

Chapter 4

Buckman's Rules of Covariation

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4.1 Introduction

Many ammonoid taxa have long been known to show a huge degree of morphological variation of their conch (for reviews, see Kennedy and Cobban 1976; De Baets et al. 2015). Morphological variability is an important subject in evolutionary studies because genetic variation and thus its morphological reflection is one of the driving factors of evolution. To some extent, intraspecific morphological variability reflects the evolvability of species and their evolutionary dynamics by promoting diversification and by protecting against extinction (West-Eberhard 1989, 2003; Wagner and Altenberg 1996; Sniegowski and Murphy 2006; Kolbe et al. 2011). High levels of morphological variability have been attributed to various ecological and developmental mechanisms, including selection for ecological generalists in an unstable environment (Simpson 1944; Parsons 1987; but see Sheldon 1993), adaptation to a variable hydrodynamic regime (Jacobs et al. 1994), inherent developmental plasticity (Yacobucci 1999), and the lack of competitors (Erwin et al. 1987; Valentine 1995). Variations in ammonoid shell forms have been rarely studied in this context, but see Yacobucci (2004b).

This very broad range of shell shapes of many ammonoid species continues to present a challenge for delimiting and distinguishing species, which becomes even more important when it concerns taxa widely used in biostratigraphy (e.g., Reeside

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and Cobban 1960; Kennedy and Cobban 1976; Dzik 1985). However, whatever the causes of morphological variation of ammonoid shells are, these morphologies were not randomly distributed. The ammonoid shell, which grew by accretion, consists of a roughly conic, chambered, calcified conch, usually coiled (more or less regularly), which may bear ornamentation consisting of ribs, tubercles, spines, or keels. Numerous characters can be used to describe the ammonoid shell (e.g., Arkell et al. 1957; Dommergues et al. 1996; Korn 2010; Klug et al. 2015a); its morphology can be separated into three major sets of characters, which are the geometry of the shell tube (including whorl shape and degree of involution), its ornamentation, and the suture shape. These three categories all display strong patterns of covariation, which were first described over a century ago (e.g., Buckman 1892; Jayet 1929; Haas 1946) and more recently have been used to characterize the intraspecific variation of ammonoids.

In his study on Bajocian (Middle Jurassic) ammonoids from Dorset (England), Buckman (1892) noted the following observation on the genera *Sonninia* and *Amalteus*: “*roughly speaking inclusion and compression of whorls correlate with the amount of ornament—the most ornate species being the most evolute, and having almost circular whorls*” (Buckman 1892, p. 313). Later, Westermann (1966) restudied the material of Buckman. He took measurements of shell characters to quantitatively evaluate the descriptive observation of Buckman (1892). He was thus able to confirm the phenomenon, which he called “*Buckman’s first law of covariation*”: “*covariation between ornament on the one hand and the whorl section and coiling [involute/evolute] on the other*” (Westermann 1966, p. 305). He also described another relationship between ornament and suture frilling: compressed variants normally have more elongated and finely frilled suture lines (“*Buckman’s second law of covariation*”; Westermann 1966). Note that these morphological patterns will be referred to here as rules (and not laws), because a law usually describes a true, absolute and unchanging relationship among interacting elements, whereas a rule describes a frequently documented pattern (with known exceptions) in the interactions of organisms and their environments, particularly in biology (e.g., Cope’s rule, Bergmann’s rule).

This chapter aims to illustrate these patterns of covariation in the ammonoid conch and then review the various explanations for the origin of this constrained morphological variation. For a discussion of intraspecific variation of ammonoids more generally, see De Baets et al. (2015).

4.2 Rules of Covariation

4.2.1 *First Rule—The More Evolute, The More Depressed, The More Ornamented*

Buckman’s first rule of covariation was coined by Westermann (1966) for the interdependence between shell geometry (involution of the shell and shape of the whorl section) and the coarseness of shell ornamentation. In other words, the more evolute,

the more depressed and the more ornamented the ammonoid shell is (Fig. 4.1). As initially defined, this pattern of covariation holds within a species (i.e., intraspecific variation) of ammonoids. Indeed, many authors have characterized a species as a variable species ranging from compressed forms that have dense, fine ribs and small, sharp tubercles to more robust forms that have fewer but more robust ribs and more rounded tubercles (e.g., the classic example of the Cenomanian *Acanthoceras*; Kennedy and Hancock 1970; Wright and Kennedy 1987).

This pattern of covariation of some shell characters has been documented in very different taxonomic groups and time periods: Devonian agoniatitins (De Baets et al. 2013), Triassic troplitids (Silberling 1959, 1962; Tozer 1971), Spathian sibiritids and dinaritids (Dagys et al. 1999; Weitschat 2008), Anisian beyrichitins, ceratitins and arctohungaritids (Silberling and Nichols 1982; Dagys and Weitschat 1993; Dagys 2001; Monnet and Bucher 2005), Jurassic cardioceratids (Callomon 1985; Wright 2012), Toarcian hildoceratids (Morard and Guex 2003), Aalenian leioceratins (Bayer 1972; Bayer and McGhee 1984; Chandler and Callomon 2009), Oxfordian-Kimmeridgian perisphinctids (Atrops and Melendez 1993), Barremian gassendiceratins (Bert et al. 2013), Aptian deshayesitids (Martin 2003), Cretaceous hoplitids (Reside and Cobban 1960; Kennedy and Cobban 1976; Reyment and Kennedy 1998), Albian mortoniceratines (Jayet 1929), Late Cretaceous acanthoceratoids (Kennedy and Hancock 1970; Kennedy and Wright 1985; Wright and Kennedy 1984, 1987, 1990; Courville and Thierry 1993), Cenomanian schloenbachiids (Wilmsen and Mosavinia 2011), Turonian collignoniceratids (Tanabe 1993; Kennedy et al. 2001), and many others (review in De Baets et al. 2015). Although abundantly described, this pattern of covariation is rarely assessed quantitatively, even though such an approach could be used to evaluate species delimitations and investigate the evolution of intraspecific variation.

The covariation pattern involves the conch geometry (shape and coiling) and the shell ornamentation (robustness and density). The ammonoid shell geometry can be quantified by using the classical linear measurements usually supplied with systematic descriptions of ammonoid species: D, shell diameter; H, whorl height; U, umbilical diameter; W, whorl width (Klug et al. 2015). Conch geometry can be approximated with the following ratios: degree of compression of whorl section (ratio H/W; ellipsoid of whorl shell aperture), and degree of involution (ratio U/D; amount of overlap between successive whorls). These ratios provide a relative metric, which allow shells of different absolute size to be compared. Note, though, that these ratios are known to change through ontogeny.

The ornamentation of the ammonoid shell is an important diagnostic character, which has frequently been interpreted incorrectly because of the lack of recognition of the intraspecific covariation of shell characters. Ornamental characters may be relatively diverse but are described mostly as qualitative characters. The degree of ornamentation can be approximated by the density of these ornaments and by their thickness. The former (often available in the literature) can be expressed as the number of (ventral) ribs (and/or tubercles) per whorl or demi-whorl at a distinct diameter (R/D). The latter (more rarely available in the literature) can be characterized by the difference of height and width of the whorl section (H and W) measured

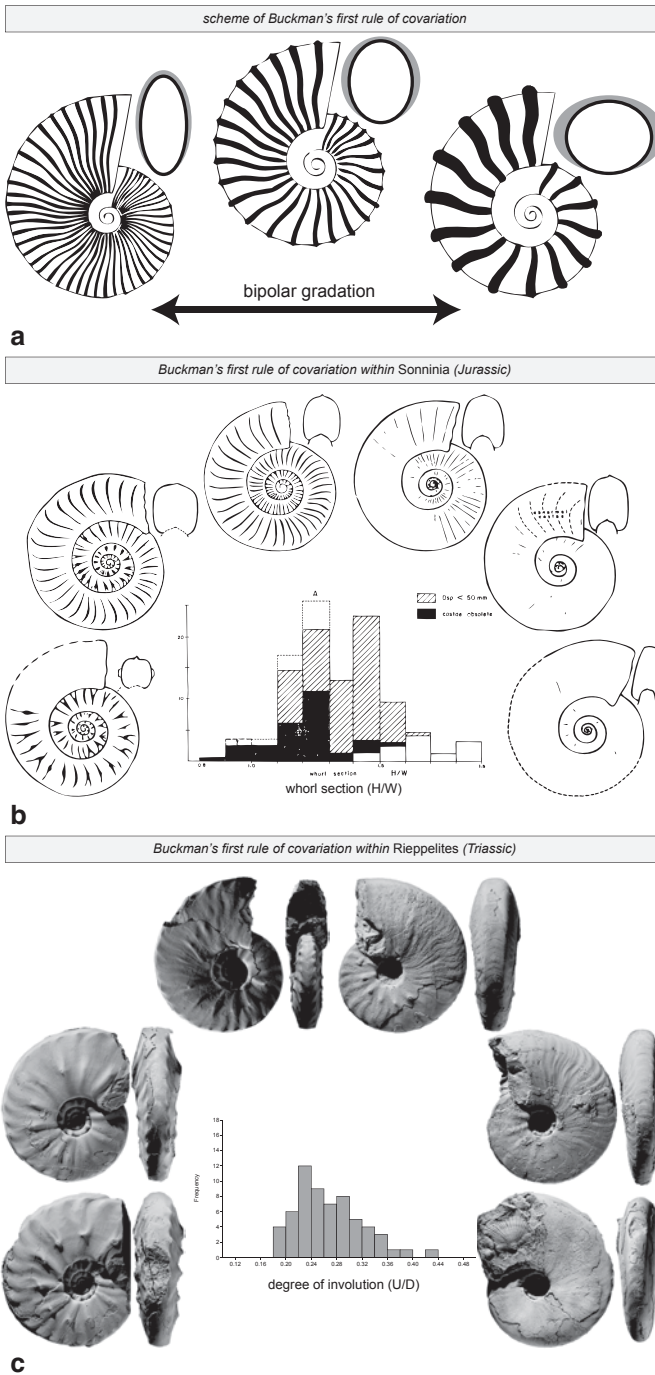


Fig. 4.1 Buckman's first rule of covariation: the more evolute, the more depressed, the more ornamented the ammonoid shell is. **a** Scheme of Buckman's first rule of covariation (modified

exactly on top of a rib and between two consecutive ribs (RH and RW, respectively; Hammer and Bucher 2005). Note that ribbing density and strength of ornamentation are mostly negatively correlated (Bert 2013; De Baets et al. 2015).

Buckman's first rule of covariation is thus the statement of a regular relationship between three characters: negative correlation between whorl compression and strength of ornamentation as well as negative correlation between whorl involution and strength of ornamentation. This kind of correlation can be evaluated by means of standard linear regression models for each pair of characters. Here, quantitative analyses have been performed using the software PAST (Hammer et al. 2001) and the statistical environment R (<http://www.r-project.org/>). These analyses and their graphical outputs are standard (e.g., Davis 2002; Hammer and Harper 2006; for a detailed application see Bert 2013). Figure 4.2 illustrates this pattern of covariation for the ammonoid species *Acrochordiceras carolinae* from the Anisian of Nevada (dataset from Monnet et al. 2010). The linear regression analysis of the covariation pattern for this species (146 specimens from a single bed) indicates that the three character sets are significantly correlated (p value lower than 1%). Whorl section (H/W) and degree of involution (U/D) are more strongly correlated ($r=0.59$), whereas density of ornamentation (R/D) is less correlated with the two other characters ($r=0.25$).

4.2.2 Second Rule—*The More Compressed, The More Frilled*

In his monographic study, Buckman (1892) also stated that in *Sonninia*, the complexity of the suture line increases in proportion to the decrease of ribbing intensity (i.e., negative correlation between suture complexity and strength of ornamentation). However, he neither illustrated nor quantified this relationship. Furthermore, this correlation had already been suggested by previous authors (for a review, see De Baets et al. 2015). Westermann (1966) referred to this covariation pattern as Buckman's second rule of covariation. Based on the first rule, a relationship between the complexity of the suture pattern and the geometry of the whorl section can be derived: the more compressed the whorl section, the more frilled the suture line (i.e. positive correlation between suture indentation and whorl compression). Contrary to the first rule, which is abundantly recognized in large samples, the second rule may not necessarily hold in all these cases (e.g., Dagens et al. 1999; Dagens 2001) or may be muted by larger constraints on suture pattern than shell shape (e.g., in *Neogastrolites* species: Yacobucci and Manship 2011).

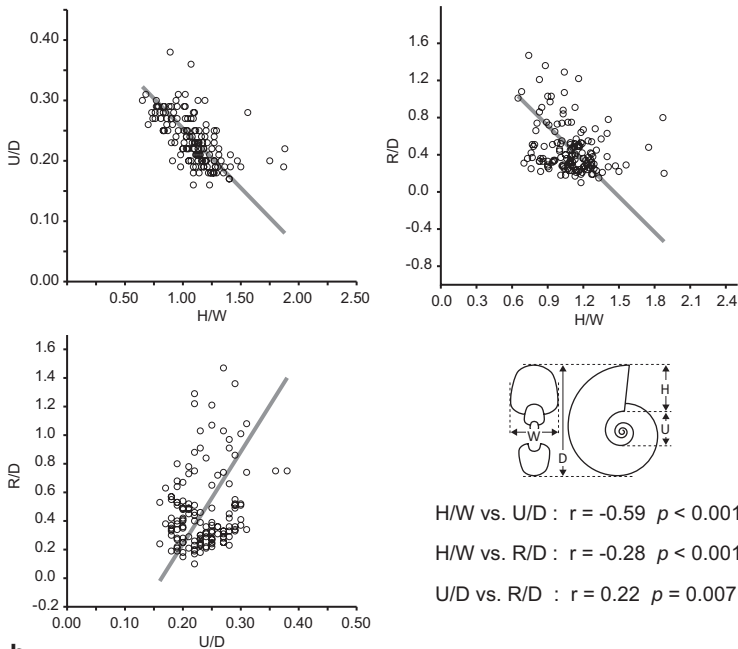
after Bert 2013): intraspecific variation of a species grades from a gracile morph (higher and tight whorl section, thin ornamentation and close umbilicus) to a robust morph (lower and broad whorl section, strong ornamentation and wide umbilicus). **b** Intergrading morphological series of *Sonninia adicra* (Bajocian) illustrating the covariation pattern between ornamentation robustness and whorl section (modified after Westermann 1966). **c** Intergrading morphological series of *Riepelites boletzkyi* (Anisian) illustrating the covariation pattern between ornamentation robustness and degree of involution (modified after Monnet and Bucher 2005)

Buckman's first rule of covariation within *Acrochordiceras* (Triassic)



a

covariation (linear correlation) between whorl compression, involution and rib density



b

Fig. 4.2 Buckman's first rule of covariation within *Acrochordiceras carolinae* (Anisian) for 146 specimens from the same stratigraphic bed. **a** Intergrading morphological series illustrating the

The suture line (imprint of septa on the conch) has been variously quantified: by simple indices such as the number of lobes (e.g., Batt 1991; Saunders et al. 1999) or by more complex indices such as fractal indices (e.g., Garcia-Ruiz et al. 1990; Boyajian and Lutz 1992; Pérez-Claros 2005; Pérez-Claros et al. 2002, 2007), by Fourier analysis (Gildner 2003; Allen 2006; Ubukata et al. 2014), by geospatial information systems (Manship 2004; Jacobucci and Manship 2011), or by Eigenshape analysis (Ubukata et al. 2010). Despite all these tools, the correlation between whorl shape, coiling and suture indentation has rarely been quantified within species. The reality of this second rule thus remains to be completely investigated. Nevertheless, shell shape and coiling are well known to have a conspicuous effect on suture pattern (Westermann 1971, 1975; Seilacher 1988; Checa and García-Ruiz 1996; Olóriz et al. 1997; Klug and Hoffmann 2015).

Note that the two rules can be merged into a single covariation pattern: the more evolute the shell, the more depressed, the more ornamented, and the less frilled is the suture. However, since the second rule is rarely tested, it is not yet known if this extended rule always holds. Finally, two additional types of covariation have been proposed. Hammer and Bucher (2006) added a potential additional rule: negative correlation between septal spacing and whorl compression (Fig. 4.3). Because of the lack of additional descriptions and datasets corroborating this latter rule, it will not be discussed further in the present study. Interestingly, Bert (2013) also described intraspecific patterns of covariation within *Gassendiceras* (Barremian), not only between two morphs like Buckman's rules of covariation, but between three morphotypes. In addition to the two classic poles usually recognized (a robust pole with thick section, evolute shell and strong ornamentation *versus* a slender pole with narrower section, involute shell and weaker ornamentation), Bert added a third morphological pole with thick section and less robust ornamentation. Additional cases are discussed by De Baets et al. (2015).

4.3 Impact of These Rules on Ammonoid Systematics

Since only hard tissues are typically fossilized for ammonoids, paleontologists necessarily define morphological species and do not have access to the interbreeding criterion of biological species (i.e., a set of interbreeding individuals reproductively isolated from other populations; e.g., Mayr 1963, 1969). Two major and opposite approaches have been used to define fossil morphospecies (for reviews on ammonoids, see Tozer 1971; Dzik 1985, 1990; Chandler and Callomon 2009; De Baets et al. 2015). The first concept ("*typological approach*") puts emphasis on every (even slight) difference in morphological characters; such an approach leads to the multiplication of species (oversplitting) and is encouraged by the concept of the

covariation pattern between ornamentation robustness, whorl section, and degree of involution. (Modified after Monnet et al. 2010). **b** Pairwise linear fitting (reduced major axis) of the three character sets (ornamentation is here evaluated by means of rib density)

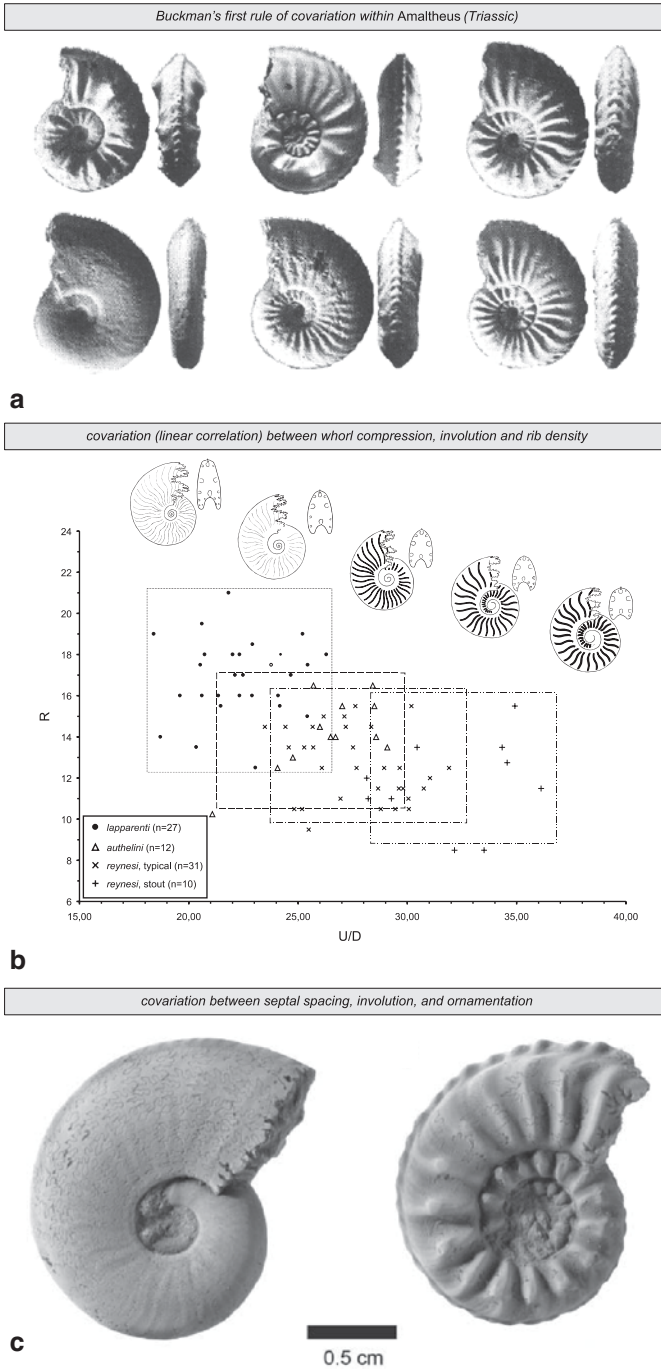


Fig. 4.3 Buckman's first rules of covariation within *Amaltheus margaritatus* (Pliensbachian). **a** Intergrading morphological series illustrating the covariation pattern between ornamentation

holotype as well as by the utility of ammonoid species as stratigraphic markers. However, many living species are known to not have such a narrow morphological variation. The second concept (population approach) takes the present-day biological species' structure into account by allowing a certain degree of morphological variation. The notion of species as an array of intergrades separated from another series of organisms between which intermediates are absent or at least rare has been formally known at least since Dobzhansky (1937). It is worth noting that it has been demonstrated that in a single interbreeding population, the quantitative, morphological characters are variable and their frequencies often follow a statistically normal distribution (e.g., Mayr 1942; Sokal and Rohlf 1995; Templeton 2006). Hence, a set of specimens showing a continuous inter-gradation of characters fitting a normal (or at least continuous and unimodal) distribution should be interpretable as variants of a single species (De Baets et al. 2015). The recognition of Buckman's rules of covariation can then serve as an aid to discriminate between ammonoid morphospecies, which may correspond to biospecies (although some discrepancies between reproductive isolation and distribution of morphological characters may inevitably occur, such as in sibling/cryptic species; e.g., Mayr 1948; Knowlton 1993; Boyle and Rodhouse 2005). Note that the criterion of normal distribution of the intergrading character states can be relaxed because it is not always strictly normal within living biospecies and because fossil populations often are biased by several geological and taphonomic processes (e.g., temporal and vertical mixing/averaging, transport; Bush et al. 2002; Kidwell and Holland 2002; Hunt 2004; review in De Baets et al. 2015).

Ammonoids, perhaps more than any other group, have suffered from taxonomic splitting (Tozer 1971; Kennedy and Cobban 1976), and authors have frequently divided intergrading populations into a whole range of typological species and even genera, which belong to what can now be regarded as a single variable species (e.g., Buckman 1892 and Westermann 1966). This problem results from the truly remarkable intraspecific variation seen among many ammonite groups (De Baets et al. 2014). Note that in some groups, end-member variants may show an extreme morphological distance and, in the absence of sufficiently large samples, may be attributed to different species or genera (e.g., taxonomic discussion in Monnet et al. 2010, p. 972; De Baets et al. 2013). The two extreme forms can be very different in their morphological proportions, but are always linked by (more frequent) intermediate forms (Weitschat 2008; De Baets et al. 2015). It is therefore critical to assess intraspecific variation from large assemblages. Recognition of this variation has led to significant simplification of the nomenclature in several cases (e.g., Reeside and Cobban 1960; Kennedy and Cobban 1976; Silberling and Nichols 1982; Wright and Kennedy 1984, 1987, 1990; Hohenegger and Tatzreiter 1992; Atrops and Melendez 1993; Weitschat 2008; Monnet et al. 2010; Bert 2013). Neglecting the population

robustness, whorl compression, and degree of involution (modified after Guex et al. 2003). **b** Scatter plot illustrating covariation of rib density and degree of involution (modified after Morard and Guex 2003). **c** Illustration of the covariation between septal density and whorl compression (modified after Hammer and Bucher 2006)

concept can lead to erroneous ecological and biostratigraphic interpretations (Dagys and Weitschat 1993) as well as overestimated values of past taxonomic richness. As a consequence, ammonoid workers have to accept that a single specimen may not necessarily be sufficient for unequivocal species identification and/ or description. This evaluation also requires that the studied assemblages are derived from a single bed in order to minimize the mixing of forms that evolved through time or that lived in different environmental settings (see Kidwell and Holland 2002). In the face of this large variation in ammonoid forms, developing species definitions is often challenging.

It is worth noting that Buckman's rules of covariation of the ammonoid shell are defined for a single species from a single sample and for regularly coiled (monomorphic) planispiral ammonoids. The systematic context for the original studies was an attempt to reduce the number of named species by recognizing that the observed range of fossil forms was, in fact, due to intraspecific variation rather than species-level differences. For instance, based on a careful re-study of *Sonninia* from the Jurassic of Dorset, which Buckman (1892) split in 64 typological species, Westermann (1966) clearly documented the pattern of covariation between the geometry of shell tube and strength of the ornamentation, and recognized a single (highly) variable species. Although a large degree of intraspecific variation in *Sonninia* is still accepted, Westermann (1966) lumped together specimens from various stratigraphic levels (e.g., Callomon 1985; Sandoval and Chandler 2000; Dietze et al. 2005) and this stratigraphic "lumping" should be avoided at the risk of synonymizing species with temporal anagenetic changes (compare Monnet et al. 2010 and Dzik 1990). Another relevant case has been described by Dagys and Weitschat (1993), who documented a case of marked intraspecific variation in a large sample of 600 specimens of *Czekanowskites rieberi* from a single concretion of Anisian age (Middle Triassic) from Arctic Siberia. Morphologically, specimens of *C. rieberi* grade from keeled, narrowly umbilicate, smooth suboxycones to widely umbilicate subcadicones with bullate, straight ribs. Dagys and Weitschat (1993) illustrated that this variation has a roughly normal distribution, which suggests that all specimens belong to a single population (for another example, see Bert 2013). Fig. 4.4 displays an example of the covariation pattern and normality of the quantitative parameters for the shells of *Acrochordiceras carolinae* from the Anisian of Nevada (dataset from Monnet et al. 2010).

A recent example of the impact of Buckman's rules of covariation on ammonoid taxonomic nomenclature has been described by Monnet et al. (2010). Based on bed-by-bed ammonoid collections in north-west Nevada, this study revised the species of *Acrochordiceras*, which is one of the most important genera of both Tethyan and North American ammonoid faunas of the Anisian (Middle Triassic). However, there was a profusion of species in the literature included in *Acrochordiceras*, mainly because of the typological taxonomic concept, which is often based on small samples and usually characterized by slight morphological differences such as a more compressed shell, coarser ribbing, or absence of tuberculation. A careful examination of these co-occurring "species" erected applying the classical typological concept reveals the presence of intermediate forms among them, thus suggesting the existence

histograms of intraspecific variation within *Acrochordiceras* (Triassic)

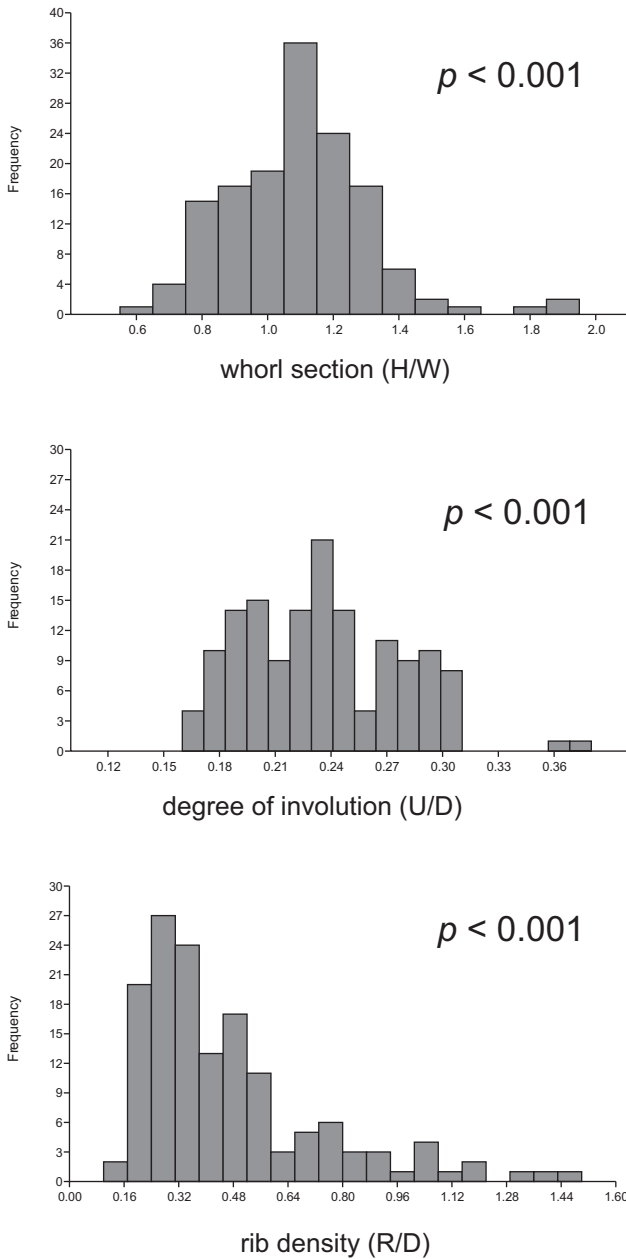


Fig. 4.4 Distribution of some characters (whorl section, coiling, and ornamentation) for 146 specimens from the same stratigraphic bed of *Acrochordiceras caroliniae* (Anisian). All characters display a normal distribution with p values significantly lower than 1 % (Shapiro–Wilk test)

of only one highly variable species. This pattern is illustrated in Fig. 4.5a, which compares the distribution of the degree of coiling (U/D) for various sizes of *Acrochordiceras carolinae* from north-west Nevada, with inclusion of values for the holotype of other synonymized species (for more details, see Monnet et al. 2010). The figure shows that *A. carolinae* has a wide range of intraspecific variation with a continuous unimodal distribution and that each old typological “species” falls within this variation. Hence, the wide range of morphological variation exhibited by acrochordiceratids illustrates Buckman’s first rule of covariation well.

When additional material is acquired through more sampling with better preserved and better stratigraphically controlled material, the revision of ammonoid species accounting for intraspecific variation usually significantly decreases species richness of ammonoid genera (Kennedy and Cobban 1976; De Baets et al. 2015). Study of additional specimens more rarely leads to the erection of additional species or the re-establishment of older ones based on previously overlooked differences in ontogeny or morphology (e.g., *Rieppelites cimeganus* in Monnet et al. 2008; *Sonninia* in De Baets et al. 2015). Therefore, the history of species taxonomy for an ammonoid genus usually is characterized by an initial rapid increase in taxonomic richness as a result of taxonomic oversplitting related to a strict typological approach, followed by a plateau with the accumulation of data, and then a decline in diversity when a better numerical grasp on intraspecific variation and finer stratigraphic resolution is achieved. The taxonomic history of the genus *Acrochordiceras* illustrates this pattern well (Fig. 4.5b). Note also that the confusion between dimorphism and continuous intraspecific variation is not uncommon, particularly when only a small sample is available (e.g., Dzik 1990; Monnet et al. 2010). Nevertheless, continuous intraspecific variation does not rule out dimorphism (see e.g., Wright and Kennedy 1984 for an example of dimorphic species in *Mantelliceras* for which each dimorph follows Buckman’s rule of covariation; further discussion in De Baets et al. 2015; Klug et al. 2015b).

4.4 Causes of Covariation

Buckman’s rules of covariation involve three sets of characters: shell shape, ornamentation, and suture patterns. What mechanism could produce such consistent and pervasive covariation across the ammonoid body plan? A helpful way to think about constraints on form was provided by Seilacher (1970) in what has come to be known as “*Seilacher’s Triangle*” (Gould 2002). The three corners of the triangle represent three categories of constraint that limit the types of forms organisms take: (1) historical/phylogenetic, (2) functional/adaptive, and (3) constructional/morphogenetic. In reality, all three types of constraint are likely to influence the anatomical forms of organisms and entangling these in fossil samples is not straightforward. Given the pervasiveness of Buckman’s covariation across a variety of ammonoid clades, phylogenetic constraints are not likely to explain the phenomenon. Several authors, though, have attempted to explain Buckman’s rules in terms of either functional or constructional constraints.

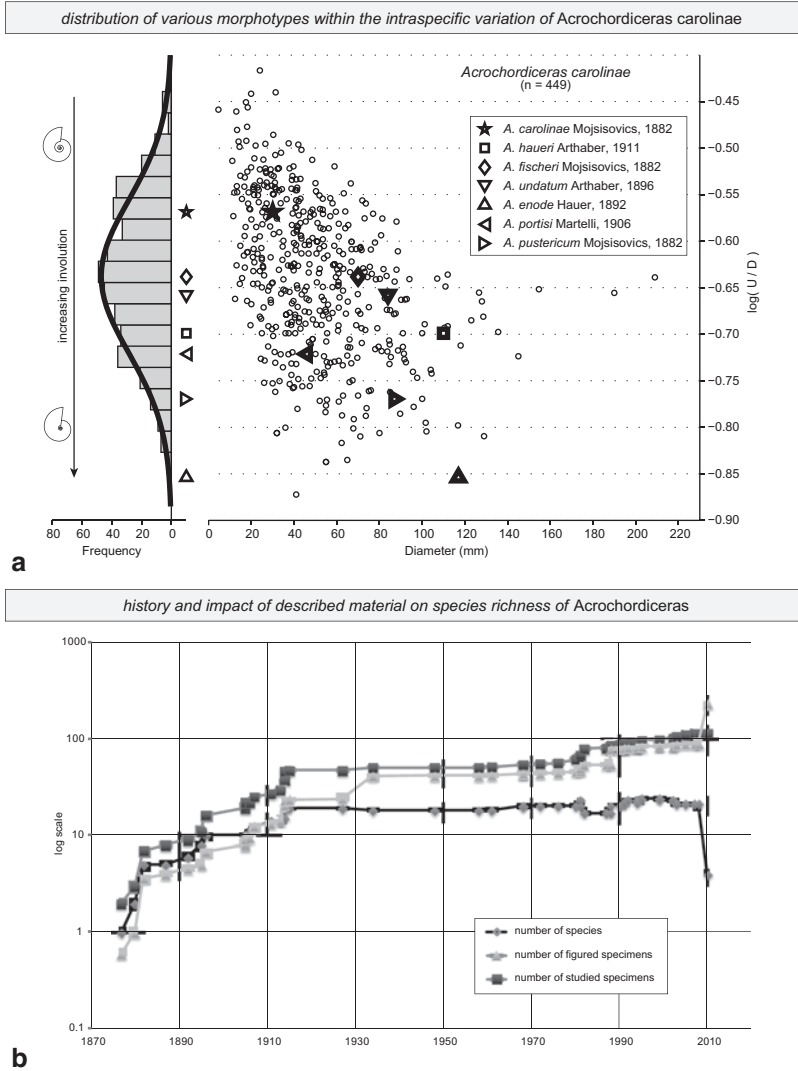


Fig. 4.5 Impact of Buckman's rules of covariation on ammonoid taxonomic nomenclature. **a** Distribution of degree of coiling (U/D) for *Acrochordiceras carolinae* Mojsisovics, 1882 in the middle Anisian from northwest Nevada (modified after Monnet et al. 2010). This diagram shows the normal distribution of U/D and the position of each species synonymized with *A. carolinae*, thus illustrating the continuous range of degree of coiling for all of the old typological species. *D* shell diameter, *U* umbilical diameter. **b** Numbers of species, figured specimens and studied specimens of the genus *Acrochordiceras* through time in the literature (unpublished data exhaustively compiling all publications with taxonomic descriptions of the genus)

4.4.1 Adaptive and Environmental Constraints

The various forms of the ammonoid shell have been largely interpreted in terms of functional needs (e.g., Dietl 1978; Jacobs 1992; Jacobs et al. 1994; Jacobs and Chamberlain 1996; Hewitt 1996; Westermann 1996; Klug and Korn 2004; Saunders et al. 2004, 2008; Klug et al. 2008), mostly in order to reconstruct the modes of life and habitats of this extinct group (e.g., Kennedy and Cobban 1976; Westermann 1996; Westermann and Tsujita 1999; Ritterbush and Bottjer 2012; Ritterbush et al. 2014). Although parts of these adaptive interpretations remain debated, the ammonoid shell has defense properties and is undoubtedly a buoyancy apparatus, which, along with shell shape, structure, and ornamentation, impose hydrodynamic limits on the animal's swimming abilities (e.g., Saunders and Shapiro 1986; Elmi 1993; Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000; De Blasio 2008; Ifrim 2013). The sometimes extreme intraspecific variation and covariation of characters of ammonoids challenge current and past ideas about a close correlation between mode of life and shell morphology in ammonoids (Dagys and Weitschat 1993; Dagys et al. 1999; reviewed in De Baets et al. 2015).

Checa et al. (1997) argued that the usual morphological covariation observed within ammonoid species (involution–whorl section–ornamentation) might result from a selection pressure to maintain a similar hydrodynamic performance among the morphotypes. Indeed, based on calculation of the center of gravity for a population of *Czekanowskites rieberi*, which illustrates Buckman's first rule of covariation well (Dagys and Weitschat 1993), Checa et al. (1997) demonstrated that, despite the extreme morphological variation, hydrostatic (orientation) and hydrodynamic (stability) properties of the population remained within narrow limits. Hence, covariation may be a way of regulating the major hydrostatic parameters at population and ontogenetic levels, thus supporting this functional interpretation of shell shape (Hammer and Bucher 2006). Kawabe (2003) documented for Cenomanian ammonoids that compressed forms tend to inhabit high-energy sandy inner shelf environments and depressed forms tend to occur in low-energy offshore mud facies, but external shell ornamentation does not necessarily vary according to lithofacies differences. A similar pattern has also been documented by Landman and Waage (1993a) for Maastrichtian *Scaphites* and by Jacobs et al. (1994) for Turonian *Scaphites whitfieldi*, which shows a similar correlation between nearshore–offshore environments and whorl shape compression (additional examples are discussed in De Baets et al. 2015). Hence, Buckman's rules of covariation may result from an ecophenotypic response to habitats with different energy. However, some authors reported the exactly opposite pattern, with more depressed and heavily ornamented forms in shallower water, thus questioning this functional interpretation (Fig. 4.6; Wilmsen and Mosavinia 2011). Batt (1989) showed that the distribution of various morphotypes of Cenomanian ammonoids in the Western Interior partially reflects environmental gradients (e.g., water depth), especially among different lineages. Furthermore, size (ontogenetic stage) probably plays an important role in controlling the amplitude of these adaptive constraints, which may be reduced at small sizes.

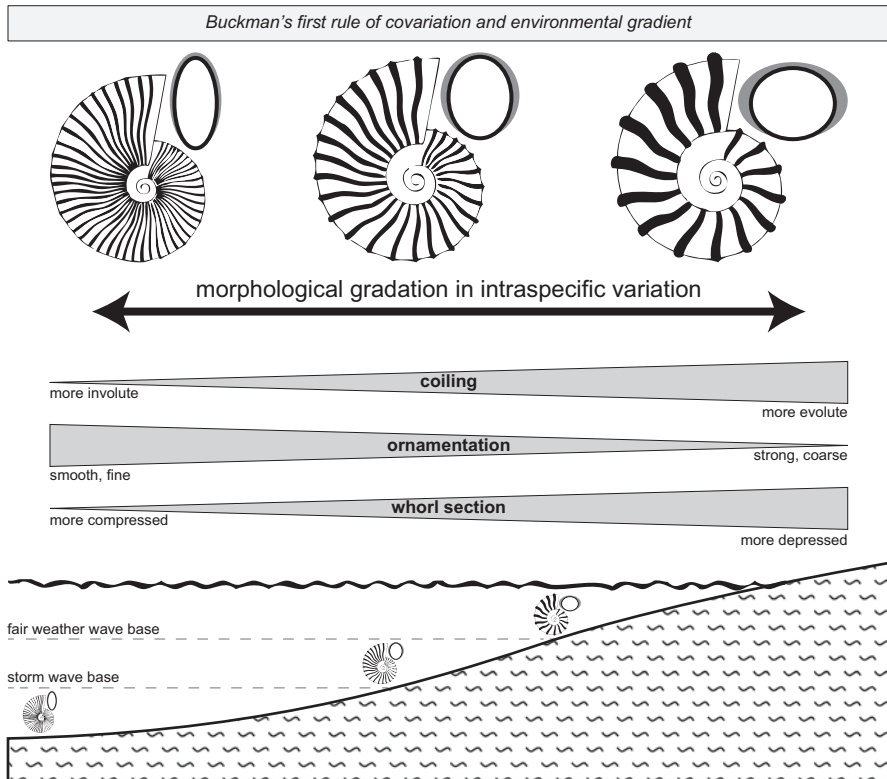


Fig. 4.6 Buckman's rules of covariation and ecophenotypism. Ammonoid intraspecific variation of its shell morphology is often reported to be ordered along a paleoenvironmental gradient (especially water depth as reflected by proximal–distal facies): strongly tuberculate, depressed forms reflect comparatively shallow, nearshore environments with higher water energy and predation pressure, whereas compressed, weakly ornamented morphs are forms of open (and deeper) marine waters. (See, e.g., Wilmsen and Mosavinia 2011; but compare with Bayer and McGhee 1984 and Jacobs et al. 1994 who reported the exact opposite pattern)

In contrast to the previous interpretations, Westermann (1966) and Reyment (1988) argued against any adaptive cause of this intraspecific covariation pattern. They maintained that the occurrence of such a large morphological variation within a single species and its abundant presence in distantly related groups through time and space is unlikely to reflect ecophenotypism. Paleogeographic differences also do not seem to impact the covariation patterns: e.g., the low paleolatitude *Acrochordiceras* and the high paleolatitude *Czekanowskites* (Anisian) show similar patterns of covariation (Dagys and Weitschat 1993; Monnet et al. 2010).

The covariation between suture indentation and shell ornamentation may also reflect functional constraints, in this case resulting from the role of suture complexity in stiffening the phragmocone (the more indented the suture, the more resistant the shell to hydrostatic pressure; Westermann 1966). However, the function of the

septal folding is still the subject of much debate and several hypotheses have been proposed (Klug and Hoffmann 2015), so the hypothesis about shell stiffening might prove to be invalid.

With regard to the covariation between septal spacing and whorl compression, Hammer and Bucher (2006) explained it in terms of hydrostatic properties. They calculated that, under equal lengthening of the body chamber during growth, the buoyancy of compressed forms is more affected. Hence, this covariation pattern can be explained by function: in order to retain neutral buoyancy, the more compressed forms must construct septa more often than the depressed morphs. However, given the often very variable septal spacing of sutures within species (e.g., Paul 2011), this covariation requires additional studies to be further tested. Kraft et al. (2008) documented cases of non-mature septal crowding in Carboniferous ammonoids and suggested that close septal spacing can be interpreted as a response to adverse ecological conditions, which caused growth deceleration.

4.4.2 *Constructional and Developmental Constraints*

With regard to the first rule of covariation (the more evolute, the more depressed, the more ornamented), several authors have argued for morphogenetic explanations. Westermann (1966) stressed that the correlation between H/W and U/D is logical, at least partially, because whorl height (H) is part of the diameter (D) (Sokal and Sneath 1963). Hence, the fact that evolute whorls are much more rounded than involute whorls in part due to a single varying dorso-ventral growth vector. Westermann (1966) also tentatively proposed that the amplitude (robustness) of shell ornamentation (ribs, spines) is a function of the growth rate for whorl width (W) and thus varies with whorl roundness (H/W). Westermann (1966) supposed that the mantle margin secreting the shell tended to more intense rhythmic lateral contraction in depressed forms than in compressed ones.

Guex et al. (2003) simulated the covariation pattern by a reaction/diffusion model of ammonoid morphogenesis, in which morphogens concentrate in shell regions of high curvature such as on the flanks of a depressed shell. The aim of this model is to fit the following observation: “*the most salient ornamentation is present where the whorls are most curved, shells with slight angular bulges often being spinose or carinate and flat ones being almost smooth*” (Guex et al. 2003). Although this model is an interesting attempt to better understand shell morphogenesis, it remains speculative. Indeed, this model makes a large number of assumptions about the nature of the underlying pattern formation system of shell morphogenesis (discussion in Hammer and Bucher 2006), which remain to be corroborated by physiological studies. Even if these reaction/diffusion models are able to reproduce color patterns of mollusks (e.g., Meinhardt 1995; Boettiger et al. 2009), it is not yet demonstrated that it upholds for shell morphogenesis as well. Additionally, this model does not yet explain the covariation of ribbing density with whorl compression and degree of involution. Other researchers (Checa 1987, 1994; Checa and Westermann 1989) argued for the opposite causal link for constructional constraints that could explain

Buckman's first rule, noting that the formation of more robust ribs during shell growth could cause the shell to automatically become more inflated and depressed.

Hammer and Bucher (2005) suggested that the first rule of covariation is "*simply*" a statement of proportionality that needs no special explanation. They assumed that robustness of ornamentation is proportional to the amount of soft parts: "*if the shell is depressed (compressed dorsoventrally), the diameter of the soft parts is small in the dorsoventral direction, and the ventral ribbing correspondingly small*". Hence, size of lateral and ventral ornamentation correlates with the proportions of the aperture (width and height). This explanation of Buckman's rule highlights simple mechanical constraints on the construction of ammonoid ornamentation. While morphogenetic pre-patterns can probably be translated into pigmentation patterns more or less directly (Fowler et al. 1992; Meinhardt 1995; Hammer and Bucher 1999; Boettiger et al. 2009), ribbing and other three-dimensional shell features involve growth, folding, and stretching of tissues, implying strong developmental constraints in terms of growth rates, mechanics, and geometry. The ratios of proportionality can vary across species (some species have stronger lateral ribs relative to shell width than others) and thus weaken the interspecific correlation between ornamentation and whorl shape (Hammer and Bucher 2005). Whatever the model, the covariation involving rib density can be explained by a domain effect if it is considered as a secondary consequence of ornamentation robustness and controlled by reaction/diffusion processes: thicker ribs tend to imply fewer ribs in the same space (Hammer and Bucher 1999).

Buckman's second rule of covariation (more compressed shell, more frilled sutures) can also be explained as a case of constructional constraint. Although the function of septal folding is subject of much debate, it has been suggested that septal formation behaves like "*viscously fingering*" liquids (Checa and Garcia-Ruiz 1996). According to this model, the degree of suture indentation depends on the space and shape available for the suture during its formation ("*domain effect*"): with equal mantle length secreting the septum, the more compressed the shell, the less space is available for the mantle, and the more constrained the suture shape will be. This domain effect on suture pattern has also been invoked to explain the evolutionary trends in suture complexity coupled with trends in involution and size increase (e.g., Monnet et al. 2011, 2015). This effect is also illustrated by increasing indentation of suture line during ontogeny (e.g., Swinnerton and Trueman 1917; Wiedmann 1966a, 1966b; Korn and Klug 2003; Pérez-Claros et al. 2007).

Hammer and Bucher (2006) argued that whorl shape and suture indentation covariation results from a heterochronic process. Because most ammonoids have rather circular whorls and simple sutures early in ontogeny, late in ontogeny the more depressed forms can be regarded as retaining their juvenile shape and suture (paedomorphosis) compared to the more compressed forms. However, this interpretation may not always hold, especially with regard to cadiconic forms in which sutures also increase their indentation, thus corroborating the domain effect hypothesis (see above). Nevertheless, Buckman's second rule of covariation may reflect intraspecific variation in development which is well known to vary within ammonoid species (e.g., Dommergues et al. 1986; Meister 1988; Courville and Crônier

2003). Similarly, Bert et al. (2013) also argued that heterochronic variation can explain the covariation between whorl compression and ornamentation coarseness, since this covariation is reflected in the ontogenetic changes of studied species (see also Courville and Crônier 2003; compare De Baets et al. 2015).

Yacobucci (2004a) studied the correlation between the variation of shell shape and of ornamentation (rib thickness and spacing). With respect to Buckman's first rule of covariation, one can expect that species with variable shell shapes would also have variable patterns of ornamentation. However, her study documented a different pattern in Cenomanian acanthoceratids of the Western Interior: groups with especially large shape variation are not those with the most intense variation in ornamentation. Hence, ammonoid shell morphogenesis is complex with some character sets more constrained than others, probably due to a different impact of developmental, constructional, environmental, and functional processes.

In conclusion, the causes of Buckman's rules of covariation for the ammonoid shell are still debated. Constructional and adaptive constraints are not mutually exclusive: both can contribute to the fabrics of structured intraspecific variation for ammonoid shells (Seilacher 1970). The recurrence of particular combinations of morphology, which are commonly regarded as strong arguments for functional constraints, can also represent "*fabricational noise*" (Seilacher 1970, 1973). Additional studies are required to test quantitatively the various hypotheses (e.g., the proportionality hypothesis of Hammer and Bucher 2005 is so far confirmed only by a single dataset). Additional insights may be found in comparative studies on the morphogenesis of living mollusks as well as from theoretical models of shell morphogenesis (e.g., Urdy et al. 2010a, 2010b; Moulton et al. 2012; Chirat et al. 2013; Moulton et al. 2015).

4.5 Extent of Buckman's Rules of Covariation

Buckman's rules of covariation appear to be a pervasive pattern of the intraspecific variation of monomorphic Mesozoic ammonoids to varying degrees. A number of questions still remain to be investigated: Does each component of the covarying character set equally contribute to the global covariation pattern? Is the degree of covariance constant during growth? Is the degree of covariance constant through time during anagenetic changes? Do dimorphic pairs show similar covariance? Does the covariation pattern apply equally within different taxonomic groups? Does the extent of covariation vary through time and phylogeny? Does it change with environmental factors and, if so, which ones? Is it related to environmental instability, developmental flexibility, or competition (Yacobucci 2004b)?

With regard to the relative contribution of each character set into the global covariation pattern, no comparative study has yet been conducted to our knowledge. Nevertheless, as can be seen with the examples of *Acrochordiceras* and *Amaltheus* (Figs. 4.2 and 4.3), pair components of the extended rule (the more evolute, the more depressed, the more coarsely ornamented, the less densely ornamented, the less frilled the sutures, and the less densely septate) are not equally correlated,

as shown by the various values of the linear correlation coefficient. Since these pair components (e.g., involution/whorl compression, or suture frilling/whorl compression) can be explained by different causes, not only are these different contributions expected, but their detailed investigation can help decipher which explanations best fit observed patterns and consequently are the most likely explanations for Buckman's rules of covariation.

Very little is known about ontogenetic patterns of covariation (De Baets et al. 2015). Since intraspecific variation of ammonoids is frequently documented to be higher in juvenile stages, one can question whether Buckman's rules of covariation uphold with the same amplitude throughout ontogeny. For instance, some covarying patterns are revealed only late in ontogeny (Monnet et al. 2010: variation of ribbing density for *Acrochordiceras* drastically decreases through ontogeny and is weakly correlated early in ontogeny). Investigating the relative proportion of covarying components through growth may help us to find the best explanation for this covariation. Understanding covariation through growth patterns may also yield insights into shell morphogenesis (e.g., Urdy et al. 2010a, 2010b; Chirat et al. 2013), such as which parameters contribute in which proportion to covariation.

With regard to the phylogenetic imprint on covariation patterns, studies have clearly focused on Mesozoic planispirally coiled ammonoids. Intraspecific variation and covariation has only rarely been quantitatively studied in Paleozoic ammonoids (Nettleship and Mapes 1993; Kaplan 1999; Korn and Vöhringer 2004; Ebbighausen and Korn 2007; Korn and Klug 2007; De Baets et al. 2013). On the one hand, Kaplan (1999) found significant covariance only in clades within the Medlicottiaceae and the Clymeniina for Paleozoic ammonoids, while on the other hand, the lack of reports of Buckman's rules from Paleozoic ammonoids is related to the rarity of studies and certainly need not reflect the true absence of covariation. According to Swan and Saunders (1987), Buckman's first rule also applies to Paleozoic ammonoids, but they discussed the correlation mostly above the species level and not in the context of intraspecific variation. Several authors reported two or more discrete morphs in Carboniferous ammonoids (e.g., McCaleb and Furnish 1964; Furnish and Knapp 1966) ranging from a more openly coiled group with a more compressed whorl section and more prominent ribbing to a less openly coiled group with a less compressed and/or less prominent ornamentation. In most cases, intergradational forms between the two or three categories were found and larger intraspecific variation exists in juvenile than in adult forms (Davis et al. 1996), which might speak for a more continuous range of intraspecific variation and covariation (for alternative interpretations, see Davis et al. 1996; Stephen et al. 2002 and De Baets et al. 2015).

Concerning covariation patterns within heteromorphic species, few studies are available and their results vary. It has often been stated that heteromorph ammonoids have a higher degree of intraspecific variation than normally coiled ammonoids (e.g., Wiedmann 1969; Dietl 1978; Ropolo 1995; Kakabadze 2004 and references therein). The phenomenon has only rarely been quantified (Urreta and Riccardi 1988; Landman and Waage 1993b; Tsujino et al. 2003; De Baets et al. 2013; Knauss and Yacobucci 2014). This might be partially related to fragmentary

preservation and problems of dealing with the unconventional shell morphology (e.g., classic Raup parameters cannot be used in some of these forms). Note that *Scaphites* is here not considered as a heteromorphic ammonoid as it only uncoils at the end of ontogeny, but see Landman et al. (2010) for a review of intraspecific variation in *Scaphites* conforming to the first rule of covariation. Nevertheless, Delaney (1997) documented that *Heteroceras emerici* (Barremian) varies between two poles interconnected by intermediates: from heterocone (large turricones and no planispiral part of the shell before the shaft) to colchicone (small turricones preceding a substantial planispiral portion before the shaft). The first pole is associated with a rather robust ornamentation and the latter pole with a rather slender ornamentation, thus illustrating a covariation between strength of ornamentation and coiling. A similar variation is also known in *Imerites* (Barremian; Bert et al. 2011). In contrast, Ropolo (1995) described *Crioceratites shibaniae* (Hauterivian) with a very variable coiling grading continuously from the criocone morphology to the tripartite morphology (coil, shaft, and hook), but without changing the ornamentation, which is very stable from one morphotype to another. Interestingly, Urrreta and Riccardi (1988) reported covariation of whorl shape and ribbing in several species of the heteromorph *Labeceras* (Albian) “with the more depressed specimens having stronger and fewer ribs and incipient tubercles on the hook’s inner margin”. Bert et al. (2013) reported similar covariation between whorl compression and ornamentation coarseness within *Gassendiceras* (Barremian). Finally, De Baets et al. (2013) described a continuous variation between more coarsely ribbed, more loosely coiled forms with a more compressed whorl section and less coarsely ribbed, but less coiled forms with a more depressed whorl section in the openly to advolutedly coiled *Erbenoceras solitarium* (Devonian). De Baets et al. (2013) reported a negative correlation between coiling and ribbing, such that more loosely coiled variants had a more densely spaced, finer ribbing, as opposed to Mesozoic coiled ammonoids where the relationship is reversed (denser, finer ribbing for more coiled variants). Therefore, it is not possible in the present state of knowledge to generalize a single rule of covariation patterns of ammonoids. They can partially follow some of Buckman’s rules or completely diverge from them.

Apparently, Buckman’s rules of covariation are valid in most ammonoid groups with regularly coiled shells throughout their long evolutionary history and as such should result from inherent constructional properties and/or common selection pressures. It is worth noting that even with sufficiently large collections, not all species follow these covariation rules, even if they coexisted (e.g., Brayard et al. 2013; Monnet and Bucher 2005; De Baets et al. 2015). The phylogenetic imprint of the strength of Buckman’s rules of covariation in ammonoids thus remains to be investigated (e.g., do phylogenetically closely related species share similar proportions of covarying characters).

Another question in evolutionary biology pertains to whether intraspecific variation can lead to interspecific differentiation (West-Eberhard 1989, 2003, 2005), because anatomical variations within populations increase the range of ecologically relevant variation that can fuel speciation (Schluter 2000, 2001; Butler et al. 2007; Nosil 2012), especially by means of heterochrony (Spicer et al. 2011; Tills

et al. 2011). In this context, Yacobucci (2004a) described a Buckman-like pattern of covariation within a Late Cretaceous clade of acanthoceratid ammonites. Entire genera could be categorized as compressed, involute, and lightly ornamented (e.g., *Metoicoceras*, *Neocardioceras*) while other, closely related genera were depressed, involute, and more heavily ornamented (e.g., *Acanthoceras*, *Plesiacanthoceras*). Similarly, within a genus, different species showed either a more compressed morph (e.g., *Metoicoceras praecox*) or a more depressed morph (e.g., *Metoicoceras geslinianum*), along with the corresponding coiling and ornamentation. Therefore, Buckman's rules of covariation may uphold (compare Swan and Saunders 1987; Yacobucci 2004a; Moulton et al. 2015), but additional datasets and studies are required to better understand this phenomenon. Particularly, such studies may help to determine whether patterns of covariation are constrained by phylogenetic heritage.

4.6 Conclusions

Ammonoids have long been known to show a large intraspecific variation of their shell morphology. This phenomenon is often, but not systematically, considerably structured and characterized by a typical covariation of characters: species can be characterized by a continuous unimodal intergradation of morphotypes following the overall rule 'the more evolute, the more depressed, the more coarsely ornamented, and the less frilled the sutures'. These covariation patterns have been labeled as Buckman's rules of covariation. Although this covariation has been abundantly documented in ammonoids of almost all geological periods and taxonomic groups, coexisting species still can have different intraspecific patterns (reviewed in De Baets et al. 2014). Competitive, but not mutually exclusive, hypotheses explain this pattern (especially adaptive vs. constructional constraints). As noted by Bert (2013), it appears that Buckman's rules of covariation are not the only covariation patterns of intraspecific variation of ammonoids, although these rules may be more common. Nevertheless, Buckman's rules of covariation and ammonoid morphogenesis are not yet fully understood (Yacobucci 2004a, 2004b). Documenting the existence of Buckman-like covariation patterns among various related groups of ammonoid species and genera will help us better understand the underlying cause(s) of these correlations. Therefore, construction of datasets (especially for ornamentation and suture) and their quantitative analyses is the next important step in order to investigate and test the various still unresolved questions about covariation rules of the ammonoid shell.

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