

Jean Guex
John S. Torday
William B. Miller Jr. *Editors*

Morphogenesis, Environmental Stress and Reverse Evolution



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Editors

Jean Guex
Institute of Earth Sciences
Geopolis, UNIL
Lausanne, Switzerland

William B. Miller Jr.
Department of Medicine
Banner Health System
Paradise Valley, AZ, USA

John S. Torday
Department of Pediatrics, Obstetrics
and Gynecology
Evolutionary Medicine Program
David Geffen School of Medicine
University of California
Los Angeles, CA, USA

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Chapter 1

Introduction



Jean Guex

Keywords Extinctions · Atavistic development · Environmental stress

This book intends to be a continuation of a prior text entitled “Retrograde Evolution During Major Extinction Crises” (Guex 2016). That initial book was restricted to the study of catastrophic evolutionary changes during such major extinctions, which were generated by extreme and sublethal environmental stresses, leading to evolutionary reversals. This introduction will be a short discussion of usual environmental stress in geology, and a condensed and reduced presentation of Guex’s 2016 book.

The concept of sublethal environmental stress denotes specific conditions that are critical to the survival or normal development of living organisms. The most common cases of environmental perturbations include pollution or poisoning by chemicals such as toxic gases, nutrient shortage, large-scale sea-level falls, major climatic changes, hydric stress, acid rain and marine anoxia. The origins of environmental stress can easily be identified and quite naturally the particular kind of stress can be hostile to some organisms and favourable to others.

The role of natural environmental stress on development and evolution is widely accepted (Badyaev 2005; Jablonka 2013). The nature of sublethal environmental stress that occurred during major extinctions such as the Permian-Triassic (PT), Triassic-Jurassic (TJ), Pliensbachian-Toarcian (Pl-To) and Cretaceous-Tertiary (KT) has been intensively investigated by means of geochemical and geochronological studies. However, most problems related to these exceptional situations belong to the realm of palaeontology, and most, if not all, such palaeontological studies are dedicated to a census of the biodiversity variations (counting how many groups survive, how many disappear, etc.) rather than to the understanding of the basic phenotypic and epigenetic variations induced by major environmental perturbations. The modes of evolution during major extinction events, the characteristics of the organisms surviving major crises and what types of transformations have affected them have not been explored. The main goal of this study is to precisely

J. Guex (✉)

Institute of Earth Sciences, Geopolis, UNIL, CH 1015 Lausanne, Switzerland

e-mail: jean.guex@unil.ch

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analyse in detail the transformations of some invertebrates during major extinction periods.

The geological record of environmental stress is naturally poor because local pollution, nutrient levels, paleotemperatures, etc. can hardly be deduced from sediments or fossils. The primary indication and proof of the sporadic sublethal environmental stress are the extinction periods themselves, which are easily recognised from the presence of major faunal turnovers reflecting the disappearance of entire phyla and their replacement by new ones.

The classical explanations of the origins of extinctions include extraterrestrial impacts, marine regressions, climatic changes, or anoxic events (Courtillot and Gaudemer 1996). The theory of giant volcanism (Courtillot 1999) has the most general explanatory power, considering the enormous potential consequences to the chemistry of seawater, global climate and temperatures. There is an almost perfect correlation between the major extinctions and periods of volcanism (Fig. 1.1, from Courtillot loc. cit.). Virtually all major extinctions are related to major ecological instability generated by giant volcanism, i.e. climatic changes and atmospheric poisoning by sulphur gases, as well as by darkening generated by fine particles and aerosols inducing major coolings

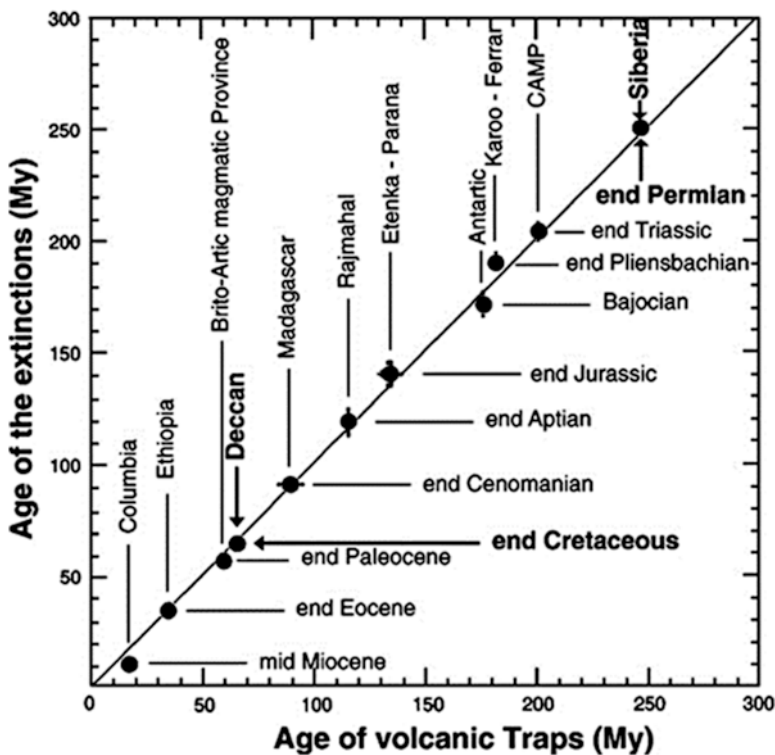


Fig. 1.1 Bivariate graph showing the correspondence between the principal mass extinctions and their geochronometrical age. From Courtillot (1999), modified

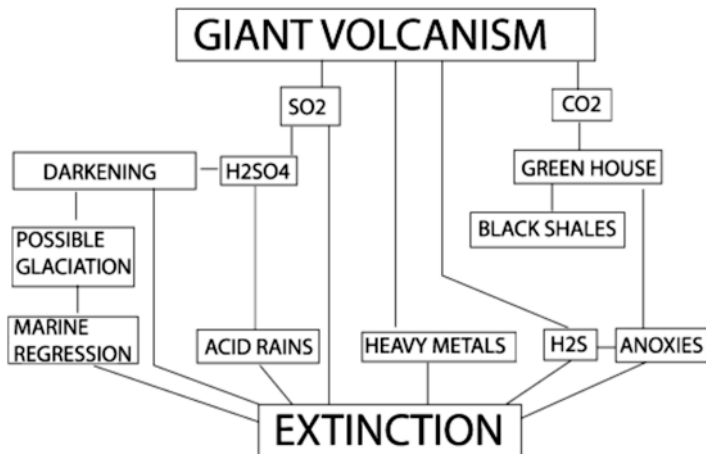


Fig. 1.2 Summary of the most obvious relationships between giant volcanism and major extinctions

and fall in the sea level (Fig. 1.2). In extremes, for example, at the Permian-Triassic boundary, the only organisms found in crisis sediments are microbialites and fern or fungus spores. Often these sediments do not contain any fossils, and hence are known as barren intervals. The post-extinction recovery is generally characterised by the explosion of simple and primitive life forms, which can be divided into two major groups:

1. Persistent opportunistic simple forms such as bacteria, fungi, ferns and some simple forms or other microfossils.
2. Primitive-looking forms derived from their immediate ancestors by retrograde evolution (a phenomenon that has been described as proteromorphosis), often associated with a reduction in body size. These organisms are not Lazarus taxa because their absence in sediments older than the ones where they are found is fully reproducible worldwide, and the duration of the intervals of time in which they are totally absent can last several millions or several tens of millions of years. In other words, a “Lazarus” explanation of such organisms cannot be reconciled with the geological record.

This introduction analyses how different groups (foraminifera, radiolaria, ammonoids, nautiloids, corals, conodonts and silicoflagellids) of invertebrates (except conodonts) survive the sublethal biotic crises during extinction episodes, and elaborates previously published works (Guex 1993, 2001, 2006). This introductory discussion also aims at developing a model explaining the heterochronous repetition of similar evolutionary lineages without invoking repetitions of identical environmental conditions.

An abundant literature has been published during the last decades concerning the Permian-Triassic boundary and the Cretaceous Paleogene boundary, which are well known for their spectacular extinctions. Two major extinctions generated by giant volcanism have been recently studied in detail by the author and his colleagues: the

Triassic-Jurassic and the Pliensbachian-Toarcian boundaries (Guex et al. 2015). These two major geological events will be discussed in light of recent geochemical and geochronological data, and will illustrate the environmental framework of the retrograde evolution observed during these events.

The End Triassic extinction has long been suspected to be related to the onset of the Central Atlantic Magmatic Province (CAMP) volcanism. However, it is only recently that U-Pb ages measured on zircons have allowed a precise correlation with the relative timescale based on the evolution of the ammonites. That correlation has been established based on very detailed stratigraphic research done in the American Cordilleras (Northern Peru and Nevada, USA) and on the discovery of ash beds deposited in the same levels as age diagnostic ammonites (Guex 1995; Schoene et al. 2010; Guex et al. 2012a). These discoveries allowed us to propose an original model explaining the precise timing of the End Triassic extinction (ETE).

One popular model to explain the ETE catastrophic event invokes super-greenhouse conditions due to extreme atmospheric CO₂ concentrations. This enrichment is often interpreted as degassing of magmatic CO₂ from huge volcanic basalt provinces (e.g. Sobolev et al. 2011 for the Permian-Triassic crisis) and/or from the degassing of carbonaceous or organic rich sediments (e.g. Svensen et al. 2009).

The second scenario invokes a short period of global icehouse conditions caused by degassing of huge volumes of volcanic SO₂, atmospheric poisoning, cooling and eustatic regression coeval with the main extinction (ETE), but probably older than the main basalt emissions. As mentioned above, this model uses the same arguments as those given below for the Late Pliensbachian cooling event.

Although both hypotheses are compatible with massive volcanic degassing related to the emission of large volumes of flood basalts, they must also be able to explain the palaeontological record in complete stratigraphic sections that display decoupling between the (marine) ammonoids and (terrestrial) plant extinctions (Guex et al. 2012a). Correlating the sedimentary and fossil records with carbon and oxygen isotope variations, and sea-level changes from the T-J and PI-To boundaries, indicates that both boundaries are related to a regressive event followed by major sea-level rise (Guex et al. 2001, 2004, 2012a).

The data allowing us to discuss the various hypotheses of recent extinction models and the timing concerning the End Triassic extinction (ETE) and the T-J boundary have been discussed in detail in Guex (2016), and will not be repeated here. This compilation synthesises the timing of sea-level changes, and $\delta^{13}\text{C}_{\text{org}}$, $\delta^{18}\text{O}$ and $p\text{CO}_2$ variations in relation with paleotemperatures, the age of the onset of the CAMP-related basaltic volcanism in the northeastern United States (Newark Supergroup) and Morocco (Argana Basin) and the ages of the two distinct End Triassic (ammonoids) and Earliest Jurassic (terrestrial plants) extinctions.

The chronology, established by ammonoids and U-Pb dating, implies that the Newark supergroup basalt postdates the ETE and the disappearance of the latest Triassic ammonite *Choristoceras crickmayi* (Guex et al. 2004; Schoene et al. 2010). The delay between the recovery of the Jurassic ammonites and the extinction of the very last Triassic ammonoids lasted at least 200 kyr (probably more), based on sedimentary rates in Northern Peru and Nevada. The extinction of the last Triassic

ammonoids in the uppermost Rhaetian correlated with a strong negative excursion of $\delta^{13}\text{C}$ and a marine regression (Guex et al. 2004). The $\delta^{18}\text{O}$ record indicates a cooling episode, which could explain the regressive event recorded in the upper Rhaetian of Austria, England and Nevada. The initial regression is followed by a significant sea-level rise potentially associated with large volcanic CO_2 emissions related to the CAMP basaltic volcanism. A major plant extinction is correlated with the greenhouse conditions that postdates the ETE by at least a few hundred thousand years. The plant extinction is recorded in Greenland (McElwain et al. 1999, 2009), and is associated with a second negative $\delta^{13}\text{C}$ recorded in the Hettangian *Psiloceras planorbis* beds (coeval with *P. pacificum*). The recovery of the ammonites after the End Triassic extinction calibrated with the geochronological data illustrated in Guex (2016) (Fig. 2.4), demonstrating a partial correlation between the $\delta^{13}\text{C}_{\text{org}}$ curve and the diversity fluctuations, and a precise correlation between the well-known first negative excursion of the organic with the peak of the Rhaetian extinction.

The second negative excursion is restricted to the *Psiloceras* zone. The mid-Hettangian slowdown of the diversification is followed by an explosion of the diversity in the Upper Hettangian, and by a new positive excursion of the organic carbon. However, we note that the minimum of the ammonite diversity (D') occurs later than the minimum of the $\delta^{13}\text{C}_{\text{org}}$ curve, which is located between the *P. pacificum* and *Kammerkarites* beds.

A similar model has been proposed for the Pliensbachian Toarcian crisis, which is known to be correlated with the onset of the Karoo-Ferrar large igneous province (Pálffy and Smith 2000). Recent high-precision U-Pb dating on zircons of major sill intrusions in the Karoo basin can be directly correlated with the well-known Toarcian Oceanic Anoxic Event (OAE), and is concomitant with these sill intrusions into organic rich sediments of that basin (Guex et al. 2012b; Sell et al. 2014). A synthesis of the major isotopic variations through the available geochronological data and major sea-level variations allows an investigation into whether and how the geochemical and biochronological data can be correlated with the magmatic activity of the Karoo-Ferrar LIP.

The end-Pliensbachian extinction, preceding the Toarcian AOE by a few hundred kyr (Dera et al. 2010), is marked by an important diversity drop (disappearance of 90% of the ammonite taxa) associated with a generalised sedimentary gap linked to a marked regression event in NW-Europe and the Pacific area.

This regression was interpreted as being due to a major short-lived glaciation (Guex et al. 2001, 2012b) coeval with the main extinction event preceding the main basalt eruptions. Our major arguments refer to an important emersion topography observed on seismic images of the North Sea (Marjanac and Steel 1997), to the evidence of polar ice storage (Price 1999) and to the deposition of thick conglomerates (Dunlap Formation in Nevada (USA) (Muller and Ferguson 1939) and Ururoa—Kawhia area, New Zealand (Hudson 2003)). The cooling model is supported by recent $\delta^{18}\text{O}$ data on belemnites (Gómez et al. 2008; Harazim et al. 2012), and by the discovery of glendonites in the upper part of the Pliensbachian (Suan et al. 2011). The origin of the major cooling is probably related to huge volcanogenic SO_2 degas-

sing during the Late Pliensbachian preceding the major CO₂ emissions of the Early Toarcian (Guex et al. 2001).

The regressive phase is followed, after a few hundred thousand years, by a worldwide transgression during the Early Toarcian, with the deposition of black shale associated with the Toarcian OAE. The Toarcian OAE itself is responsible for a second extinction affecting mainly benthic foraminifera populations and brachiopods. Radiolarians were also affected, but their extinction was apparently slightly delayed in comparison with the benthos, and probably coincided with a drastic fertility drop just after the OAE.

The succession of ice house conditions immediately followed by super-greenhouse conditions can be explained thanks to a petrological model explaining the SO₂-dominated vs. CO₂-dominated degassing couplet generating the successive cold and hot conditions (Guex et al. 2016). The model invokes a thermal erosion of the cratonic lithosphere, inducing giant H₂S/SO₂ release from sulphur-bearing basal continental crust before CO₂ becomes the dominant gas associated with the giant basalt emission.

During moderate (i.e. not sublethal) environmental stress, the morphological response of many invertebrates consists often of a loss of symmetry (is this reverse evolution?), very well described by Hoffmann and Parsons (1991). Some paleontological examples will be described further in this book by Venec Peyre and Lipp.

During the major extinctions, several phyla tend to reverse their evolution and give rise to primitive-looking forms. Such reversal can be illustrated diagrammatically using one single relatively simple curve discovered by Thom (1972): the cusp catastrophe.

The catastrophe theory is a domain of the differential topology, which was invented by René Thom (1972). It aims at building the simplest continuous dynamic model, which can generate a morphology, given empirically, or a set of discontinuous phenomena.

Thom's theory concerns the phenomena where a gradual and relatively slow change produces a sudden jump of the state of the system. Such phenomena are called catastrophes. The graphical representation known under the name of "cusp catastrophe" is ideal to describe empirically the cases of the evolutionary jumps, which arise during gradual changes in the environmental stress. The surface illustrated in Fig. 1.3 represents the variable, which characterises the more or less advanced state of a taxonomic group, which varies during evolutionary space-time. This state is controlled by two parameters, which, in our case, are environmental stress and time factor.

When these parameters vary, the curve of the state of the taxonomic group under study follows a trajectory, which depends on the time and intensity of the environmental stress. When the stress gradually reaches a certain threshold, the evolutionary state of the evolving system arrives at the border of the cusp, and a jump occurs towards a previous state of a more primitive aspect. In this introduction we will use such simple diagrams to describe reverse phenomena characteristic of retrograde evolution.

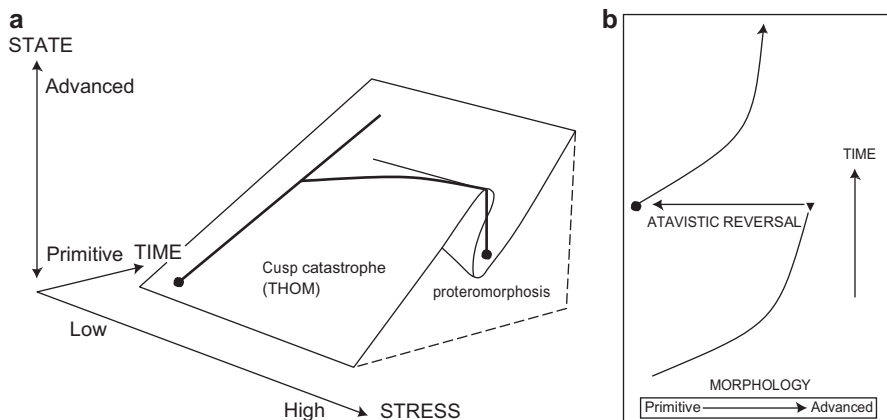


Fig. 1.3 The cusp catastrophe of Thom. (a) Stress and time are the parameters controlling the state of the evolving system (primitive–advanced). (b) Simplified graphic representation of (a)

One Example of Planktonic Foraminifera

A fundamental example of a Cretaceous planktonic foraminiferal anagenetic lineage starting from a very primitive form (evolute with simple rounded chambers), and giving rise to more complex forms with an involute and carinated shell, was recently identified in the lineage *Ticinella-Thalmaninella* (Desmares et al. 2008; Fig. 3.1). During the major Cenomanian oceanic anoxic event OAE2, the end forms of the lineage (group of *Thalmaninella greenhornensis*) gave rise to a very simplified atavistic group (*Thalmaninella multiloculata*, also called “*Anaticinella*”), which is a quasi-homeomorph of its ticinellid ancestor. Here we present these discoveries (Desmares et al. 2008) in light of what is known about the influence of high environmental stress on the development and variability of some other marine invertebrates.

The stratigraphic interval considered in the present section spans from the Late Albian to Late Cenomanian. There are records of two major environmental perturbations in this period: the Mid-Cenomanian Event and the Oceanic Anoxic Event called OAE2. These two anoxic events have markedly influenced the evolution of the *Ticinella-Thalmaninella* lineage, as well as two diverging lineages represented by *Rotalipora montsalvensis-praemontsalvensis* and *montsalvensis-planconvexa* (Gonzalez-Donoso et al. 2007). The stratigraphic distribution and outline of the phylogeny of these lineages are shown in Fig. 3.1 (from Desmares et al. 2008, modified; see also Caron 1985; Robaszynski and Caron 1995 for the stratigraphic details, and Guex et al. 2012b for discussion) (Fig. 1.4).

The anagenetic *Ticinella-Thalmaninella* lineage represents an example of geometrical transformation, which is quite similar to what is known for many lineages of ammonites.

The “*Anaticinella*” plexus:

During the onset of the anoxic event OAE2, the intraspecific variability of *Thalmaninella greenhornensis* increases remarkably; this group gives rise to *Thalmaninella multiloculata*, a “species” (morphospecies) with an indistinctly

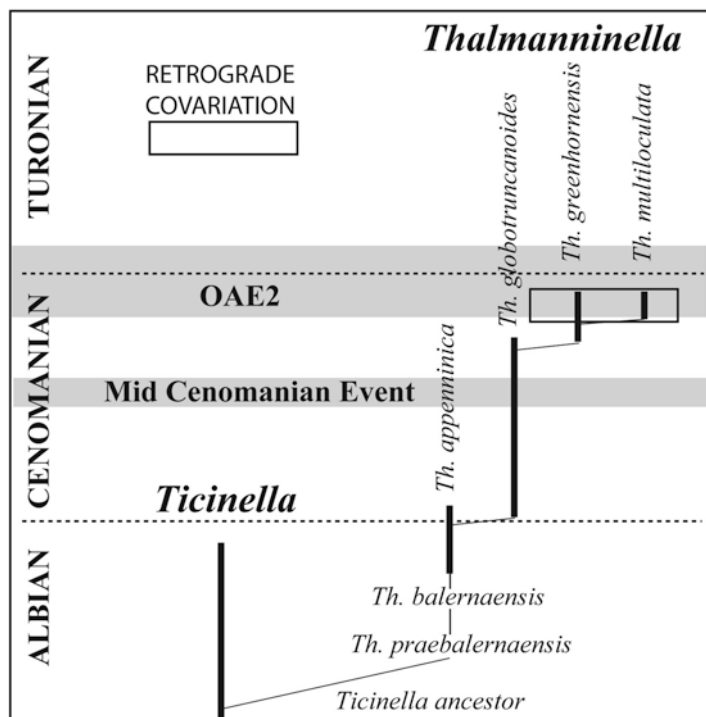


Fig. 1.4 The *Ticinella*-*Thalmaninella* lineage

marked or absent keel, which is the last member of the *ticinellid-thalmaninellid* lineage (Desmares et al. 2008).

Th. greenhornensis is a complex trochospiral species that displays raised sutures on the spiral side, supplementary apertures on the umbilical side and a single keel. It further presents umbilical secondary apertures and non-inflated chambers on the umbilical side.

Globular morphotypes with supplementary apertures also occur in the same assemblages as the keeled ones. They were initially referred to as *Anaticinella multiloculata* (Eicher 1972), which was first described in the North American Basin (Eicher 1972) (Fig. 1.5).

In all Upper Cenomanian Western Interior Seaway outcrops, transitional specimens between the keeled forms of *Th. greenhornensis* and the globular morphotypes of *Th. multiloculata* were observed (Desmares et al. 2008). These morphotypes do not have a keel on all chambers of their final whorls. Where present, the keel is more or less pronounced, i.e. from indistinctly marked to thick and protruding. From *Th. greenhornensis* to *Th. multiloculata*, the chambers evolve progressively from crescentic to globular shape, the raised sutures become more depressed and the periumbilical flanges disappear progressively on the umbilical side. The junction between the sutures and the periphery that is oblique in *Th. greenhornensis*

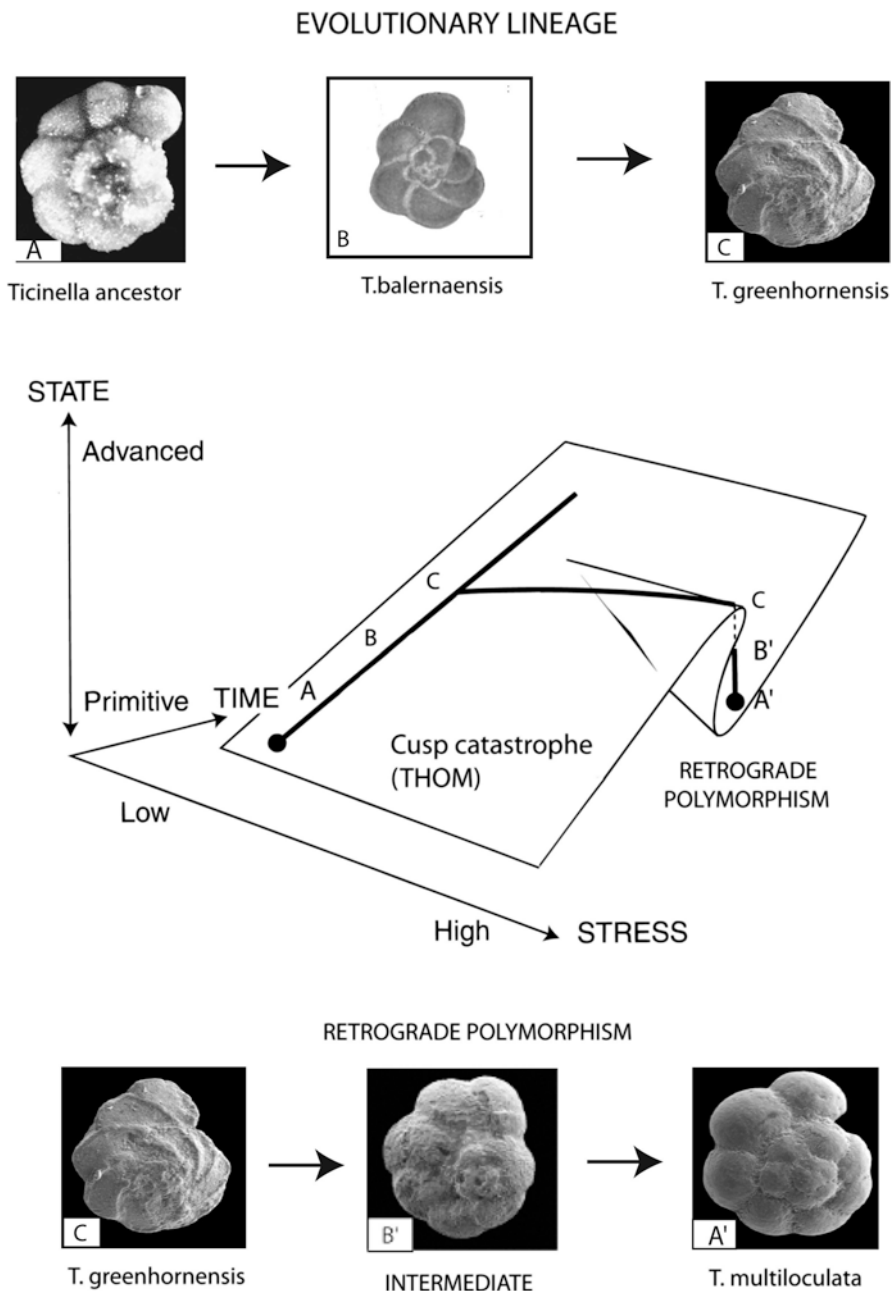


Fig. 1.5 Retrograde polymorphism affecting the *Thalmaninella* lineage during the upper Cenomanian anoxic event (data reinterpreted from Desmares et al. 2008; see Guex et al. 2012b)

becomes perpendicular in *Th. multiloculata*. In lateral view, specimens of *Th. greenhornensis* that are compressed in form gradually change to a globular shape (Desmares et al. 2008).

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Chapter 2

The Controversial Cope's, Haeckel's and Dollo's Evolutionary Rules: The Role of Evolutionary Retrogradation



Jean Guex

Abstract The goal of this chapter is to discuss old problems and recent polemics related to the famous Cope's, Dollo's and Haeckel's rules. The first concerns phyletic size increase: that sort of trend is observed in a multitude of phyla and shows several exceptions during periods of environmental stress. The second rule is discussed with some details because evolutionary reversions of trends are also frequent during stress episodes. The third trend, terminal addition, is very common and one can observe numerous cases where characters that are added late in phylogeny are also the first to be deleted during external stress phases. The addition of new elements at the end of ontogeny is frequently concomitant with size increases (Cope's trend).

There are many sorts of stress that are recorded in the stratigraphical data: major pollutions due to the development of massive volcanism (large igneous provinces), major climate changes due to plate tectonics, etc.

Our main examples of reverse evolution are observed in nautiloids, conodonts, planktonic foraminifera, benthic foraminifera, ammonoids, silicoflagellids, corals, trilobites, etc.

Keywords Cope's · Dollo's · Haeckel's rules · A short review

2.1 Cope's Rule

2.1.1 *Some of Its Consequences*

The best documented evolutionary trend in the paleontological record is the famous "rule" of size increase, also known as "Cope's rule", eponymously named for the American vertebrate specialist who described it for the first time in 1896 (Cope 1896; see also Stanley 1973). A fascinating global view of that phenomenon has

J. Guex (✉)

Institute of Earth Sciences, Geopolis, UNIL, CH 1015 Lausanne, Switzerland

e-mail: jean.guex@unil.ch

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been published recently in the Atlas of Vertebrates by Escher and Marchant (2016): almost all the vertebrate lineages show a clear tendency to increase their size over long periods of time, except during periods of major stress, when they show either a decrease in size or an extinction. The trend in size increase is more often observed at the beginning of evolutionary lineages, and much less often at the end of lineages, when organisms have attained their maximal size. They can remain unchanged for long periods, or show fluctuations in size, directed just as well towards size increase as towards size reduction, depending on environmental variations (water temperature, chemistry, etc.). The ignorance of this fact has often led to ill-founded criticisms of the Cope's rule (Gould 1996; Jablonski 1997; see Thom 1983, p. 127). The goal of this chapter is, in part, to show that this rule could be a particular case of a more general rule stating that the increases in size, surface and volume vary independently (Guex 2003). This has significant consequences for the general geometry and ornamentation of the different groups discussed in our recent book on reverse evolution concerning nautiloids, conodonts, planktonic foraminifera, benthic foramina, ammonoids, silicoflagellids and corals (Guex 2016). Major evolutionary trends observable in many groups of marine invertebrates suggest that multiple trends in the increasing involution of coiled shells (often correlated with the development of smooth forms), or of ornamental characters, are directly connected to the geometrical variations affecting the size of the organism. The evolutionary trend most frequently observed in Mesozoic ammonoids, particularly at the family level, is where the ancestral forms have an open umbilicus (evolute), and where the descendants tend to develop a narrow umbilicus (involute and less ornamented). This trend was recognised more than 100 years ago by Hyatt (1869) in Liassic ammonites, and it appeared for the first time during the Devonian, at the beginning of the history of this group (Erben 1966). When it is completely realised, this trend starts with an open umbilicus and increases the overlap of the coiling (i.e. this is an independent consequence of the usual Cope's trend, accompanied by a surface increase of the mantle). Over the course of time, this leads to the genesis of lenticular forms (oxycones), or more or less spherical (sphaerocones) ones, or a section being depressed (cadicones). The ammonites also often show a trend to increase the sinuosity of the growth lines, and many show an increase in sutural complexity in the course of time. The major trend with increasing involution observed in the ammonites is also observed in nautiloids (Sobolev 1994) and in some gastropods (Runnegar 1987).

This trend also affects many unicellular groups like benthic and planktonic foraminifera at various stages of their development (e.g. the appearance of *Orbulina* (Cifelli 1969; Hottinger and Drobne 1988; Septfontaine 1988; Adams 1983)). Some benthic foraminifera develop an increase in lateral elongation (Hottinger and Drobne 1988), which geometrically corresponds to the development of cadicone coiling in ammonites. Other groups of microorganisms like the nassellarian radiolarians display a similar phenomenon, with the increase in sphericity and reduction amongst segments (Riedel and Sanfilippo 1981), and, as an ultimate result, cryptocephalisation and cryptothoracisation (Dumitrica 1970). Spherical forms like *Paracannopilus* also develop from spicular forms in

the silicoflagellids (chrysophytes). Note in passing that these transformations can also be concomitant with an increase in the size of the organism. The specialists who have described these trends almost always provide an adaptive explanation, and an ad hoc morphofunctional origination such as improvement of the hydrodynamism. The increasing involution observed in ammonites is generally explained by a minimisation of the quantity of shell necessary to protect the animal, or by an increased hydrodynamism (Raup 1967). The discrepancy between lenticular, involuted and spherical shells seems however to show that it is not about a mechanism of optimisation of the use of shell material because the lenticular, involuted or laterally compressed forms are very frequent in the fossil record, and are far from being optimal from this point of view. Other authors explain the increasing involution of the shells and the complexification of the suture lines as an increase in the mechanical resistance to hydrostatic pressure. In benthic foraminifera, the increase in surface is supposed to facilitate the exchange of oxygen, and the increase in the elongation of the test would also increase the mobility of the animal in the loose sediment. These trends are all observed in very diverse phyla like planktonic organisms, as well as in benthic or burrowing forms. It is well known that in itself, the increase in size can be lethal, in the more or less short term, in lots of descendants. Ad hoc functional explanations are hardly satisfactory because the trends discussed above are observed in very diverse phyla, including planktonic, nektonic, benthic and burrowing organisms. Moreover, it is also well known that continuous size increase usually leads to gigantism, which can prove to be fatal within 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 in involution. Similarly, a decrease in linear size that is not accompanied by a decrease in volume will also lead to a drastic increase in 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 for by a simultaneous increase in the 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 in volume not compensated by a decrease in the mantle surface can explain the small juvenile bulges observed in the inner whorls of the earliest 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's stop in shell secretion is followed by a delayed restart of the soft parts' growth, generating a rotation of the growth lines.

2.1.2 Technical Remark About Some Criticisms of Cope's Rule

In “Full House”, one of the most famous books by Gould (1996), the author tries to demonstrate the absence of a global increase in complexity during the evolution of living organisms. His main argument, already discussed in Guex (2016), is that the most abundant organisms present on Earth, the bacteria, have not really evolved morphologically over the last 3 billion years. In this book, Gould uses quantitative arguments like size variations observed in the Cretaceous and Cenozoic foraminifera, and the fractal dimensions of the Ceratite suture lines during the late Palaeozoic and early Mesozoic. We will briefly examine these two quantitative arguments. His Fig. 25 (1996, p 160) shows the size variations of planktonic foraminifera during the Late Cretaceous and the Cenozoic. 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 for 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) in fact 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 lines of most ceratitids become more complex during evolution. This has been illustrated in Fig. 5.3 (Guex 2016), which shows that the ceratitic suture line of the ancestor of the highly complex phylloceratids has a fractal dimension of about 1.2, whereas 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.

2.2 Haeckel's Rule of Terminal Addition

The great Haeckel (1874) had the sad privilege of being one of the most criticised palaeontologists of his time, together with the great Lamarck. As an example, we can quote Gilbert and Barresi (2016), who wrote the following text (Internet posting): “A disastrous union of embryology and evolutionary biology was forged in the last half of the nineteenth century by the German embryologist and philosopher, Ernst Haeckel. Based on the assumption that the laws by which species arose on this planet (phylogeny) were identical to the laws by which the individuals of the species developed (ontogeny), he viewed adult organisms as the embryonic stages of more advanced organisms. This view was summarised in his “biogenetic law”, that ontogeny recapitulates phylogeny. In other words, development of advanced species was seen to pass through stages represented by adult organisms of more primitive species. In this view, the creation of new phyla is a step towards the completion of human development. In earlier epochs, only the initial stages of this development occurred, producing protists and cnidarians. Later, more stages were added sequentially until a human being evolved”. The absence of real fraud by Haeckel was established by the great biologist Richards (2008, 2009).

Ontogeny is the set of steps followed by the organism during the development of its structure. This can also be described as the series of steps appearing in the structure of the organism. This kind of rule would generate a great variety of forms deriving from the ontogeny of the first ancestor, and, as a by-product, the different possible evolutionary paths followed by the descendants of that hypothetical ancestor. This is of course too complex to be done experimentally nowadays, but it would obviously connect Haeckel's controversial biogenetic rule to the actual relationships between ontogeny and phylogeny.

Gilbert (loc. cit.) continues his criticism about Haeckel's *law of terminal addition*. “The embryo evolved new species by adding a step at the end of the previous ones. In such a view, humans evolved when the embryo of the next highest ape added a new stage. This provided a linear, not a branching, phylogeny. This is a critically important departure from what we usually consider as Darwinian evolution”. In one of his concluding remarks, Gilbert wrote also, “Indeed, half of Stephen J. Gould's 1977 book *Ontogeny and Phylogeny* is spent exorcising the ghost of Haeckel so that we could discuss evolutionary developmental biology without having to deal with the biogenetic law”. We disagree with this last statement.

Within the invertebrates, we can observe the validity of the terminal addition rule, which is very common and well recorded in the fossil record. In the modern classification of the radiolarians, based and elaborated on the ontogeny of these organisms, most of the lineages established by Dumitrica in a multitude of papers are based on the geometry of the early stages of these organisms (microsphere), which are very stable over time (see Dumitrica, in De Wever et al. 2001). The same trend can be observed in multiple foraminifera lineages. We can add that terminal addition is very common (see examples in Guex 2016), and one observes numerous cases where characters which are added late in phylogeny are also the first to be

deleted during external stress phases. The addition of new elements at the end of ontogeny is frequently concomitant with size increases (Cope's trend). Examples can be found in dinosaurs (*Diplodocus* with an important increase in the cervical vertebrae), elephants with the defences, sabretooths, felines, etc.

Torday and Miller Jr (2018; Chap. X) have provided a mechanistic explanation for terminal addition based on the principle of cell–cell communication in evolution (Torday and Rehan 2012). Since such cellular interactions are mediated by growth factors stimulating the production of second messengers, it would be inefficient to modify this stepwise process by adding on at the beginning or in the middle, hence the “terminal” addition.

2.3 Catastrophe and Retrograde Evolution

We will come back here to a very didactic example found in ammonites (Phymatoceratinae and Hammatoceratinae of the Middle and Late Toarcian) illustrated in Fig. 2.1.

At the end of the Middle Toarcian, the Euro-Boreal province was affected by a major regional regression generated by the insurrection of the western Tethys' rift shoulder (Stampfli 1993). That regressive event began a major faunal turnover, culminating 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 Grammocerotidae, which were dominant

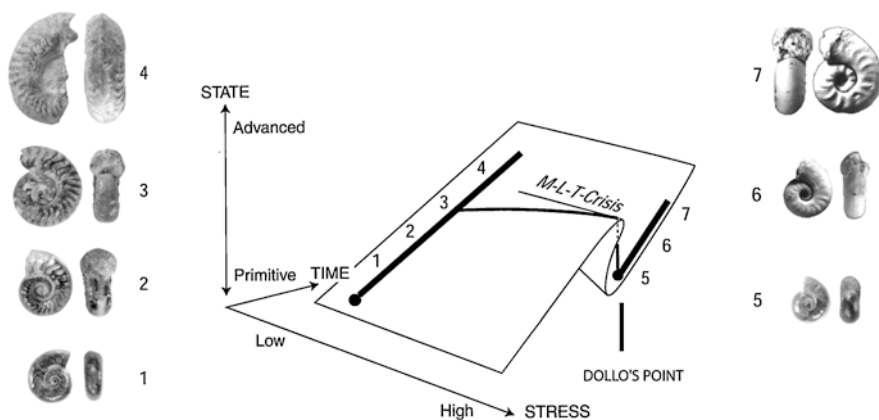


Fig. 2.1 Evolution of the lineages *Paronychoceras* (1 and 2), *Pseudobrodieia* (3) and *Brodieia* (4) in the Middle-Early Late Toarcian. Recovery of homeomorphs to extinct forms in *Onychoceras planum* (5), *O. tenue* (6) and *O. differens* (7) in the Late Toarcian. MLT = Middle-Late Toarcian Crisis. Species 5–7 appearing at the Middle-Late Toarcian crisis are quasi-homeomorphs of 1–3. Diagram not to scale. From Guex (2016), modified

during the Late Toarcian. During this stratigraphic interval, a prototypical example of atavistic reversals is observed in the microconch lineage *Paronychoceras*-*Brodieia* of the middle Toarcian Phymatoceratinae. That lineage, illustrated in Fig. 2.1, is characterised by a drastic increase in ornamental complexity, involution and size. In the Late Toarcian, that sequence is followed by the *Onychoceras* lineage, a group of unkeeled microconchs of hammatoceratids, which is atavistic and practically homeomorphic with its ancestral *Paronychoceras* (Fig. 2.1).

That case study can be analysed schematically to demonstrate the relationship between Cope's rule, terminal addition of characters and retrogradation of those characters until an atavistic point that we call "Dollo's point", beyond which the reversion would be lethal, or the shell would be lost. Figure 2.1 (1) shows the ancestor of the microconch lineage: it is smooth, with slightly evolute coiling. Its direct descendant (Fig. 2.1 (2)) is bigger and starts to develop slight ribs without a ventral keel. The next (Fig. 2.1 (3)) develops a bigger shell, and the beginning of a keel, and it is followed by forms with bifurcate ribs and a keeled venter. The end form (Fig. 2.1 (4)) is about two times bigger and develops lappets.

The Middle-Upper Toarcian crisis occurs at the boundary between the two substages; the ancestral lineage developed from *Paronychoceras* disappears, and is replaced by a new lineage starting with *Onychoceras* (Fig. 2.1 (5–7)), which follows an evolutionary morphological path identical to the ancestral one (Fig. 2.1 (1–4)).

This case study is particularly interesting because of its completeness. It shows very well the point to which the retrograde lineage cannot go further back: the Dollo's point, which will be discussed further below.

2.4 Dollo's Law of Irreversibility

Dollo's law of irreversibility of evolution was clearly explained in Dollo's (1893) seminal work on the laws of evolution in 1893. About this, he wrote "that an organism cannot return, even partially, to a previous state already realised in its ancestral series". That important sentence was rewritten by Gould 1970 as "An organism never returns exactly to a former state even if it finds itself placed in conditions of existence identical to those in which it has previously lived. But by virtue of the indestructibility of the past it always keeps some traces of the intermediate stages through which it is passed". The general opinion is that the loss of complex features in evolution is irreversible (e.g. loss of teeth in birds or loss of legs in whales). For example, Dollo had observed correctly that the protoconch of uncoiled ammonoids is fundamentally different from the initial ontogenetic stages of ancestral straight nautiloids. In fact, the existence of evolutionary inversions is extremely frequent during extinction periods (Guex 2016), but it generally does not affect the initial ontogenetic stage: there is a ratchet acting on the potential evolutionary reversal that we will discuss briefly below. Such reversals of evolution, contradicting in part Dollo's law, are generally observed during the major extinction periods, and are discussed in detail in Guex (2016: "Retrograde Evolution") (see also Marshall et al. 1994; Porter and Crandall 2003; Protas 2007).

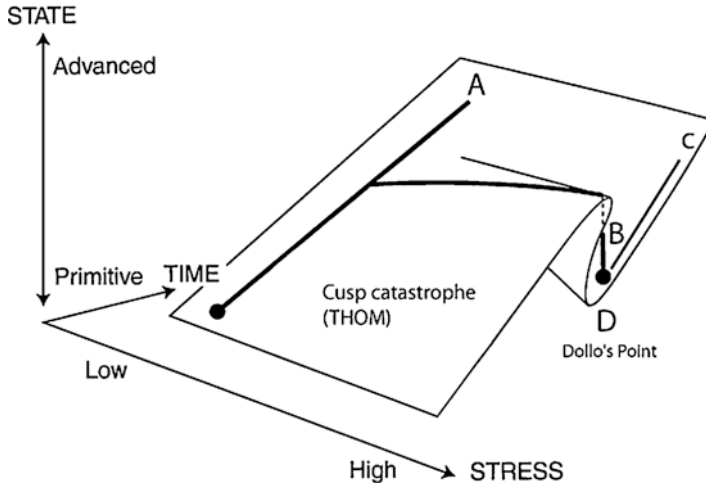


Fig. 2.2 Evolutionary trajectories of a hypothetical organism (several real examples in Guex 2016). (A) Cope's rule, terminal addition; (B) proteromorphosis, retrogradation; (C) recovery of lost characters; (D) Dollo's point

As already mentioned, we have illustrated here (Fig. 2.1) one of the cases where Cope's rule, Dollo's law and terminal addition are all observed to act in parallel in a single lineage through time. The same kinds of geometrical transformations are clearly observed in nautiloids, conodonts, planktonic foraminifera, benthic foramina, ammonoids, silicoflagellids and corals (Guex 2016). Cases of reversal not related to environmental stress are discussed in Collin and Cipriani (2003), Collin and Miglietta (2008), Teotonio and Rose (2001), Whiting et al. (2003) and Kohlsdorf and Wagner (2006).

A diagrammatic representation of the above discussion is summarised in Fig. 2.2.

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Chapter 3

Impact of the Environmental Stress on the Late Permian Pollen Grains from Zechstein Deposits of Poland



Anna Fijalkowska-Mader

Abstract Analyzing the material from the Polish Zechstein deposits, the appearance of morphologically changed gymnosperm bisaccate pollen grains was observed. These changes concern the number of sacci, their shape and size, as well as thickening of the central body exine. Most of the malformed grains were found within the *Lueckisporites virkkiae* and *Jugasporites delasaueci* conifer species, being the dominant component of the Polish Late Permian miospore assemblages. The reason for the emergence of these abnormal forms was environmental stress caused by enhanced ultraviolet-B (UV-B) irradiation connected with Siberian Trap volcanism in the Late Permian.

Keywords Environmental stress · Pollen · Late Permian

3.1 Introduction

Late Permian gymnosperm bisaccate pollen grains are characterized by a relatively large share of malformed specimens. Properly shaped wind-dispersed bisaccate pollen grain consists of a circular central body and two half-moon-shaped, symmetric air sacci, usually lighter color than central body. Bladderlike sacci enlarge volatile surface of pollen and allow them to be transported over long distances both in air and on water (Leslie 2008). By abnormal (teratological) pollen grains the number of sacci ranges from zero (asaccate form) to a few and exine (outer part of cell wall) of the central body can be thicker. In addition a limb of exine, extending over the central body, can appear.

In the Central European Basin area (named also German Basin; Fig. 3.1a) most of the malformed grains were found within the *Lueckisporites* Potonié et Klaus, *Jugasporites* Leschik, and *Triadispora* Klaus genera (Potonié and Schweitzer 1960;

A. Fijalkowska-Mader (✉)

Polish Geological Institute—National Research Institute, Holy Cross Branch, Kielce, Poland

e-mail: anna.mader@pgi.gov.pl

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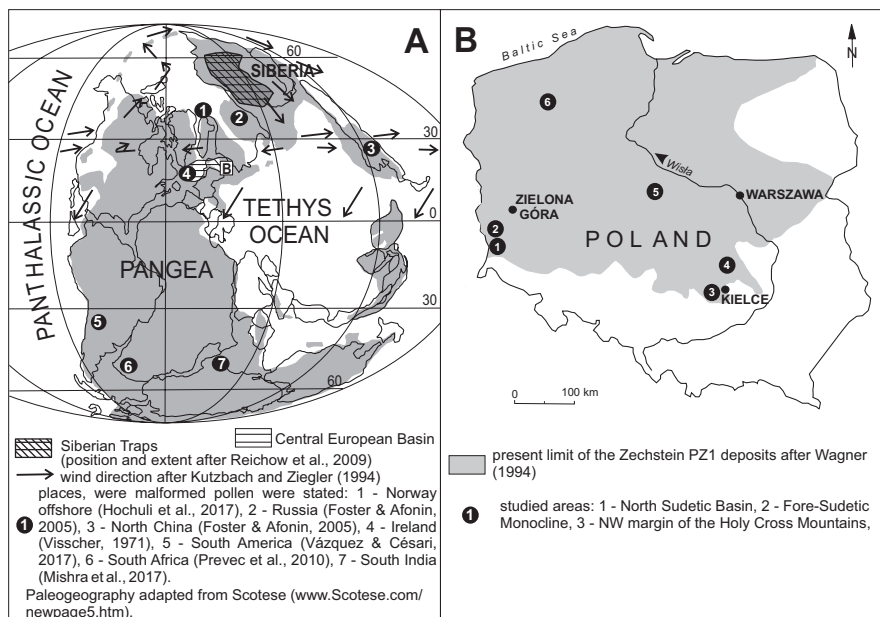


Fig. 3.1 (a) Location of Poland (b) against the paleogeographic map of the Late Permian with marked places of malformed pollen grain occurrence, (b) location of the studied areas in Poland

Grebe and Schweitzer 1962; Visscher 1971, 1972; Dybova-Jachowicz 1981; Fijałkowska-Mader 2012). All these taxa are the conifer pollen produced by *Ullmannia bronni* Goepfert, *U. frumentaria* (Schlotheim) Goepfert, and unspecified Voltziales, respectively (Potonié and Schweitzer 1960; Visscher 1971). To illustrate morphological variability within *Lueckisporites* and *Jugasporites* genera, Visscher (1971, 1972) introduced the “palynodeme” term, calling modified specimens morphological norms and marked with the symbolism from Aa and Ab—the unchanged forms—to E in case of the *Lueckisporites* palynodeme (Fig. 3.2), which were to arise through gradual, evolutionary changes. Although palynodeme concept was generally rejected by the palynologists (cf. Vázquez and Césari 2017), the norms of *Lueckisporites*, treated as malformed pollen, are still a useful tool, especially in palynostratigraphy of the Zechstein deposits in the Central Europe (cf. Visscher 1973; Fijałkowska 1994, 1995; Fijałkowska-Mader 1997; Fijałkowska-Mader 2013; Dybova-Jachowicz and Chłopek 2003; Fijałkowska-Mader et al. 2018).

Other Late Permian pollen do not show such strong variability. Within the *Jugasporites* genus it relates to the shape of the grain, number and shape of sacci, and shape of the tetrad mark. Based on these features, Visscher (1971) distinguished two morphological norms A and B.

Another example of malformed pollen grain is the trisaccate species *Triadispora visscheri* (Visscher) Fijałkowska. A similar specimen was described by Foster and Afonin (2005; Fig. 4f) from the Upper Permian of North China as a teratological form of the *Alisporites* sp.

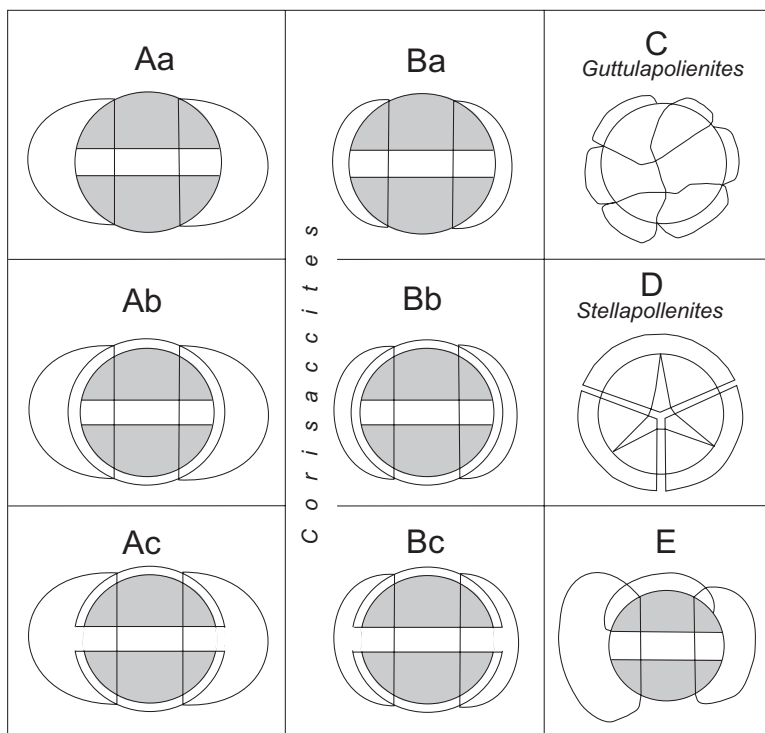


Fig. 3.2 Morphological norms within the *Lueckisporites* palynodeme after Visscher (1971, 1972)

The impulse for the author (Fijałkowska-Mader 2012) to revise the views on the causes of morphological norms within late Permian pollen grains and rejection of the theory of gradual evolutionary changes and individual variability was the work of Foster and Afonin (2005), illustrating changes in the morphology of pollen grains of the species *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius and *Alisporites* sp. from Russia and China. The authors claimed environmental stress, caused by catastrophic climate change at the end of the Permian, connected with extensive Siberian Trap volcanic activity, as the reason for these changes. Studies of Visscher et al. (2004), Hochuli et al. (2016, 2017), Black et al. (2014), Benton (2018), and Benca et al. (2018) confirmed their suggestion.

3.2 Materials and Methods

At the end of the Permian area of Poland was an eastern margin of the epicontinental Central European Basin, called also the Zechstein Basin (Fig. 3.1a), where the cyclic sedimentation of the shallow water deposits took place. Each of the four cyclothems (PZ1–PZ4; Fig. 3.3) began with marine carbonates and, through