# Covariation patterns in ammonoids : observations, models, and open questions.

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Since Westermann's (1966) reinterpretation of Buckman's (1887) work on Sonninids, covariation patterns have been found repeatedly among ammonoids. The observation that "roughly speaking, inclusion and compression of the whorls correlate with the amount of ornament – the most ornate species being the more evolute (i.e. lossely coiled) and having almost circular whorls ..." (Buckman, 1887) implied that the 64 distinct "species" separated in the cited work were merely morphological varieties pertaining to a single monospecific series of covariants (Westermann, 1966). Many more similar examples can be found in the literature on Cretaceous, Jurassic, Triassic, and - possibly - Paleozoic faunas (see Morard & Guex, 2003 for a review). Our own studies on Lower Jurassic faunas from western European and peri-tethyan localities have shown that covariation patterns are quite ubiquitous among Liassic ammonites. We therefore investigated more thoroughly the relationships between dimensional, ornamental and sutural shell parameters in order to better understand the dependencies of these parameters on each other and on possible third factors (internal and/or external). Moreover, theoretical simulations have shown that morphogenetic models based for example on reaction-diffusion processes could explain some of the observed links (Guex et al., 2003).

Covariation patterns were found to occur for three kinds of parameters :
1) purely dimensional (Raup's law of covariation): we observe a non random distribution of actual shell shapes in potential morphospace
2) ornamental (Buckman's law of covariation): tuberculation, rib prominence, spacing and trajectory depend on whorl proportion
3) sutural (Buckland's law of covariation): suture line complexity depends on the geometry of the inner shell tube whereas septal spacing is linked to coiling type
These patterns were studied biometrically in several Liassic families (fig.1): Domerian *Amaltheidae*, Lower Toarcian *Dactylioceratidae*, Middle-Upper Toarcian Harpoceratinae (Morard & Guex, 2003). Qualitative observations were also made on Upper Sinemurian Schlotheimiidae, Domerian Protogrammoceratinae and Upper Toarcian Phymatoceratinae.

All these data show that geometric dependencies, biomechanical constraints, as well as physiological requirements, have to be integrated in morphogenetic models. Moreover "size effects" appear to be of prime importance in ammonite growth and evolution. They can result in different morphological trends. Indeed, unidimensional changes may be accomodated by complex shape modifications (coiling, overlap, rib trajectory), rather than absolute size changes (Guex, 2001). The aim is now to try and explain the links between coiling parameters, rib formation and septal spacing through physico-chemical interactions and/or integrated growth programs. Covariation patterns indicate that a few crucial parameters might control the overall development of ammonite shells, although the final morphological expression will also be modulated by phylogenetic contingencies. Biologically, ammonite shell shape, ornamentation and structure are the product of a unique growth process with dynamically interconnected parameters.

The exact cause and evolutionary consequence of sudden bursts of variability are not yet clear, but our work revealed that covariation patterns are often linked to episodes of environmental stress. Whether it is a response to deteriorating living conditions or an effect of stress relaxation is still under investigation. Accurate multiproxy stratigraphical analyses are needed to discriminate between alternative hypotheses. Understanding the origin of variability has fundamental implications in evolutionary theory. It should be added that, within the investigated species, the widest variability spectrum is found among juvenile or subadult individuals, although initial whorls are rigorously identical. Adult morphologies tend to converge again by adopting similar mature traits (differential constraints on successive growth stages, ageing, ...).

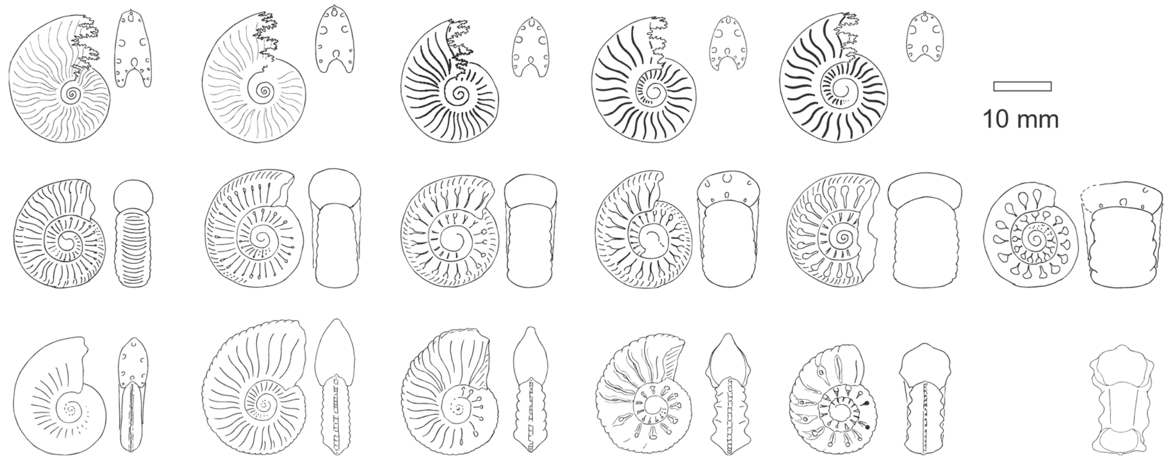


Figure 1. Examples of covariation patterns in three Liassic ammonite genera (in each case all specimens were sampled from the same bed):
Top: Upper Toarcian *Osperleioceras* from the Causses Basin
Middle : Lower Toarcian *Dactylioceras* from the Lusitanian Basin
Bottom : Middle Domerian *Amaltheus* from the Causses Basin

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