

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 94 (2001)
Heft: 3

Artikel: Environmental stress and atavism in ammonoid evolution
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DOI: <https://doi.org/10.5169/seals-168897>

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Environmental stress and atavism in ammonoid evolution

JEAN GUEX

Keywords: Evolutionary trends, reversals, atavistic forms, environmental stress, ammonites, extinctions

ABSTRACT

The most common trends observed in ammonoid evolution during ecologically stable periods are characterized by an increase of shell curvature (e.g. evolute to involute), by the development of more complex ornamentation (flexuosity of ribbing, appearance of nodes and spines) and by a long term increase of the suture line's fractal dimension. Major evolutionary jumps in ammonoids occur during severe extinction events, and are characterized by the sudden appearance of simple, primitive-looking forms which are similar to remote ancestors of their more complex immediate progenitors. Such forms are interpreted as atavistic. According to this hypothesis, homeomorphic species generated during such sublethal stress events can be separated by several millions of years.

RESUME

Les tendances évolutives les plus communément observées chez les ammonites au cours des périodes de stabilité environnementale sont caractérisées par une augmentation de la courbure de la coquille (passage de formes évolutes vers des formes involutes), par le développement d'une ornementation plus complexe (flexuosité des côtes, apparition de nodosités ou d'épines) et par une augmentation, dans le long terme, de la dimension fractale de la ligne de suture (passage de sutures goniatitiques vers des sutures ammonitiques). Les sauts évolutifs majeurs surviennent au cours des événements d'extinctions majeures et sont caractérisés par l'apparition soudaine de formes d'aspect primitif qui sont semblables aux ancêtres de leurs progéniteurs immédiats, plus complexes, et que nous interprétons comme ataviques. Les espèces homéomorphes engendrées au cours de telles périodes de stress subléthal peuvent être séparées par des intervalles de plusieurs millions d'années.

Introduction

In recent years, biologists have renewed interest in the influence of environmental stress on evolution and development. For example, Rutherford & Lindquist (1998) demonstrated that impaired or mutant heat shock protein Hsp90 was responsible for a great variety of abnormalities in the development of *Drosophila melanogaster*. These abnormal forms were shown to be fertile and their anomalies are inheritable under artificial selection. From their experiments the authors concluded that external stress, such as abnormal temperature or chemical stress, could uncover morphological variants for selection to act upon, allowing some of the rapid morphological radiations observed in the fossil record. These conclusions follow the fundamental experiments of Waddington (1953, 1956) who applied sublethal artificial chemical stress and high temperatures to developing *Drosophila* pupae, thus obtaining inheritable resurgences of atavistic structures, such as the bithorax and crossveinless abnormalities which are deleterious under natural selection. Waddington's experiments proved that external stress applied to an organism at an early stage of development during a very short time could drastically alter its later devel-

opment. Long periods of environmental stress (see below) should increase the probability of generating viable modified organisms.

Other recent work concluded that the effects of external stress on morphological development should increase the rate of mutation and recombination, generating an important increase of the intraspecific variability (Williamson 1981) and initiate the appearance of asymmetries (Hoffman & Parsons 1991). Phenomena which could be attributed to such effects have been widely observed in the fossil record (Almeras & Elmi 1987; Guex 1992, 1993) and it has been proposed that many evolutionary novelties occurred in stressed nearshore environments (Jablonski et al. 1983; Lewin 1983).

This paper describes the influence of environmental stress on evolutionary trends in some Mesozoic ammonite lineages. Ammonites are characterized by exceedingly rapid evolutionary rates, encompassing a very wide range of morphologies, which makes them very useful tools for precise chronostratigraphic correlations in marine sediments. In the first part of the paper the major causes of environmental stress which can

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affect the development of organisms are briefly discussed. The second part describes some of the main patterns of morphological changes shown by the evolution of ammonites during periods of extinction generated by high environmental stress.

Cope's rule and size decrease

Classical scientific literature provides numerous descriptions of evolutionary trends characterized by increases in the size (Cope's rule) and anatomical and morphological complexity of organisms (Newell 1949; Valentine et al. 1994). Paleontological literature also provides several examples of the repetitive and recurrent character of such trends (Foraminifera: Cifelli 1969; Ammonites: Haas 1942; Conodonts: Hirsch 1994). On the other hand, size reductions generated by environmental constraints such as marine regressions, anoxic episodes and thermal or nutritional stress have also been reported (Hallam 1978; Mancini 1978). There is quantitative evidence in several foraminiferal lineages that such size reductions in themselves do not necessarily disrupt trends toward size increase or toward increasing geometrical complexity (Hofker 1963; Fig.1).

It is widely considered that small forms with short life spans and rapid proliferation are favoured during stressful episodes to the detriment of larger organisms which are more vulnerable to extinction (r-selection) (McKinney 1990; Hallam 1998). This idea supports the belief that new evolutionary lineages are often developed iteratively from persistent stocks of small opportunistic forms. As a corollary, reversals of the long-term trends towards higher complexity have sometimes been explained by an elimination of more complex forms during extinction events (Saunders et al. 1999).

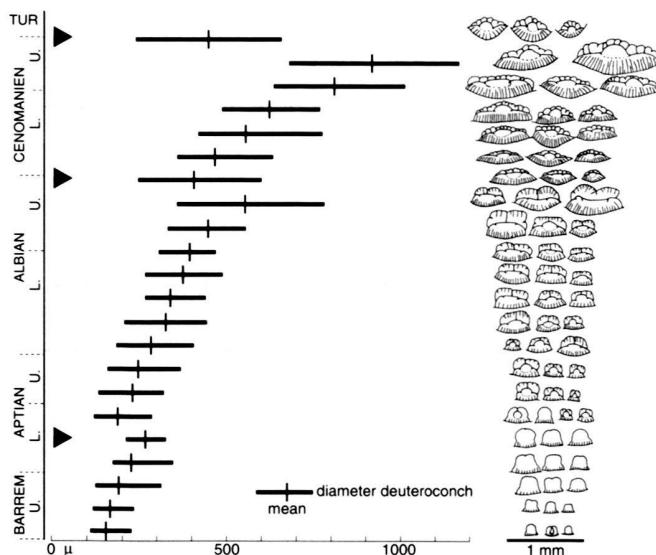


Fig. 1. Abrupt size decreases generated by major Cretaceous anoxic events (arrows) during overall global size and morphological complexity increase in the deutoconch of *Orbitolina* (redrawn and reinterpreted from Hofker, 1963)

Evolution of ammonites differs from this model because the primitive groups, which are the source of the new evolutionary lineages, are systematically absent from the known stratigraphic record separating the respective first appearances of these distinct lineages. This absence seems therefore to be real and not due to incomplete fossil documentation. On the other hand, when the fossil record is good enough, it is possible to follow the more or less gradual transformation of the primitive groups into more elaborate forms through time.

Few studies explore the way some advanced groups (outcome of evolutionary trends) can yield globally simplified and primitive-looking forms. When this question is addressed, heterochronies like progenesis or neoteny are inferred (McKinney & McNamara 1991). Such forms often appear in an abrupt manner during episodes of intense environmental stress, generating polymorphism oriented towards a global simplification of the phenotypes belonging to the advanced ancestral group. Such abrupt transitions can be schematically represented on Thom's fold catastrophe model (Fig. 2) (Thom 1972; Guex 1981). In such cases the evolutionary jumps are characterized by the appearance of forms which are atavistic and homeomorphic with remote ancestors of their own lineage, a phenomenon termed proteromorphosis (i.e. characterized by a primitive morphology).

Stress factors

For paleontologists, the most obvious and reliable indicators of major environmental stress consists of extinction periods, whatever their causes (Hart ed. 1996; Hallam & Wignall 1997).

The most important stress factors affecting marine faunas and generating major extinctions are: i) large-scale regressions (Grabau 1936), ii) climatic variations (Valentine 1968) and iii) major volcanic eruptions (Courtillot 1999). Marine anoxic

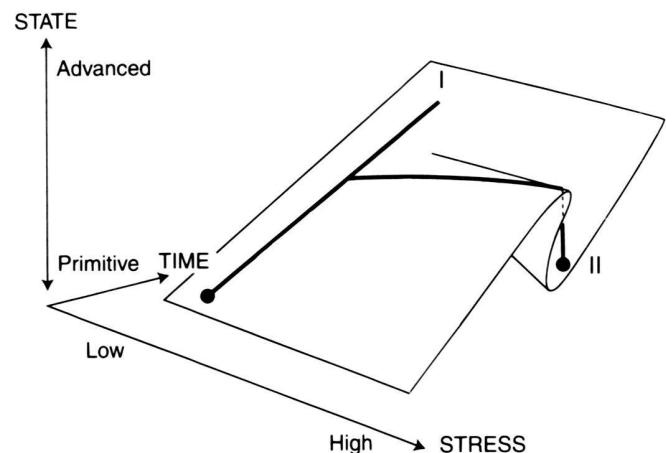


Fig. 2. Diagrammatic representation of a punctuated anagenesis. Path I = anagenetic lineage. Path II = catastrophic reappearance of atavistic forms (simplified from Guex, 1981)

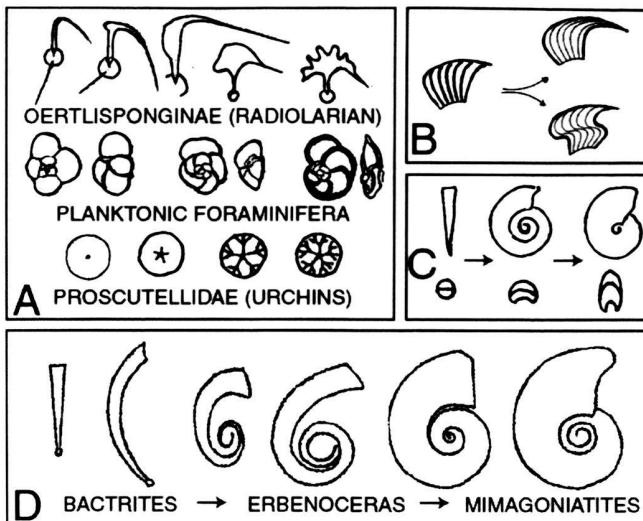


Fig 3. (A) Increasing morphological complexity observed in the evolution of some fossil groups. (B) Increasing curvature of growth lines and ribs observed in different ammonite lineages. (C) Increasing curvature of shell geometry. (D) Phylogeny of the earliest ammonoids during the Devonian, redrawn and simplified from Erben (1966)

events are also often concomitant with climatic variations, themselves correlated with important sea level changes. Such events should generate nutritional stress and/or chemical pollution (e.g. acid rains) in marine environments. The major regressions are easy to identify in the stratigraphic record and the most important ones were already recognized during the nineteenth century (Suess 1888). Unfortunately, major short-term temperature changes are more difficult to detect in pre-Cenozoic times because they rarely impart clear sedimentary or isotopic signatures.

Geometrical and ornamental complexity of ammonite shells

For many authors (e.g. Valentine et al. 1994) the complexity of an organism or its skeleton increases as a function of the number of its parts (organs, types of cells, number of structural elements etc). In the case of the ammonites it is impossible to provide a precise definition of the term „complexity“ when comparing the state of evolutionary development in distinct evolutionary lineages; an advanced evolutionary state in one particular group of a given evolutionary lineage can well correspond to a primitive state in another group of another lineage. Nevertheless, within an homogeneous phyletic lineage, relative complexity may be defined in an empirical way. Fig. 3 illustrates some typical cases of evolutionary transformations that are reasonably imputed to an increase in morphological complexity of the group of organisms under consideration.

Ammonites have three main morphological parameters: the suture line, the ornamentation and the geometry of the shell. The most evident trait of ammonite morphological evo-

lution consists of an increase in the complexity of their suture line through time; the sutures of the primitive ammonites like the Goniatites have a fractal dimension close to 1 while that of very elaborate groups like the Phylloceratids have a dimension that is close to 1.6 (Guex 1981). The numerical quantification of sutural complexity by its fractal dimension is of considerable interest because this dimension can be a useful ecological indicator such as the depth at which the different representatives of a given group lived (Batt 1991; Oloriz & Palmqvist 1997). The ornamental complexity of ammonite shells can be evaluated by means of immediate empirical criteria such as those illustrated in Fig. 3B.

Another important factor in understanding phylogenies is morphological covariation. First observed by Buckman (1887) in *Sonninia* and *Amaltheus* and rediscussed later by Westermann (1966), covariation was originally described as follows: „Roughly speaking, inclusion and compression of the whorls correlate with the amount of ornament - the most ornate species being the more evolute (= loosely coiled) and having almost circular whorls...“ It is now known that covariation depends on internal shell geometry (Guex 1999), namely the lateral and ventral curvature of the shell which controls the thickness of the mantle and the concentration of morphogens present in that shell-secreting epithelium (see below). The most salient ornamentation is present where the whorls are the most curved, shells with slight angular bulges often being spinose or carinate and flat ones being almost smooth. As a general rule, juvenile ammonites belonging to peramorphic lineages are more evolute and have a greater lateral curvature of the whorl than the adult ones. This explains the common observation of ancestral spinose or coarsely ornate forms giving rise to involute „smooth“ or weakly ornamented descendants. These observations have recently been tested by André Koch (pers. comm.) within the conceptual framework of Meinhardt's reaction - diffusion models (Meinhardt 1995). Koch simulated the distribution of morphogens in a quadrangular body chamber and demonstrated that morphogen maxima are located in those parts of the mantle situated in the angular parts of the shell.

The global geometry of conical ammonite shells ranges between two extreme types: straight or completely involute (notwithstanding exceptional cases such as the trochospirals and nipponitoid coiling). The passage from a straight shell to an involute one (sphaerocone or oxycone) results from a twofold increase in the curvature of the cone (following the direction of the growth and in the plane continually orthogonal to that of the growth (Fig. 3C)). This can be described as an increased geometrical complexity of the coiling (Guex 1992; Rivier & Goldar 1998).

Main evolutionary trends during stable periods

The most frequent evolutionary trend observed in Mesozoic ammonites is where the ancestral group has an open umbilicus (=evolute form) and where the descendants are involute (=

tightly coiled). This trend was first described in Liassic ammonites (*Arietitidae*, Hyatt 1869) and later recognized in Devonian ammonites, at the beginning of the history of the group (Erben 1966) (Fig. 3D).

The trend towards increasing involution of initially evolute shells leads either to lenticular (oxycones) or more or less spherical shells (sphaerocones). The recurrent character of this trend was discussed in the early 1940's to explain the multitude of heterochronous homeomorphies observed within this group (Schindewolf 1940; Haas 1942). Geometrically, primitive uncoiled ammonites are more "simple" than their tightly coiled descendants. The increasing involution often observed in Mesozoic ammonites is only a repetition of the initial evolutionary trend illustrated in Fig. 3D. In many lineages, ammonite ornaments start to be modified in the juvenile stage of the ancestral forms and the novel structures (spines, collars, flexuous ribs or even smooth whorls) more or less rapidly invade the mature stage of the descendants. Such evolutionary novelties are never acquired during stressful episodes.

In most oxycone groups (end of lineages) the involute compressed geometry of the shell is acquired in a peramorphic manner (increasing involution is accentuated during the subadult stage). In other groups such as the *Amaltheidae* and the *Cardioceratidae* the ogival shape of the whorl section arises from an increase of the ventral projection of the mantle. Once established, such families can survive for long periods without exhibiting subsequent oriented transformations.

Inversion of the trends during stress episodes

Long before the Cretaceous/Paleogene boundary when the ammonites disappeared, this group had experienced two other major crises: the extinctions at the end of Permian and Triassic times. In both cases, post-extinction diversification started basically from smooth evolute forms with simple suture lines: *Xenodiscus-Ophiceras* in the beginning of the Triassic and *Psiloceras* in the beginning of the Jurassic. The detailed phylogeny of the ancestors of the Xenodiscidae is not known but it is well established that this group gave rise to all the Triassic Ceratitina. In the same fashion the smooth and evolute *Psiloceras*, the Lower Jurassic homeomorph of *Ophiceras*, gave rise to all the Jurassic ammonites except the *Phyllocerataceae* from which it derived (Guex 1982; Tozer 1984; Schlatter 1994; Keupp 2000; v. Hillebrandt 2000).

The Triassic-Jurassic boundary and the appearance of the Psiloceratina (Fig. 4)

In the late Rhetian, the transition between the relatively involute *Phyllocerataceae* with complex suture lines and the resulting group (*Psiloceras*) is characterized by a drastic simplification of the morphology concomitant with the major late Triassic extinction event.

The geometrical simplification which characterizes the *Psiloceras* is often accompanied by a loss of the sutural sym-

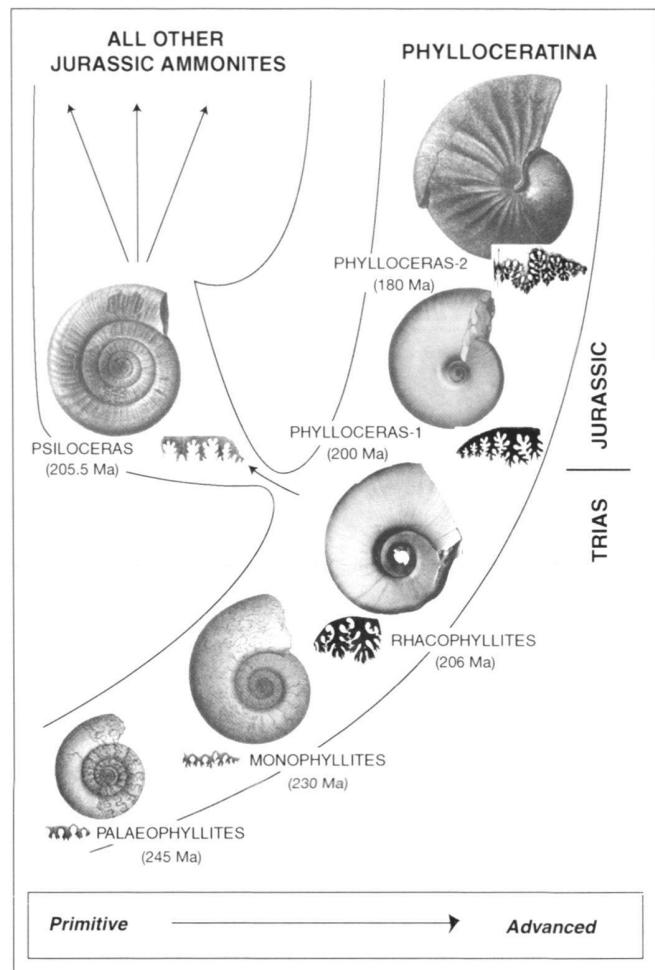


Fig. 4. Evolution of the Triassic *Phyllocerataceae* and passage to the earliest Jurassic ammonite, *Psiloceras*, ancestor of all Jurassic ammonites. Not to scale. 245 Ma = Spathian; 230 Ma = Ladinian; 206 Ma = Rhaetian; 205 Ma = Early Hettangian; 200 Ma = Late Hettangian; 180 Ma = Toarcian.

metry (lateral displacement of the siphuncle) which persists in some descending lineages such as the *Discamphiceratinae*. This helicoidal coiling of the siphuncle associated with a trend towards the uncoiling of the shell prompted a reconsideration of *Psiloceras* as aborted heteromorphs (Guex 1992, 1993).

The sudden appearance of extremely evolute (= serpentine) forms deriving from platycone ancestors during, or at the end of, severe extinction events is very common (e.g. *Dactylioceras* and *Emaciaticeras* at the end of the Pliensbachian, *Grammoceras* during the Middle-Late Toarcian crisis etc.).

The great middle - late Toarcian regression in NW-Europe

At the end of the middle Toarcian, the Euro-Boreal province was affected by a major regional regression generated by the surrection of the western Tethys' rift shoulder (Stampfli 1993). With that regressive event began a major faunal turnover cul-

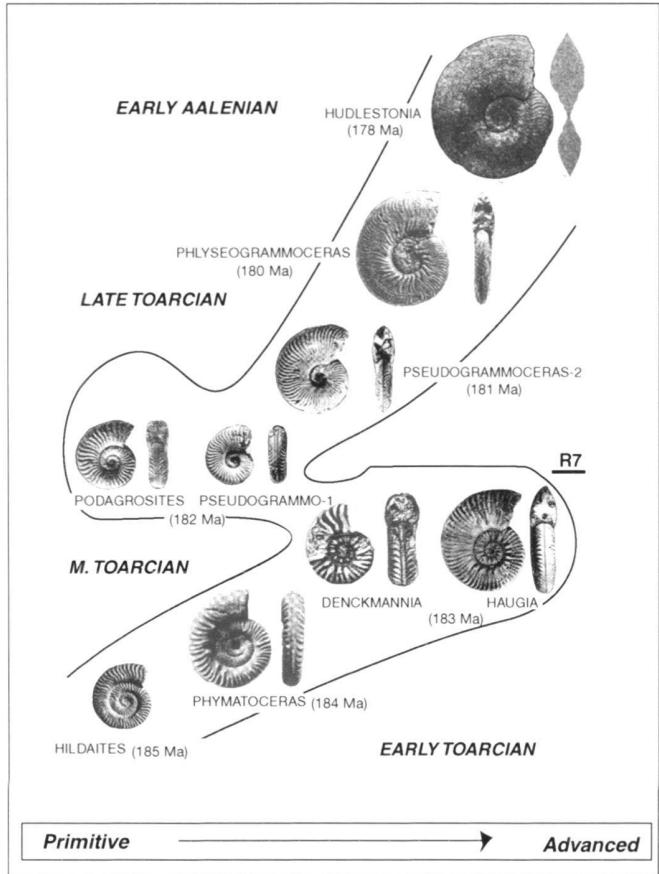


Fig. 5. Evolution of the *Phymatoceratinae* and *Grammoceratidae* during the early to late Toarcian times; R7 is the middle-late Toarcian regressive event. Not to scale.

minating in the extinction of late Liassic ammonites such as the *Hildoceratinae*, the *Mercaticeratinae*, the *Dactylioceratidae* and most of the *Phymatoceratinae*. The disappearance of those groups was concomitant with the development of two new families, the *Hammatoceratidae* and the *Grammoceratidae*, which were dominant during the late Toarcian.

Fig. 5 schematically illustrates the evolution of the *Phymatoceratinae* and one of their derivatives, the *Grammoceratidae*. This lineage is rooted in evolute forms of the Lower Toarcian which belong to the genus *Hildaites*, and which evolved into the involute group of *Haugia* via *Phymatoceras*. During the late middle Toarcian, the variability of *Haugia* increased and gave rise to a very simply ribbed ammonite, *Podagrosites*, which is a homeomorph of the ancestral *Hildaites*.

Starting from the *Podagrosites* pole, a continuous morphological transition exists towards the different species of *Pseudogrammoceras* eventually giving rise to the involute and fasciculate *Phlyseogrammoceras* and to the smooth oxycone *Hudlestonia*.

In our opinion, this example demonstrates clearly that the passage from involute forms (which are the outcome of a

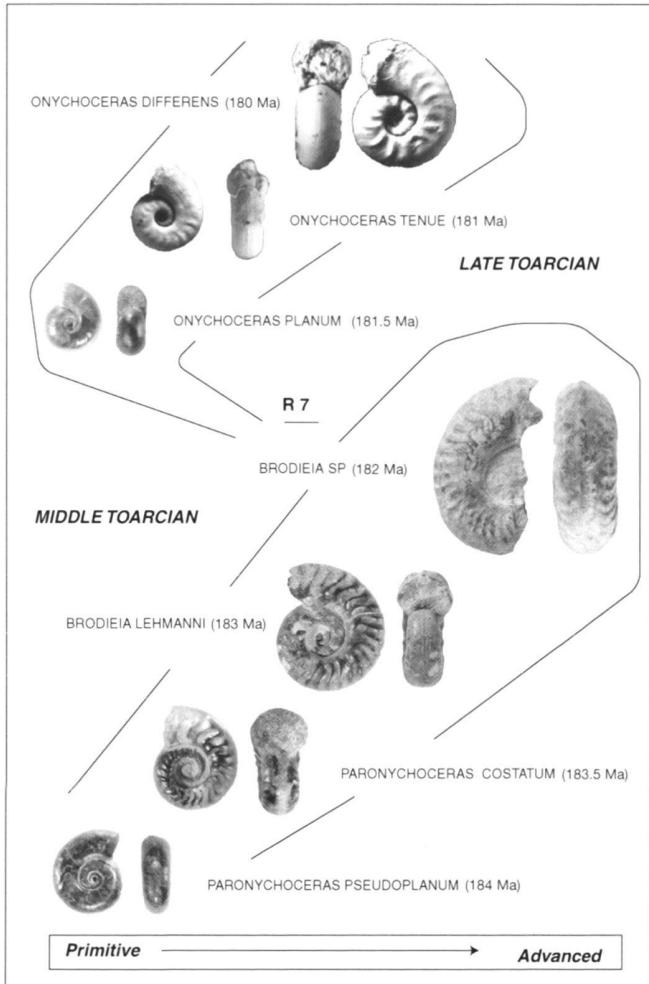


Fig. 6. Evolution of the microconch genera *Paronychoceras* and *Onychoceras* during the middle to late Toarcian times; R7 is the middle-late Toarcian regressive event. Not to scale.

major evolutionary trend) towards a primitive looking evolute form is realized through an increase of the polymorphism of the ancestral advanced group during an episode of stress (Guex 1992, 1993).

It should be noted that such a transformation is global (i.e. it affects the whole ontogeny) and does not result from a simple heterochrony like neoteny or progenesis. The simplified resulting pole of the reversed lineage resembles much more closely its remote ancestors than the juvenile of its immediate progenitor. In the case illustrated here, the appearance of *Podagrosites* occurs about 2 million years after the disappearance of its homeomorphic remote ancestor *Hildaites*.

During the same stratigraphic interval, another interesting example of atavistic reversal is observed in the microconch lineage *Paronychoceras* → *Brodieia* of the middle Toarcian *Phymatoceratinae*. That lineage, illustrated in Fig. 6, is characterized by a drastic increase of the ornamental complexity, invo-

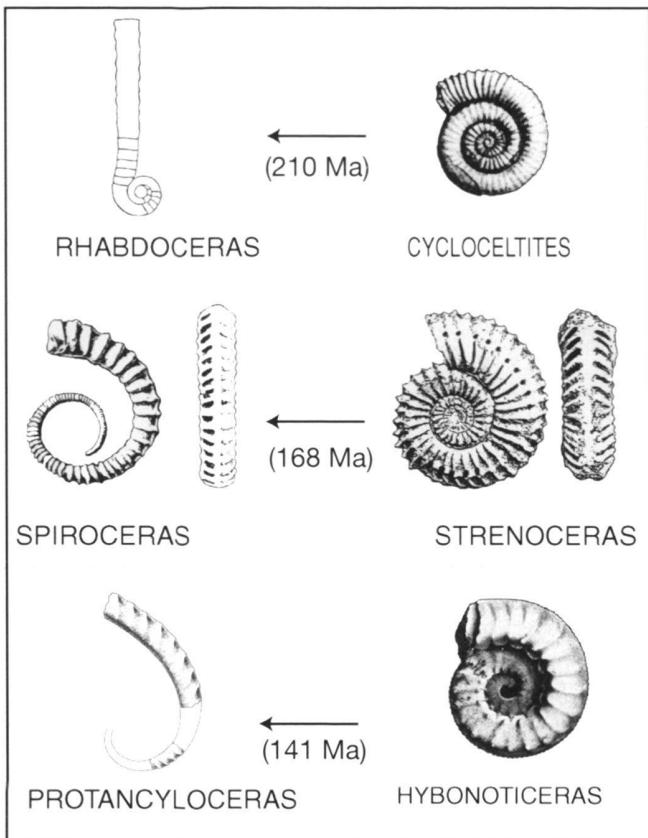


Fig. 7. Catastrophic transitions between normally coiled and heteromorph ammonites. The heteromorphs illustrated in that figure are not inter-connected phylogenetically. Not to scale. 210 Ma = Late Norian; 168 Ma = Late Bajocian; 141 Ma = Early Tithonian.

lution and size. In the late Toarcian, that sequence is followed by the *Onychoceras* lineage, a group of unkeeled microconch Hammatoceratids, which is atavistic and practically homeomorph of its ancestral *Paronychoceras* (Fig. 6).

Heteromorph ammonites

The most spectacular reversals of the trends towards increasing involution are observed among ammonites called „heteromorphs“ (uncoiled or with helicoidal coiling) which appear abruptly at various periods of the Triassic and of the Jurassic and which proliferate during the whole Cretaceous (Fig. 7).

The oldest uncoiled Mesozoic group belongs to the genus *Rhabdoceras* and derives from the normally coiled *Sympolyculus/Cycloceltites* group. *Rhabdoceras* appears at the end of the middle Norian, during an important extinction (disappearance of 50 % of the ammonoid families existing at that time (Taylor et al. 2000)) which can be correlated with a major regressive event. *Rhabdoceras* itself generates semi-uncoiled ammonites such as *Choristoceras* (Spath 1933), *Peripleurites* and the heli-

coiled *Cochloceras*. The late Triassic heteromorph *Choristoceras* proliferated during the whole Rhetian when most other typical Triassic ammonoids disappeared.

Similar occurrences are observed during the Middle and Late Jurassic with the appearances of *Spiroceras* and *Protancyloceras*, deriving from normally coiled ammonites (Fig. 7). Note again that uncoiling is a global process: uncoiled ammonites do not at all resemble juveniles of their ancestors and, therefore, they cannot be considered as „paedomorphs“.

Conclusions

Drastic simplifications of shell geometry take place during periods of extinctions generated by high environmental stress. They cannot be attributed to reverse spontaneous mutations occurring during low selective pressure conditions (Wiedmann 1969; Delanoy & Magnin 1994). Contrary to popular belief, the early representatives of a new species generated under such stressfull conditions are neither progenetic paedomorphs nor r-selected extinction resistant forms. This is evident because they are always extremely rare at the beginning of their existence (e.g. first *Psiloceras* or first *Protancyloceras* etc...). The proliferation of the new species characteristically takes place only after the extinction event which resulted in markedly decreased competition for habitats. Note also that the heteromorphs were not less adapted than their „advanced“ ancestors because they often proliferated throughout post-extinction periods without being affected by minor sea level variations or anoxic events. One explanation could be that the heteromorphs had different trophic behaviors than their normally coiled ancestors which allowed them to explore new ecological niches (Cecca 1997).

It is also noted that the forms which we believe to be atavistic are not only generated by environmental stress but that they are favoured by selection during and after mass extinction events (but not before!). The obvious reason for this is that such forms are unspecialized compared to their specialized direct ancestors. They have therefore a great potential to occupy most of the available ecological niches.

What these observations suggest is that ancestral development programs are partially preserved in the advanced forms of any single evolutionary lineage. The problem is to know if part of the genetic information accumulated during the preceding trend could suddenly be lost or inhibited during sublethal stress episodes or if the appearance of the atavistic forms is simply the result of certain processes comparable to the Hsp90 disfunction described by Rutherford & Lindquist (1998).

Whatever the cause (genetic or biochemical) of the reversal processes postulated above, it is very easy to inhibit the development of morphological novelties accumulated during several millions of years. In any case it is clearly a result of such reversals that the ammonoids were able to survive drastic extinctions like the end-Permian and end-Triassic (i.e. generating exceedingly simple forms such as *Ophiceras* and *Psiloceras*) and to regenerate a full diversity during their subsequent evolution.

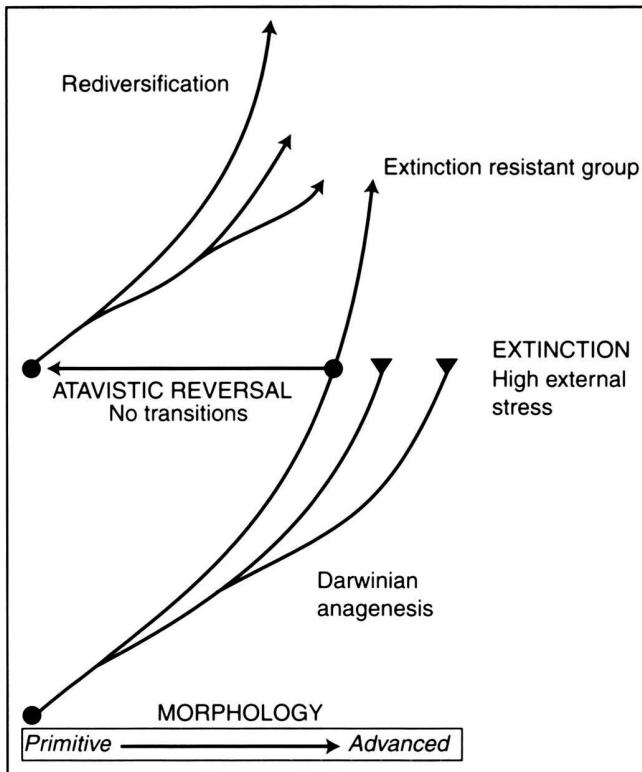


Fig. 8. Diagrammatic representation of the phylogenies illustrated in Figs. 4 to 6

Extrapolating our observations to evolutionary jumps observed in other groups like planktonic foraminifera, it would not be surprising if the extant primitive hedbergellid-like forms had more genetic affinities with the benthic foraminifera ancestral to the Cretaceous globigerinids than with their own direct globigerinid ancestors.

The most extreme simplification which can affect a skeleton is its own disappearance. For example, loss of skeleton under severe external stress is well known in silicoflagellids (Van Valkenburg & Norris 1970; Thomas et al. 1980; Moestrup & Thomsen 1990). Such skeletal disappearances probably occurred in corals during the major Permian-Triassic extinction. We can also expect that such a phenomenon is wide-spread in radiolarians because simple and cryptogenic spicular forms regularly occur in the stratigraphic column.

These observations, summarized in Fig. 8, ultimately suggest that direct experiments could produce atavistic forms under sublethal stress applied to organisms during their early development.

Acknowledgements

I thank A. Escher, M. Cosca, N. Rivier, F. Hirsch, J. Marcoux, J. Sandoval, D. Taylor, P. McGough, E. S. Carter, S. Gorican, L. O'Dogherty, J. Remane, F. Reuse, F. Rothen, P. DeWever, F. Cecca and H. Bucher for discussions and comments and G. Monin for technical assistance. Supported by Swiss NSF grant 2000.55220.98/1

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Manuscript received October 3, 2001

Revision accepted November 1, 2001