bajocian to Bathonian) (Plate 4.12, figs 5-6).

**Subfamily Levantinellinae** Fourcade, Mouti and Teherani, 1997
Characterised by having a single layer of cyclical chambers, undivided by pillars. Jurassic.

• *Levantinella* Fourcade, Mouti and Teherani, 1997 (Type species: *Mangashtia? egyp-tiensis* Fourcade, Araf and Sigal, 1984). Peneropliform and compressed axially. A simple proloculus followed by a planispiral evolute stage and a later uniserial stage. The first chambers are simple, and then subdivided by zigzag pillars with perforations. Late Jurassic (Oxfordian to Kimmeridgian) (Plate 4.4, fig. 2).
• *Syriana* Fourcade and Mouti, 1995 (Type species: *Syriana khouryi* Fourcade and Mouti, 1995). This form is characterised by a compressed flaring test with bilateral symmetry, with multiple apertures successively disposed in rows. The numerous chambers are subdivided by many vertical radial subepidermal partitions arranged in a well-developed uniserial stage. Middle Jurassic (late Callovian) (Plate 4.9, fig. 6B).

**Superfamily Nezzazatoidea** Hamaoui and Saint-Marc, 1970
The test is trochospiral or planispiral, later occasionally uncoiled. The wall is simple nonlamellar, microgranular, and may possess internal plates or simple partitions. The aperture is simple or multiple with tooth plates. Middle Jurassic (Bajocian) to Holocene.
Family Mayncinidae Loeblich and Tappan, 1985
The test is biumbilicate or very compressed, planispirally enrolled, and rarely uncoiling. Chambers increase rapidly in height. The septa are monolamellar. The wall is simple, solid and microgranular. Middle Jurassic to Late Cretaceous (Bajocian to Santonian).

- *Daxia* Cuvillier and Szakall, 1949 (Type species: *Daxia orbignyi* Cuvillier and Szakall, 1949). The test is planispiral, completely involute, lenticular, bilaterally symmetrical with a moderately sharp margin. Chambers are very narrow. There is a single aperture, that is basal, rounded and central. Late Jurassic to Late Cretaceous (Kimmeridgian to Cenomanian) (Plate 5.3, fig. 11; Plate 5.4, fig. 7).

- *Freixialina* Ramalho, 1969 (Type species: *Freixialina planispiralis* Ramalho, 1969). The test is biumbilicate, planispiral, with sutures that are slightly curved. The wall is finely agglutinated. The aperture is an areal slit in the middle of apertural face. Jurassic (Bajocian to Tithonian) (Plate 4.5, fig. 3).

Superfamily Biokovinoidea Gušić, 1977
Members of this superfamily have a free test with a trochospiral or planispiral early stage, that later may be uncoiled. The septa are homogenous and massive. The walls have an imperforate outer layer and a canaliculate inner layer. The aperture is basal to areal, single to multiple. Early Jurassic (Sinemurian) to Late Cretaceous (Maastrichtian).

Family Biokovinidae Gušić, 1977
The test is planispirally coiled, later it may be uncoiled. Endoskeletal pillars may be present. Walls are canaliculate, with alveoles that open both to the exterior or interior. Early Jurassic to Cretaceous.

- *Bosniella* Gušić, 1977 (Type species: *Bosniella oenensis* Gušić, 1977). This genus is characterised by having a well-developed uncoiled later stage with thick, widely spaced and gently curved septa. The aperture is single in the coiled stage becoming cribrate in the uncoiled part. The presence or absence of alveoles in the wall is still debatable. Septfontaine (1988, p. 242) put the genus *Bosniella* in synonymy with *Mesoendothyra* Dain, 1958, as “the presence or absence of keriotheca which is not always visible due to diagenesis, is not a reliable criterion for the distinction between the taxa *Mesoendothyra* and *Bosniella*”. The type species of *Mesoendothyra* had been originally described as having alveolar within the wall structure. However, in my specimens the wall structure is solid and I still consider the two taxa as being separate. Early Jurassic (late Sinemurian to early Pliensbachian) (Plate 4.16, figs 1-2).

Family Charentiidae Loeblich and Tappan, 1985
Early stages are planispiral or streptospiral. Walls are finely canaliculated. Apertures are single or multiple. Middle Jurassic to Late Cretaceous (Callovian to Maastrichtian).

- *Karaisella* Kurbatov, 1971 (Type species: *Karaisella uzbekistanica* Kurbatov, 1971). Tests have streptospiral early coiling but later are planispiral. The base of septum against the previous whorl is thickened and chomata-like as in *Charentia* (see Chapter 5). Late Jurassic (Oxfordian) (Plate 4.16, fig. 11).
Tests are planispirally coiled but later may be uncoiled. Walls have coarse alveoles. Early Jurassic.

- *Lituolipora* Gusić and Velic, 1978 (Type species: *Lituolipora polymorpha* Gusić and Velic, 1978). Tests have a later stage that may be irregularly coiled, uncoiled and rectilinear. Walls are microgranular with coarse alveoles. Early Jurassic (Sinemurian to Pliensbachian) (Plate 4.17, fig. 7).

Superfamily Spiroplectammonoidea Cushman, 1927
Tests are planispirally coiled or biserial in early stages, but later biserial. Walls are agglutinated, non-canaliculate. Carboniferous to Holocene.

Family Textulariopsidae Loeblich and Tappan, 1982
Members of this family have a biserial early stage, later they may be loosely biserial or uniserial. Walls are agglutinated. Early Jurassic (Sinemurian) to Late Cretaceous (Maastrichtian).

- *Textulariopsis* Banner and Pereira, 1981 (Type species: *Textulariopsis portsdownensis* Banner and Pereira, 1981). On the basis of a single (type) species, Banner and Pereira (1981, p. 98) defined their new genus as “Wall: agglutinated with calcareous cement, solid, imperforate, lacking canaliculi or pseudopores; proloculus succeeded by a rectilinear series of chambers, all biserially arranged; aperture: anteromarginal, a simple basal, narrow slit. Differs from other small benthic *Spirorutilus* Hofker in its lack of a planispiral initial stage, from *Textularia* Defrance in its lack of canaliculate, pseudoporous walls, and from *Pseudobolivina* Wiesner by its low aperture and structurally insignificant chitinous endoskeleton”. Two new Cretaceous species were assigned to the genus by Loeblich and Tappan (1982), plus three other Cretaceous species from the North America, and *T. areoplecta* from the Early Jurassic (Pliensbachian to Toarcian) of northern Alaska, which had previously been assigned to *Textularia*. BouDagher-Fadel et al. 2001 confirmed that this seemingly largely Cretaceous genus had originated by the Sinemurian. Early Jurassic to Cretaceous (Sinemurian to Maastrichtian) (Plate 4.8, fig. 25).

Superfamily Textularioidea Ehrenberg, 1838
Tests are trochospiral, biserial or triserial in early stages but later may be uniserial or biserial. Walls are agglutinated and canaliculate. Early Jurassic (Sinemurian) to Holocene.

Family Chrysalidinidae Neagu, 1968
Tests are high trochospiral, with quinqueserial, quadriserial, triserial or biserial coiling modes, or with certain consecutive pairs of these. The aperture is central along the axis of coiling. In quadriserial or quinqueserial forms, an umbilicus is present and the aperture is covered with a broad umbilical flap, which may be penetrated by multiple accessory apertures. Internal pillars may develop between successive
intraumbilical flaps. Banner et al. (1991) divided this family into two subfamilies; the mainly Cretaceous Chrysalidininae (see Chapter 5), which evolved as a single lineage developing pillars in the centre of the test, and the mainly Jurassic Paravalvulininae (see below) which survived into the Valanginian and possibly the Hauterivian. This classification is followed here and in the Chapter 5.

**Subfamily Paravalvulininae Banner, Simmons and Whittaker, 1991**

This subfamily was created by Banner et al. (1991) to include all initially quadriserial or quinqueserial forms, becoming quadriserial or quinqueserial in neanic growth (a postnepionic growth stage with the architecture of an adult shell, see Hottinger, 2006), and then quinqueserial, quadriserial or triserial in the adult. Jurassic (Sinemurian to Kimmeridgian).

- **Paravalvulina** Septfontaine, 1988 (Type species: *Paravalvulina complicata* Septfontaine, 1988). Internal pillars between successive umbilical flaps. The early test is quadriserial, later becoming uniserial. Jurassic to?Cretaceous (Bathonian to?Hauterivian) (Plate 4.11, fig. 1).

- **Pseudomarssonella** Redmond, 1965 (Type species: *Pseudomarssonella maxima* Redmond, 1965). Forms with cribrate apertures and an umbilicus that is concave with no internal umbilical pillars. Umbilical apertural flaps of successive whorls are broad and are axially separated by a narrow space. Adult tests are quadriserial or quinqueserial. Jurassic (Bathonian to Callovian) (Plate 4.8, fig. 26; Plate 4.11, figs 2-4).

- **Redmondoides** Banner, Simmons and Whittaker, 1991 (Type species: *Pseudomarssonella media* Redmond, 1965). The test is quadriserial in the adult form. The umbilicus is concave with no internal umbilical pillars. Apertural flaps of successive whorls are well separated. Septa are flattened with narrow umbilicus. Jurassic (Bajocian to Kimmeridgian) (Plate 4.11, figs 5-7).

- **Riyadhella** Redmond, 1965 (Type species: *Riyadhella regularis* Redmond, 1965). Forms with septa and terminal faces that are highly convex. Redmond’s species of *Riyadhella* were known to him only as solid specimens extracted from their matrix. Banner et al. (1991) revised the genus and its four assigned species partly on the basis of thin sections of type material, providing amended descriptions of the Redmond (1965) species *R. arabica, R. elongata, R. inflata* and *R. regularis* and placing his species *R. hemeri, R. intermedia* and *R. nana* in synonymy with *R. regularis*. They reassigned the genus to the Family Chrysalidinidae rather than to the Family Prolixoplectidae (as by Loeblich and Tappan 1988). BouDagher-Fadel et al. (2001) recorded a new, more primitive species *R. praeregularis* in the Sinemurian of the western Mediterranean that reveals canaliculi within the test wall and extended the stratigraphic range of the genus down into the Early Jurassic, and its geographic range significantly westwards within Tethys. Jurassic (Sinemurian to Kimmeridgian) (Plate 4.11, figs 10-13).

- **Riyadhoides** Banner, Simmons and Whittaker, 1991 (Type species: *Pseudomarssonella mcclurei* Redmond, 1965). Tests are quadriserial in the adult with flattened septa, or with septa and terminal face concave. Jurassic (late Bajocian – Tithonian) (Plate 4.11, figs 8-9).
Order Miliolida Delage and Hérouard, 1896
The miliolines have tests that are porcelaneous and imperforate, made of high Mg-calcite with fine randomly oriented crystals. They range from the Carboniferous to the Holocene.

Superfamily Milioloidea Ehrenberg, 1839
Tests are coiled commonly with two or more chambers arranged in varying planes about the longitudinal axis, later they may become involute. Advanced forms may have secondary partitions within the chambers. Late Triassic (Norian) to Holocene.

Family Nautiloculinidae Loeblich and Tappan, 1985
Tests are free, lenticular, planispiral, and involute with secondary thickening in the umbilical region. Apertures are equatorial. Middle Jurassic to Late Cretaceous.

• *Nautiloculina* Mohler, 1938 (Type species: *Nautiloculina oolithica* Mohler, 1938). It has been variously placed in previous systematics. It was originally described by Mohler (1938, p. 18) as calcareous and imperforate, compared to porcelaneous *Planispirina*. Loeblich and Tappan (1964b, p. 443) placed the genus into the miliolines. They subsequently (1985, p. 92; 1988, p. 71) reallocated this genus into the lituoloids. I do not agree with this classification as *Nautiloculina* does not possess a microgranular agglutinated wall. Yet, it is not a member of the calcareous rotalilides with the hyaline calcitic perforate wall. The multi-layered imperforate wall of *Nautiloculina* is very difficult to separate from simple fusulinines such as the Carboniferous *Millerella* Thompson, 1942. Nonetheless, the considerable time gap between the Palaeozoic Loeblichiiidae and the Jurassic-Cretaceous Nautiloculinidae would make it difficult to explain a relationship between them. Presently, *Nautiloculina* has been placed systematically in the Milioloidea (see Noujaim Clark and BouDagher-Fadel, 2001) because some of the miliolides (such as *Austrotrillina, Quinqueloculina*, etc.) display double layered walls like *Nautiloculina*, although the thin dark layer is internal to the thick transparent layer of the wall of the normal miliolides, but it is external to the wall of *Nautiloculina*. Consequently, the thin dark layer may be basal to the wall of the normal miliolides, while the later part of the wall grow inwards toward the chamber lumen; in *Nautiloculina* the thin dark layer of the wall could equally be basal to the development of the thicker translucent part of the wall which also would have grown inwards towards the chamber lumen. Tests are biumbonate, nautiliform with chambers increasing slowly in height. Late Jurassic (Bajocian) to Early Cretaceous (Aptian) (Plate 4.9, figs 6A, 7-12; see Chapter 5, Fig. 5.23).

4.3 Biostratigraphy and Phylogenetic Evolution

4.3.1 General Biostratigraphy

Following the mass extinction in the marine realm at the end of the Triassic, foraminifera did not make a full recovery until the middle of the Sinemurian. Hettangian
foraminifera were rare and simple, and were predominately small Involutinoidea and Pfenderinoidea (see Figs 4.7, 4.8). *Siphovalvulina* and *Textularia* dominated the early Sinemurian (BouDagher-Fadel, 2000; BouDagher-Fadel et al., 2001; Bosence et al., 2009; Scherreiks et al., 2010). However, from the Sinemurian onwards, the Early Jurassic witnessed the steady development of these textulariides from small simple forms to internally complicated forms, which became abundant from the Pliensbachian onwards, yielding a high biostratigraphic resolution for the Tethyan carbonate facies. The Pfenderinoidea and Textularioidea dominated assemblages in the Bathonian and Callovian, but the Lituoloidea/Loftuioidea seem to have taken over during the Late Jurassic (see Fig. 4.9). The abundance of the agglutinated textulariides (see Chart 4.1) in the Jurassic and their short ranges makes them an invaluable biostratigraphical resource (e.g. Noujaim Clark and BouDagher-Fadel, 2004; BouDagher-Fadel and Bosence, 2007).

![Fig. 4.8. The phylogenetic development of the Involutinoidea through the Jurassic.](chart)
<table>
<thead>
<tr>
<th>Period, Epoch, Stage</th>
<th>Age (Ma)</th>
<th>Involutinoidea</th>
<th>Textularioidea</th>
<th>Pfenderinoidea</th>
<th>Lituoloidea/Loftusioidea</th>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Early</td>
<td>174.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Triassic</td>
<td>188.3</td>
<td></td>
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</table>

*Fig. 4.9.* Biostratigraphic ranges and diversity of the main Jurassic superfamilies of Tethys. Details of the genera and their ranges are shown in Chart 4.1 online.
Importantly in this epoch, dasyclad algae became abundant and flourished in a reefal environment. As foraminifera became large, they developed blind chambers (alveoles) in their test walls, which housed these symbiotic algae (see Fig. 4.10). From the middle to late Sinemurian, forms with internal pillars, such as *Pseudopfenderina* (Plate 4.6, figs 10-16), and fine alveoles in the walls, as in *Everticyclammina* (Fig. 4.10), began to appear in the Western Mediterranean. Such features developed in later forms, with larger and more consistent alveoles, in the Pliensbachian to the Late Jurassic and Cretaceous, becoming very important components of Mesozoic rocks.

Septfontaine (1981) had proposed a standard Jurassic biozonation on the basis of 56 foraminiferal generic ranges, which took account of work by earlier authors. His scheme began with an *Orbitopsella* range zone approximately equivalent to the Pliensbachian: none of his genera were confidently recorded from the underlying Sinemurian. Later, Septfontaine (1984) recorded *’Siphovalvulina’* from the Sinemurian-Pliensbachian (Domerian) of Morocco and distinguished a biozone of *’Siphovalvulina’* and *Mesoendothyra*, characterized by a fauna of small, primitive lituoloids: the two index genera plus *Everticyclammina praevirguliana*. Plate 4.16, fig.3), *Glomospira* sp. and *Earlandia* sp. These taxa occurred in all six biozones that he distinguished in the Moroccan Early Jurassic (Hettangian to Pliensbachian), but the lower boundary of this ‘interval zone’ was defined by the first appearance of *Lituosepta recoarensis* (Plate 4.16, figs 7-8), the index fossil for the overlying zone. A similar scheme was applied to the Buffadero Member of the Gibraltar Limestone (BouDagher-Fadel et al., 2001). More recently, Fugagnoli (2004) recorded that the Hettangian-early Sinemurian interval belongs to his Dasyclades Zone, early most late Sinemurian to?*Lituosepta recoarensis* zone, while the lower part of the Sinemurian and early Pliensbachian belongs to the *Orbitopsella* zone and finally the late Pliensbachian belongs to the *Planisepta compressa* zone. On the other hand, the Toarcian is dominated by forms with internal radial partitions (e.g. *Haurania*).

Later, BouDagher-Fadel and Bosence (2007), while systematically studying the Early Jurassic foraminifera, divided the Hettangian to Pliensbachian into four biozones, that correlate with strontium isotope dating. In this book, these biozones are revised and the entire Jurassic biozones are plotted (Fig. 4.11). These Jurassic biozones are:

- the *Siphovalvulina colomi* biozone, corresponding to the early Sinemurian and includes S. colomi (Plate 4.1, figs 3-6), S. gibraltarensis (Plate 4.1, figs 7-8), Duotaxis metula (Plate 4.6, fig. 1), Riyadhella praeregularis (Plate 4.11, figs 10-11), Involutina liassica, *Pseudopfenderina butterlini* (Plate 4.6, fig. 10-16);
- the *Everticyclammina praevirguliana* biozone, which corresponds to the mid Sinemurian and coincides with the first appearance of *E. praevirguliana* (Plate 4.16, fig. 3) and includes Siphovalvulina colomi, S. gibraltarensis, *Textulariopsis sinemurenensis* (Plate 4.8, Fig. 25), Riyadhella praeregularis, Duotaxis metula. Foraminifera of the *Everticyclammina praevirguliana* biozone occur in micritic limestones with associated algae/cyanobacteria (*Cayeuxia*, Plate 4.18, figs 1-2; *Thaumatoporella*, Plate 4.18, figs 3-4 and *Palaeodasycladus mediterraneus*, Plate 4.18, figs 5-7);
Evolution and Geological Significance of Larger Benthic Foraminifera
Fig. 4.10. Alveolar exoskeleton and polygonal network. Scale bars = 0.5mm. A) simple alveolar layer in *Everticyclammina virguliana* (Koechlin), Zakum-1, core 9536 ft, ARAB, Kimmeridgian; B) *Pseudocyclammina lituus* (Yokoyama), equatorial section, Hauterivian, Umm Shaif-3, cuttings 6710 ft, THAMAMA IV; C) Enlargement of *P. lituus* (Yokoyama), from the Early Cretaceous of the Persian Gulf, showing continuity between the labyrinthic hypodermis and the septa, and the wholly areal position of the septal apertures. It shows the inclusion of small exotic benthic foraminifera in the labyrinthic part of the hypodermis; D) *Alveosepta jaccardi* (Schrodt), from early Kimmeridgian of the Persian Gulf, Dukhan-51, core 7444 ft, stratotype DAR (Darb 2/3 boundary), equatorial section of a microspheric specimen showing delicately labyrinthic hypodermis and discontinuity between the alveolae of successive septa; E) *Everticyclammina virguliana* (Koechlin), early Kimmeridgian, after Hottinger (1967), showing the alveolar wall, closer spacing of narrow alveolae like these would mimic the canaliculate wall of *Charentia* (see Chap. 5). Note that the lower parts of the septa (S) often points forward (as in *Spinoendothyra*), producing very convex, almost conical septa, in which the aperture may be surrounded by a short, thick neck (N); these features are not typical of the Cretaceous *Everticyclammina greigt* (Henson) (see Chap. 5), the probable descendants of *E. virguliana*; F) *Rectocyclammina cf. chouberti* after Ramalho (1971), “Purbeckian”, Tithonian, Portugal, much larger and with elaborately structured hypodermis than in the type *R. chouberti*; G) *Pseudocyclammina sphaeroidalis* Hottinger, type specimen from the Kimmeridgian of east Morocco, after Hottinger (1967). It is distinguished from *P. lituus* (above) by having a simpler alveolar hypodermis and spheroidal test; note the very simple septa, often showing only one aperture in any one equatorial cut; H) *Streptocyclammina liasica* Hottinger, syntypes figured from the Early Jurassic of Morocco. Only the streptospirality readily distinguishes the heavily agglutinated forms of this species from *Pseudocyclammina bukowiensis* (Plate 4.10, figs 7-10) and the exceptionally rectilinear forms of this species (see Hottinger, 1967) from *P. vasconica* (Plate 4.10, fig. 9).
**Lituosepta recoarensis** and **Orbitopsella** spp. biozone, corresponding to the late Sinemurian. It coincides with the first appearance of *L. recoarensis* (Plate 4.16, figs 8-9) and includes *Siphovalvulina* sp., *Haurania deserta* (Plate 4.11, figs 18-20; Plate 4.12, figs 1-4), **Orbitopsella praecursor** (see Figs 4.18, 4.19; Plate 4.17, figs 2-3), *Amijiella amijii* (Plate 4.4, figs 8-9), **Pseudopfenderina** sp., and *Bosniella oenensis* (Plate 4.16, figs 1-2);

**Planisepita compressa** biozone which corresponds to the early Pliensbachian and coincides with the first appearance of *P. compressa* (Plate 4.9, figs 1-3). It includes *Pseudocyclammina* sp., *Haurania deserta*, *Amijiella amijii*, *Riyadhella* sp., *Siphovalvulina* sp., *Siphovalvulina colomi*, *Siphovalvulina gibraltarensis*, *Textulariopsis* sp., *Duotaxis metula*, *Éverticyclammina* sp., *Pseudocyclus* sp., *Orbitopsella* sp., *Haurania* sp., *Lituosepta recoarensis*, *Orbitopsella “circumvulvata”*, *Textularia* sp., *Siphovalvulina* sp., small miliolids, *Orbitopsella praecursor*, *Bosniella oenensis*, *Amijiella amijii*, *Haurania deserta*, *Pseudopfenderina* sp., and *Buccicrenata* sp. (see Chart 4.1);

**Socotraina serpentina** biozone which corresponds to the Toarcian. The beginning of this biozone coincides with the last appearance of **Planisepita**. It includes forms with pillared or partitioned central zone, e.g. *Socotraina serpentina*, *Haurania deserta*, *Amijiella amijii*, and *Cyclorbitopsella tibetica*. The top of this biozone marks the disappearance of **Orbitopsella** (see Fig. 4.11);

**Gutnicella cayeuxi** biozone which corresponds to the Aalenian. This biozone coincides with the first appearance of *Timidonella* (Plate 4.12, figs 13-16), which replaced **Orbitopsella** and **Gutnicella**. It includes *Gutnicella bizonorum*, *G. minoricensis*, *G. cayeuxi* and *Timidonella sarda*;

**Kurnubia palastiniensis** biozone, corresponding to the Bajociian. This biozone coincides with the first appearance of *Kurnubia*, *Pfenderina* and *Conicopfenderina*. It includes *Pseudopfenderina butterlini*, *Kurnubia palastiniensis*, *K. jurassica*, *Pfenderina salernitana*, *P. trochoidea*, *Conicopfenderina mesojurassica*, *Gutnicella cayeuxi*, *Timidonella sarda*, *Amijiella slingeri*, *Rectocyclammina ammobaculitiformis*, *Pseudocyclus* maynci and *Pseudocyclus bukowiensis*;

**Ataxella occitanica** biozone, corresponding to the Early Bathonian. It coincides with appearance of *Andersenolina elongata* (Plate 4.1, fig. 4) and includes *Trocholina granosa*, *T. conica*, *Redmondoides lugeoni*, *Kurnubia palastiniensis*, *K. jurassica*, *Pfenderina salernitana*, *P. trochoidea*, *Conicopfenderina mesojurassica*, *Paravalvulina complicata*, *Pseudocyclus maynci*, *P. bukowiensis* and *Spiraloconulus perconigi*;

**Alzonorbitopsella arabia** biozone, corresponding to the Late Bathonian. It coincides with the range of *Alzonorbitopsella arabia* (Plate 4.2, figs 5-10) and it includes *Redmondoides medius*, *R. inflatus*, *Pseudomarssonella maxima*, *P. bipartita*, *Pseudocyclus maynci* and *P. bukowiensis*. The top of this biozone witnesses the disappearance of *Haurania deserta*;

**Kilianina preblancheti** biozone, corresponding to the Early Callovian. It includes *Trocholina transversaria*, *Andersenolina alpina*, *Kurnubia palastiniensis*, *K. jurassica*, *Pfenderina salernitana*, *P. trochoidea*, *Pseudopfenderina maxima*, and *Kilianina blancheti*;

**Pseudopfenderina sp.** biozone, corresponding to the Late Callovian. It includes *Rectocyclus ammobaculitiformis*, *Pseudocyclus maynci*, *Pseudocyclus bukowiensis*, *Kurnubia palastiniensis*, *K. jurassica*, *Pfenderina salernitana*, *P. trochoidea*, *Pseudopfenderina smouti* and *Kilianina blancheti*.
### Jurassic Larger Benthic Foraminifera Biozones

<table>
<thead>
<tr>
<th>Period, Epoch, and Stage</th>
<th>LBF Zones</th>
<th>Diagnosis First Occurrence</th>
<th>Diagnosis Last Occurrence</th>
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<tr>
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</tr>
<tr>
<td>Early</td>
<td>Freixialna planispiralis</td>
<td>Kiliarnia lata</td>
<td>Paragurongina ochiispiralis</td>
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<td>Anchiopora protistiatica</td>
<td>Pseudospiricyclina smouti</td>
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<tr>
<td>Late</td>
<td>Evergulvulina sinemurensis</td>
<td>Meyendorfina septatrophina</td>
<td>Siphovalvulina coloni</td>
</tr>
</tbody>
</table>

*Fig. 4.11.* Jurassic larger benthic foraminifera biozones defined in this study with diagnostic first and last occurrences.
• *Anchispirocyclina praelusitanica* biozone, corresponding to the Early Oxfordian. It coincides with the first appearance of *A. praelusitanica* and includes *Septatrocholina banneri*, *Rectocyclammina annacobaculitiformis*, *Pseudocyclammina maynci* and *Pseudocyclammina bukowiensis*;

• *Parurgonina caelinensis* biozone, corresponding to the Late Oxfordian. It includes *Choffatella tingitana*, *Torinosuella peneropliformis*, *Anchispirocyclina praelusitanica* and *Alveosepta jaccardi*. The top of this biozone witnesses the disappearance of *Septatrocholina*;

• *Kilianina lata* biozone, corresponding to the Kimmeridgian. It includes *Kilianina lata*, *Neokilianina rahonensis*, *Freixialina atlastica*, *Buccicrenata primitiva*, *Pseudocyclammina ukrainica*, *P. sphaeroidalis*, *Rectocyclammina chouberti*, *Redmondellina powersi* and *Pseudospirocyclina mauretanica*. The top of this biozone marks the disappearance of *Conicokurnubia*;

• *Freixialina planispiralis* biozone, corresponding to the Tithonian. It includes *Anchispirocyclina neumanni*, *Everticyclammina virguliana*, *E. praekelleri*, *Pseudocyclammina lituus* and *Anchispirocyclina lusitanica*. The early part of this biozone witnesses the disappearance of *Kurnubia* (Plate 4.8, figs 3-21), while the top is marked by the disappearance of *Parurgonina*, *Pseudospirocyclina*, *Kastamonina* and *Labyrinthina*.

The Middle and Late Jurassic have been intensively studied from the Middle East (Henson, 1948), Eastern Mediterranean (Noujaim Clark and BouDagher-Fadel, 2002, BouDagher-Fadel and Lord, 2002; Noujaim and BouDagher-Fadel, 2004) and the Western Mediterranean (Septfontaine, 1988, BouDagher-Fadel and Bosence, 2007; Bosence et al., 2009), and phylogenetic evolutions have been traced for different groups, such as the Textularioidea (Banner et al., 1991) and the Lituoloidea (Septfontaine, 1988). The Middle Jurassic is rich with foraminifera filled with internal pillars (e.g. *Haurania*), while for assemblages in the Late Jurassic, foraminifera with narrow internal alveoles dominate (see Fig. 4.12). Chart 4.1 summarises the ranges of most important species in the Jurassic, and Chart 4.2 shows the range of the major textulariine superfamilies.

Below are discussed the evolutionary lineages and revised phylogenetic evolutions of the most important superfamilies in the Jurassic, namely the Pfenderinoidea, the Lituoloidea, the Textularioidea, and the Involutoidea.

### 4.3.2 The Pfenderinoidea of the Jurassic

In the Hettangian, small simple textulariides developed a twisted siphonal canal connecting the successive apertures (Figs. 4.13, 4.14, 4.15). These forms evolved gradually from the Sinemurian to the Bathonian into *Pseudopfenderina*, a form with high, loose spires with separate pillars filling the narrow central zone (see Fig. 4.7), which in turn evolved forms, such as *Pfenderella*, with single subcameral tunnels, short chambers with secondarily deposited material but without secondary septa (Plate 4.7, figs 21-24). These forms are probably the ancestors of *Pfenderina*, which developed a solid central core in the Bajocian. The pillars in the centre of *Pfenderina* fuse and coalesce in a strong central zone (Fig. 4.13A, Plate 4.7, figs 6-7). *Pfenderina* persists into the Early Cretaceous. In the Bathonian, *Pfenderina* evolved into *Palaeopfenderina*, with a
The Mesozoic Larger Benthic Foraminifera: The Jurassic

<table>
<thead>
<tr>
<th>Age (Ma)</th>
<th>Period, Epoch and Stage</th>
<th>Cymbriaella</th>
<th>Orbitopsella</th>
<th>Bosniella</th>
<th>Everticyclammina</th>
<th>Haurania</th>
<th>Playhaynania</th>
<th>Amidella</th>
<th>Socorina</th>
<th>Pseudocyclusammina</th>
<th>Ilyamella</th>
<th>Palaeocyclusammina</th>
<th>Litsepta</th>
<th>Planisephta</th>
<th>Palaeocyclammina</th>
<th>Guornicella</th>
<th>Timidonella</th>
<th>Meyendorffina</th>
<th>Alzamella</th>
<th>Bostia</th>
<th>Anchispirecyclina</th>
<th>Alveosepta</th>
<th>Redmondellina</th>
<th>Labyrinthina</th>
<th>Levamilla</th>
<th>Kastamonina</th>
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</thead>
<tbody>
<tr>
<td>145.0</td>
<td>Jurassic</td>
<td></td>
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<tr>
<td>163.5</td>
<td></td>
<td>Cymbriaella</td>
<td>Orbitopsella</td>
<td>Bosniella</td>
<td>Everticyclammina</td>
<td>Haurania</td>
<td>Playhaynania</td>
<td>Amidella</td>
<td>Socorina</td>
<td>Pseudocyclusammina</td>
<td>Ilyamella</td>
<td>Palaeocyclusammina</td>
<td>Litsepta</td>
<td>Planisephta</td>
<td>Palaeocyclammina</td>
<td>Guornicella</td>
<td>Timidonella</td>
<td>Meyendorffina</td>
<td>Alzamella</td>
<td>Bostia</td>
<td>Anchispirecyclina</td>
<td>Alveosepta</td>
<td>Redmondellina</td>
<td>Labyrinthina</td>
<td>Levamilla</td>
<td>Kastamonina</td>
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<tr>
<td>174.1</td>
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<td>199.3</td>
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Fig 4.12. The biostratigraphic ranges of the Lituoloidea in the Jurassic.
superficial position of the tunnel, with a groove at the surface of the columella, and by the filling of the inter-pillar spaces with calcitic material. In the Bathonian, *Sanderella* (Plate 4.7, fig. 17), the ancestral form of the terminally uncoiled forms, evolved from *Pfenderina* by developing a flaring, flattened, peneropliform test. In *Sanderella*, the spiral canal may bifurcate in the rectilinear portion forming multiple subcameral tunnels. In the late Bathonian, forms with a subcylindrical, lituoliform test evolved from *Satorina* (Plate 4.7, figs 15-16), with the tunnel partly or wholly surrounding the rectilinear columella, and other forms appear at the same time, with conical, coskinoliniform tests, but with pillars becoming separated in a broad central zone and the tunnel of the rectilinear part being reduced and discontinuous. In the late Bathonian, *Chablaisia* (Plate 4.7, figs 12-13) may have evolved directly from *Pfenderina* by developing a spiral canal and calcitic fillings in the chambers. In the Bathonian, *Pseudoeggerella* (Plate 4.7, fig. 14) evolved from *Pfenderella* (Plate 4.7, figs 21-24) by developing a narrow columella and calcitic protuberances in the chambers. In the Oxfordian, *Steinekella* (Plate 4.7, figs 18-20) replaces *Pfenderella* by developing a massive, central, continuous columella and multiple subcameral tunnels.

*Pfenderella* (Plate 4.7, figs 21-24) probably is also ancestral to *Kurnubia* (Plate 4.8, figs 3-8), which developed a peripheral zone divided by radial partitions in the Bajocian (Fig. 4.14). The high, loose, slender trochosiral test with a columella made of thickened innermost septal buttons of *Kurnubia* developed transverse partitions to form *Praekurnubia* in the Bathonian to Callovian. This latter in turn developed a broad central zone of a rectilinear cone, with scattered pillars and thickened inner ends of radial partitions, to form *Conicokurnubia* (Plate 4.8, figs 1-2) in the Oxfordian to Kimmeridgian. *Pfenderina*, with secondary infillings and internal partitions, appeared in the Late Jurassic (Oxfordian) and ranged into the Early Cretaceous (Valanginian) of southern Europe, but in the Middle East, survived until the Late Cretaceous (Chart 4.2).
The Valvulinidae show the first known example of a crosswise-oblique stolons system (the marginoporiform structure of Hottinger and Caus, 1982) (Fig. 4.16). They evolved a trochospiral test, with a valvular tooth plate, *Valvulina*. This form gives rise to conical tests, where central septa are thickened in a broad central zone (*Kilianina*, Plate 4.1, fig. 9B) in the Bathonian to Callovian. In the Oxfordian to Tithonian they are replaced with highly conical forms, possessing septa breaking in the umbilical region to form sub-conical pillars (*Parurgonina*, Plate 4.10, figs 17-18), which in turn gives rise in the early Kimmeridgian to forms with a high number of chambers per whorl and a strongly pillared centre (*Neokilianina*, Plate 4.10, Figs 13, 15-16), while compressed tests with cyclical chambers with numerous pillars evolved in the Oxfordian to Kimmeridgian (*Levantinella*, Plate 4.10, fig. 19).
**Evolution and Geological Significance of Larger Benthic Foraminifera**

<table>
<thead>
<tr>
<th>Principle Characteristics</th>
<th>Generic characteristics and forms</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>No pillars: a low trochospire. Wall possibly alveolar (canaliculate).</td>
<td>Chablaisia Septfontaine</td>
<td>C. chablaensis Septfontaine (Bath. - Cal.)</td>
</tr>
<tr>
<td>High, loose &quot;arenobuliminid&quot; spires with broad chamber spaces</td>
<td>Pseudopfenderina Hottinger</td>
<td></td>
</tr>
<tr>
<td>High or low trochospires with reduced chamber spaces</td>
<td>Pfenderina Henson</td>
<td></td>
</tr>
<tr>
<td>Test flaring, flattened, peneropliform</td>
<td>Tunnel may bifurcate in rectilinear portion</td>
<td>Sanderella Redmond</td>
</tr>
<tr>
<td>Test subcylindrical, lituoliform</td>
<td>Tunnel partly or wholly surrounds rectilinear columella</td>
<td>Satorina Fourcade and Chorowicz</td>
</tr>
<tr>
<td>Test conical, coskinoliform</td>
<td>Tunnel of rectilinear part is reduced and discontinuous</td>
<td>Conicopfenderina Septfontaine, 1988</td>
</tr>
<tr>
<td>Trochospiral throughout</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pillars separated, discrete, in narrow central zone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pillars fuse, coalescent in strong central zone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pillars coalescent into massive columella</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Radial peripheral partitions only, no chamberlets in series</td>
<td>Praekumbia Redmond, 1964</td>
<td>P. crusei Redmond (Bath. - E. Oxf.)</td>
</tr>
<tr>
<td>Radial partitions produce one tier of peripheral chamberlets in each rectilinear chamber</td>
<td>Conicokumbia Septfontaine</td>
<td>Conicokumbia orbitoliniformis Septfontaine, 1988 (Oxf. - Kim.)</td>
</tr>
<tr>
<td>Peripheral zone divided by radial partitions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High loose, slender trochospires</td>
<td>Kumubia Henson</td>
<td></td>
</tr>
<tr>
<td>Columella made of thickened innermost septal ends &quot;buttons&quot; without pillars</td>
<td></td>
<td></td>
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<tr>
<td>with lateral chamberlets alternating in several tiers</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Broad central zone of rectilinear cone with scattered pillars and thickened inner ends of radial partitions</td>
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</tbody>
</table>

**Fig. 4.15.** Morphological characteristics of the key species of the pfenderinids.
<table>
<thead>
<tr>
<th>Principle Characteristics</th>
<th>Generic Characteristics</th>
<th>Specific Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial high trochospire of 2 to 4 whorls</td>
<td>Walls of hummocks not thickened or coalescent; no massive central zone</td>
<td>Paragonina Cuvillier et al., 1968</td>
</tr>
<tr>
<td>Hummocks and arches convexly curved; no rectangular peripheral chamberlets</td>
<td>Wall of hummocks are thickened in a broad central zone</td>
<td>Kllanina Pfender, 1933</td>
</tr>
<tr>
<td>Initial spire reduced to one whorl only</td>
<td></td>
<td>Urgonina (Paragonina) caelinensis Cuvillier et al., 1968 late Oxfordian to Tithonian</td>
</tr>
</tbody>
</table>

Test conical; central zone arches not thickened into an almost solid mass

Test flaring, concavo-convex; central zone still with open passage ways; chambers highly arched

Test conical, central zone arches thickened and coalescent into an almost solid mass

K. rahonensis Foury and Cincent (Early Kim.)

K. lata Oberhauser (Kim.)

K. blanchei Pfender (Bath-Early Oxf.)

Fig. 4.16. Morphological characteristics of key species of the valvulinids.
4.3.3 The Lituoloidea of the Jurassic

Jurassic lituoloids (see Figs 4.12, 4.17) evolved rapidly, exhibiting a marked dimorphism between microspheric and megalospheric generations. Their rapid evolution, combined with their short ranges, gives the group a very useful biostratigraphic role in the Jurassic. In the Hettangian, the ancestor form of the lituoloids evolved from a simple form, Lituola, with early planispirally enrolled whorls, which later became uncoiled and rectilinear with a solid wall. Lituola evolved into Cymbriaella at the beginning of the Jurassic by developing a coarse irregular subepidermal polygonal network. In the late Sinemurian, Cymbriaella evolved into a form with radial partitions, Haurania. This form evolved into Socotraina in the Pliensbachian by filling the uniserial chambers with vertical subradial partitions. Haurania in turn gives rise to Platyhaurania in the latest Sinemurian, which possesses cylindrical chambers in the uncoiled part. Socotraina gives rise, in the Middle Jurassic, to forms with open flabelliform chambers filled centrally with pillars, with subepidermal nets of alternating horizontal and vertical pillars in Timidonella, and a central zone with irregular pillars of different sizes in Gutnicella. Meyendorffina replaced Timidonella in the Bathonian by losing the horizontal pillars.

Early forms, such as Haurania, Amijiella had a comparatively coarse structure with no clear differentiation of an epiderm, just a thin outer wall covering the polygonal network (Fig. 4.20). They also have radial partitions and pillars in the central zone with no orderly differentiation of beams and rafters. This group evolved into forms such as Orbitopsella, which developed an alveolar microstructure in the Sinemurian (Fig. 4.18). Large, complex, internally complicated agglutinating benthic foraminifera with pillars and/or intramural alveoles, such as Orbitopsella and Cyclorbitopsella, did not appear until latest Sinemurian to Pliensbachian times (Fig. 4.19). Orbitopsella have a flaring second stage, that becomes a well-developed uncoiled part in Lituosepta, and completely annular in Cyclorbitopsella. Lituosepta became planispiral and laterally compressed in Palaeomayncina, and developed vertical partitions and pillars in Planisepta. In the Late Jurassic, Labyrinthina developed a more important spiral stage than that in Lituosepta.

Amijiella evolved in parallel to Haurania in the late Sinemurian by having strong radial partitions, but unlike Haurania it has no pillars in the central zone (Fig. 4.20). Other planispiral forms became uncoiled and developed pillars superficially united by a coarse network (Ijdranella), or in the central zone with thin septa and uncoiled test (Spiraloconulus), or with a central zone filled by complex reticulum of densely spaced pillars (e.g. Pseudospirocyclina, Anchispirocyclina). There appear to be a grade through Pseudospirocyclina smouti (Plate 4.5, figs 9-10), and/or P. mauretanica (Plate 4.5, figs 11-12), and/or P. maynci (Plate 4.5, figs 13, 15), into Anchispirocyclina husitanica (Plate 4.15, figs 6-9) in Early Kimmeridgian. Other uncoiled forms are found without pillars, but develop a subepidermal reticulate mesh, which continues in the septa (Alzonella), or have irregular transverse radial partitions (Bostia). Kastamonina replaces Amijiella in the Kimmeridgian to Tithonian by developing a much reduced early coil and a more complex internal structure.
Fig 4.17. The phylogenetic development of the Lituoloidea through the Jurassic.
Fig. 4.18. Scale bars = 0.5mm. The structure of *Orbitopsella*, having a discoidal test formed by a simple exoskeleton and a pillared endoskeleton: A) Oblique section of a megalospheric *Orbitopsella primaeva* (Henson) (= *Coskinolinopsis primaevus* Henson, 1948), type species figured by Henson (1948) from the Early Jurassic of the Musandan limestone, Oman. B) Oblique section of a microspheric *Orbitopsella praecursor* (Günbel), Milhala, Oman; C) An enlargement of B showing (a) the alternating pattern in the disposition of the foramen, which are the openings that allow communication between the consecutive chambers, providing passages for functional endoplasm, and (b) oblique centered section of a megalospheric specimen showing the spherical protoconch.
4.3.4 The Loftusioidea of the Jurassic

The Jurassic planispiral forms with no pillars in the central zone, similar to *Lituola*, but with an alveolar wall, first appeared in the Sinemurian (*Everticyclammina praevirguliana*, Plate 4.16, fig. 3). This was immediately followed in the Pliensbachian by *Pseudocyclusammina*, forms with areal cribrate apertures spread over the apertural face, a labyrinthic hypodermis, and a reticulate subepidermal skeleton. The early primitive
<table>
<thead>
<tr>
<th>Principle Characteristics</th>
<th>Generic Characteristics</th>
<th>Specific Characteristics</th>
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<tbody>
<tr>
<td>With fine pillars in central zone</td>
<td>Radial partitions delicate, often bifurcating vertically to form a partial tier of peripheral chamberlets</td>
<td><em>Haurania</em> Henson</td>
</tr>
<tr>
<td>No pillars in central zone</td>
<td>Radial partitions strong, tending to become thickened in transverse section towards central zone, only rarely bifurcate vertically to form few, scattered chamberlets</td>
<td><em>Amijiella</em> Loeblich and Tappan (late Sin. to Bath. or ?Cal.)</td>
</tr>
<tr>
<td>Vertical pillars that project a short distance inward from the outer wall</td>
<td>Vertical partitions thickened in central zone to form a solid or vesicular central mass, arching becoming rectangular peripherally</td>
<td><em>Meyendorffina</em> Arouze and Bison, 1958 (Bath)</td>
</tr>
</tbody>
</table>

Chambers high, septa very arched, initial coil very small

Chambers low, septa thick and weakly arched, initial coil larger

A. amiji (Henson) Late Sin. - Bath.

A. sp. = "Ivanjaca slingeri" (Golesstaneh) (Baj.-Bath-?Cal.)

Septa arched convexly in central zone, but quadrately peripherally, producing rectangular peripheral chamberlets

*Myendorffina* n. sp. aff. *bathonica* Cal./Oxf.

*Myendorffina* *bathonica* Arouze and Bison (Bath.)

*Fig. 4.20. Morphological characteristics of key species of the hauraniids.*
\textit{Pseudocyclammina} has coarse simple alveoles, but soon several independent evolutionary modifications of the test occur, such as an increased complexity of the hypodermis which reached acme in the Santonian with \textit{Martiguesia} (see Chapter 5), and to increased test compression and coiling rate (e.g. \textit{Torinosuella}, Plate 4.15, fig. 5). Other lineages deriving from \textit{Pseudocyclammina} in the Oxfordian to Kimmeridgian are forms with walls with fine and complex alveoles and septa with many apertures (\textit{Alveosepta}), and with pillar-like hypodermal extensions (\textit{Redmondellina}). A very few forms from the Jurassic survived into the Early Cretaceous, (e.g. \textit{Everticyclammina}, \textit{Pseudocyclammina}).

\textit{Rectocyclus} in the Kimmeridgian has the apertural characters of \textit{Everticyclammina} and probably grades into it; \textit{R. chouberti} (Plate 4.12, fig. 18) is very close to \textit{E. gr. virguliana} (Plate 4.16, fig. 6), however, its internally thickened aperture is close to that of \textit{Feurtillia}. The latter evolved, in latest Jurassic possibly from \textit{Ammobaculites} by the development of an alveolar hypodermis and thick septa, but with the retention of the simple aperture with the strong apertural neck (see Chapter 5).

\textbf{4.3.5 The Biokovinoidea of the Jurassic}

Quite independently a group of foraminifera with canaliculate walls appear in the Sinemurian, the uncoiled Early Jurassic biokovinids and lituoliporids and the coiled planispiral to streptospiral charentiids. The charentiids that appear later in the Callovian have planispiral to streptospiral walls and are finely canaliculate.

\textbf{4.3.6 The Nezzazatoidea of the Jurassic}

In the Kimmeridgian, the biumbilicate nezzazatoids made their first appearance. They are distinguished by their simple nonlamellar, microgranular walls and by the simple internal partitions and their apertural tooth plates. Their oldest representative, \textit{Freixialina} is essentially a Jurassic form, ranging from the Bajocian to the Tithonian, while \textit{Daxia} that appear much later in the Kimmeridgian has a completely involute test and more curved sutures. It survived the Jurassic-Cretaceous boundary, only to die out in the Late Cretaceous.

\textbf{4.3.7 The Spiroplectamminoidea of the Jurassic}

The representative of the Jurassic spiroplectamminoids, \textit{Textulariopsis} first appeared in the Sinemurian (BouDagher-Fadel et al, 2001). This essentially Cretaceous genus lacks the early planispiral coil and canaliculi.

\textbf{4.3.8. The Textularioidea of the Jurassic}

Within the Textularioidea, the chrysalidinoids evolved in the Jurassic from simple textulariide forms with triserial, quadriserial or quinqueserial tests (with simple interiors) into forms with convex septa and canaliculi in the walls (\textit{Riyadhella}) (see Fig. 4.21).
These forms developed umbilical apertural flaps with a narrow umbilicus in the Bajocian to Kimmeridgian (*Redmondoides*), and flattened septa in the late Bajocian to Tithonian (*Riyadhoides*). Internal pillars between successive umbilical flaps appeared in the Bathonian (*Paravalvulina*), while in the Bathonian to Kimmeridgian forms with no internal pillars, but with apertural flaps separated only by a narrow space, thrived (*Pseudomarssonella*).
4.3.9. The Involutinoidea of the Jurassic

After their first appearance in the Late Triassic, *Trocholina* (Figs. 4.3, 4.6) and *Involutina* (Figs 4.4, 4.5) continue to thrive in the Jurassic. Forms, with rapidly enlarging and loosely coiled planispiral with many chambers (*Protopeneroplis*), first appeared in the Middle Jurassic, at the beginning of the Aalenian. In the Bathonian, *Trocholina* gave rise to forms with a thick outer wall and a deeply fissured umbilicus, *Neotrocholina*, and forms with a perforated plate covering the umbilicus. In the Callovian, *Septatrocholina* developed rudimentary septa and survived into the Oxfordian. Most of the involutinids survived the Jurassic-Cretaceous boundary, but this order completely disappeared at the end of the Cenomanian.

4.3.10. The Milioloidea of the Jurassic

The large miliolids are rare in the Jurassic, however, in the Late Bajocian, a lenticular, planispiral, and involute form, *Nautiloculina* with secondary thickening in the umbilical region made its first appearance. This form has been variously placed in previous systematics, but it is placed here because it displays double layered walls like the miliolides (see explanation above). *Nautiloculina* survives the Jurassic - Cretaceous boundary and is commonly found in the backreef/reefal environments of the Cretaceous.

4.4 Palaeoecology of the Jurassic Larger Foraminifera

The Jurassic period saw warm tropical greenhouse conditions world-wide. The sea level gradually rose (O’Dogherty et al., 2000) and the shallow warm waters of Tethys and the Proto-Atlantic flooded large portions of the continents and spread across Europe. The level of oxygen in the atmosphere was recovering gradually through the Jurassic (see Fig. 3.9). The Jurassic sedimentary sequences around the Mediterranean were dominated by warm-water, shallow-marine carbonates that are of crucial importance both as a record of climatic/oceanic conditions but also as hydrocarbon reservoirs. These deposits are dominantly biogenic in origin, consisting primarily of larger benthic foraminifera and algae, with hermatypic corals. Coral reefs were common in the Jurassic, just as they are today.

In the Hettangian, the diversity of Tethyan foraminifera was poor, and was made up of small agglutinated forms such as *Textularia, Siphovalvulina, Duotaxis* (Plate 4.6, fig. 1), and small microgranular and porcelaneous forms such as *Glomospira*. These small foraminifera were widespread on the platform and have been considered as very tolerant (Septfontaine, 1984; Fugagnoli, 2004). They occur in marginal environments (oligohaline, with terrestrial influx) and in deeper marine environments that reflect elevated levels of organic carbon influx (Rettori, 1995), and with high rates of micritic production (Fugagnoli, 2004). The presence of these small foraminifera, with the complete absence of larger forms, points to a stressed environment or an ecosystem that suffered severe environmental fluctuations.
In the early Sinemurian, larger benthic foraminifera were mostly textulariides. The biota as a whole is characteristic of inner carbonate platform environments that were widespread along the rifted western margins of the Early Jurassic Tethys. They are more primitive than species well-known from the later Early Jurassic (Pliensbachian). These Sinemurian assemblages still included distinctive smaller foraminifera, such as *Siphonvalvulina* (with depressed chambers). Microflora are present as the probable cyanobacterium *Cayeuxia piae* (Plate 4.18, fig 1-2), the dasyclad green alga *Palaeodasycladus mediterraneus* (Plate 18, figs 5-7), and the disputed alga *Thaumatoporella parvovesiculosifera* (Plate 4.18, figs 3-4, 9). *Thaumatoporella* were in general widespread in Early Jurassic platform carbonate of Tethys. *Palaeodasycladus* was abundant and is well-preserved, consistent with deposition in shallow marine, inner platform conditions. These small foraminifera and dasycladacean algae are all found within limestones that show a range of shallow carbonate platform lithologies, largely packstones and grainstones that were subjected to periodic emergence, calcrete formation, and erosion along the margin of Tethys (BouDagher-Fadel et al., 2001; BouDagher-Fadel and Bosence, 2007).

The late Sinemurian is characterized by the presence of larger benthic foraminifera, with large, test-wall surface area, as in *Orbitopsella*, with many small chamberlets, which may have been used for hosting endosymbionts (Hottinger, 1982). Such larger foraminifera are highly adapted to mesotrophic and oligotrophic (nutrient-deficient) conditions (Fugagnoli, 2004). The *Orbitopsella* assemblages are present in peloidal wackestone/packstone deposits of the inner platform, together with *Lituosepta*, *Pseudopfenderina*, *Everticyclammina* and *Haurania* in Morocco and Spain (BouDagher-Fadel and Bosence, 2007). Such an assemblage is not very tolerant of environmental change (Fugagnoli, 2004), and is encountered in shallow water carbonate facies all along the southern Tethyan margin (Septfontaine, 1984). These complex and highly diverse faunas point to the establishment of stable ecosystems.

*Orbitopsella* is found throughout the Pliensbachian, together with the appearance of new forms with a so-called subepidermal network, which is described by Hottinger (1996) as a shell architecture adapted to avoid photoinhibition in the lowermost photic zone. Forms with coarsely alveolar tests, such as *Pseudocyctammina*, made their first appearance. These large hypodermal alveoles may well have had a function of harbouring photosymbionts, which would have thrived in the shallow palaeoenvironment populated by these foraminifera (Banner and Whittaker, 1991). These forms such as *Haurania*, *Amijiella* (which appeared in the late Sinemurian), *Socotraina* and *Lituosepta* (which first appeared in the Pliensbachian) indicate established shallow warm waters along Tethys in that period of the Early Jurassic.

The early Toarcian transgression is marked by a brief period of global warming (Jenkyns, 2003) and the occurrence of organic carbon rich shales in large parts of western Europe and other parts of the world. There is a positive carbon isotope excursion of pelagic limestones in several of the Tethyan sections. The widespread occurrence of the early Toarcian shales is explained by an Oceanic Anoxic Event (OAE) (Jenkyns, 1988; Jenkyns and Clayton, 1997). Despite these highly unfavourable living conditions for benthic foraminifera, the number of forms going extinct is low, with new forms appearing at the Pliensbachian-Toarcian boundary possessing the so-called
subepidermal network and alveolar walls. Extinctions may have occurred regionally or locally, however, where relative sea level low stands resulted in enclosed stagnated basins with adverse environments.

The Aalenian saw the gradual recovery for the shallow carbonate environment. However, it was not before the Bajocian to Bathonian that an explosion of these large complicated forms became prominent in the shallow carbonate facies of Tethys, extending from the shallow carbonates of Japan to those of the Middle East, Europe, and Tanzania.

The “cold snap” at the Callovian-Oxfordian (Jenkyns, 2003) might have triggered the extinction of many elongated, internally complicated forms such as the pfenderinoids. Shallow water forms with large intramural alveoles persisted into the Tithonian and were in association with green algae (e.g. *Clupeina jurassica*, Plate 4.18, fig. 11) and stromatoporoids (e.g. *Cladocoropsis mirabilis*, Plate 4.18, fig. 12). Forms with narrow alveoles and a regularly labyrinthic hypodermis (e.g. *Alveosepta*, *Redmondellina*, *Choffatella*) occurred from Portugal through North Africa and southern Europe to the Middle East, ranging from the late Oxfordian to Kimmeridgian and occupied a deeper water palaeoenvironment than the contemporaneous forms with larger alveoles and irregularly labyrinthic hypodermis (e.g. *Everticyclammina*). Their appearance seems to have extended the distribution of these foraminifera further into outer neritic waters, as they appear to have inhabited deeper waters (outer neritic) than *Pseudocyclammina* (with large hypodermal alveoles), or to have tolerated water richer in argillaceous suspensions. According to Banner and Whittaker (1991), they seem to have thrived under reduced illumination, in which conditions codiacean and dasyclad algae were rare or absent. It is possible that the narrow hypodermal alveoles allowed ionic exchange between internal cytoplasm and surrounding seawater, through the extremely thin hypodermis. Hughes (2004) in analyzing the significance of alveoles in *Pseudocyclammina*, and in the light of its occurrence with deep water foraminifera in the Hanifa Formation, Saudi Arabia, argued that the interpreted function of broader alveoles needs further consideration. While agreeing with Banner and Whittaker (1991) that the presence of alveoles may have enabled the organism to construct a test of the required size in a muddy environment, it is also possible low oxygen availability may have been their main rationale. The alveoles gave the organism greater protection from anoxic, hostile sulphide-enriched bottom waters. Low oxygen availability has also been discussed by Preece et al. (2000), who considered that the complex wall structure and presence of alveoles are a means to increase the surface area to volume ratio for gaseous exchange under conditions of low oxygen availability. On the other hand, the increased internal surface area provided by the alveoles may have increased the efficiency of the symbiotic algae, by sheltering them from abnormal water chemistry within the photic zone. *Pseudospirocyclina* and *Anchispirocyclina* are not recorded from the Kimmeridgian (at the *Alveosepta jaccardi* horizon) of the eastern Mid East Gulf; probably both these genera were restricted to shallower, more inner shelf environmental than *Alveosepta jaccardi*.

By the end of the Kimmeridgian crisis the short lived forms with narrow alveoles had disappeared (except for *Choffatella*, Fig. 4.22), and only robust forms characteristic of shallow clear waters survived the Tithonian and crossed over to the Cretaceous.
4.5 Palaeogeographic Distribution of the Jurassic Larger Foraminifera

During the Jurassic, Pangea continued to disintegrate and the extent of the oceans was far more widespread than in the Triassic. The supercontinent fragments began to drift in different directions forming rift valleys, and one of these opened to form the southern part of the North Atlantic Ocean (Fig. 4.23). Polar ice caps were still lacking throughout the Jurassic period (Hallam, 1995), and larger foraminiferal distribution indicates that warm conditions extended to much higher latitudes than today.

The Jurassic, which according to Hallam (1978) marks the end of the ancient stages of Earth evolution, was the period where newly evolved characters in the foraminiferal communities became established, thrived and went on to dominate the Cretaceous shallow marine environment. The development of this new biota in the Jurassic occurred against the background of significant events in the Earth’s history: the termination of the early Cimmerian orogeny, the opening of the North Atlantic, the Triassic-Jurassic reef destruction of the Tethyan carbonate platform, the pre-Cretaceous late Cimmerian uplifts, and climatic changes that resulted in increased differences between the microfaunas in the different palaeogeographic provinces (Basov and Kuznetsova, 2000). Nonetheless, there is no clear evidence of a catastrophic extinction event during the Jurassic. On the contrary, as is evident from larger benthic foraminifera evolution, many forms experienced expansions in distribution, and forms appeared in new niches, such as the appearance of deeper-water larger benthic foraminifera (Choffatella) in
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the Late Jurassic, and most notably the first occurrence (see Fig. 4.24) in the Middle Jurassic of planktonic foraminifera (see BouDagher-Fadel et al., 1997; 2015).

The similarity of the Mediterranean Jurassic assemblages with those recorded from Southern Turkey, Iran, Saudi Arabia, Iraq and the Gulf States, Syria and Israel is remarkable (Noujaim Clark and BouDagher-Fadel, 2001). This commonality may be surprising given the presence in the Tethys of palaeo-highs, and vertical tectonic movements affecting differentially subsided and uplifted platform blocks, but obviously oceanic circulation must have allowed a cosmopolitan distribution of larger benthic foraminifera. Despite their widespread occurrence, the larger Jurassic forms had a significant evolutionary history. The factors driving their evolution involved climatic, paleo-oceanographic, tectonic (or impact) processes, and below is outlined how all of these factors affected their test structure, phylogenetic evolution and distribution.

As discussed in the previous Chapter, the Triassic-Jurassic boundary marks one of the five largest mass extinctions in the past 500 Ma. However, there is still debate as to

Fig. 4.23. Palaeogeographic and tectonic reconstruction of the Early Jurassic, (by R. Blakey http://jan.ucc.nau.edu/~rcb7/paleogeographic.html).
### Fig 4.24

The parallel evolution of the early planktonic foraminifera compared with the lituoloids in the Jurassic.

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- Redmondella
- Alveospira
- Archispiraculina
- Kiheina
- Bsoina
- Alcoella
- Meyendorfina
- Spiroconulus
- Conoglobinella
- Conoglobigera
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the cause of this extinction. This might have happened, as explained in Chapter 3, as a response to an impact at the Triassic-Jurassic boundary (e.g. Boslough et al., 1996), which in turn might have triggered the eruption of a large igneous flood basalt province (e.g. Jones et al., 2002). The Tr-J boundary, is contemporaneous with the eruption of one of the world’s largest known continental igneous province, the Central Atlantic Magmatic Province (Marzoli et al., 2004). This event would have caused a climatic and biotic crisis at the Tr-J boundary, triggered by the emission volcanic gases and would have been responsible for the abrupt turnover of faunas that occurred at the Rhaetian-Hettangian boundary (Fowell and Olsen, 1993; Fowell and Traverse, 1995; McElwain et al., 1999; Olsen et al., 2002a, 2002b; Percival et al., 2017). These gases could have also caused the short-lived global warming, of possibly 2–4 °C, that has been implicated as a cause of the Tr-J mass extinction (McElwain et al., 1999; Beerling and Berner, 2002), and that has been inferred from a marked negative carbon isotope ($\delta^{13}$C) anomaly observed in marine and terrestrial Tr-J boundary strata from Hungary, Canada, and England (Ward et al., 2001; Hesselbo et al., 2002). This crisis at the Tr-J boundary would have inhibited photosynthesis in the shallow seas of Tethys. According to Vermeij (2004) starvation and habitat loss triggered by these conditions would lead to widespread collateral extinction of species. Vermeij argues that conditions traditionally identified by palaeontologists as initiating mass extinction, such as oxygen deprivation, oversupply of nutrients and poisoning (by carbon dioxide, methane and sulphides) are manifestations of the ecological avalanche triggered by a crisis among primary producers, and are therefore considered consequences rather than primary causes of extinction.

In the aftermath of the Tr-J event, the small involutinides (see Fig. 4.8) with a planispiral to trochospiral enrolled tubular second chamber survived and continued into the Jurassic as “disaster forms”. Common in pre-extinction shallow marine assemblages, Involutina and Trocholina are rare and small in the immediate post-extinction aftermath. Urbanek (1993) introduced the term “Lilliput effect”, which describes a temporary, within lineage size decrease of the surviving organisms through an extinction event. This effect, which is the morphological manifestation of a post-crisis ecological stress, explains the pattern of size change which is seen through the Hettangian and early Sinemurian.

Following the Kauffman and Erwin (1995) post-extinction event recovery model, Twitchett (2006) divided the post-extinction “repopulation interval” into an initial “survival interval” and a later “recovery interval”. In the Hettangian, blooms of small opportunistic genera such as Duotaxis dominate sparse assemblages of new, small textulariine forms, such as Siphovalvulina, that represent the “survival stage”. By the middle Sinemurian, there was a recovery, with an increase in new genera, as new forms evolved to fill the niches which had been vacated by the end Triassic extinction event. This recovery continued through the Sinemurian to the Pliensbachian with no major extinction at the boundary, but with more evolved taxa becoming established through the Pliensbachian. The filling of the larger benthic foraminiferal niches continued through the Pliensbachian, where new forms of lituoloids appeared that went on to play an important role in the evolutionary development of this group throughout the Jurassic and Cretaceous.
The development of the carbonate facies of the western Mediterranean, from the late Pliensbachian onwards, was affected by events which led to the drowning of the Trento Platform (Zempolich, 1993). This stopped the further development of the benthic foraminifera in the Jurassic carbonates of the western Mediterranean. However, despite well documented mass extinctions of other faunas, the Pliensbachian and Toarcian show only modestly enhanced (but seemingly not catastrophic) levels of extinction amongst the larger foraminifera. Towards the end of the Pliensbachian, 33% of the larger foraminifera became extinct (see Fig. 4.25). This extinction was followed by rapid diversification in the late Toarcian. Hallam (1986) proposed that to speak of an end Pliensbachian extinction was misleading, and that it was in fact a low-level event, particularly among benthic marine invertebrates, and not focused at the Pliensbachian-Toarcian boundary, but spreading over into the early Toarcian. This was, he suggested, caused by ocean bottom-water anoxia in Western Europe, evidenced by the development of widespread units of laminated organic-rich shale (see Vermeij, 2004). In addition, Hallam (1986) argued that there is no evidence for contemporary organic-rich shale sequences (reflecting low bottom-water oxygenation) or extinctions, in South America. Thus, he concluded that the early Toarcian extinction was a regional European event only and that global explanations were irrelevant, although even in Western Europe organic-rich shale facies is not universal. However, there were

![Jurassic Genera](image)

**Fig. 4.25.** The total number of genera, new appearances and extinctions of larger foraminifera throughout the Jurassic. The extinctions correspond to the end of each stage and the appearances of new genera with the beginning of the following stage.
major global extinction events in the early Toarcian, for example in benthic ostracods (Boomer et al. 2008).

Little and Benton (1995) in studying the distribution of the macrofauna in Europe at the Pliensbachian-Toarcian boundary argued that there is no evidence for a single family-level mass-extinction event at the end of the Pliensbachian stage (Sepkoski, 1989, 1990). Rather, there is a five-zone phase of extinction from the late Pliensbachian to early Toarcian. The event has a global distribution because, although the majority of the family extinctions occurred within Boreal north-western Europe, there were also extinctions in the Tethyan and Austral realms.

Of the many events that happened during the Pliensbachian, one of the drivers for possible ecological stress, which may have caused the observed, but diffuse, enhanced extinction rates, is the Karoo-Ferrar flood basalt event (Palfy and Smith, 2000). The Karoo province in South Africa and the Ferrar province in Antarctica (Fig. 4.26) are disjunct parts of a once contiguous Gondwanan large igneous province. It ranks among the most voluminous flood basalt provinces of the Phanerozoic (Rampino and Stothers, 1988) and extends for 4000 km². The vast majority of the lava volume appears to have been extruded at 183 Ma in about 1 Ma. The anoxic event identified by Hallam (1961) and Wignall (2001) in NW European marine sections and in South America,

Fig. 4.26. The Pliensbachian world showing the position of the Karoo-Ferrar flood basalts.
Evolution and Geological Significance of Larger Benthic Foraminifera

may have been triggered by the eruption of volcanic CO$_2$ and ensuing global warming (Jenkyns, 1999; Wignall et al., 2005). Unlike the Tr-J boundary, where the CAMP volcanism seems to have triggered a major catastrophic extinction, the Pliensbachian event is more diffuse. The reduced impact of the Karoo-Ferrar large igneous province (LIP) eruption may be related to the fact that it occurred at high paleolatitudes, and so may not have globally affected the paleoclimate so rapidly.

As conditions ameliorated during the Aalenian, the biota became more diverse and gradually began to resemble pre-extinction biotas (Harries and Little, 1999). Many forms which survived the Pliensbachian-Toarcian event flourished in established niches during the Toarcian and only very few new forms appeared. The Aalenian, through to the Bathonian, shows a major expansion of larger benthic genera. This may be associated with the global recovery in O$_2$ levels (Fig. 3.10), or the opening up of new habitats as the incipient North Atlantic began to widen as a result of the rifting induced by the CAMP volcanism at the end of the Triassic (see Figure 4.27).

Fig. 4.27. Palaeogeographic and tectonic reconstruction of the Middle Jurassic (by R. Blakey [http://jan.ucc.nau.edu/~rcb7/paleogeographic.html](http://jan.ucc.nau.edu/~rcb7/paleogeographic.html)).
Following the Aalenian-Bajocian regional anoxic event, which is recorded in the Carpathian part of the Western Tethys, the most intense foraminiferal turnover took place at the Bajocian-Bathonian boundary, and coincides with a maximum diversity of Ammonites (O’Dogherty et al., 2000, see here Plate 4.18, fig. 8). In the Bajocian-Bathonian, the diversity of the larger benthic foraminifera is also at its maximum in the carbonate platforms and reefs of Tethyan margins. There was a major influx of new genera (~30%, see Fig. 4.25) at the beginning of the Bajocian and continued towards the Bathonian (~42% of new genera). These foraminifera were mainly agglutinated and were characterized by the noticeable development of multiple alveoles in their walls (Basov and Kuznetsova, 2000). The Bajocian saw also the most important event in the history of foraminiferal evolution, namely the appearance of planktonic foraminifera (BouDagher-Fadel et al., 1997; BouDagher-Fadel, 2015). These foraminifera, for unknown reasons, began a meroplanktonic mode of life (benthic in the early stage, becoming planktonic in the last stage). These foraminifera were represented by Conoglobigerina (Fig. 4.24) which had a restricted geographic occurrence; they all occurred in present-day South-Central and Eastern Europe. They did not become cosmopolitan and holoplanktonic (fully planktonic) until the late Bathonian, with the occurrence of Globuligerina (see BouDagher-Fadel et al., 1997; BouDagher-Fadel, 2015).

The end Bathonian and Callovian were also associated with enhanced extinction rates (see Fig. 4.25 and Chart 4.2). This might just reflect the vigorous increase in the number of genera to be found, which reached a maximum in the Bathonian, and which would have produced a more competitive evolutionary environment, and hence a higher background rate of extinctions. However, this Middle Jurassic epoch also coincides with at least two major impact events that gave rise to the 80km diameter Puchezh-Katunki crater in Russia and the 20 km diameter Obolon crater in the Ukraine. These events might also have contributed to enhanced environmental stress that could have been responsible for part of the enhanced extinction rate in these stages.

The transition from the Middle to the Late Jurassic was characterized by significant changes in oceanography and climate. These changes were accompanied by modifications in the global carbon cycle as shown in the carbon isotope record (Louis-Schmid et al., 2007). They were triggered by the opening and/or widening of the Tethys-Atlantic-Pacific seaway and a massive spread of shallow-marine carbonate production leading to higher $P_{CO_2}$, and according to Louis-Schmid et al. (2007) this increase in $P_{CO_2}$ may have triggered changes in the biological carbon pump and in organic carbon burial in the mid Oxfordian.

The Oxfordian and Kimmeridgian show another burst of larger foraminifera speciation (Fig. 4.25) that maintained the overall number of genera at a high level, but increased extinction rates at the end of the Kimmeridgian and Tithonian saw numbers of genera decline as the Jurassic came to an end. This general decline may be related to the final opening of the proto-North Atlantic, and a consequent change in global circulation patterns. The larger foraminifera in the Oxfordian developed special features, such as narrow alveoles and a regularly labyrinthic hypodermis (e.g. Alveosepta), which helped them to occupy deeper waters than the contemporaneous forms with larger alveoles and irregularly labyrinthic hypodermis (e.g. Everticyclammina). They became
cosmopolitan and can be found from Portugal through North Africa and southern Europe to the Middle East, and range from the late Oxfordian to Kimmeridgian. In parallel to their evolution, planktonic foraminifera occupying the upper waters of the oceans became more established, wholly planktonic and cosmopolitan.

The end Kimmeridgian saw only a minor extinction, and these were of forms which colonized deeper waters, while no new larger foraminifera appeared to occupy these empty niches in the Tithonian. Around 30% of the larger benthic foraminifera became extinct towards the end of the Tithonian. The end Jurassic (~145Ma) coincides with two major events: (a) a series of large terrestrial impact events (see Glikson, 2005) including Moroweng (70 km), Mjolnr (40 km) and Gosses Bluff (24 km), and (b) a major sub-marine flood basalt event that created the Shatsky Rise, which is the oldest of the great Pacific plateaus with an estimated flood basalt volume of 4.3x10^6 km^3. Mahoney et al. (2005) suggest that this feature is consistent with an impact origin. These events might have been the reasons for the disappearance of long ranging, well established Jurassic larger foraminifera, such as *Pseudospirocyclina*. However, a number of Jurassic agglutinated foraminifera continued through to the Cretaceous where they flourished and thrived, before their final extinctions within the early Cretaceous.
Plate 4.1  Scale bars: Figs 1, 9 = 0.5mm; Figs 2-3, 6-8 = 0.25mm; Figs 4-5 = 1mm. Fig. 1. *Involutina liassic* (Jones), axial section, Early Jurassic, Italy, UCL coll. Fig. 2. *Neotrocholina* sp., Callovian/Oxfordian, Saudi Arabia, UCL coll. Fig. 3. *Neotrocholina valdensis* Reichel, Callovian, Saudi Arabia, UCL coll. Fig. 4. *Andersenolina elongata* (Leupold), late Bathonian, Saudi Arabia, UCL coll. Fig. 5. *Andersenolina alpina* (Leupold), Kimmeridgian/Barriasian, Lebanon, UCL coll. Fig. 6. *Trocholina conica* (Schlumberger), Callovian/Oxfordian, Saudi Arabia, UCL coll. Fig. 7. *Trocholina cf. granosa* (Frentzen), Bajocian/Bathonian, Saudi Arabia, UCL coll. Fig. 8. *Trocholina palastiniensis* Henson, holotype, Jurassic, Kurnub, South Israel, NHM P38477. Fig. 9. *Haplophragmoides* sp., *Trocholina palastiniensis* Henson, holotype, *Kurnubia jurassica* (Henson), Jurassic, Kurnub, South Israel, NHM P38477.
Plate 4.2  Scale bars: Figs 1-4 = 0.25; Figs 5-10 = 0.5mm. Septatrocholina banneri, BouDagher-Fadel, first described by BouDagher-Fadel (2008) and validated in BouDagher-Fadel (2016); 1-3) NHM coll., BP 7702, from 8172 ft in Juh-1 core, Qatar; Callovian-Oxfordian, upper Araej Formation; fig. 4, NHM coll., BP 7701, from 9880 ft in Um-Shaif-4 core; Upper Bathonian, basal Uweinat Formation; Abu Dhabi. 1) Paratype, tangential section showing rudimentary Septa; 2) Holotype, equatorial section showing the globular proloculus followed by a trochospirally enroled divided tubular second chamber with rudimentary septa; 3) Paratype, tangential axial section showing the rudimentary septa; 4) Paratype, axial section in which septa are not visible. Figs 5-10. Alzonorbitopsella arabia, BouDagher-Fadel, first described by BouDagher-Fadel (2008) and validated in BouDagher-Fadel (2016), 5) holotype NHM BP 6626, equatorial section of the annular holotype with large megalospheric proloculus; 6, 9, 10) NHM BP 6627, from 9879 ¼ ft, 6) Paratype, equatorial section showing the annular test with no septulae, 9) Paratype, oblique axial section showing the delicate reticulate hypodermis of beams and rafters, 10) Paratype, enlargement of the axial section to show that the reticulate hypodermis of beams and rafters does not continue onto the septa; 7, 8) NHM BP 6623, from 9880 ft; Umm-Shaif-4 core; Upper Bathonian, basal Uweinat Formation, Abu Dhabi, 7) Paratype, equatorial section showing the large megalospheric proloculus, 8) Paratype, oblique equatorial section showing the annular chambers immediately following the large megalospheric proloculus.

Plate 4.3  Scale bars: Figs 1-6 = 0.6mm. Figs 1-6. Septatrocholina banneri BouDagher-Fadel, 1-3, 5-6) Callovian-Oxfordian, Upper Araej Formation, from 8172 ft in Juh-1 core, Qatar, NHM BP 7702; 4) late Bathonian, basal Uweinat Formation, from 9880 ft in Um-Shaif-4 core Abu Dhabi, BP 7701.
Plate 4.4 Scale bars: Fig. 1 = 0.25mm; Figs 3-4 = 1mm; Figs 5-7, 10-12 = 0.5mm; Figs 8-9 = 0.3mm. Fig. 1. Trocholina palastiniensis Henson, paratype, Late Callovian, Kurnub Anticline, Israel, NHM P38477. Fig. 2. Levantinella egyptiensis Fourcade, Arafa and Sigal, type figured by Fourcade et al. (1997), Oxfordian, Jibal As Sahiyleh, Syria. Fig. 3. Kilianina lata Oberhauser, paratype figured by Oberhauser (1956), Kimmeridgian, Karadag, West Taurus, Turkey. Fig. 4. Sanderella laynei Redmond, holotype figured by Redmond (1964), Bathonian/Callovian (probably Early Callovian), basal Upper Dhruma, ARAMCO T-60-60A, 40-50ft. Fig. 5. Haurania deserta Henson, paratype, figured by Henson (1948), Bathonian, Muhaiwir Formation, West Iraq, NHM P35859. Fig. 6. Socotraina serpentina Banner et al., identified wrongly as Milahaina tortuosa Smout unpublished species and genus by Smout MS, probably Bajocian, Wadi Milaha, Oman. Fig. 7. Amijiella sp., identified wrongly as Iranica stingeri Gollestaneh MS (1965), probably Bajocian, Wadi Milaha, Oman. Gollestaneh wrongly described it as possessing an initial high trochosphere, but is undoubtedly an Amijiella. The species name (nomen nudum) was published by Gollestaneh (1974), but the species has never been validly named. Figs 8-9. Amijiella amiji (Henson), paratypes, Bathonian, Muhaivir Formation, Wadi Amij well, West Iraq, NHM M/3869-3870. Fig. 10. Ataxella occitana (Peybernés), figured by Pelissié et al. (1984) as “Paracoskinolina occitana”, late Bathonian, Pyrénées, France. Fig. 11. Everticyclammina prekelleri Banner and Highton, paratype, Kimmeridgian to Tithonian, Broumana, Lebanon, NHM P52255. Fig. 12. Robustoconus tisljari Schlagintweit, Velič and Solac axial, oblique sections showing microspheric specimens (courtesy of Dr Schlagintweit), figured by Schlagintweit (2013), early Bajocian, Croatia.

Plate 4.5 Scale bars: Figs 1-6, 8-16 = 0.5mm; Fig. 7 = 0.3mm. Figs 1-2. Choffatella tingitana Hottinger, type specimens figured by Hottinger (1967), Kimmeridgian-Tithonian, Morocco, 1) holotype, equatorial B-form; 2) paratype, off-centered axial B-form. Fig. 3. Freixialina planispiralis Ramalho, holotype, figured by Ramalho (1969), Kimmeridgian-Tithonian, NW of Freixial, Portugal. Fig. 4. Dhrumella evoluta Redmond, paratype figured by Loeblich and Tappan (1986), Bathonian, Saudi Arabia. Figs 5-6. Mesoendothyra izumiana Dain, type specimens figured by Dain (1958), Kimmeridgian, Russia, 5) equatorial section; 6) axial section. Fig. 7. Protopenorolpis striata Weynschenk, holotype, figured by Weynschenk (1950), Middle/Late Jurassic, Austria. Fig. 8. Buccicrenata primitiva BouDagher-Fadel, holotype, equatorial section of microspheric form, NHM 66907. Figs 9-10. Pseudospirocyclina smouti (Banner), late Callovian-early Oxfordian, 9) holotype figured by Banner (1970), Zakum 1, Upper Araej, Umm Shaif, Persian Gulf showing irregular, sporadic extensions of the hypodermis; 10) oblique vertical section, Lebanon, UCL coll. Figs 11-12. Pseudospirocyclina mauretanica Hottinger, types specimens figured by Hottinger (1967), Kimmeridgian, Morocco, 11) axial section; 12) equatorial section. Fig. 14. Pseudospirocyclina muluchensis (Hottinger), types figured by Hottinger (1967), Kimmeridgian, Morocco. Figs 13, 15. Pseudospirocyclina maynei Hottinger, type specimens figured by Hottinger (1967), Kimmeridgian, Morocco, 13) paratype; 15) holotype. Fig. 16. Pseudocyyclammina sphaeroidalis Hottinger, type specimen figured by Hottinger (1967), Kimmeridgian, East Morocco (distinguished from P. lituus by simpler alveolar hypodermis and sub-spheroidal test).
Plate 4.6  Scale bars: Figs 1-8, 16 = 0.15mm; Figs 9-15, 17-21 = 0.5mm. Fig. 1. Duotaxis metula Kristan, vertical section showing a conical multi-serial test, BouDagher-Fadel et al., 2001, Sinemurian, NHM P.66938, Sample L7, Gibraltar, UCL coll. Fig. 2. A). Thaumatoporella?parovesiculifera (Raineri), B) Siphovalvulina sp., Sinemurian, showing the columellar-siphon, Sample CQ 87,UCL coll. Figs 3-6. Siphovalvulina colomi BouDagher-Fadel et al. 2001, Sinemurian, Apennines, Mt Bove, 3) megalospheric form showing the initial coiled part of the test, Sample MB 63; 4) microspheric form showing the nearly parallel sides in later growth; 5) holotype, vertical section, NHM P66910, Sample G27; 6) paratype, transverse section. Sample L6, NHM P66911b. Figs 7-8. Siphovalvulina gibraltarensis BouDagher-Fadel et al., 2001 Sinemurian; 7) figured holotype, NHMP66912, Sample G8; 8), figured paratype, NHM P66930, Sample D20. Fig. 9. A) Siphovalvulina beydouni BouDagher-Fadel, holotype, B) Kilianina blancheti Pfender, figured by Noujaim Clark and BouDagher-Fadel (2004), Kesrouane Limestone Formation, Lebanon, UCL coll. Fig. 10. Pseudopfenderina butterlini (Brun), Sinemurian- Pliensbachian, Morocco, UCL coll. Fig. 11. A specimen supposed by Sepfontaine (1967) to be intermediate between Siphovalvulina and Pseudopfenderina, Bathonian, Cevennes, France. Figs 12-14. Pseudopfenderina butterlini (Brun), type species figured by Hottinger (1967), Sinemurian-Plensbachian, Morocco. Fig. 15. A reconstruction by Hottinger (1967) of Pseudopfenderina. The columella reconstructed by Hottinger seems to be too elaborate for typical P. butterlini, and the incipient tunnels of Pseudopfenderina are not drawn in the reconstruction. Fig. 16. Pseudopfenderina butterlini (Brun), oblique vertical section figured by Noujaim Clark and BouDagher-Fadel (2004), Bathonian, Kesrouane Limestone Formation, Lebanon, UCL coll. Figs 17-21. Palaepfenderina salernitana (Sartonia and Crescenti), Bathonian, Uwainat, Qatar, NHM P44639.

Plate 4.7  Scale bars: Figs 1, 2 = 0.15mm; Figs 3-5, 20, 21 = 0.5mm; Figs 6-11, 14 = 0.3mm; Figs 18-19 = 1mm. Figs 1-2. Palaepfenderina salernitana (Sartonia and Crescenti), Bathonian, Uwainat, Qatar, NHM P43712, 1) vertical section; 2) transverse section. Figs 3-5. Palaepfenderina trochoidea (Smout and Sugden), 3) type figure, Bathonian, Uwainat Limestone, Qatar, showing sub- cameral tunnel and the pilared coalescent septal structure of the pfenderid columella; 4) paratype, NHM P43715; 5) paratype, NHM P42967. Figs 6-7. Pfenderina neocomiensis (Pfender), syntypes of Eorupertia neocomiensis Pfender (1938), Valanginian, near Toulon, France, 6) vertical section; 7) transverse section. Figs 8-11. Conicopfenderina mesojurassica (Mayne), 8) type figure, late Bathonian, Switzerland, figured by Septfontaine (1981); 9) late Bathonian of Upper Kesrouane Limestone Formation, Lebanon,UCL coll; 10 -11) Bathonian, Switzerland, 10) figured by Septfontaine (1981); 11) figured by Septfontaine (1978). Fig. 12. Chablaisia chablaensis (Septfontaine), types figured by Septfontaine (1977), Bathonian?-Callovian, French Pre-Alps. Fig. 14. Pseudoeggerella elongata Septfontaine, type figured by Septfontaine (1988), Bathonian, Pre-Alps, Switzerland. Figs 15-16. Satorina apuliensis Fourcade and Chorowicz, type figures, Bathonian-Callovian, Yugoslavia, 15) holotype. Fig. 17. Sanderella sp. Section showing bifurcating sub-cameral tunnel in the flaring, rectilinear growth stage, figured by Altiner and Septfontaine (1979), Callovian, Tauras, Turkey. Figs 18-20. Steinekella steinekei Redmond, Oxfordian, Tuwaiq Mountain Formation, figured by Redmond (1964), 18-19) holotype; 20) superficially eroded paratype showing exoskeletal partitions and peripheral chamberlets. Figs 21-24. Pfenderella arabica Redmond, 21) type species from Middle Jurassic (Bathonian or Callovian), Saudia Arabia; 22-24) sketches showing; 22) high trochosiral, test with somewhat inflated chambers; 23) the aperture covered by a finely perforate hemispherical apertural plate; 24) secondary intercameral foramina connected by subcameral tunnel that spirals around the axis of coiling.
**Plate 4.8** Scale bars: Figs 1-2, 8-12, 14-25 = 0.5mm; Figs 3-7, 13, 26 = 0.3mm. Fig. 1. *Conicokurnubia orbiloliniformis* Septfontaine, figured by Septfontaine (1988), Oxfordian-Kimmeridgian, Pre-Alps, Switzerland. Fig. 2. *Conicokurnubia* sp., figured by Septfontaine (1981), Kimmeridgian, Turkey. Figs 3-8. *Kurnubia jurassica* (Henson), late Oxfordian, Shuqraia Beds, Kurnub, Israel. 3) NHM P39087; 4) NHM P39129; 5) NHM P39086; 6) paratype, Jurassic, Israel, NHM M38/40; 7-8) Kimmeridgian, Saudi Arabia, UCL coll. Figs 9-14. *Kurnubia palastiniensis* Henson. 9) paratype, NHM M3836; 10) holotype, revised by Maync (1966), late Oxfordian, Kurnub, Israel, NHM P39089; 11-12) oblique vertical section of “B-form”, figured by Noujaim Clark and BouDagher-Fadel (2004), Oxfordian-early Kimmeridgian, Bannes Complex, Lebanon; 13) transverse section of a paratype; 14) figured by Noujaim Clark and BouDagher-Fadel (2004), Oxfordian, Kersouane Limestone Formation, Lebanon. Figs 15-21. *Kurnubia wellingsi* Henson. 15-17) figured paratypes, late Oxfordian, Shuqraia Beds, Kurnub, Israel; 15) solid specimen, NHM P39083; 16) transverse section, NHM P43718; 17) vertical section, NHM P43718; 18-19) figured by Noujaim Clark and BouDagher-Fadel (2004), Oxfordian, Kersouane Limestone Formation, Lebanon; 18) oblique vertical sections; 19) transverse section; 20-21) figured by Hottinger (1967), Oxfordian, Morocco; 20) transverse section; 21) vertical section. Figs 22, 24. *Praekurnubia crusei* Redmond, figured by Noujaim Clark and BouDagher-Fadel (2004), Oxfordian, Kersouane Limestone Formation, Lebanon. Fig. 23. A) *Praekurnubia crusei* Redmond, B) *Meyendorffina bathonica* Aurouze and Bizon, figured by Noujaim Clark and BouDagher-Fadel (2004), Oxfordian, Kersouane Limestone Formation, Lebanon. Figs 25. *Textulariopsis sinemurenensis* BouDagher-Fadel and Bosence, vertical section, holotype, Sample G8, Gibraltar, NHM P66936. Fig. 26. *Pseudomarssonella maxima* Redmond, late Bathonian-early Callovian, paratype, solid specimen, American Museum of Natural History (AMNH) FT-1270.

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**Plate 4.9** Scale bars: Figs 1-6, 11-14 = 0.5mm; Figs 7-10 = 0.15mm. Figs 1-3. *Planisepcta compressa* (Hottinger), 1-2) types figured by Hottinger (1967), Sinemurian, Morocco, microspheric specimens, 1) holotype, 2) paratype; 3) megalospheric specimen from Betics, Gavillan Formation, Southern Spain, UCL coll. Figs 4-5. *Labyrinthina mirabilis* Weynschenk, figured by Fourcade and Neumann (1966), Kimmeridgian, Spain, 4) vertical section; 5) oblique transverse section. Fig. 6. A) *Nautiloculina circularis* (Said and Barakat), B) *Syriana khouri* Fourcade et al., figured by Noujaim Clark and BouDagher-Fadel (2004), Callovian, Lebanon. Figs 7-8. *Nautiloculina oolithica* (Mohler), Bajocian-Bathonian, Persian Gulf, NHM coll; 7) oblique axial section, Um Shaif-4, core, 9961ft, Lower ARAEJ; 8) equatorial section showing double septa, Umm Shaif-4, core, 9969ft, Lower ARAEJ. Figs 9-10. *Nautiloculina circularis* (Said and Barakat), Callovian, Persian Gulf, NHM coll, Um Shaif-4, core, 9705ft; 9586ft. Figs 11,13. *Nautiloculina cretacea* Arnaud-Vannieu and Peybernés, types figures from Arnaud-Vannieu and Peybernés (1978), Berriasian-Aptian, France. Fig. 12. *Obitammina elliptica* (d’Archaig), figured by Hottinger (1967), late Bajocian, Chaumont, France. Fig. 14. A) *Redmondellina powersi* (Redmond), B, D) *Nautiloculina oolithica* (Mohler), C) *Kurnubia wellingsi* (Henson), early Kimmeridgian, Lebanon, UCL coll.
Plate 4.10  Scale bars: Figs 1-2 = 0.25mm; Figs 3, 5, 7-10, 12-13; Figs 4, 11, 14-19 = 0.5mm. Fig. 6 = 0.15mm.

1. *Kastamonina abonica* Sirrel, type specimens figured by Sirrel (1993), Kimmeridgian-Tithonian, Turkey. Fig. 2. *Palaeomaynina termieri* (Hottinger), figured by Septfontaine (1988), Sinemurian-Pliensbachian, Swiss Pre-Alps. Figs 3, 5, 6. *Pseudocyclammina lituus* (Yokoyama), 3) equatorial section with the beginnings of a rectilinear terminal chamber series; this is rare in *P. lituus* but common in *P. vasconica* (see Chapter 5), Haueterivian, Saudi Arabia; 5) axial section of a toptype figured by Maync (1959), Kimmeridgian, Japan; 6) Early Cretaceous, Iran, NHM P52300. Fig. 4. *Pseudocyclammina kelleri* Henson, syntype, Awasil no.5, Ramadi, Iraq, Middle Jurassic, NHM P35968. Figs 7-8. *Pseudocyclammina bukoviensis* Cushman and Glazewski, Kimmeridgian, Saudi Arabia, 7) axial section; 8) equatorial section; 8) axial section;) late Valanginian, uppermost Zangura Formation, NHM P52301; 9) axial section; 10) equatorial section. The thick-walled, coarsely agglutinated, inner hypodermal alveolae distinguish this form from *P. lituus*. Fig. 9 *Pseudocyclammina vasconica* Maync, Kuwait, Mutriha-2, cuttings, 12,540ft, MINAGISH-D, Valanginian, rectilinear growth stages and initial coil in tangential section. Fig. 10. *Meyendorffina n.* sp. aff. *Bathonica* (see key in Fig. 4.20), showing peripheral rectangular chamberlets, Callovian/Oxfordian, Upper Araej, Um Shaif-3, NHM coll. Note the smaller test size and less complex alveolar wall than in *P. lituus*. Note the range of *P. vasconica* in the Tethyan carbonate shelf seems to be demonstrated to be throughout the Valanginian to Aptian, although it occurs in floods as a local Valanginian index in Saudi Arabia and SE Mid East Gulf.

Fig. 11. *Spiraloculina perconigi* Allemann and Shroeder, holotype figured by Allemann and Shroeder (1972), Bathonian, Spain. Fig. 12. *Kilianina blanchetti* Pfenner, Oxfordian, Upper Kesrouane Limestone, Lebanon, UCL coll. Figs 13, 15-16. *Neokilianina rahonensis* Foury and Vincent, 13, 15) types figured, Kimmeridgian, Chaussin, 13) holotype, axial section; 15) transverse section; 16) vertical section, basai Kimmeridgian, Lebanon, UCL coll. Fig. 14. *Kilianina preblanchetti* BouDagher-Fadel and Noujaim Clark, types figured by Noujaim Clark and BouDagher-Fadel (2004), Early Callovian;14A) holotype, axial section; 14B) oblique equatorial section. Figs 17-18. *Parurgonina coelinsensis* Cuvillier, Foury and Romano, 17) type specimen figured by Cuvillier et al. (1968), Kimmeridgian, Italy; 18) an oblique central section showing the septa breaking in the umbilical region to form pillars, Oxfordian, Lebanon, UCL coll. Fig. 19. *Levantinella egyptiensis* (Fourcade et al.), oblique equatorial section, Oxfordian, Lebanon, UCL coll.

Plate 4.11  Scale bars: Figs 1-4, 6, 8-9, 11-13, 20 = 0.3mm; Figs 7, 10, 17-19 = 0.5mm; Figs 5, 15-16 = 0.15mm; Fig. 14 = 0.25mm. Fig. 1. *Paravalvulina* sp., Bathonian, Uwainat Formation, United Arab Emirates, NHM P52625. Fig. 2. *Pseudomarssonella maxima* Redmond, paratype sectioned and figured by Banner et al. (1991), late Bathonian-early Callovian, Saudi Arabia, American Museum of Natural History (AMNH) FT-1270. Fig. 3. *Pseudomarssonella plicata* Redmond, Bajocian-Bathonian, Persian Gulf, Umm Shaif-3, cuttings, 10,084ft (caved from Lower ARAEJ). Fig. 4. *Pseudomarssonella bipartia* Redmond grading into *P. inflata* Redmond, Callovian, Idd-el-Shargi, core, 8740ft, Upper Uwainat Formation, United Arab Emirates, NHM coll. Fig. 5. *Redmondoides rotundatus* (Redmond), paratype figured and sectioned by Banner et al. (1991), mid/late Bathonian, Saudi Arabia, AMNH FT-1293A. Fig. 6. *Redmondoides medius* (Redmond), note chamber walls straight, perpendicular to the septa, Callovian-Oxfordian, Persian Gulf, Umm Shaif-4, cores, basal Upper Araej, NHM coll. Fig. 7. *Redmondoides lugeoni* (Septfontaine), metatypic topotype, axial sectioning showing broad, plate-like apertural lips, Bathonian-Callovian, near Cheblais, France, NHM P52616. Figs 8-9. *Riyadhoides mcehleri* (Redmond), late Bajocian, 8) paratype, AMNH FT-1272, 9) sectioned and figured by Banner et al. (1991), Saudi Arabia, Dhruma, NHM coll. Figs 10-11. *Riyadhella praeregularis* BouDagher-Fadel et al., 2001, figured types, Sinemurian-Early Pliensbachian, Gibraltar, 10) holotype, axial section showing thin, convoluted septa and canaliculated test wall, NHM P66947, Sample D20; 11) paratype, NHM P66916. Fig. 12. *Riyadhella regularis* Redmond, mid/late Bathonian, paratype of the synonymous *R. nana* Redmond, figured by Banner et al. (1991), Aramco well, Saudi Arabia. Fig. 13. *Riyadhella* sp., Callovian, Upper Uweinat, Persian Gulf, NHM coll. Fig. 14. *Cymbriaella lorigae* Fugagnoli, figured by Fugagnoli (1999), Sinemurian-Pliensbachian, Italy. Fig. 15. A sketch showing *Vulvulina* sp. and the tooth-like aperture from Banner’s collection, UCL. Figs 16-17. *Gutnicella cayeuxi* (Lucas), 16) type specimen figured by Lucas (1939), Aalenian, Algeria; 17) figured by Gutnic and Moullade (1967), Aalenian, West Taurus, Turkey. Figs 18-20. *Haurania desert* Henson, Bathonian, 18) paratype from Muhaiwir Formation, NHM P35859; 19) paratype, Jurassic, Wadi Amij well, West Iraq M/3846, NHM P35863; 20) paratype, transverse thin section, NHM P3856.
Plate 4.12  Scale bars: Figs 1-3, 5, 7, 9, 14, 17-20 = 0.25mm; Fig. 4 = 1mm; Figs 6, 8, 11 = 0.15mm; Figs 10, 12-13 = 0.3mm; Fig. 15 = 1mm; Fig. 16 = 2mm. Figs 1-4. *Haurania deserta* Henson, 1948, 1-2) figured by BouDagher-Fadel and Bosence (2007), Middle Jurassic, 1) Betics, Gavillan Formation, Southern Spain, Sample RA-01-203; 2) High Atlas, Jebel Rat Formation, Morocco; 3) longitudinal section, Toarcian, Yemen, NHM P53894; 4) vertical section figured by Hottinger (1967), Morocco. Fig. 5-6 *Meyendorffina bathonica* Arouze and Bizon, 5) figured by Furrer and Septfontaine (1977), late Bathonian, Swiss Pre-Alps; 6) figured by Noujaim Clark and BouDagher-Fadel (2004), late Bathonian, Lebanon. Fig. 7. *Gutnicella oxi- tanica* (Peybernes), late Bathonian-late Callovian, Upper Kessrouane Limestone, Lebanon, UCL coll. Fig. 8. *Gutnicella bizonorum* (Bourrouilh and Moullade), figured paratype, Bathonian, Minorca. Fig. 9. *Gutnicella minoricensis* (Bourrouilh and Moullade), type figured, Bathonian, Algeria. Figs 10-11. *Socotraina serpentina* Banner et al., Early Jurassic, Socotra, Yemen, 10) holotype, microspheric specimen, vertical section, NHM P53883; 11) paratype, transverse section, NHM P53892. Fig. 12. *Platyhaurania subcompressa* Bassoullet and Boutakiout, type specimen figured by Bassoullet and Boutakiout (1996), late Sinemurian, Morocco. Figs 13-16. *Timidonella sarda* Bassoullet, Chabrier and Fourcade, type figures, Bajocian-Bathonian, Sardinia, 13-14) A-forms; 15-16) B-forms. Fig. 17. *Trochamijiella gollesstanehi* Athersuch et al., type specimens figured, Bathonian, Oman. Fig. 18. *Rectocyclammina chouberti* Hottinger, type specimen figured by Hottinger (1967), early Kimmeridgian, Morocco. Fig. 19. *Meyendorffina* sp., Bathonian, France, UCL coll. Fig. 20. *Alveosepta jaccardi* (Schrodt), equatorial section of a B-form, early Kimmeridgian, Qatar, Dukhan-51, 74441/2ft, NHM coll.

Plate 4.13  Scale bars: Figs 1-8 = 0.5mm Figs 1-3. *Alveosepta jaccardi* (Schrodt), late Oxfordian, 1) topotype figured by Hottinger (1967), Switzerland; 2-3) figured by Noujaim Clark and BouDagher-Fadel (2002) from Bhannes Complex, Lebanon, 2) axial section; 3) oblique equatorial section. Figs 4-5. *Redmondellina powersi* (Redmond), Early Kimmeridgian, figured by Noujaim Clark and BouDagher-Fadel (2002) from Bhannes Complex, Lebanon, 4) oblique equatorial section showing the “clear line” in septa, and median lamella cut lengthwise in last chamber; 5) transverse section of a microspheric form showing pillar-like hypodermal extensions, UCL coll. Figs 6-8. *Alzonella cuvillier* Bernier and Neumann, type figures, 6) showing partitions “beams” which subdivide the chamberlets, Bathonian, Alzon, France; 7) Bathonian, Mas-del-Pont Well, France; 8) Callovian, Uweinat, Umm Shaif-3, Persian Gulf, NHM coll.
Plate 4.14  Scale bars: Figs 1-6 = 1mm. Figs 1-6. Alzonorbitopsella arabia BouDagher-Fadel, 5) BP 6626; 6,9,10) BP 6627, from 9879 ¼ ft; 7, 8) BP 6623, from 9880 ft; Um-Shaif-4 core; Upper Bathonian, basal Uweinat Formation, Abu Dhabi, NHM coll.
Plate 4.15  Scale bars: Figs 1, 7-13 = 0.5mm; Figs 2, 5 = 0.3mm; Figs 3-4 =0.15mm; Fig. 6 = 1mm. Fig. 1. *Palaeocyclammina complanata* Bassoullet, Boutakiout and Echarfaoui, holotype F62025, figured by Bassoullet et al. (1999), Pliensbachian, Morocco. Figs 2-4. *Amijiella amiji* (Henson), type specimens, Bathonian, Muhaiir Formation, Wadi Amij well, West Iraq, 2) solid specimen, holotype, NHM P35869; 3-4) paratypes, 3) transverse section, 4) axial section, NHM P35866. Fig. 5. *Torinosuella penneropliformis* (Yabe and Hanzawa), Thamama Formation, Oman, Umm Shaif-3, cuttings, 7255ft, NHM coll. Figs 6-7. *Anchispirocyclina lusitanica* (Egger), 6) figured by Ramalho (1971), equatorial section of B-form, Kimmeridgian, Portugal; 7) figured by Hottinger (1967), Kimmeridgian, Morocco. Figs 8-9. *Anchispirocyclina praelusitanica* (Maync), near topotypes, B-forms figured by Hottinger (1967), Oxfordian, Israel (note: Hottinger referred *praelusitanica* to *Alveosepta (=Redmondellina powersi)*, but *praelusitanica* lacks the septal “clear line” of *Redmondellina* and has pillars spread throughout the whole chamber lumen, not merely in the median plane). Figs 10-11. *Bostia irregularis* Bassoullet, type figured by Bassoullet et al. (1999), late Bathonian, France, 10) holotype, axial section; 11) paratype, axial section. Figs 12-13. *Ijdranella altasica* Bassoullet et al., type specimens figured by Bassoullet et al. (1999), Pliensbachian, Morocco, 12) holotype, equatorial section; 13) oblique vertical section.

Plate 4.16  Scale bars: Figs 1-6, 8, 10 = 0.5mm; Figs 7, 9, 11 = 0.3mm. Figs 1-2. *Bosniella oenensis* Gušić, Sinemurian-Pliensbachian, Jebel Rat Formation, southern High Atlas, Morocco, UCL coll. Fig. 3. *Everticyclammina praevirguliana* Fugagnoli, Sinemurian-Pliensbachian, Gibraltar, UCL coll.. Fig. 4. *Everticyclammina kelleri* (Henson), paralectotype, equatorial section, Berriasian-Valanginian, Zangura Formation, Iraq, NHM P35968. Fig. 5. *Everticyclammina greigi* (Henson), paratype, basal Cretaceous, Qatar, NHM P35795. Fig. 6. *Everticyclammina virguliana* (Koechlin), Kimmeridgian, Persian Gulf, Zakum-1, core, 9536ft, NHM coll. Fig. 7. *Streptocyclammina parvula* (Hottinger), figured by Hottinger (1967), Kimmeridgian, Morocco. Figs 8-9. *Lituosepta recoarense* (Cati), 8) microspheric form figured by Hottinger (1967), Middle Jurassic, Morocco; 9) megalospheric form, Betics, Gavillan Formation, Spain. Fig. 10. *Orbitopsella primaeva* (Henson, 1948), microspheric forms, Betics, Gavillan Formation, Spain, UCL coll.. Fig. 11. *Karaisella uzbekistanica* Kurbatov, figured from Kurbatov (1971), Oxfordian, Uzbekistan.
Plate 4.17  Scale bars: Fig. 1 = 1mm; Figs 2-3 = 0.3mm; Figs 4-9 = 0.5mm. Fig. 1. Orbitopsella dubari Hottinger, megalospheric form, figured by Hottinger (1967), Middle Jurassic, Morocco. Fig. 2-3. Orbitopsella praecursor (Gümbel), syntypes, Sinemurian, Jabal Milaha, Oman, NHM P35780. Figs 4-6. Orbitopsella primaeva (Henson), syntypes, Middle Jurassic, Jabal Milhaha Oman, Davies collection, 4) NHM 35791; 5) NHM P35789; 6) NHM 35788. Fig. 7. Lituolipora polymorpha Gusić and Velić, figured by Gusić and Velić (1978), Early Jurassic, Yugoslavia. Fig. 8-9. Cycloorbitopsella tibetica Cherchi, Schroeder and Zhang, Pliensbachian, 8) holotype, figured by Cherchi, Schroeder and Zhang (1984), Pupuga Formation, South Tibet; 9) Betics, Gavillan Formation, Spain, UCL coll
Plate 4.18 Scale bars: Figs 1-12 = 0.5mm. Figs 1-2. *Cayeuxia? piae* Frollo, Sinemurian-Pliensbachian, 1) Lebanon, UCL coll.; 2) figured by BouDagher-Fadel and Bosence (2007), High Atlas, Jebel Rat Formation, Morocco. Figs 3-4, 9. *Thaumatoporella? parvovesiculifera* (Raineri), Sinemurian, 3) Betics, Gavilan Formation, Spain, figured by BouDagher-Fadel and Bosence (2007); 4) Gibraltar Limestone Formation, NHM P66949; 9) sample MB 49, UCL coll. Figs 5-7. *Palaeodasycladus? mediterraneus* (Pia), figured by BouDagher-Fadel et al. (2001), Sinemurian, Gibraltar Limestone Formation 5) NHM P66945; 6-7) NHM P66931-32. Fig. 8. *Ammonites* spp, Pliensbachian, Italy, UCL coll. Fig. 10. *Orbitopsella* spp., Early Jurassic, Pakistan, UCL coll. Fig. 11. *Clypeina jurassica* Favre, early Kimmeridgian, Kesrouane Limestone, UCL coll. Fig. 12. *Cladocoropsis mirabilis* Felix, Kimmeridgian, Greece, UCL coll.