A generalization of Cope's rule

JEAN GUEX[1]

Keywords. – Cope's Rule, Increasing involution, Ammonites, Radiolarians, Foraminifera.

Abstract. – For numerous shelly invertebrates, Cope's rule is shown in this paper to merely describe the particular case where volume increase is strictly coupled with diameter or length. Allometries, which are frequently observed in the evolution of the shells' geometry, mean that their size, volume and surface can vary independently. The consequences of this can be summarized as follows : 1) volume increase not coupled with an increase of diameter or length of the organisms generates increasing involution and/or lateral width in the shell of cephalopods, foraminifera and radiolarians ; 2) an increase of the biomineralizing surface, not coupled with volume increase, generates increasing apparent complexity in the sutures and growth lines in ammonites, and an increase in the complexity and number of chambers in foraminifera.

Généralisation de la règle de Cope

Mots clés. – Règle de Cope, Involution croissante, Ammonites, Foraminifères, Radiolaires.

Résumé. – Nous montrons ici que la fameuse "Règle de Cope" décrit uniquement les cas particuliers où l'accroissement phylétique de la taille des organismes est strictement couplé à un accroissement concomitant de leur dimension linéaire. Les allométries que l'on observe souvent dans l'évolution de la forme des organismes montrent que leur taille, volume et surface peuvent varier de façon indépendante.Les conséquences de ceci sont les suivantes. Un accroissement du volume qui n'est pas couplé avec un accroissement de la dimension linéaire des organismes induit un accroissement de l'involution et/ou de l'élongation chez les céphalopodes à coquille externe, chez les foraminifères et chez les radiolaires. Un accroissement de la surface biominéralisante non couplé avec un accroissement concomitant du volume induit une augmentation de la complexité des lignes de sutures et de la trajectoire des stries de croissance chez les ammonites et un accroissement dans le nombre et la complexité des chambres chez les foraminifères.

INTRODUCTION

Paleontologists 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 1982 ; 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 paleontologist who first observed it in the nineteenth century [Cope, 1896 ; Stanley, 1973 ; Guex, 2001a]. The most famous case, illustrated in many paleontological text-books, is the evolution of horses.

Before going further, we should note that size increase is by no means a true 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 [Guex, 1992 ; Jablonski, 1997]. One spectacular case of drastic size decrease is the one observed in planktonic foraminifera below the Cretaceous-Tertiary boundary [Guex, 1992], which could be due to the environmental stress generated by the giant volcanism of the Deccan traps dated by Courtillot and his colleagues [see Courtillot, 1995]. Such size fluctuations and trend reversals are usually dependent on environmental variations [Guex, 2001b], and increasing size mainly affects the beginning of phyletic lineages.

We also note that the term "size" is used here in a generalized sense describing simultaneously the main linear dimensions of an organism (e.g. diameter of an ammonite shell, height or length of a nasselarian radiolarian, and so on) and its volume. It is however obvious that these two parameters can vary independently from each other and, when necessary, the distinction between them will be clearly made in the following discussion.

The goal of this study is to propose a generalization of Cope's Rule. We will show that major evolutionary tendencies towards more complex features, like the apparent complexification of some ornamental traits or of geometrical features that are observed within many marine shelly invertebrates seem to be indirectly related to this "rule" (see remark below).
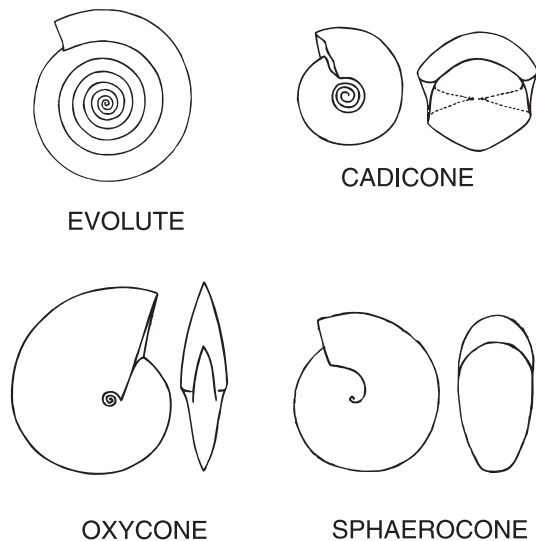
FIG .1. – Principal morphologies deriving from evolute forms observed in ammonites.
FIG. 1. – *Principales tendances à l'involution croissante observées chez les ammonites.*

FREQUENT EVOLUTIONARY TRENDS

The most frequent evolutionary trend observed in Mesozoic ammonites is where the ancestral group has an open umbilicus (i.e. evolute form) and where the descendants are involute (i.e. tightly coiled). This trend was first described in Liassic ammonites [Arietitidae : see Hyatt, 1889] and later recognized in Devonian ammonites, at the beginning of the history of the group [Erben, 1966].

The trend towards increasing involution of originally evolute shells leads either to lenticular (oxycones) or more or less spherical shells (sphaerocones) (fig.1). 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].

Some ammonite lineages also show a broad trend towards increased sinuosity of the growth-lines and, on a large time scale, this group shows an overall increase in suture line complexity.

The major trend towards increased involution in ammonites is similarly seen in nautiloids [Sobolev, 1994] and certain gastropods [Runnegar, 1981].

It is also noted that this tendency equally affects many unicellular organisms such as planktonic and benthic foraminifera (e.g. the appearance of *Orbulina*) at various stages of their development [Hottinger and Drobne, 1988 ; 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 cadicone coiling in ammonites (fig.1).

In other groups of microfossils, 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), we find that globular forms such as *Cannopilus* have evolved from simple spicular forms [Guex, 1993]. Figure 2 (A-E) represents various modes of increasing shell curvature through evolution. Notice 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.

MORPHO-FUNCTIONAL INTERPRETATIONS

Paleontologists who describe 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 involution and greater complexity of sutures increases the shells 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 morpho-functional (better resistance to predators) or pseudo-statistical (nowhere but up !) [Stanley, 1973 ; McKinney, 1990].

DECOUPLING OF VOLUME, AREA AND LENGTH

The above ad hoc explanations are hardly satisfactory because the trends discussed in this paper 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 sphaerocone ammonites (fig.1). 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 etc.

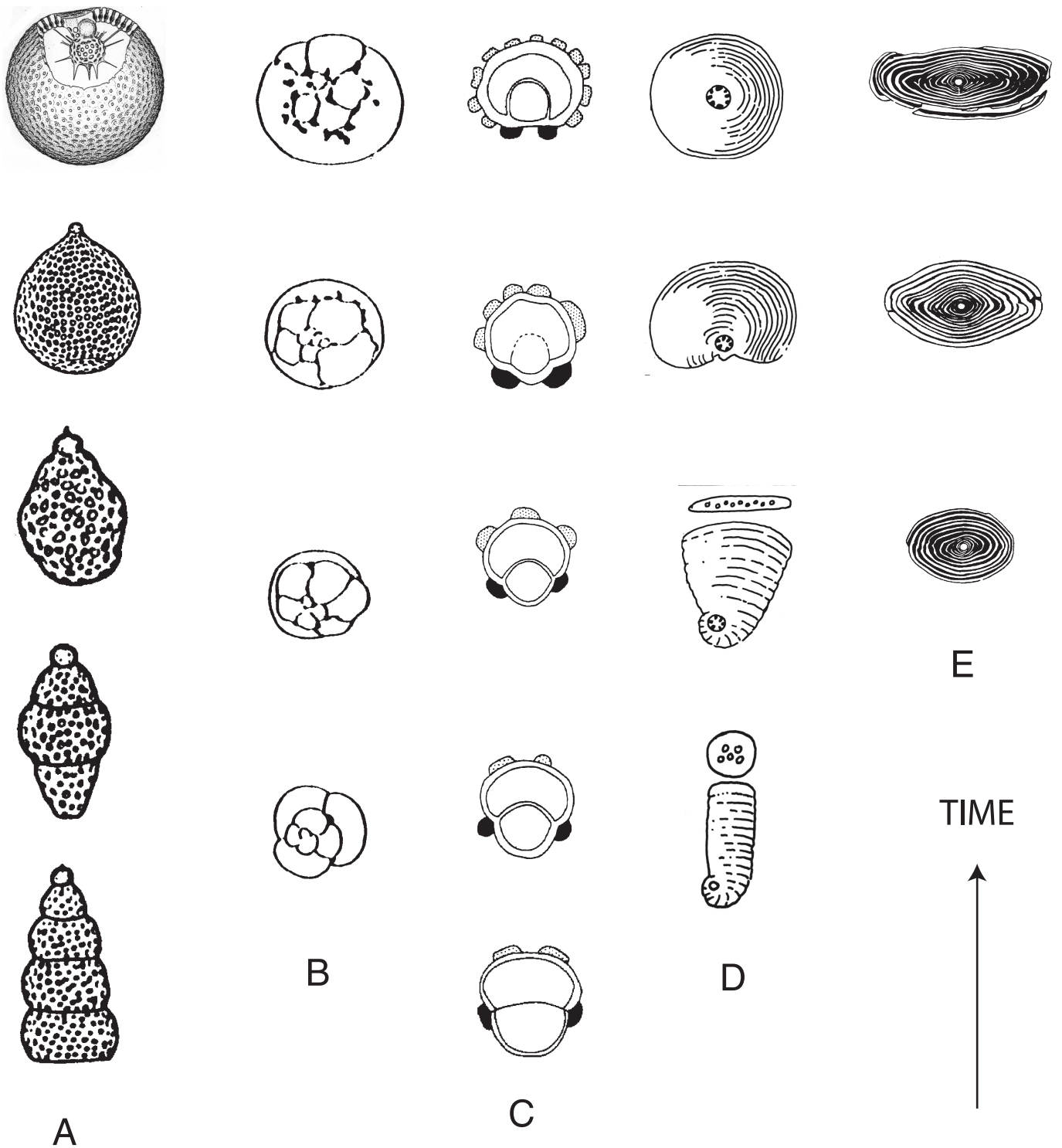An increase in involution and in complexification of internal structures observed in tests of many foraminifera,

FIG. 2. – A) Increasing involution leading to a cryptothoracisation in some nasselarian radiolarians [Sanfilippo and Riedel, 1970 ; Dumitrica, 1970]. B) Increasing involution in the *Orbulina* lineage (planktonic foraminifera [Blow, 1956 ; Cifelli, 1969]). C) Crypto-proloculinisation in *Lepidocyclina* (benthic foraminifera [Adams, 1983]). D) Increasing involution in lituolids (benthic foraminifera [Septfontaine, 1988]). E) benthic foraminifera elongation in alveolinids (benthic foraminifera [Hottinger and Drobne, 1988]).

FIG. 2. – A) *Involution croissante aboutissant à une cryptothoracisation chez certains radiolaires nassellaires [Sanfilippo et Riedel, 1970 ; Dumitrica, 1970]. B) Involution croissante dans la lignée des* Orbulina *(foraminifères planctoniques) [Blow, 1956]. C) Crypto-proloculinisation chez* Lepidocyclina *(foraminifère benthique) [Adams, 1983]. D) Involution croissante chez les lituolidés (foraminifères benthiques) [Septfontaines, 1988]. E) Augmentation de l'élongation chez les alvéolinidés (foraminifères benthiques) [Hottinger et Drobne, 1988].*

gastropods, nautiloids, radiolarians, and others clearly result from the same process. This can be summarized as follows.

From a geometric point of view, all the above trends are the result of an increase of the organism's biomineralizing surface. If the increase of that biomineralizing surface is not compensated by an increase of its main linear dimensions, there is an increase in tests' curvature.

From this we conclude that :

1) volume increase not coupled with an increase of the diameter or length generates increasing involution and/or elongation in shelly cephalopods, foraminifera and radiolarians ;

2) an increase of the biomineralizing surface, not coupled with volume increase, generates increasing apparent complexity in the sutures and growth lines in ammonites and an increase in the complexity and number of chambers in foraminifera ;

3) Cope's rule is merely a particular case of the more general rule where linear dimensions, volume and surface vary independently ;

4) most peramorphic heterochronies observed in the fossil record can be explained by a general evolutionary trend towards an increase of the biomineralizing surface.

REMARK ON A POSSIBLE LINK WITH GENOME SIZE

The absence of evident correlation between genome size and overall complexity of an organism is usually admitted [Ohno, 1970 ; Raff and Kaufman, 1983]. In spite of the above evidence, it is tempting (and not contradictory) to explain the existence of evolutionary trends that are orientated towards more complicated geometries and ornamentation by sporadic duplication of some genes or gene groups.

Finally, it should be noted that Ohno [1970] highlighted an inverse correlation between the geological age of fish and the size of their genome. According to Ohno's research (but see also Knight, 2002], the genome of very ancient, 'primitive' groups found today, is much larger than that of more recently appearing groups. In our view, genetic loss (or elimination) of redundant genes can occur during times of excess environmental stress leaving only a functional genome of reduced size [Guex, 1992, 2001b].

References

ADAMS C.G. (1983). – Speciation, phylogenesis, tectonism, climate and eustasy : factors in the evolution of Cenozoic larger foraminiferal bioprovinces. – *Syst. Assoc. Spec. Pub.* **23**, 255-289.

BLOW W.H. (1956). – Origin and evolution of the foraminiferal genus *Orbulina* D'Orbigny. – *Micropaleontology,* **2**, 57-70.

CIFELLI R. (1969). – Radiation of Cenozoic planktonic foraminifera. – *Syst. Zool.*, **18**, 154-168.

COPE E.D. (1896). – The primary factors of organic evolution. – Open Court Publishing Company, Chicago. 547 p.

COURTILLOT V. (1995). – La vie en catastrophes. – Fayard, 278 p.

DUMITRICA P. (1970). – Cryptocephalic and cryptothoracic *Nasselaria* in some Mesozoic deposits of Romania. – *Rev. Roum. Géol. Géoph.*, **14**, 45-124.

ERBEN H.K (1966). – Über den Ursprung der Ammonoidea. – *Biol. Rev.*, **41**, 641-658.

GUEX J. (1992). – Origine des sauts évolutifs chez les ammonites. – *Bull. Soc. vaudoise Sci. Nat.,* **82**, 117-144.

GUEX J. (1993). – Simplifications géométriques liées au stress écologique chez certains protistes. – *Bull. Soc. vaudoise Sci. Nat.*, **82**, 357-368.

GUEX J. (2001a). – Involution croissante et règle de Cope. – *Bull. Soc. vaudoise Sci. Nat.*, **87**, 373-379.

GUEX J. (2001b). – Environmental stress and atavism in ammonoid evolution. – *Eclogae. Geol. Helv.,* **94**, 321-328.

HASSAN M.A., WESTERMANN G. E.G., HEWITT R.A. & DOKAINISH M.A. (2002). – Finite-element analysis of simulated ammonoid septa (extinct Cephalopoda) : septal and sutural complexities do not reduce strength. – *Paleobiology*, **28**, 113-126.

HOTTINGER L. (1982). – Larger foraminifera, giant cells with a historical background. – *Naturwissenschaften,* **69**, 361-371.

HOTTINGER L. & DROBNE K. (1988). – Alvéolines tertiaires : quelques problèmes liés à la conception de l'espèce. – *Rev. Paléobiol. Genève*, *Vol. Spéc.*, **2**, 665-681.

HYATT A. (1889). – Genesis of the Arietitidae. – *Mus. Comp. Zool. Harvard Mem.*, **16**, 1-238.

JABLONSKI D. (1997). – Body-size evolution in Cretaceous molluscs and the status of Cope's rule. – *Nature*, **385**, 250-252.

KNIGHT J. (2002). – All genomes great and small. – *Nature*, **417**, 374-376.

LESS G. & KOVACS L. O. (1996). – Age-estimates by European Paleogene Orthophragminas using numerical evolutionary correlation. – *Geobios*, **29**, 261-185.

MCKINNEY M.L. (1990). – Trends in body-size evolution. *In* : K.J. McNamara, Ed., Evolutionary trends. – Belhaven Press, London.

OHNO S. (1970). – Evolution by gene duplication. – Springer Verlag, NY.

PEYBERNÈS B., FONDECAVE-WALLEZ M.J., GOURINARD Y. & EICHENE P. (1997). – Comparative sequence stratigraphy and grade-dating by planktonic foraminifera from the Campanian-Maestrichtian and Paleocene of several sections in southwestern Europe and North Africa. – *C. R. Acad. Sci.,* Paris, **324**, 839-846.

RAFF R.A. & KAUFMAN T.C. (1983). – Embryos, genes, and evolution. – Macmillan Publ. Co.

RAUP D. (1967). – Geometric analysis of shell coiling : coiling in ammonids. – *J. Pal.*, **41**, 43-65.

RUNNEGAR B. (1981). – Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. – *Lethaia*, **14** , 311-322.

SANFILIPPO A. & RIEDEL W.R. (1970). – Post-Eocene "closed" theoperid radiolarians. – *Micropal.*, **16**, 446-462.

SCHINDEWOLF O.H. (1940). – Konvergenz bei Korallen und Ammoniten. – *Fortschr. Geol. Palaeontol.*, **12**, 387-491.

SEPTFONTAINE M. (1988). – Vers une classification évolutive des Lituolidés (Foraminifères) jurassiques en milieu de plate-forme carbonatée. – *Rev. Paléobiol. Genève*, *Vol. Spéc.*, **2**, 229-256.

SOBOLEV E.S. (1994). – Stratigraphic range of Triassic boreal Nautiloidea. – *Mém. Géol. Lausanne*, **22**, 127-138.

STANLEY S.M. (1973). – An explanation for Cope's rule. – *Evolution,* **27/1**, 1-26.