Chapter 1
Evolutionary Trends During Periods of Relative Ecological Equilibrium

1.1 Introduction

The global crises which punctuate Earth History and are responsible for the classical extinctions that took place—for example, during the Permian Triassic or at the Cretaceous Tertiary boundary—are framing periods of relative ecological equilibrium during which gradual, slow evolutionary trends lasting millions of years develop.

These trends often start with "simple" organisms and end with much more "advanced" ones. These rather obvious trends have been widely studied during recent decades at the expense of researching the evolutionary reactions of the living organisms during the crisis.

The goal of the present book is to analyse the reversals of the most common evolutionary trends observed in the fossil record of some selected invertebrates (ammonoids, radiolarian, foraminifera and conodonts) during periods of ecological disequilibrium and extinctions. It is therefore necessary to describe first the basic trends observed during periods of ecological dynamic equilibrium.

Then we will describe the reversals affecting the organisms which survived major extinctions generated by ecosystem collapses due to both extrinsic (physical and/or chemical) and intrinsic (biotic) stresses.

Palaeontologists generally use the term "evolutionary trend" to describe the oriented morphological transformations occurring in stratigraphic sequences of one particular species or in phyletic series of closely related species. In some cases, trends seem to be gradual and are used as a biochronological clock for stratigraphic correlations (Peybernes et al. 1997; Hottinger 1981; Less and Kovacs 1996). However, in most cases, they appear as discrete sequences of closely related species belonging to a single lineage showing an oriented morphological variation.

The phyletic increase in body size is the most frequently quoted evolutionary trend. It is known as Cope's Rule, named after the American vertebrate palaeontologist who first observed it in the nineteenth century (Cope 1896). The most famous case, illustrated in many palaeontological textbooks, is the controversial evolution of the horse.

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1.2 Evolutionary Trends in Ammonites

1.2.1 Initial Trends

Today it is banal to observe that the most frequent long-lasting evolutionary trend observed in Mesozoic ammonites is that where the ancestral group has an opened umbilicus (evolutes form) and the derived group has a closed umbilicus (involute form). This tendency was recognized more than hundred years ago (Hyatt 1889) and the same trend characterizes the Devonian bactritids from the very beginning of their history (Erben 1966) (Fig. 1.1). When completely accomplished, the increasing spiralization of initially evolute shells gives rise to lenticular (oxycones) or spherical (sphaerocones) forms (Fig. 1.2). In the following discussion

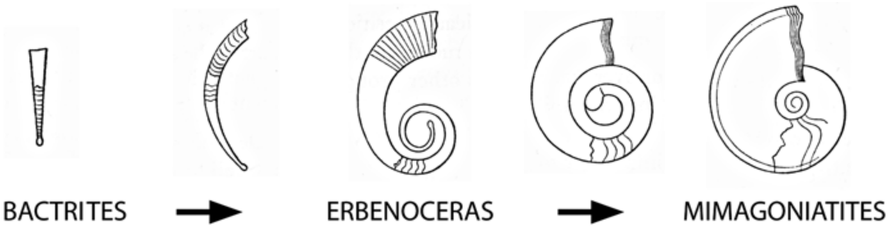

Fig. 1.1 First coiling observed in the Devonian ancestors of ammonoids (Redrawn and modified from Erben 1966. From Guex (2001))

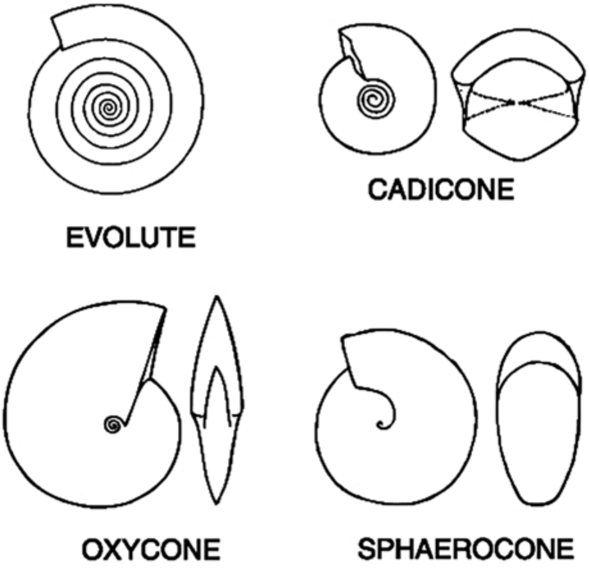

Fig. 1.2 Some typical involute shells generated by an evolute ancestor

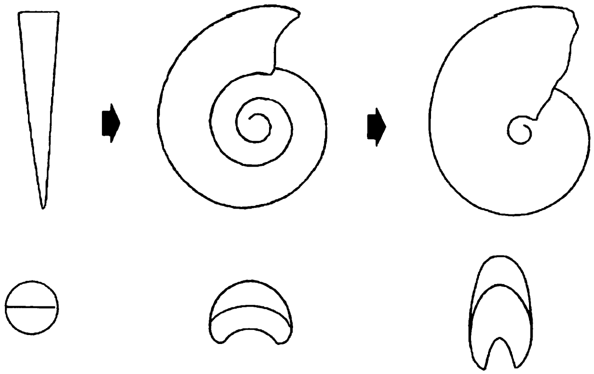

Fig. 1.3 Increasing curvature leading to involute geometry

we consider that the spiralization increase corresponds to an elevated apparent geometrical complexity of the shells because it is the consequence of a double increase of the curvature of these shells: first the spiralization of the originally straight tube and second the increase in involution (tight coiling) (Fig. 1.3). Similar trends are also seen in nautiloids (Sobolev 1994) and certain gastropods (Runnegar 1987).

Generally speaking such increases of the shell curvature are related to the surface increase "rule" observed in so many fossil lineages and described as the "generalized Cope's rule" by Guex (2001, 2003).

1.2.2 *Size and Involution Increase in the Acrochordiceratidae*

Monnet et al. (2012a, b) analysed the evolutionary trends of the family Acrochordiceratidae Arthaber from the Early to Middle Triassic (251–228 Ma). The study was based on very large samples of this ammonoid family which were obtained from strata in north-west Nevada and north-east British Columbia. They enable quantitative and statistical analyses of its morphological evolutionary trends and demonstrate that the monophyletic clade Acrochordiceratidae underwent the classical evolute to involute evolutionary trend associated with an increase in its adult shell size (diameter) and an increase in the complexity of its suture line. This trend in ammonoid geometry is a beautiful illustration of Cope's rule with an accommodation of the increase of the shell diameter and involution (Fig. 1.4).

The recurrent character of this kind of trend was first discussed in the early 1940s to explain the multitude of heterochronous homeomorphies observed within this group (Schindewolf 1940; Haas 1942). Some ammonite lineages also show a broad trend towards increased sinuosity of the growth lines and, on a large timescale, this group shows an overall increase in suture line complexity.

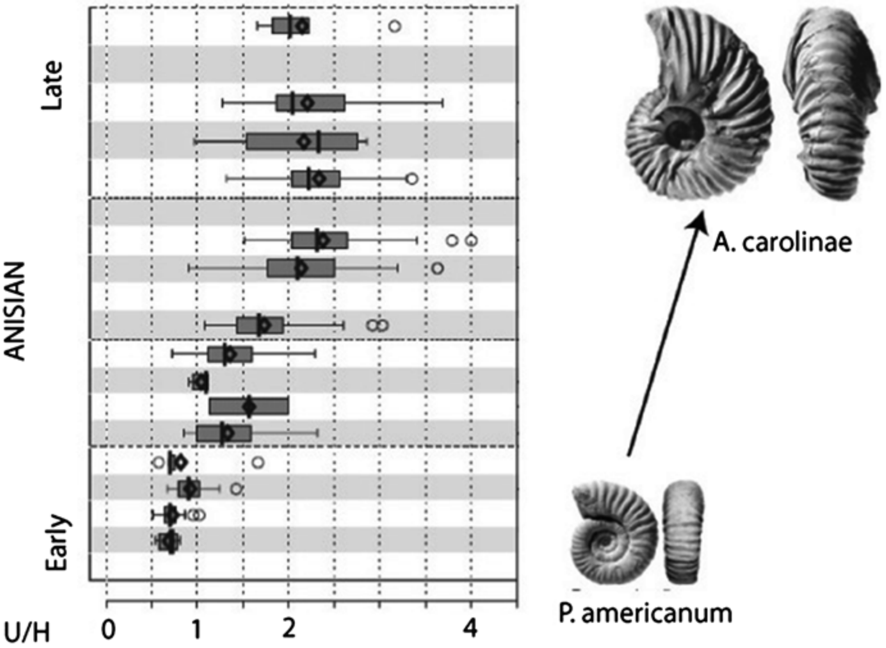

Fig. 1.4 Increasing size and involution (U/H = umbilicus vs. height) in the Acrochordiceratinae during the Middle Triassic (From Monnet et al. 2012a, b)

A sharp description of the iterative evolution of the ammonoids has been produced by Haas (1942, p 643): «…not only types and groups of types reiterate themselves in the history of ammonites, but also certain evolutionary cycles, each proceeding along definite anagenetic trends, e.g., from evolute, sturdy forms with coarse costation to more involute and discoidal ones with a finer and more sigmoidal ribbing»

1.2.3 Paedomorphic Genesis of a Sphaerocone Ammonite

During the middle and late Early Sinemurian, some microderoceratids start to develop a tendency to form globose geometry in the juvenile, prefigurating the proterogenetic (paedomorphic) transformation of the evolute spinose Microderoceras (Early Sinemurian Eoderoceratid) into a sphaerocone Liparoceras (Early Pliensbachian) via an intermediate group called Tetraspidoceras (Late Sinemurian) (Fig. 1.5).

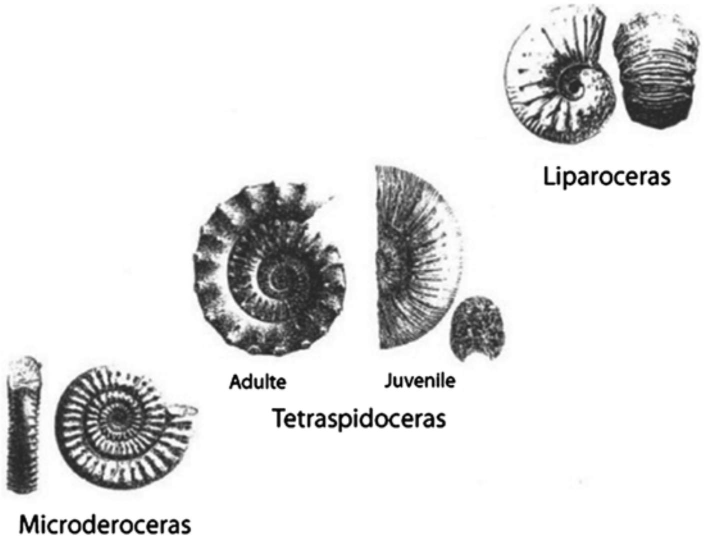

Fig. 1.5 Paedomorphic genesis of a sphaerocone *Liparoceras* within *Tetraspidoceras* starting from an evolute spinose ancestor *Microderoceras* (not to scale)

1.2.4 Rates of Changes in the Involution of Some Ammonites

Following the major End Triassic Extinction we can follow the evolution of several genera deriving from the smooth and very simple *Psiloceras* of the Lower Hettangian: *Kammerkaroceras* via *Discamphiceras* (Discamphiceratinae, Psiloceratacеae), *Angulaticeras* via *Saxoceras* and *Kammerkarites (Schlotheimiidae, Psiloceratacеae), Pseudaetomoceras* via *Caloceras* and *Alsatites (Arietitidae, Arietitaceae), Badouxia* via *Caloceras* and *Sunrisites*. Thanks to new geochronological data produced by Guex et al. (2012a), the rate of change in the involution can be quantified and expressed by the variation of the ratio U/D (=umbilicus vs. diameter) in some typical phylogenetical lineages mentioned above (Fig. 1.6).

1.3 Increasing Involution in Foraminifera

The increase in involution equally affects many unicellular organisms such as planktonic and benthic foraminifera (e.g. the appearance of *Orbulina*) at various stages of their development (Septfontaine 1988; Adams 1983; Blow 1956; Cifelli 1969). Certain benthic foraminifera exhibit an increase in lateral elongation (Hottinger and Drobne 1988) that geometrically corresponds to the development of

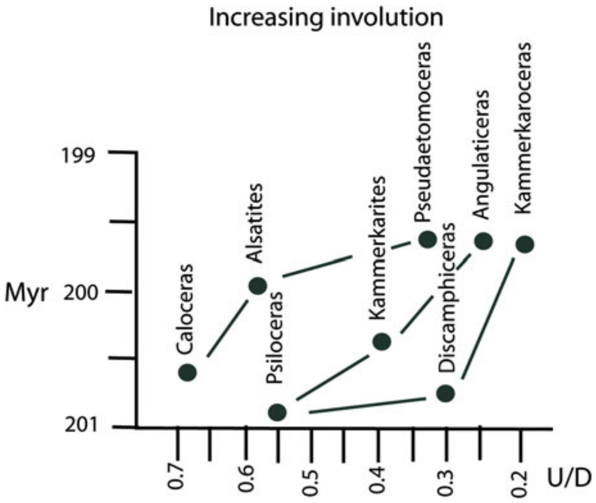

Fig. 1.6 Increasing involution in Lower Jurassic main subfamilies (Guex et al. 2012a)

cadicone coiling in ammonites (Fig. 1.2). In other groups of microfossils discussed below in more detail, such as nassellarian Radiolaria, a similar phenomenon is observed, namely increased sphericity and reduction in the number of segments (Sanfilippo and Riedel 1970). This results in the development of cryptocephalic and cryptothoracic forms (Dumitrica 1970). Similarly, within silicoflagellates (Chrysophytes) discussed in Chap. 8, we find that globular shells such as *Cannopilus* have evolved from simple spicular forms (Guex 1993). Figure 1.7a–d represents various modes of increasing shell curvature through the evolution of foraminifera. Note that (1) these modes of transformation are sometimes associated with an increase in size and (2) the increased involution can occur at any stage of the development but it is more frequently peramorphic than paedomorphic.

1.4 Morpho-Functional Interpretations

Palaeontologists who described the above-mentioned trends have frequently proposed ad hoc adaptive and morpho-functional explanations. Observed increase in involution among ammonites is generally explained in terms of optimal use of the shell material, shell strength and/or improved streamlining (Raup 1967). However, the geometrical antinomy between involute lenticular shells and spherical shells means that the trend towards increasing involution is not uniquely the result of an optimization mechanism for shelly material usage. This is in fact because involute lenticular forms, which are abundant in the fossil record, are far from an optimal geometry from this point of view. Other authors suggest that increased shell

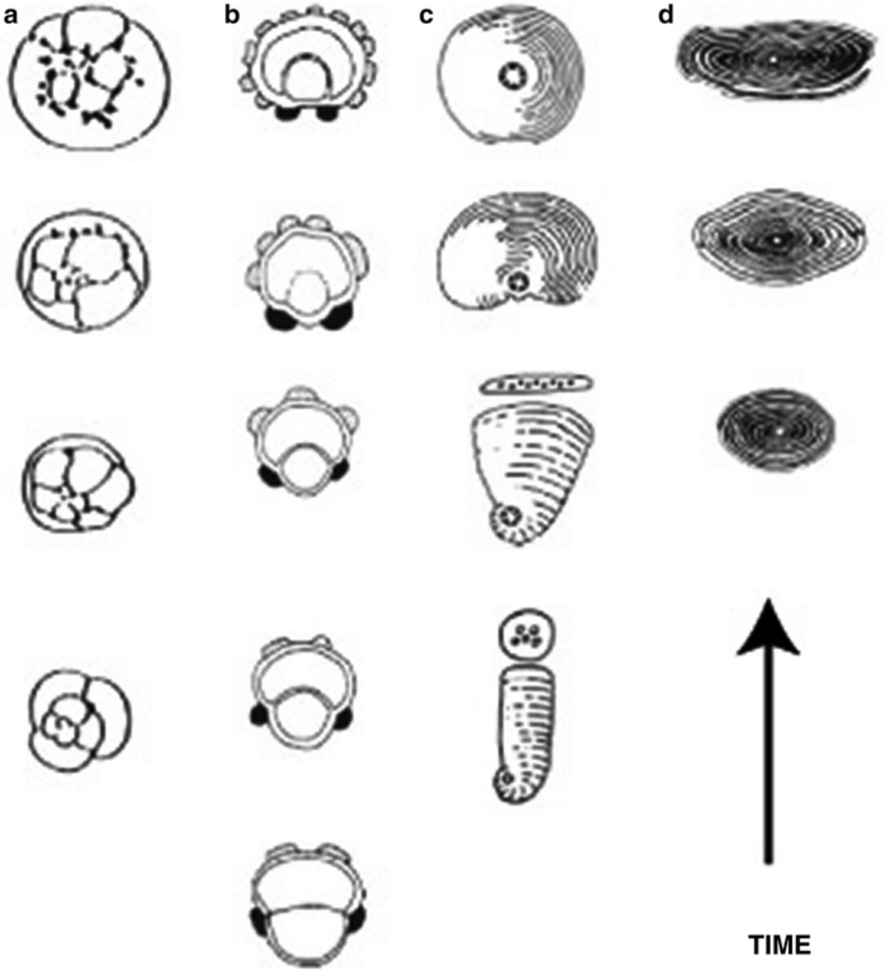

Fig. 1.7 Foraminifera: (**a**) Increasing involution in the *Orbulina* lineage (planktonic foraminifera (Blow 1956; Cifelli 1969)). (**b**) Cryptoproloculinization in *Lepidocyclina* (benthic foraminifera (Adams 1983)). (**c**) Increasing involution in lituolids (benthic foraminifera (Septfontaine 1988)). (**d**) Benthic foraminifera elongation in alveolinids (benthic foraminifera (Hottinger and Drobne 1988)). From Guex (2003)

involution and greater complexity of sutures increase the shell's resistance to hydrostatic pressure (Hassan et al. 2002). Increased surface area of benthic foraminifera is usually interpreted as aiding oxygen exchange. Similarly, elongation of the test is sometimes explained as an optimization of the animal's motility within unconsolidated sediment. As for size increase, the most frequent explanation is morphofunctional (better resistance to predators) or invokes the famous mantra "*nowhere but up*!" (Stanley 1973; McKinney 1990).

1.5 Decoupling of Volume, Surface and Linear Dimension

The above ad hoc explanations are hardly satisfactory because the trends discussed in this introduction are observed in very diverse phyla, including planktonic, nectonic, benthic and burrowing organisms. Moreover, it is also well known that continuous size increase usually leads to gigantism, which can prove to be fatal in a more or less short time. The allometries observed during the geometrical/morphological evolution of shelly invertebrates show that size (i.e. diameter or length: see above), volume and surface can vary independently.

Within ammonites, an increase in volumetric size, which is not accompanied by an increase in linear size (i.e. the diameter; note that the body chamber's length is often unknown for preservational reasons), will result in an increase of involution. Similarly, a decrease in linear size which is not accompanied by a decrease in volume will also lead to a drastic increase of involution. Such a process certainly accounts for the geometry of the lower Triassic small cryptogenic ammonites such as the spherical Isculitids deriving from the serpenticone Columbitids. We also note that an increase in the mantle's surface area, if not compensated by a simultaneous increase in volume of the animal, results in an increase in suture complexity and/or flexuosity of growth lines at the aperture. On the other hand, a decrease of the volume not compensated by a decrease in the mantle surface can explain the small juvenile bulges observed in the inner whorls of the primitive Psiloceratids such as the "Knötchenstadium" of *P. spelae* (syn. *P. spelae tirolicum*).

Another interesting by-product of the above-described morphogenetic rules is the "stop and go" growth of the ammonites followed by an oblique reorientation of the growth lines (Guex 1967, pp 328–329). This is obviously due to the fact that the growth stop of the shell secretion is followed by a delayed restart of the soft parts' growth, generating a rotation of the growth lines.

1.6 Radiolarian Evolutionary Trends

1.6.1 Introduction

Radiolarians are Cambrian to recent holoplanktonic marine protists with morphologically very diverse siliceous skeletons. In the Mesozoic, two main groups are differentiated: nassellarians (mostly conical, composed of one or more consecutive segments) and spumellarians s.l. (generally spherical, composed of one or more concentrical shells). Following the extensive radiolarian research over the past decades, it is now possible to trace the development of some Mesozoic radiolarians through time and to reliably reconstruct several phyletic lineages. In this section we analyse some lineages with well-marked trends in skeletal development (and compare these trends with those observed in other marine organisms). The most usual geometrical transformations occurring in radiolarians are characterized by an increase of the surface of the shell. In several nassellarians, we observe a progressive inflation of the test, leading to a spherization. In some groups such a trend leads to cryptocephalization (Dumitrica 1970), a phenomenon analogous to the orbulinization of some Tertiary foraminifers. The development of a terminal tube or of apertural arches is also frequent in the nassellarians. In many respects, the transformations observed in the spumellarians are related to the same kind of geometrical modifications. For example, the addition of an arch to a polar spine in *Baumgartneria*, of a ring in the Saturnalids, of a button or spine also in the ring of *Aurisaturnalis*, are clear examples of an increase of the shell surface through time. Several examples of evolutionary reversals are given in Chap. 4 where the radiolarian is discussed. For a comprehensive and general discussion on radiolarian systematics and terminology the reader is referred to the monograph by De Wever et al. (2001).

1.6.2 Peramorphic Trends and Isometric Size Increase

Isometric size increase (i.e. without change in shape) is rare in radiolarians. Good examples are found in *Spongostichomitra* (Fig. 1.8) and *Obeliscoites*. *Spongostichomitra* has a conical to cylindrical test with very thick and unconstricted spongy wall.

Primitive forms have a small number of chambers, which are not visible in evolved species. Broken specimens show that the segmental divisions are lacking or poorly developed. This group shows an exceptional size increase between the Albian-Cenomanian transition.

Fig. 1.8 Isometric size increase in *Spongostichomitra* from the Albian-Cenomanian (scale bar 100 µm). Guex et al. (2012b)

1.6.3 Peramorphic Trends and Surface Increase: Spherization of the Test

The most frequent and best described trend is spherization of the test where the increase of volume is not or only weakly coupled with an increase of the length of the shell (Riedel and Sanfilippo 1981; Sanfilippo et al. 1985; Carter and Guex 1999). A similar trend was first described by Sanfilippo and Riedel (1970, 1982) in the Cenozoic Thecotylidae where it is accompanied by a reduction of the cephalothorax. It is also well illustrated in *Palinandromeda* (Fig. 1.9) and *Mirifusus* (Fig. 1.10).

Palinandromeda is a broadly conical amphipyndacid with 5–7 segments and a large basal aperture (Fig. 1.9). The cephalis is dome shaped, poreless and usually has an apical horn. The thorax is small, cylindrical and directly joined to the cephalis. The abdominal and postabdominal segments are trapezoidal or bell shaped with large pores increasing in size distally. The evolution of this group is characterized

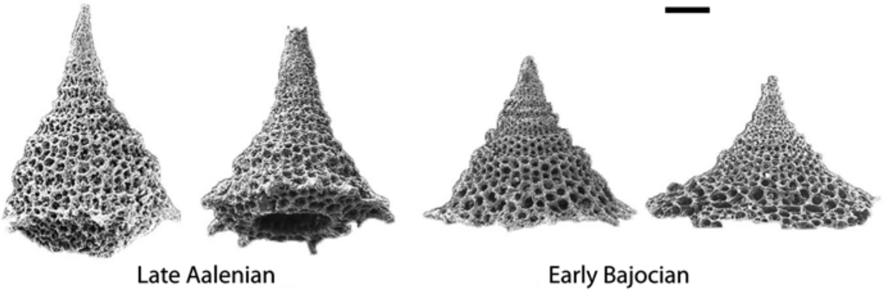

Fig. 1.9 Evolution of *Palinandromeda* from the Late Aalenian-Early Bajocian. Scale bar 100 μm. From Bartolini in Guex et al. (2012b)

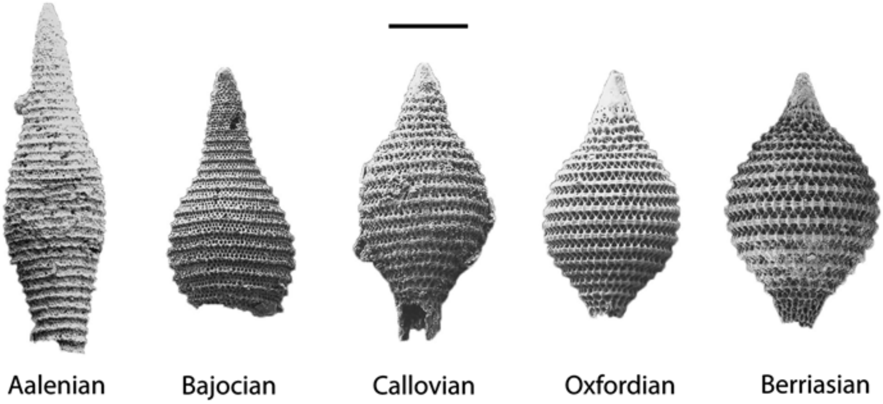

Fig. 1.10 Spherization of the test in *Mirifusus* from the Aalenian-Berriasian. Scale bar 100 μm. Guex et al. (2012b)

by an increase in the flatness of the abdominal segment, developing a planar basal surface. This evolutionary transformation is an extreme exaggeration of the spherization trend whereby the radius of the sphere becomes so large that this nassellarian becomes widely bell shaped and flat during its phylogeny.

The test of *Mirifusus* (Fig. 1.10) is spindle shaped during the Aalenian except in the earliest forms such as *Mirifusus proavus*, and is probably derived from *Parvicingula*-like nassellarians, where it is still slightly conical with the lower part of the spindle poorly developed. The proportions and shape of the conical proximal and inflated median part of the test is highly variable but during its evolution, *Mirifusus* shows a strong increase in sphericity and many species of this genus tend to become spindle shaped and even can develop a terminal tube. It is interesting to note that the duration of the main evolutionary transformation from *M. proavus* to *Mirifusus minor* lasts roughly 20 million years (late Aalenian to late Oxfordian). Then *M. minor* remains practically unchanged for more than 20 million years until the late Hauterivian, when it becomes extinct. This clearly means that the end form can survive successfully for a long period of time if environmental conditions remain favourable.

Another important case of spherization occurs in the williriedellids (Fig. 1.11), which show an extreme increase of the involution, analogous to that observed in Neogene orbulinid foraminifers (Kennett and Srinivasan 1983; Bolli and Saunders 1985; Guex 1992, 1993, 2003). This phenomenon was described as cryptocephalization by Dumitrica (1970).

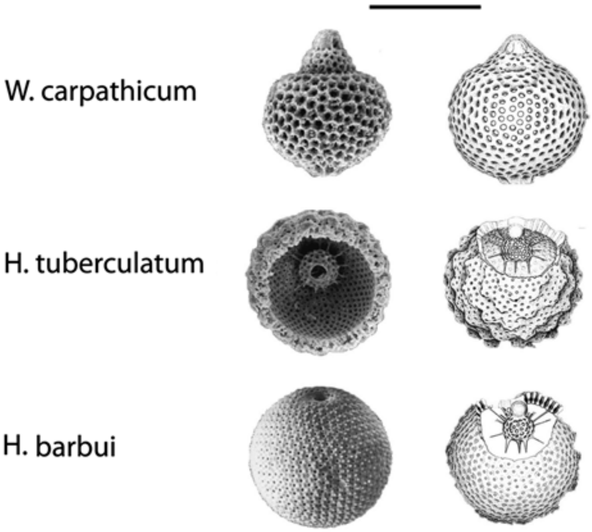

Fig. 1.11 Cryptocephalisation within the family Williriedelidae (*Williriedelum carpathicum, Holocryptocranium tuberculatum* and *H. barbui*). Scale bar 100 µm. From Dumitrica 1970 in Guex et al. (2012b)

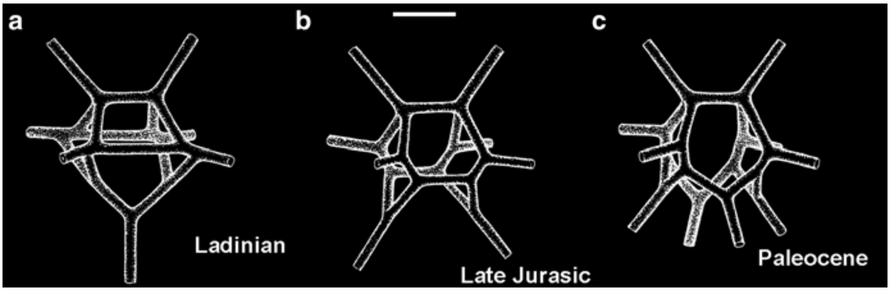

Fig. 1.12 Duplications of the antapical spine in Centrocubus between the Ladinian and Paleocene. Scale bar 100 µm. From Dumitrica in Guex et al. (2012b)

1.6.4 Paedomorphic Trends in Centrocubidae

Proterogenesis occurs sometimes in nassellarians and spumellarians s.l., especially in the Pyloniaceae and Centrocubidae where new structures first develop in the earliest ontogenetic stage. The initial antapical spicule of Centrocubids frequently evolves by doubling or quadrupling of the antapical spine, leading to entirely new modes of growth in subsequent descendants and to forms which are cryptogenic with regard to their ancestors. The evolution of the microsphere of some selected *Centrocubus* is illustrated in Fig. 1.12.

1.7 Cope's Rule, Surface Increase and Apparent Complexity

Before going further we should briefly discuss the concept of complexity applied to living organisms which is used, most of the time, from a purely intuitive point of view (Fig. 1.13) (see McShea 1991; Lloyd 2001).

In some cases it is possible to assign a numerical value to the apparent complexity of a particular character. For example, an ammonite suture line with a high value of its fractal dimension will look more "complex" than a suture line with a low fractal dimension (Guex 1981). The global curvature of a shell provides also a measure of its geometrical complexity, a straight shell looking more "simple" than one which is highly contorted or tightly coiled (Figs. 1.1 and 1.2). It should also be clear that two concepts should be distinguished from the very beginning, with the concept of geometrical complexity coming first and the idea of ornamental complexity being secondary. Sometimes the two variables covary during the ontogeny and sometimes they do not.

This distinction is important when analysing the covariation under the light of the very frequent evolutionary trend of phyletic size increase.

The size increase, however, is not a truly general evolutionary rule because many lineages do not increase in size during their evolution and numerous cases of size decrease are known in the fossil record. For example, a remarkable case of drastic

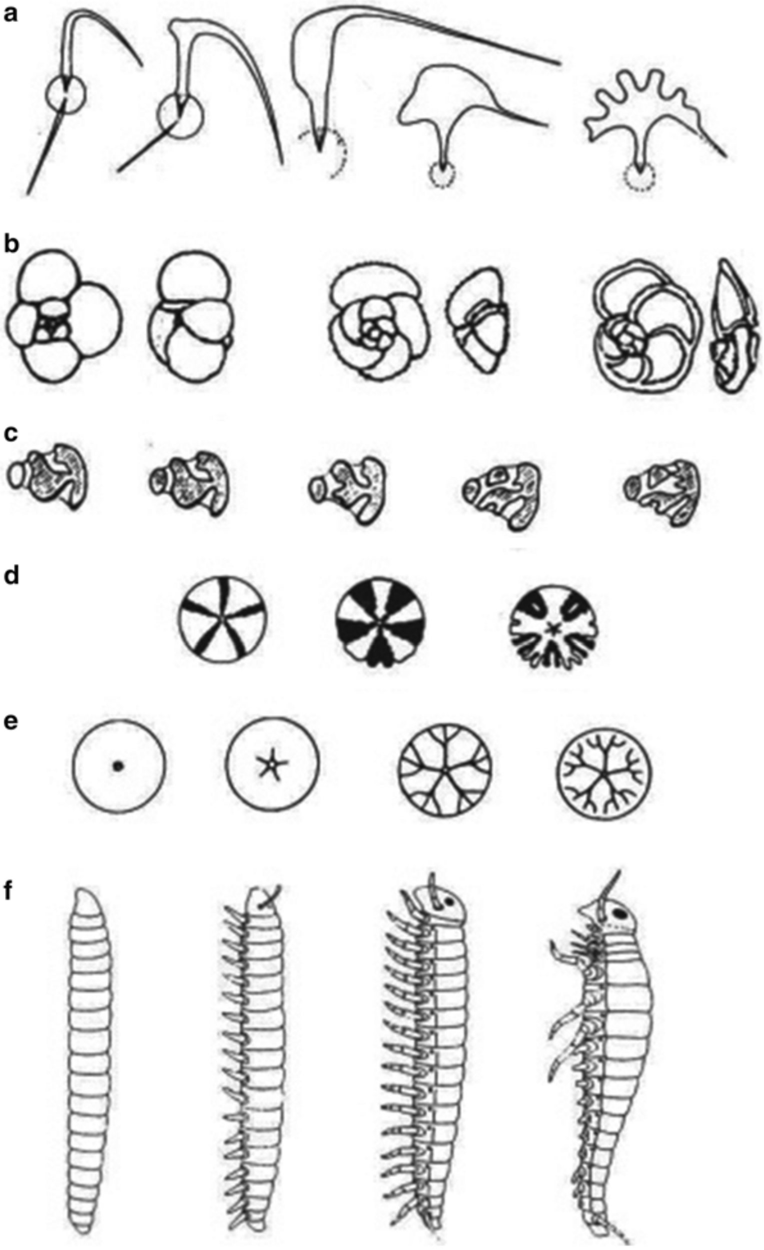

Fig. 1.13 Examples of the surface increase rule generating an apparent complexity increase. All figures simplified and not to scale (from Guex 1992). (**a**) *Oertlisponginae* (Dumitrica 1970). (**b**) Development of the carina in planktonic foraminifera (Cifelli 1969). (**c**) Complexification of the teeth in the *Piezodus-Prolagus* lineage (Hürtzeler 1962). (**d**) Development of the marginal notches in *Rotulidae* (Durham 1966). (**e**) Development of the actinal groves in *Proscutellidae* (Durham 1966). (**f**) Transitions from annelids to insects via onychophorids and myriapods (Raff and Kaufman 1983). From Guex (1992)

size decrease has been observed in planktonic foraminifera below the Cretaceous-Tertiary boundary which is certainly due to the environmental stress generated by the giant volcanism of the Deccan traps (see Courtillot 1999). These size fluctuations and trend reversals are usually dependent on environmental variations and increasing size is mainly observed at the beginning of phyletic lineages.

The allometries observed during the geometrical/morphological evolution of shelly invertebrates show that size (i.e. diameter or length), volume and surface can vary independently. Within ammonites, an increase in volumetric size, which is not accompanied by an increase in linear size (e.g. the diameter), will result in an increase of involution (Figs. 1.1 and 1.2). Similarly, a decrease in linear size which is not accompanied by a decrease in volume will also lead to an increase of involution, leading to subspherical forms. It is obvious that an increase in the mantle's surface area, if not compensated by a simultaneous increase in volume of the animal, results in an increase in sutural complexity and/or flexuosity of growth lines at the aperture in ammonoids, etc. An increase in the involution and in the apparent complexity of internal structures observed in tests of many foraminifera, as well as the increasing complexity of some ornamental traits or of geometrical features that are observed within many marine shelly invertebrates is indirectly related to this generalized Cope's rule (rule of surface increase). To summarize we can say that from a geometrical point of view, all the trends described above are the result of an increase of the surface of the membrane responsible for the biomineralization. The ornaments themselves are subordinated to the general geometry of the shell, specially the details of the local curvature of its secreting membrane, as shown below (Chap. 5, Fig. 5.10).

1.8 Technical Remark About "Full House" (Gould 1996)

In 1996, Gould published a famous book, "Full House", in which he tried to demonstrate the absence of a global increase in complexity during the evolution of living organisms. His main argument is that the most abundant organisms present on the Earth, the bacteria, did not really evolve morphologically during the last 3 billion years. In this book, Gould uses quantitative arguments like size variations observed in the Cretaceous and Cainozoic foraminifera and the fractal dimension of the Ceratites suture lines during the late Palaeozoic and early Mesozoic. We will briefly examine those two quantitative arguments.

His figure 25 (1996, p 160) shows the size variations of planktonic foraminifera during the Late Cretaceous and the Cainozoic. These diagrams are supposed to demonstrate that the rule of size increase (Cope's rule) is meaningless because it is often represented by zigzag variations, as is the case in the planktonic foraminifera observed during that period. We consider that Gould's argument is invalid because size decreases are always related to environmental stress, a phenomenon known since the beginning of the twentieth century (Shimer 1908; see also Mancini 1978). Gould's diagrams (his Fig. 25) just illustrate in a perfect manner that the size reductions occurred during the KT boundary, Late Eocene and Late Oligocene, which are periods of high environmental stress responsible for more or less pronounced extinctions (see Zachos et al. (2001) and Schmidt et al. (2004) for recent quantitative data).

His second quantitative argument concerns the fractal dimension of some ammonoid suture lines during the late Palaeozoic and Triassic times (loc.cit Fig. 35, p. 210). The measurements representing these relationships, as constructed by Gould, are distributed in a completely chaotic way and are supposed to demonstrate that there are no relationships between sutural complexity and time during that period.

The problem is that Gould overlooked the fact that he should have connected the dots representing the various measurements following two criteria. First the ontogeny: small juvenile specimens have a suture line, which always looks less complex than an adult one. And secondly the phylogeny within each separate lineage: the suture line of most ceratitids becomes more complex during the evolution. This is well illustrated in our Fig. 5.3 which shows that the ceratitic suture line of the ancestor of the highly complex phylloceratids has a fractal dimension of about 1.2 when the resulting advanced *Phylloceras* has a suture line dimension of about 1.6 (see Guex 1981). The psiloceratid *Neophyllites* generated during the TJB extinction period also shows a drastic reduction of its sutural complexity.