Chapter 4
Trend Reversals in Radiolaria During Extinction Periods

4.1 End Permian Event and the Entactinids

Since the Cambrian period when they first appeared, radiolarians have experienced several quasi extinctions but survive well until the present time. One of the most severe extinctions in their life history occurred at the end of the Permian and a careful review of the way they survived the Permian Triassic crisis was recently published (De Wever et al. 2006). It is demonstrated that following the Permian extinction some forms, such as the entactinarian *Parentactinia*, reduced the complexity of their skeleton by partial loss of the outer spherical shell that surrounds the spicule. Incidentally, many earliest Triassic spicular forms belonging to the entactinids are the result of a loss of the outer skeleton (De Wever et al. 2006). The evolutionary process leading to simple and primitive looking end-forms under the influence of high environmental stress in radiolarians is very similar to what is observed in the Silicoflagellids and Foraminifera. Such simplifications often correspond to the reappearance of ancestral geometries in the *Ticinella* lineage discussed above. Three examples illustrating such phenomena are given below.

4.2 Retrograde Evolution of the *Albaillella* Lineage During the Permian-Triassic Crisis

The first detailed evolutionary study of the genus *Albaillella* in the Upper Permian of Japan demonstrated that the *Albaillella* lineage starts with a small form having a conical shell with six narrow transverse bands and a ventral wing called *A*. sp. *G* (Kuwahara 1999 and Fig. 4.1). The apical part of the shell of this ancestral form is almost straight with a ventral wing protruding from near the last transverse band. It is followed by *Albaillella yamakitai* Kuwahara, which has a conical shell with five transverse bands, a dorsal bulge and one ventral wing. Next in the sequence is

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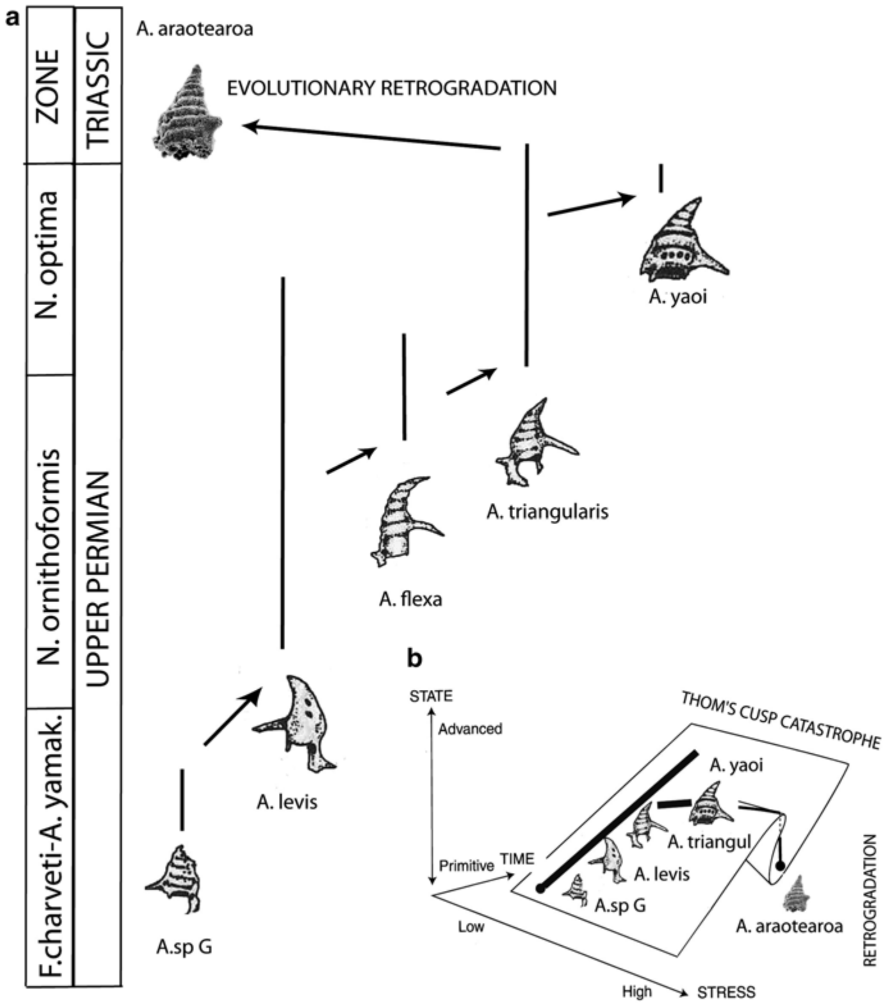

Fig. 4.1 (**a**) Anagenetic evolution of *Albaillella* during the *Upper* Permian showing increasing convexity of the conical shell and reversal of the trend above the Permian-Triassic boundary. (**b**) Diagrammatic representation of the evolutionary catastrophe observed in the Albaillellids at the Permian Triassic transition (from Guex et al. 2014)

Albaillella sp. *A*. with a conical shell and one ventral wing with dimple-like holes. The shell is small, conical, flattened with a ventral wing and a strongly pentagonal form. The upper part of the shell starts to be slightly curved on the ventral side. *A*. sp. A is followed by *Albaillella protolevis* Kuwahara and *A. levis* Sashida and Tonishi, characterized by a conical, smooth and inflated shell with one ventral wing.

Albaillella lauta Kuwahara shows a ventrally curved upper part and shell height is greater than in *A. levis*. The next one, *A. flexa* Kuwahara, has a ventro-apical shell that is remarkably curved. It is followed by *A. angusta*, which is slightly less curved and by *A. excelsa*, which is smooth and elongated. The last three representatives of the lineage, *A. triangularis*, *A.* sp. D and *A. yaoi* show extreme curvature of the apical part of the cone.

To summarize, the phyletic sequence is gradual with most intermediate forms represented and with the derived forms replacing progressively the ancestral forms. In other words there is no place for a persistent opportunistic form surviving during the development of the lineage. Of note, Kuwahara's uppermost Permian section is cut by a fault. Nevertheless, we have a perfect record of the geometrical transformations of *Albaillella* during that critical evolutionary interval. Following the greatest extinction in the history of the Earth, the oldest Lower Triassic record of *Albaillella*, is provided by Takemura and Aono (2007) with the discovery of *Albaillella aotearoa* Takemura at Arrow Rocks (Oruatemanu), New Zealand. This Triassic species has a small, somewhat flattened conical shell with a ventral wing. The upper part of the shell is almost straight in outline and is clearly a homeomorph of *Albaillella* sp. *G* and *A. yamakitai* described by Kuwahara at the beginning of the Upper Permian lineage, providing a nice example of morphological retrogradation (=proteromorphosis).

4.3 The Evolution of the Saturnalids During the KT Crisis

The fundamental studies on the evolution of the oertlispongids and their direct derivatives, the saturnalids, provide an outstanding illustration of the long-term complexification of some radiolarian skeletons (Dumitrica, 1982, 1985). In the Early Paleocene, which immediately followed the End Cretaceous Extinction, this group was marked by the appearance of a very simplified radiolarian group, the Axopruninae, a saturnalid that lost its equatorial ring and retained only two polar spines. The Triassic oertlispongids are represented by a simple spongy spherical shell with two spines. The upper spine of these radiolarians was transformed into an arch with increasingly complex geometry, suggesting at the same time an affinity of this group with the saturnalids (Dumitrica, 1982). Subsequently it was established that Lower Jurassic saturnalid evolution is characterized by the transformation of the spongy inner shell into a sequence of two concentric latticed medullary shells, surrounded by an external shell. Further extrapolation of these initial discoveries showed that saturnalids derived from the oertlispongids by a similar complexification of the lower spine, followed by a fusion of the two arcs, leading to the genesis of typical saturnalids with an equatorial ring (Kozur and Mostler, 1983, 1990). Similarly several Cenozoic forms with simple subspheric cortical shells with two axial spines (*Axoprunum*, *Xyphosphaera*) derived from the usual saturnalids by loss of the equatorial ring, a characteristic of this large family (Dumitrica, 1985). This major geometrical simplification occurred suddenly within the Lower Paleocene and it clearly results from the major crisis leading to the Cretaceous-Tertiary extinction. The loss of the equatorial ring is comparable with the loss of the basal ring of the silicoflagellids at times of artificial or natural ecological stress (Fig. 4.2).

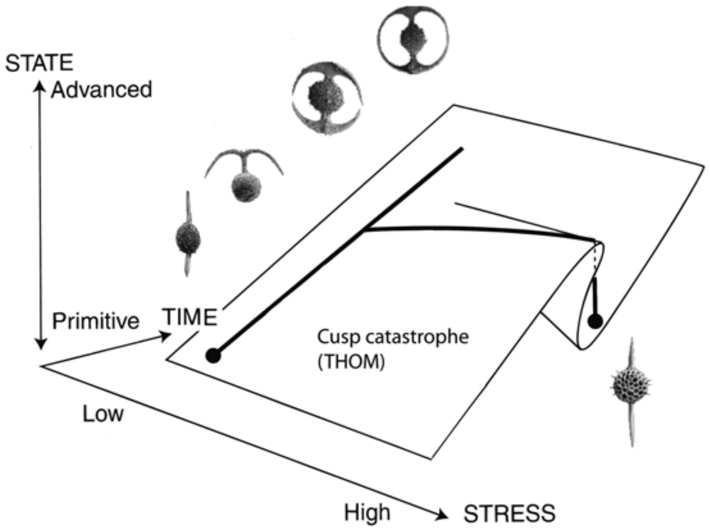

Fig. 4.2 Idealized view of the evolution of the saturnalids and loss of the equatorial ring at the Cretaceous-Cenozoic boundary. Not to scale (constructed after a diagram of Guex 1993)

4.4 Untwisting of Spines Around the Triassic–Jurassic Boundary Crisis

Drastic retrogradation in spine geometry occurs during the Triassic–Jurassic Boundary crisis. *Tipperella* is a late Norian to Hettangian genus characterized by having a simple subspherical test with four spines in the tetrahedral position. The cortical shell wall is thick and variable in appearance, composed of either small polygonal pore frames or spongy meshwork. The interior cavity is filled with spongy meshwork that is frequently dissolved. Spines are triradiate and strongly twisted through most of the Rhaetian stage (see Fig. 4.3), but towards the end of it they begin to untwist. This contrasts remarkably with basal Hettangian forms whose spines are straight and circular in cross section, similar to many Permian radiolarians.

A similar case of untwisting can also be seen in *Betraccium* during the TJ crisis (see Guex et al. 2012). This middle Norian pantanelliid has a subspherical cortical shell with coarse polygonal meshwork and three radially arranged primary bladed spines in the same plane. *Betraccium smithi* Pessagno and other Norian species such as *B. deweveri* Pessagno and Blome, *B. maclearni* Pessagno and Blome and *B. yakounense* Pessagno and Blome have twisted spines. All species with strongly twisted spines disappear around the Norian–Rhaetian boundary, and all subsequent species have straight three-bladed spines (Carter, 1993).

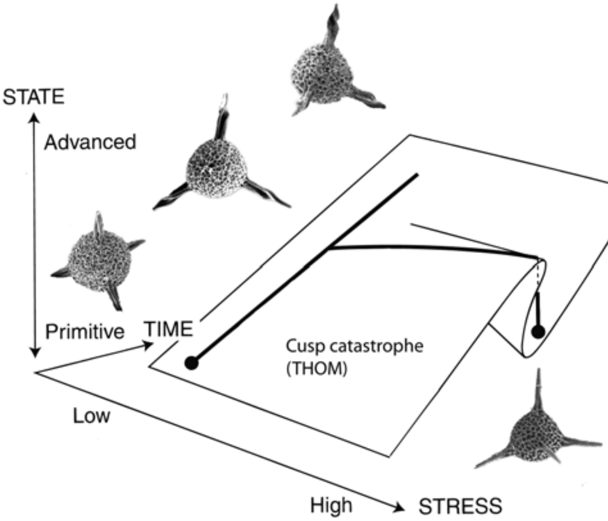

Fig. 4.3 Loss of the twisting of the spines in *Tipperella* at the Triassic–Jurassic boundary. Diagram, not to scale (from Guex et al. 2012a)

4.5 The Evolution of *Eucyrtidiellum* During the Pliensbachian Toarcian Stages

In this section we will study the evolution of the genus Eucyrtidiellum during the Lower Jurassic and its reaction during the Pliensbachian Toarcian major crisis. To give a clear picture of the rate of faunal turnover among radiolarian during that period, we expressed it as the number of species with FAD (first appearance datum) against the number of species with LAD (last appearance datum) in a given biochronological unit, called Unitary Association (see Guex et al. 2015a, b). A special tool of the UAgraph program (Hammer et al. 2015) called "Cumulated FADs/LADs" was used to construct Fig. 4.4 and we used the cumulative number of FADs plotted against the cumulative number of LADs. Each Unitary Association is represented by a point on the curve. Gentle slopes of the curve indicate high diversification rates (great number of FADs vs. low number of LADs) and steep slopes indicate high extinction rates (low number of FADs vs. great number of LADs). Take notice of the problem that the beginning and the end of such a curve are biased by the fact that the base and the top of the original range chart record truncated ranges: all taxa in the lowest biochronological unit may range downward and all taxa in the highest unit may range upward. These parts of the curve must obviously be ignored. The advantage of this method is that it analyses the relationship between FADs and LADs and not only their absolute numbers. This means that the analysis is not biased by exceptional preservation, which is a common phenomenon in the radiolarian fossil record.

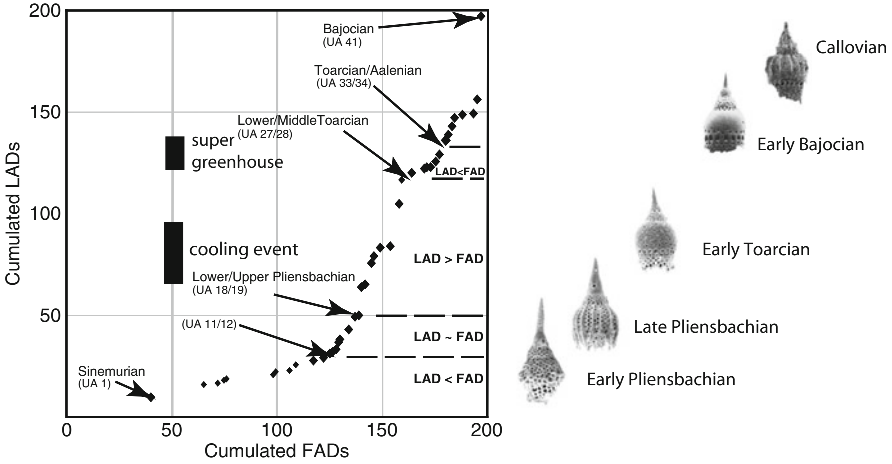

Fig. 4.4 Cumulated FADs vs. cumulated LADs of the radiolarian during the Sinemurian-Bajocian interval and the evolution of Eucyrtidiellum during the Pliensbachian-Callovian interval. Quantitative stratigraphic data from Carter et al. (2010), Gorican et al. (2006) and Gorican et al. (2013)

Eucyrtidiellum is a very common Jurassic nassellarian looking like a tiara. In the Pliensbachian *E. nagaiae* with an abdomen typically ornamented with strong vertical costae, evolves from *E. gunense* (Gorican et al. 2006). During the topmost Pliensbachian–Early Toarcian major crisis, these forms give rise to smooth derivatives without the abdominal costae (*E. disparile*), that evolve to smooth poreless forms (*E. unumaense*) in the early Middle Jurassic. Abdominal costae gradually reappear in the Bathonian (*E. dentatum—E. pustulatum—E. semifactum, E. ptyctum* and later *E. pyramis*). The pores on the abdomen progressively close in this lineage.

The drastic simplification of the ornamentation and retrograde evolution of Eucyrtidiellum during the Pliensbachian-Toarcian crisis is clearly related to the major environmental perturbation which occurred during that period (Gorican et al. 2006). That crisis is also well known to be correlated with the onset of the Karoo-Ferrar large igneous province discussed in Sect. 2.2.