Chapter 5
Evolutionary Patterns of Ammonoids: Phenotypic Trends, Convergence, and Parallel Evolution

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5.1 Introduction

Ammonoids are characterized by high evolutionary rates. Because taxa evolved and became extinct rapidly, ammonoids are extremely useful tools for dating strata. For instance, due to their high turnover rates, ammonoid species can often enable the construction of biozones spanning less than 100,000 years duration (see e.g., House 1985; Monnet et al. 2015a). In addition to this outstanding time marker property, ammonoids also can provide significant insights into evolutionary biology. They have repeatedly been proven valuable study objects to develop or test evolutionary hypotheses and to investigate patterns of biodiversity (e.g., Schindewolf 1933, 1940, 1950; Kennedy 1977, 1989; Kennedy and Wright 1985; Landman 1988; Korn 1995, 2003; House 1996; Saunders et al. 1999; Guex 2001, 2003, 2006; Korn and Klug 2003; Gerber et al. 2008; Neige et al. 2009; Brayard et al. 2009; Monnet et al. 2011; De Baets et al. 2012; Korn et al. 2013a). Seilacher (1988, p. 67) correctly summarized this fact in his famous phrase stating that ammonoids "*are for paleontologists what* Drosophila *is in genetics*". This is the result of exceptional properties such as their high abundance, widespread occurrence, high evolutionary rates, high taxonomic diversity and morphological disparity, usually well-known stratigraphic framework (e.g., Stanley 1979; Sepkoski 1998; Foote and Sepkoski 1999), and their

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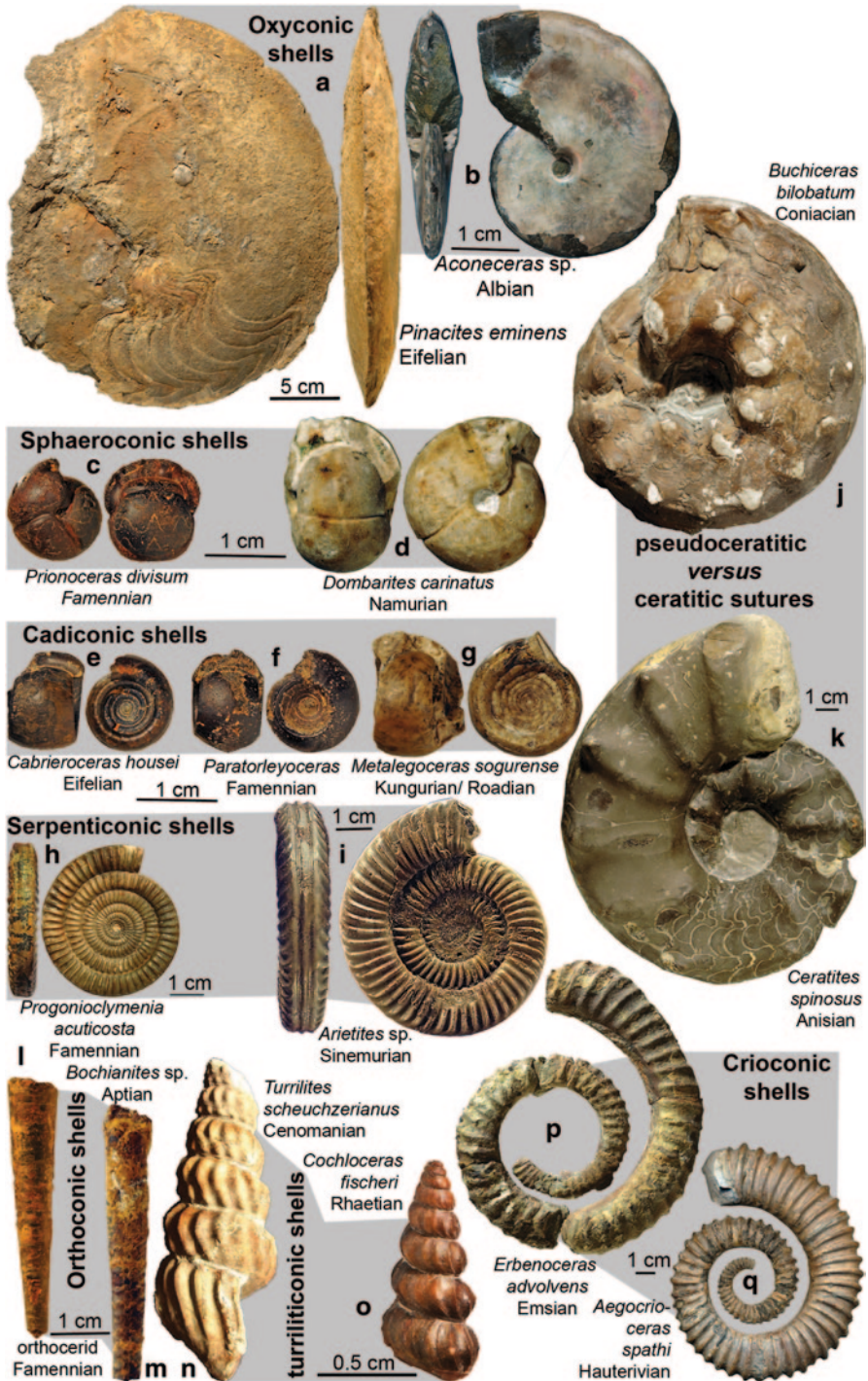e-mail: kenneth.debaets@fau.de

Fig. 5.1 Some cases of convergence in shell form and suture line course. **a** *Pinacites eminens*, PIMUZ 31078, Eifelian, Jebel El Mrakib, Morocco. **b** *Aconeceras* sp., Albian, Mahajanga,

accretionary mode of shell growth that recorded the complete development (ontogeny) of the animals from the embryonic and juvenile stages to adulthood. In the fossil record, ammonoids are well-known to display major evolutionary patterns in shell morphology. They often evolved homeomorphic lineages and experienced numerous long-term (often several million years) morphological evolutionary trends, many of which were iterative or even parallel over time. This review will focus on these two points.

Homeomorphy has been recognized frequently among ammonoids (e.g., Schindewolf 1933, 1940; Haas 1942; Reyment 1955; Kennedy and Cobban 1976; Kennedy 1977; Wright and Kennedy 1979; Bayer and McGhee 1984; Kennedy and Wright 1985; Hewitt 1989; Page 1996; Bujtor 2010). Homeomorphy can be defined as the result of the evolution of close morphological similarities between species that are not closely related, or as the recurrence of phenotypic similarity within unrelated clades that evolved independently (Neville 1962; Lauder 1981; Wake 1991; Sanderson and Hufford 1996; Hall 2007; Futuyma 2009; McGhee 2011). It is generally thought to result from adaptation to similar modes of life or similar functions in different organisms or parts of organisms (but not always; see e.g., Reyment 1955). Homeomorphy can be the outcome of convergent evolution (McGhee 2011) when animals exploit similar habitats/ecological niches in similar ways and thus likely arrive at morphologically similar solutions independently. The wings of birds, bats and pterosaurs are a classic example of homeomorphy, having evolved independently in three separate lineages from joint ancestors lacking this character as a means of achieving the functional requirements of flight. In order to determine the common origin, homology of the homeomorphic organs has to be examined.

Among animals with an external shell, convergent evolution leading to homeomorphic taxa has always been common and thus has been abundantly documented (e.g., Rudwick 1965; Horne 2005). For ammonoids, which are limited to a tubular external shell with finite limits of variation in coiling, ornament and suture imposed by constructional constraints, evolutionary convergence is widespread (Fig. 5.1). In the most extreme cases, Mesozoic forms developed "atavistic" shell shapes reminiscent of Paleozoic ammonoids. Some examples (out of countless) are the shell shapes or suture lines of Triassic Arcestina resembling Paleozoic Goniatitina

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Madagascar. **c** *Prionoceras lamellosum*, PIMUZ 31072, middle Famennian, Madene El Mrakib, Morocco. **d** *Dombarites carinatus*, PIMUZ 31075, Namurian, Aktubinsk, Kazakhstan. **e** *Cabrieroceras housei*, PIMUZ 31076, late Eifelian, Oued Chebbi, Morocco. **f** *Paratorelyoceras globosum*, PIMUZ 31077, early Famennian, Oued Chebbi, Morocco. **g** *Metalegoceras sogurense*, PIMUZ 31084, Kungurian/Roadian, Aktubinsk, Kazakhstan. **h** *Progonioclymenia acuticosta*, Famennian, South Urals, Orenburgskaya Obl., Russia. **i** *Arietites* sp., Sinemurian, Mögglingen, Germany (Staatliches Museum für Naturkunde Stuttgart). **j** *Buchiceras bilobatum*, Coniacian, Peru. **k** *Ceratites spinosus*, Anisian, Garnberg (Muschelkalkmuseum, Ingelfingen, col. H. Hagdorn). **l** Orthocerida gen. et sp. indet., PIMUZ 31074, Late Famennian, Lambidia, Morocco. **m** *Bochianites* sp., PIMUZ 31073, Albian, Anges, France. **n** *Turrilites scheuchzerianus*, Cenomanian, Pas de Calais, France (col. H. Chatelier, France). **o** *Cochloceras fischeri*, Rhaetian, Sandling, Austria (col. H. Keupp, Berlin, MAm-1131). **p** *Erbenoceras advolvens*, GPIT 1849–2002, early Emsian, Gart El Anz, Morocco. **q** *Aegocrioceras spathi*, Hauterivian, Resse, Germany. All specimens at the Palaeontological Institute and Museum of the University of Zurich if not mentioned otherwise. Images: i and p: W. Gerber (Tübingen), n: H. Chatelier (France), o: H. Keupp (Berlin), q: R. Hoffmann (Bochum)

(Page 1996), or members of the Cretaceous Flickiidae with a simplified suture line and shell form similar to some Devonian Anarcestina (Wright and Kennedy 1979). These morphological similarities are no evidence for phylogenetic relationships but of convergent evolution. In some cases, ammonoids have developed very similar morphologies in most aspects generally accepted to be of diagnostic, taxonomic value that can lead to erroneous phylogenetic inferences or classification when not taking into account the stratigraphic gap separating these taxa. The situation is even more precarious when these forms co-occur or follow each other closely in time and where homeomorphic characters might be used to infer phylogenetic relationships.

Among ammonoids, examples of long-term morphological evolutionary trends are numerous (e.g., Haas 1942; Guex 1973, 1981, 1992, 2001, 2006; Kennedy 1977; Thierry 1982; Bayer and McGhee 1984, 1985; Kennedy and Wright 1985; Dommergues et al. 1989; Dommergues 1990; Neige et al. 1997; Korn and Klug 2003; Klug et al. 2005; Monnet et al. 2011, 2013; De Baets et al. 2012). These long-term phenotypic evolutionary trends are persistent and directed changes of morphological characters through significant periods of geological time (often several million years) within a monophyletic group (e.g., Gould 1988, 1990). Furthermore, these repeated trends can be independent, but often are organized in convergent, iterative and parallel patterns over time (Haas 1942; Guex 2001, 2003). Last but not least, all these patterns can contribute in a major way to the understanding of homeomorphic characters in ammonoid shells.

Parallel evolution (e.g., Serb and Eernisse 2008) can be defined as the independent evolution of similar biological traits in at least two different lineages having similar phenotypic trajectories driven by common (developmental) constraints. Parallel evolution is often confused with convergence (Webb 1994) since both can result in taxa with highly similar characters, but the two concepts remain distinct (Serb and Eernisse 2008) even if there may be a continuum between parallelism and convergence (Gould 2002; Donoghue 2005). On the one hand, superficially similar features are formed by different developmental pathways in convergence. On the other hand, parallel evolution is thought to involve similar developmental modifications that evolved independently (often in closely related organisms). Parallel evolution is a moderately common phenomenon in extinct and extant lineages (e.g., Averoff and Patel 1997) and often assumed to be the product of adaptation by means of natural selection. The literature on ammonoid evolution contains several references to parallel evolution or "parallelism" (parallelism is sometimes used in a slightly different meaning: Monnet et al. 2011), but many of these studies are spurious because they do not account for dimorphism and intraspecific variability and they rely only on qualitative description (Kennedy 1977). However, there are now convincing examples based on data for which their taxonomy, stratigraphy and phylogeny have been revised by quantitative methods (e.g., Meister 1993; Monnet et al. 2011).

Homeomorphic character states can evolve convergently or in parallel. They are major patterns of phenotypic evolution. Such examples of homoplasy (Lankester 1870) present opportunities to discover the foundations of morphological traits and determine processes and mechanisms of evolution (Wake et al. 2011). Furthermore,

understanding what is driving the high degree of homeomorphy within ammonoids is of great importance for taxonomy (e.g., Hewitt 1989; Webb 1994) and phylogeny as it might result in a high degree of homoplasy (Wake 1991; Yacobucci 2012). Understanding the long-term morphological trends is also of prime importance as they are at least partially responsible for the high degree of homeomorphism among ammonoids and may provide significant insights into evolutionary constraints operating on the ammonoid shell. However, the processes behind these common evolutionary patterns are still not well understood. As noted by Kennedy and Wright (1985, p. 142), the evolution of Cretaceous ammonoids shows "*repeated patterns that reflect the selection of features whose adaptive significance in most cases escapes the observer*". For ammonoids, this situation may partly arise from two major sources of noise. First, the phylogeny of ammonoids at the species rank is only rarely reconstructed by means of state-of-the-art, recent phylogenetic methods (Neige et al. 2009; Yacobucci 2012) and consequently prevent the valuable use of ammonoids in evolutionary studies despite having a huge potential. Second, studies on ammonoid evolution are very often carried out using qualitative/descriptive approaches without real quantification and statistical testing. However, these phenotypic evolutionary patterns can only be confidently assessed by novel quantitative and statistical methods. The major aim of this chapter is to review some of these methods and their application to ammonoids, which reflect the potential of ammonoids for providing insights into evolutionary patterns and processes.

5.2   Macroevolutionary Trends

5.2.1   Definition

> *One of the crowning achievements of paleontology, and of surpassing importance in the development of evolutionary theory, has been the discovery of innumerable graded morphological series of fossils showing progressive change as we ascend the geological scale of time. Many of the evolutionary modifications follow simple patterns, or trends, which recur again and again in related, or even unrelated stocks.* (Newell 1949, p. 103)

One of the intriguing outcomes of biological evolution (as described by Newell above) is the frequent occurrence of long-term evolutionary trends. These patterns are persistent and directed changes of morphological characters through significant periods of geological time within a monophyletic group (Fig. 5.2; Simpson 1953; Gould 1988, 1990; McKinney 1990; McShea 1994; McNamara 2006). The fossil record displays numerous examples of lineages persistently evolving during several million years toward greater "*complexity*" and/or toward larger body size (Cope 1887, 1896; Depéret 1909; Matthew 1926; Newell 1949; Simpson 1953; Rensch 1959; Stanley 1973; Hallam 1975; Kennedy and Wright 1985; Fisher 1986; MacFadden 1986, 1992, 2005; Gould 1988, 1990, 1996, 1997; Jablonski 1987, 1997; McShea 1991, 1994, 1996; Boyajian and Lutz 1992; Valentine et al. 1994; Kaiser and Boucot 1996; Wagner 1996; Trammer and Kaim 1997; Alroy 1998, 2000;
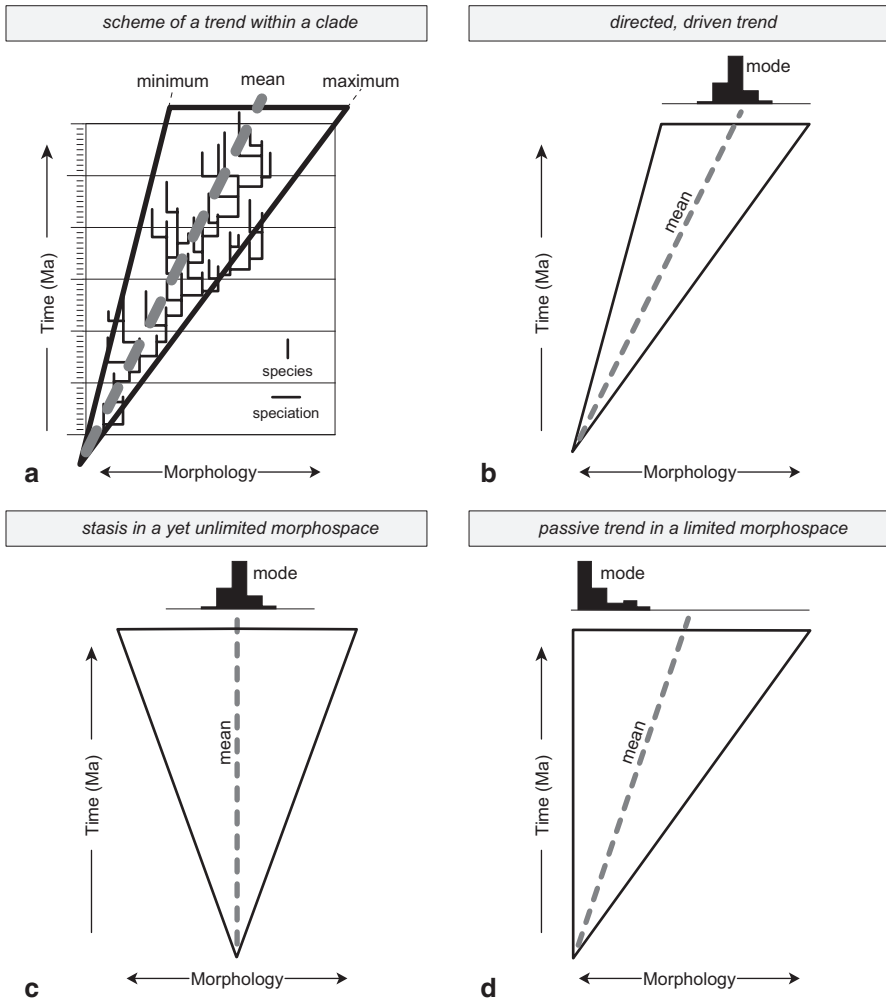
Fig. 5.2 Schemes of long-term phenotypic macroevolutionary trends of a lineage through time (modified after McShea 1994). **a** The vagaries of the morphology (origination and extinction of species) of a clade through time are mainly characterized by its mean and range in its phenotypic space. **b** A long-term trend is characterized by a protracted shift of the entire range and mean morphology of the studied group. **c** Absence of changes in this morphological mean illustrates stasis. **d** A seemingly driven trend may occur in a phenotypic space limited by physical/constructional boundaries, but in this case the most abundant forms still remain similar to the root of the clade (compare with b)

Saunders et al. 1999; Adami et al. 2000; Wang 2001; Gould and MacFadden 2004; Guex 2006; Hunt and Roy 2006; Adamowicz et al. 2008; Novack-Gottshall and Lanier 2008; McGhee 2011). Such trends occur in almost all metazoan groups and probably reflect a pervasive pattern of evolution. This sustained directionality of morphological evolution is one of the oldest and most important aspects of

evolution, and is therefore an important research program in paleobiology (McNamara 1990). The occurrence, generality and causes of long-term evolutionary trends have been intensively studied and debated, and have significant implications for an overall understanding of patterns and processes of evolution.

5.2.2 Phenotypic Trends in Ammonoid Shell Characters

Ammonoids are characterized by a septate, univalved, usually coiled shell, basically conic, with or without an external sculptured ornamentation. This shell can be described by multiple qualitative (for a list of ammonoid characters, see e.g., Arkell et al. 1957; Dommergues et al. 2002; Korn 2010) and quantitative characters, some of which will be illustrated here (for their definition, see Monnet et al. 2011 and Klug et al. 2015b). Among quantified ammonoid shell characters, there are four that commonly display long-term evolutionary trends through time: adult body size, degree of involution (coiling), strength (or spacing) of ornamentation, and indentation of suture line (Kennedy 1977; Kennedy and Wright 1985; Dommergues 1990; Saunders 1995; Saunders and Work 1996; Saunders et al. 1999; Guex 2001, 2006; Korn and Klug 2003; Klug and Korn 2004; Monnet et al. 2011 and references therein). The general tendency for body size to increase during the evolution of a group of animals is known as Cope's rule (Rensch 1948) or as the law of phyletic increase in size (Depéret 1909). With regard to ammonoids, several authors have illustrated and discussed examples of increasing shell size (Stanley 1973; Hallam 1975; Thierry 1982; Kennedy and Wright 1985; Guex 2003; Dommergues et al. 2002; Monnet et al. 2011, 2012; De Baets et al. 2012). For instance, Hallam (1975) described Cope's rule in some Jurassic ammonoid families but he focused only on maximum shell size, whereas Dommergues et al. (2002) documented no preponderant trends (but without phylogenetic data) in an almost exhaustive compendium (more than 1000 species) of Early Jurassic ammonoids. Furthermore, trends of decreasing shell size might also occur (Korn 1995b).

Another repeatedly documented evolutionary trend within ammonoids is that from an openly umbilicate ancestral group (evolute) toward a descendant group with a smaller or closed umbilicus (involute; Fig. 5.3a). Such trends have been documented already by Hyatt (1889) for Liassic arietitids. This pattern has even been documented in the earliest history of ammonoids: during the Early Devonian, ammonoids showed a progressive coiling from straight orthocerids via curved bactritoids to coiled ammonoids (Erben 1966; Wiedmann 1966; Klug 2001; Klug and Korn 2004; De Baets et al. 2009, 2012, 2013b). This increasing shell involution (protracted closure of the umbilicus by increasing overlap of the whorls) is also the most commonly described long-term morphological trend among more derived ammonoids (e.g., Hyatt 1889; Schindewolf 1940; Haas 1942; Guex 1973, 1981, 1992; Bayer and McGhee 1984, 1985; Dommergues 1990; De Baets et al. 2009, 2012; Klug et al. 2010, 2015a; Monnet et al. 2010, 2012, 2013; see also Monnet et al. 2011 and references therein). Note that uncoiling of ammonoids has also been documented repeatedly (e.g., Wiedmann 1969; Cecca 1997).
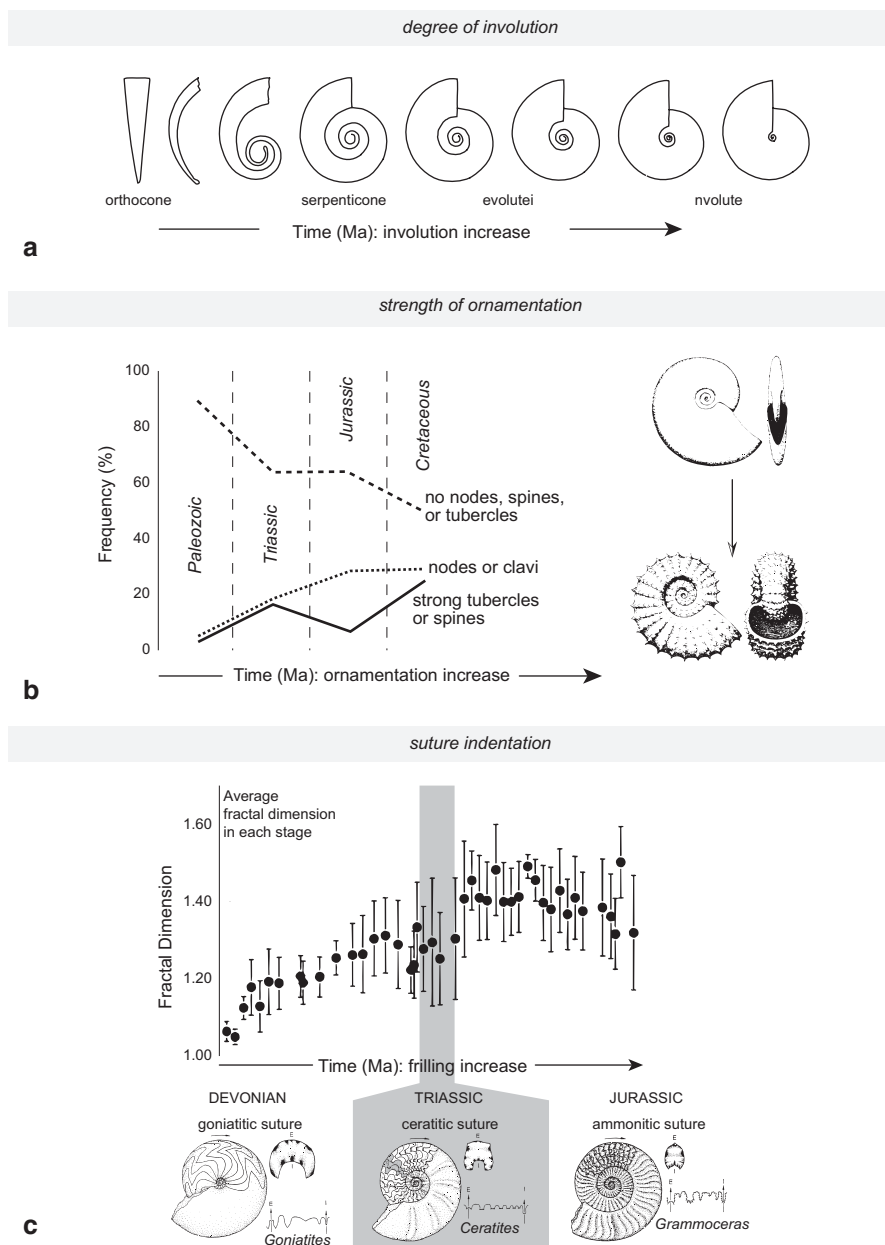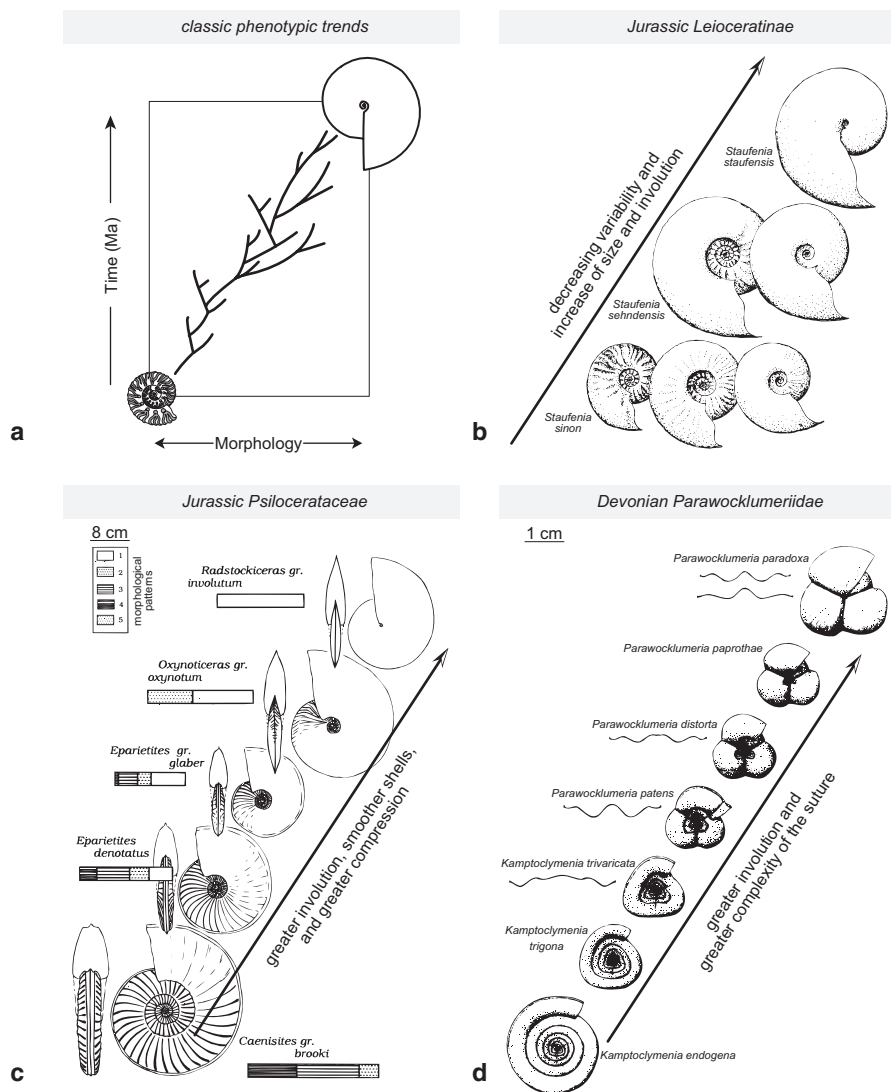
Fig. 5.3 Global long-term evolutionary trends of the ammonoid conch. **a** Scheme of the initial trend in the degree of involution within Devonian early ammonoids (modified after Wiedmann 1966). **b** Scheme of the trend toward more ornamented shells (modified after Ward 1981). **c** Scheme of the trend toward greater complexity of the suture line (modified after Boyajian and Lutz 1992)

With regard to shell ornamentation, various authors (Ward 1981, 1996; Vermeij 1987; Westerman 1996) showed that the whole ammonoid clade reveals a trend toward more ornamented forms (Fig. 5.3b). Although the authors interpreted this pattern as a response to the evolution of increasing numbers of shell crushing predators, the qualitative data of Ward (1981) suggest a passive trend constrained by a left-wall effect. For instance, convergent evolution of spines in marine mollusk shells have classically been interpreted as having repeatedly evolved as a defense in response to shell-crushing predators (e.g., Vermeij 1987; Kröger 2005; Ifrim 2013), but other interpretations are also available (see Ifrim 2013). Recent studies (Moulton et al. 2012, 2015; Chirat et al. 2013) have demonstrated that a large diversity of ornamentation and spine structures can be accounted for through small variations in control parameters of the mechanical interaction between the secreting mantle edge and the calcified shell edge, which suggests that convergent evolution of spines can also be understood through a generic morphogenetic process without selective pressures. By contrast, simplification of shell ornament through the evolution of a clade was also frequently observed at a lower taxonomic scale (e.g., Bayer and McGhee 1984, 1985; Kenney and Wright 1985).

Finally, ammonoid evolution is also characterized by an overall increase in the intensity of indentation of adult sutures (= frilling or "complexity") (Fig. 5.3c): from agoniatitic (smooth lobes and saddles), via goniatitic (smooth lobes, pointed saddles), to ceratitic (smooth saddles, denticulate lobes), and to ammonitic (frilled lobes and saddles). This increasing suture indentation has been quantified by fractal or Fourier analyses by several authors (e.g., García-Ruiz et al. 1990; Boyajian and Lutz 1992; Saunders and Work 1996, 1997; Saunders et al. 1999; Pérez-Claros et al. 2002, 2007). For instance, Saunders et al. (1999) documented a bias in the direction of speciation toward more indented sutures (within 475 ancestor/descendant pairs; descendants were more than twice as likely to be more complex than their ancestors). They also noted that mass extinctions acted in opposition to this long-term trend by eliminating more indented forms and thus resetting the trend (which might be linked with the elimination of extreme morphologies like oxycones and cadicones, which tend to have more sutural elements). Interestingly, this role of lineage sorting by means of increased extinction rates of particular morphologies has also been emphasized either as resetting trends (Guex 2001, 2006) or as strengthening trends (De Baets et al. 2012). At lower taxonomic ranks and shorter time intervals, evolutionary trends in suture indentation are also common and include not only patterns of increasing indentation, but also decreasing indentation and smoothing of sutures (see e.g., Kennedy and Wright 1985; Checa 1987). In addition, this statement holds for every character (size, ornamentation, coiling, and suture): both increasing and decreasing trends have been documented (see review of Kennedy and Wright 1985).

Interestingly, the morphological trends described above often happened simultaneously. This lead to a particular evolutionary pattern characterized by lineages originating with small, ornamented, evolute and depressed forms, which more or less progressively changed and ended with large, smooth, involute and compressed shells (Fig. 5.4a; e.g., Silberling and Nichols 1980; Bayer and McGhee 1984,

Fig. 5.4 Examples of long-term phenotypic evolutionary trends of the ammonoid shell within lineages. **a** Scheme of the most frequently described ammonoid trend: it starts with more evolute, more depressed, and more ornamented shells and evolves toward more involute, more compressed, and smoother shells. **b** Morphological trend of *Staufenia* during the Jurassic of Germany (modified after Bayer and McGhee 1985). **c** Peramorphic trend of Psilocerataceae (modified after Dommergues 1990). **d** Devonian transition from *Kamptoclymenia* to *Parawocklumeria* in the Rhenish Massif (modified after Korn 1995a)

1985; Klinger and Kennedy 1984; Guex 2001, 2003, 2006; Monnet et al. 2012). Figure 5.4b–d reports examples of such phenotypic trends. These trends are also recognized to occur successively several times within a clade leading to a repetitive pattern of similar trends ("*evolutionary cycles*" of Haas 1942). The frequency,

combination and proportion of these morphological trends within the evolution of ammonoids remain however to be investigated. Moreover, Kennedy and Wright (1985) recognized that Late Cretaceous ammonoids experienced almost all combinations of trends and it is not yet clear if one pattern predominates or not.

5.3   Univariate Phenotypic Trends in Ammonoids

5.3.1   Classic Descriptive Stratophenetics

Evolutionary changes of the ammonoid shell through time are classically investigated by means of a stratophenetic approach (Gingerich 1979, 1993; Raup and Crick 1981, 1982; Bookstein 1988; Roopnarine et al. 1999) regardless of its phylogenetic interpretation. It usually includes a graphic illustration of the morphological range of a character through successive time slices such as beds or biozones (e.g., Raup and Crick 1981; Thierry 1982; Bayer and McGhee 1984; Kennedy and Wright 1985; Dommergues et al. 1989; Dommergues 1990; Klug et al. 2005; Monnet et al. 2011, 2012; De Baets et al. 2012). Patterns of phenotypic evolution of quantitative characters are usually examined separately by means of bivariate plots depicting their quantile distribution (or descriptive statistics such as mean, minimum, maximum, median and/or quartiles). These plots enable an empirical evaluation of the presence or absence of directed evolutionary changes (trends) for each character.

A recent example of morphological trends of the ammonoid shell investigated by a classic stratophenetic approach has been published by Monnet et al. (2012). Therein, details of the long-term phenotypic evolution of Acrochordiceratidae during the Anisian (Middle Triassic) were analyzed. Morphological changes of the acrochordiceratid shell were quantified based on large collections (more than 700 specimens) from Nevada (USA). This study showed (Fig. 5.5a) that the monophyletic clade of Acrochordiceratidae (i) underwent a significant increase (possibly with several steps) of its adult shell diameter (i.e. Cope's rule), (ii) showed an evolute to involute evolutionary trend (i.e. an increase of the degree of shell involution), and (iii) experienced a qualitative increase of indentation of its suture line. The protracted changes in shell morphology of the Acrochordiceratidae are robust and non-random (Monnet et al. 2012). They can be interpreted as being constrained by the persistent, common selection pressure on this mostly anagenetic lineage with relatively moderate evolutionary rates during an ecologically stable period (Fig. 5.5c). As discussed by Monnet et al. (2011), such trends of morphological evolution in the ammonoid shell may suggest that their morphology is mainly controlled by adaptive and constructional constraints. Interestingly, not all quantified characters showed trends such as whorl shape compression and ribbing density (Fig. 5.5b).
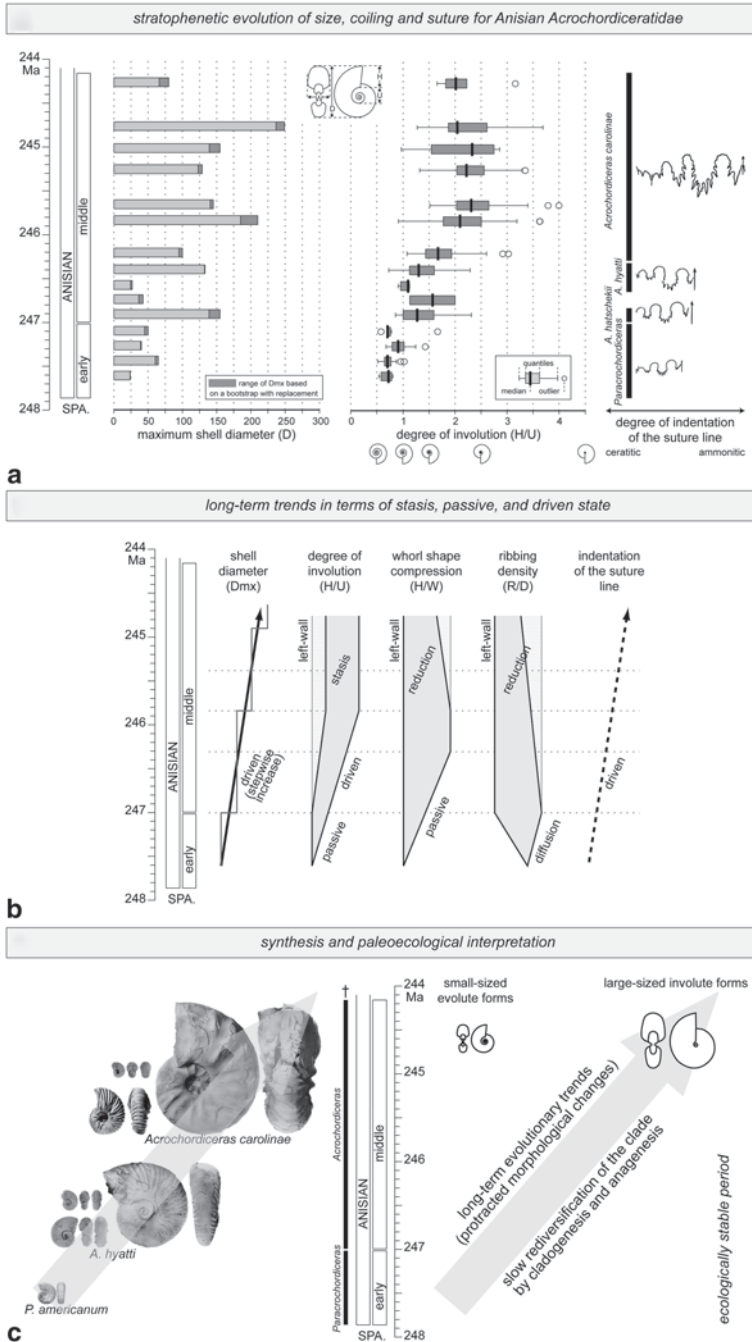
Fig. 5.5 Evolution of maximum shell diameter, degree of involution and suture shape for Acrochordiceratidae during the Anisian (Middle Triassic) (modified after Monnet et al. 2012). **a** Stratophenetic patterns of some conch characters showing a trend of their mean. **b** The corresponding

## 5.3.2 Passive and Driven Trends and Lineage Sorting

The ammonoid literature is rich in descriptions of phenotypic trends through time (references in 5.3.1). However, a crucial question is whether these evolutionary trajectories are robust and not just random fluctuations in phenotypic space. Indeed, the classic stratophenetic approach is a subjective graphic approach, which impedes distinguishing random fluctuations from persistent trends (e.g., Roopnarine et al. 1999; Hunt 2006). The method has been criticized because it lacks a means of evaluating the robustness of the documented pattern. This is not always straightforward in fossil organisms due to, e.g., low sample size combined with large variation in fossil groups (De Baets et al. 2015). The absence of quantitative methods adapted to the study of the incomplete and time-averaged fossil record lead in the past to biased descriptive studies. In addition, Gould (1988, 1990) pointed out two major common misinterpretations of stratophenetic trends: (i) biases may result from the systematic search of gradual evolution between species by arbitrary picking out only part of a clade and ignoring the entire complex phylogenetic tree (“*anagenesis faith*”); (ii) other biases may arise from a focus on extreme values (maximum) instead of accounting for the entire variance. Furthermore, Raup et al. (1973) showed that trends can be simulated even if both direction and frequency of speciation and extinction are allowed to vary randomly. To overcome such problems, several approaches have been developed and/or used during the past decades for evaluating trends, especially for stratophenetic data and with or without a phylogenetic framework.

One major advance in the understanding of trends came with the recognition of the “*left-wall effect*” (Stanley 1973; Gould 1988; McShea 1994). Indeed, many patterns could arise via (random) fluctuations from a fixed boundary, as when a clade originates near a minimum viable morphology (Fig. 5.1d); in this case, the mean of the studied lineage can increase because change in one direction is blocked by a boundary in some region of the morphological space. For instance, the coiling of ammonoids is bounded on one side by “*straight conch*” and on the other side by “*fully occluded umbilicus*”. Such boundary-limited trends were referred to as “*passive*” in opposition to “*active*” trends, which display a shift of the entire range of the morphology (McShea 1994; see also discussion of Alroy 2000). Note that “*passive*” is not identical with “*random*”, because a passive trend can still result from different processes acting independently and heterogeneously (McShea 1994). Since such passive trends arise owing to the topography of the adaptive landscape (Kaplan 2008; Pigliucci 2008), it is useful to identify them in order to avoid over-interpretation (usually adaptive) of the patterns and help discriminate the limiting effects of structural constraints from natural selection (Gould 1988).

Long-term phenotypic changes can arise by means of a wide range of mechanisms, and different dynamics can operate simultaneously, in opposition or in concert, at different levels (Stanley 1973; Vrba and Gould 1986; Gould 1988, 2002;

patterns in terms of long-term trends (stasis, left-wall effect, directed shift) showing that some characters have very different evolutionary patterns. **c** Interpretation of the typical documented pattern (illustrated ammonoids are at the same scale)
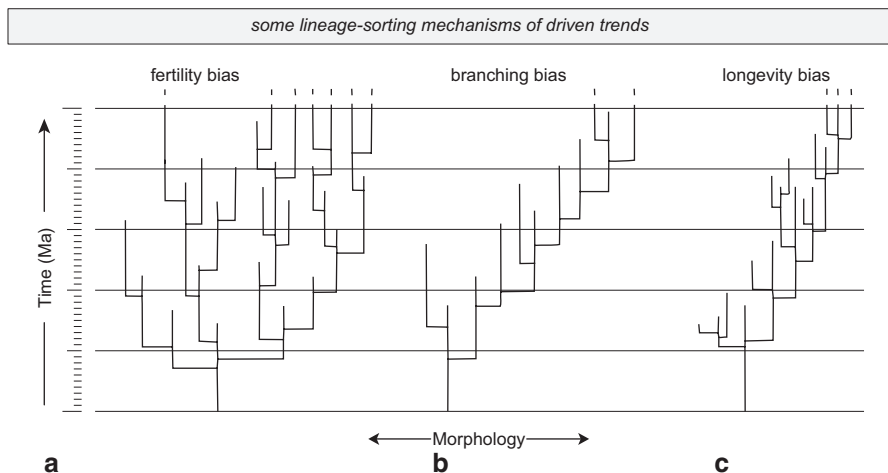
Fig. 5.6 Some lineage-sorting mechanisms leading to phenotypic patterns of among-species, driven trends (modified after Gould 1988). **a** The trend results from a higher speciation rate of a part of the morphospace of the studied lineage. **b** The trend is triggered by a preferred direction of speciation. **c** The trend is induced by longer persistence of species from a particular part of the morphospace

McNamara 1990; McShea 1994; Foote and Miller 2007). For instance, a trend may be underlain by transformation of its constituent species, by preferential origination of new species, by random speciation followed by differential survival or proliferation in the direction of the trend, or by any combination of these very different processes (Stanley 1973; Gould 1988; Jablonski 2007). For example, Gould (1988) showed that one process or the combination of several processes might cause a driven process (Fig. 5.6): (i) a bias in the direction of speciation ("*branching bias*": is the number of speciation events equally distributed among decreasing and increasing phenotypic changes?); (ii) a bias in the magnitude of speciation ("*fertility bias*": are speciation rates similar throughout the morphospace?); (iii) a bias in the amount of extinction ("*longevity bias*": do species located in a particular part of the morphospace survive longer?).

Evolutionary trends can also result from mechanisms acting at different hierarchical levels, leading to the concept of "*lineage sorting*" (Vrba and Gould 1986): (i) trends can be driven by organism-level traits (within-lineage sorting) such as body size or habitat preferences that can also be translated into patterns of among-species evolution (Vrba 1980, 1983, 1984); or (ii) trends can be driven by emergent properties at the species level (among-lineage sorting) such as geographic range, speciation rates, or longevity (Stanley 1979; Gould 2002). From a methodological viewpoint, several authors discussed several tests to discriminate passive and driven trends, globally for a clade (Gould 1988; McShea 1994; Wagner 1996; Wang 2001, 2005), mainly by focusing on the biases listed above. Alroy (2000) also proposed additional approaches to analyze phenotypic macroevolutionary trends. However, none of these tests have been applied to ammonoids.
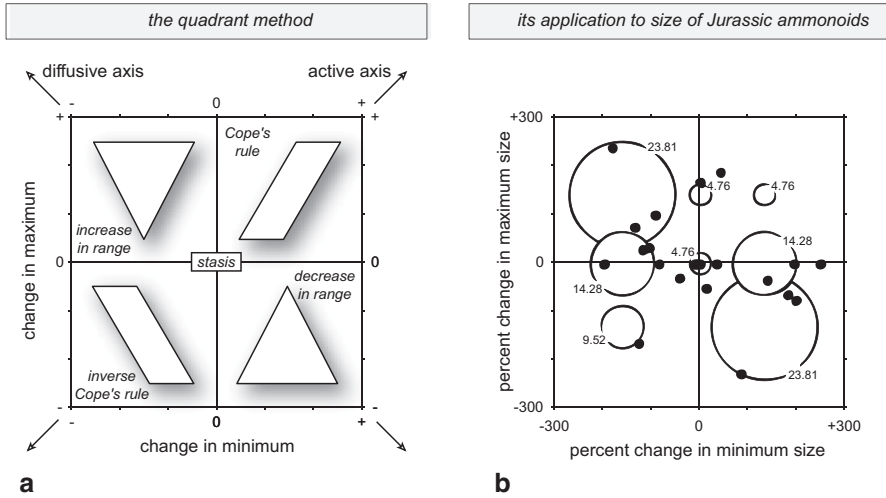
Fig. 5.7 The quadrant method and its application to quantify the relative proportion of passive and driven trends within a linage. **a** The quadrant method of Jablonski (1997) reports phenotypic changes between pairs of successive stratigraphic intervals or phylogenetic data in terms of changes in variance. The top right quadrant corresponds to an increase in the studied morphology, the bottom left quadrant to a decrease, the top left quadrant to an increase in range, and the bottom right quadrant to a decrease in range. **b** Styles of size change in Early Jurassic ammonoids (black circles are the difference between two successive sets of biozones; circle diameter is proportional to frequency in the corresponding quadrant) (modified after Dommergues et al. 2002)

Another major approach to quantify the relative proportion of passive and driven trends within a lineage is that of Jablonski (1997; see also Trammer and Kaim 1999). He proposed the "*quadrant*" method as a graphic approach to evaluate the relative proportion of evolutionary changes between the minimum and maximum of the range of a character (Fig. 5.7a). This approach thus focuses on changes in variance (*sensu* Gould 1988) and can accommodate stratophenetic series or for phylogenetic sequences. In this approach, a graph reports and synthesizes the complete series within a clade of the differences of morphological values of some characters either between an ancestor and its descendant or between two successive stratigraphic intervals. The four quadrants represented four possible trends in character evolution. This enables the comparison of the relative proportion of increases, stases, and decreases within the studied clade and thus evaluates if one macroevolutionary pattern dominates or not. By accounting for the changes at the lower and upper phenotypic bounds, these analyses essentially correspond to the test based on "the behavior of the minimum" for distinguishing passive from active (directional) trends. Jablonski (1997) applied the method to evaluate Cope's rule within Cretaceous mollusks and found no support for a predominance of body size increase. For ammonoids, Dommergues et al. (2002) applied the method also to evaluate the pervasiveness of Cope's rule in the Jurassic. Their study highlighted the absence of sustained trends for shell size and even emphasizes the predominance of random fluctuations in shell size (Fig. 5.7b).
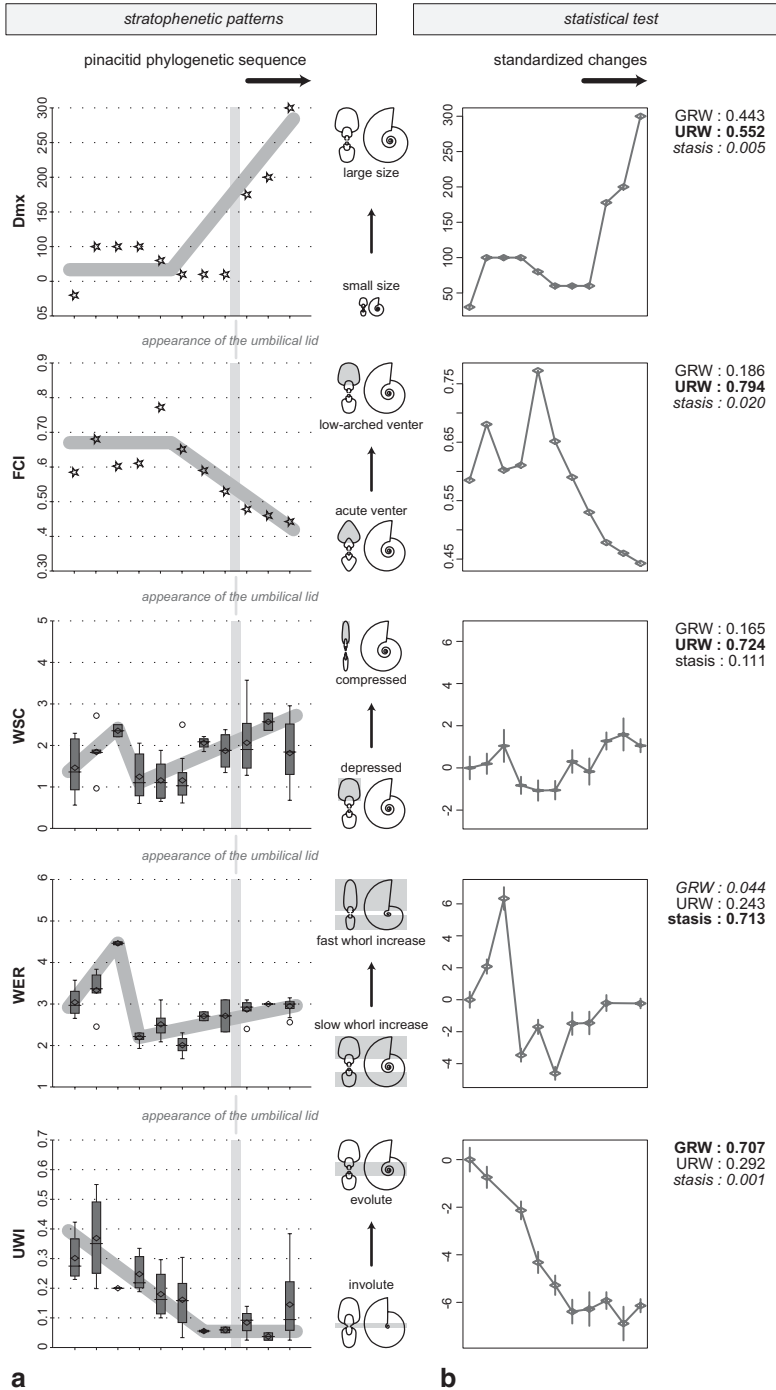
Fig. 5.8 Phenotypic trajectory analysis of univariate shell characters of Devonian ammonoids (modified after Monnet et al. 2011). **a** Stratophenetic patterns of some conch parameters and

5.3.3   Random Walks and Univariate Phenotypic Trajectory Analysis

Previously described approaches aim to describe and quantify the relative phenotypic changes of a lineage through time and phylogeny, usually at the species rank. However, trends in evolutionary series can be produced randomly (Raup and Gould 1974; Raup and Crick 1981; Bookstein 1987, 1988; Raup 1997; Roopnarine et al. 1999; Sheets and Mitchell 2001). Hence, previously empirically identified evolutionary trends must be tested statistically before examining the discrimination of patterns and processes of macroevolutionary trends. For this purpose, several methods exist, which are based on random walk models, to test and characterize observed trends and to distinguish the three modes of evolutionary change commonly considered in paleontological studies: directional change (GRW, general random walk), random walk (URW, unbiased random walk), and stasis (Gingerich 1993; Roopnarine 2001; Sheets and Mitchell 2001; Hunt 2006). The evolutionary changes of each character can be evaluated by means of the maximum likelihood method of Hunt (2004, 2006, 2007) and Hunt et al. (2008). The method performs well even when evolutionary sequences are incompletely sampled, which is likely for empirical sequences of fossils (Hunt 2006). It has been implemented as a package ("paleoTS"; Hunt 2006) in the freely available statistical and scientific environment R (http://www.r-project.org/). The method evaluates the maximum likelihood of producing the observed trends for the three evolutionary modes (GRW, URW, stasis). The relative support of each of these three models is assessed using statistical means such as Akaike weights (Anderson et al. 2000; Hunt 2004, 2006; Hunt et al. 2008). Methods to study phenotypic evolution and evolutionary trends in a phylogenetic framework have also been developed (e.g., Hunt and Carrano 2010).

For ammonoids, a recent application of random walk methods is the study of Monnet et al. (2011). Therein, the evolution of two lineages of Early to Middle Devonian age (405–395 Ma) was investigated. Eight quantitative shell characters were analyzed (Monnet et al. 2011; Klug et al. 2015b). The stratophenetic evolution of some of these shell characters for the lineage that includes the Pinacitidae is shown in Fig. 5.8a. Within this lineage, the maximum adult shell size (Dmx), the number of lobes of the suture (NLb), their relative depth of the lateral lobe (OLb), as well as the acuteness of the venter (FCI) increased simultaneously, especially among the more derived species. The umbilical width index (UWI) and the imprint zone rate (IZR) also display trends but these occur only among the more primitive species. Evolutionary changes of whorl shape compression (WSC) and whorl expansion rate (WER) display different, slightly more complex evolutionary patterns: a quick increase in the most primitive species, an abrupt reset and then a slight increase in the most derived species, giving the trend a sigmoid course.

sketch of the impact on the ammonoid shell. Boxes represent the inter-quartile range of individual values for each character and species. **b** Statistical assessment of the same macroevolutionary trends by means of the random walk method of Hunt (2006). Akaike values of the three tested evolutionary modes (GRW—directional trend, URW—random walk, and stasis) are reported and significant when greater than a half unit

This ammonoid lineage thus displays empirical morphological evolutionary trends of some shell characters. The statistical evaluation of the three evolutionary modes (directional trend, random walk, stasis) by means of the method of Hunt (2006) is illustrated in Fig. 5.8b. Among the three tested evolutionary patterns, the studied quantitative characters are mainly characterized by random trends and/or stasis (Akaike weights>0.5). The only well-supported directional trend is for UWI (increasing degree of involution). Two other shell characters may display possible directed trends (Dmx, NLb), which have negligible values for stasis and moderate values for random walks. Thus, the studied ammonoid lineage displays directed trends for UWI with certainty, and probably for Dmx and NLb, while all other characters remain devoid of directional trends. In other words, through time and phylogeny, pinacitids acquired larger, more involute and oxyconic shells and more complex sutures. With the appearance of the umbilical lid (an extension of the lateral shell wall covering the umbilicus), the trends toward greater involution (decreasing UWI) leveled off (Fig. 5.8a). This leveling off corresponds to a "left-wall effect", i.e. the trend cannot go further once the umbilicus is closed, because this marks a constructional boundary (successive whorls completely overlap). Given the variety of patterns illustrated by the various quantitative shell characters studied, this example illustrates the necessity to test statistically for the likelihood of the three evolutionary modes. This prerequisite test is crucial to avoid over-interpretation of the evolutionary patterns and their suspected causes. Studies of phenotypic evolution of ammonoid shells can thus greatly benefit from these recent quantitative approaches (see chap. 5.5).

5.4   Multivariate Phenotypic Trends in Ammonoids

Investigating morphological macroevolution of a lineage through time by focusing on a single character (univariate) enables one to distinguish two major patterns: either stasis (absence of significant changes), or trend (directional or random walk; Fig. 5.9a). Based on these two primary patterns of morphological evolution, a series of additional patterns can be distinguished based on the relative evolution among multiple trends (multivariate): convergence, divergence, and parallel evolution (Fig. 5.9b). In a phenotypic space, convergence and divergence describe that the youngest forms are closest and farthest from the oldest forms, respectively; magnitude, shape, and direction of this change do not have to be similar. Parallel evolution is defined as the independent evolution of similar biological traits in at least two different lineages having similar magnitude, shape, and direction of their phenotypic trajectories. Cases of convergence and divergence are frequent but the concepts are broad. Demonstrated cases of parallel evolution are less frequent but concern a more precise pattern. Assessing quantitatively the significance and robustness of any of these evolutionary patterns is a difficult task, for which two statistical methods became available recently. The difficulty is to model and compare curves (evolutionary trajectories) within a multidimensional space constituted by the studied morphological characters (morphospace). These two methods were applied to ammonoids to test for parallel evolution.
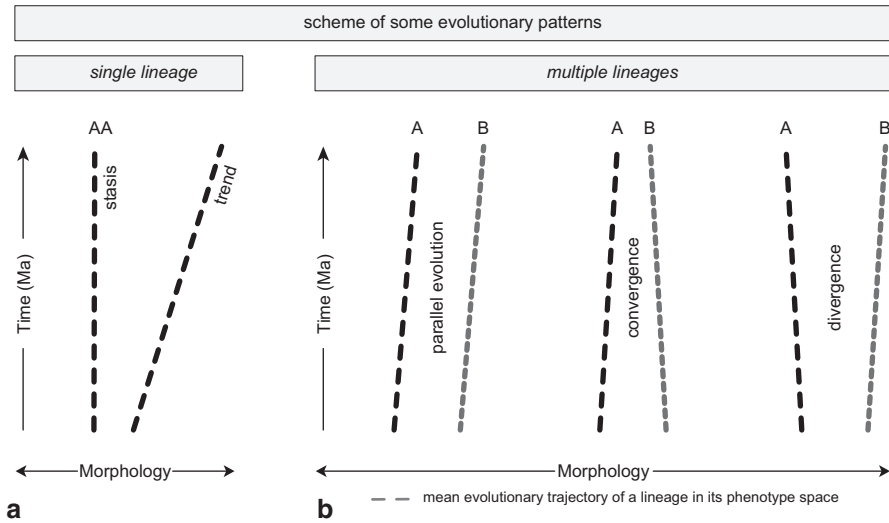
Fig. 5.9 Scheme of some macroevolutionary patterns of a lineage in its morphological space. **a** Accounting for a single character enables distinction of stasis and directed/random trend. **b** Accounting for multiple characters enables distinction of convergence, divergence, and parallel evolution

The relative evolution of a subset of characters within a morphological space can be evaluated by a method developed by Adams and Collyer (2009) for comparing evolutionary trajectories of phenotypic change (see also Collyer and Adams 2013). According to this method, the phenotypic evolution of a lineage is defined as a trajectory across a set of evolutionary levels in a multivariate morphological space. Attributes of these trajectories (magnitude, direction and shape) are quantified and statistically compared across pairs of taxa by means of a residual randomization permutation method (Collyer and Adams 2007, 2013; Adams and Collyer 2009), and a summary statistic is used to determine the extent to which patterns of phenotypic evolution are concordant. This method is very powerful since it can be used to evaluate various evolutionary patterns. One constraint is that it currently requires the same number of comparable evolutionary levels (e.g., the same number of species) between the two compared lineages. Within this method, parallel evolution of two lineages can be defined by a similar origin in the morphological space, and by similar magnitude and direction of their evolutionary trajectories.

A second method to test parallel evolution of two lineages has been proposed by Monnet et al. (2011). It follows an approach proposed by Mitteroecker et al. (2005) for comparing ontogenetic trajectories. This method is a permutation test based on within-lineage multivariate regression of the characters hypothesized to be involved in the parallel evolution. If the two lineages evolved in parallel, then their phylogenetic trajectories are identical in the morphological space defined by the subset of characters involved. This hypothesis is tested by comparing the summed squared distances of a linear total least square regression for each lineage separately between the two original lineages and for random series of two lineages obtained
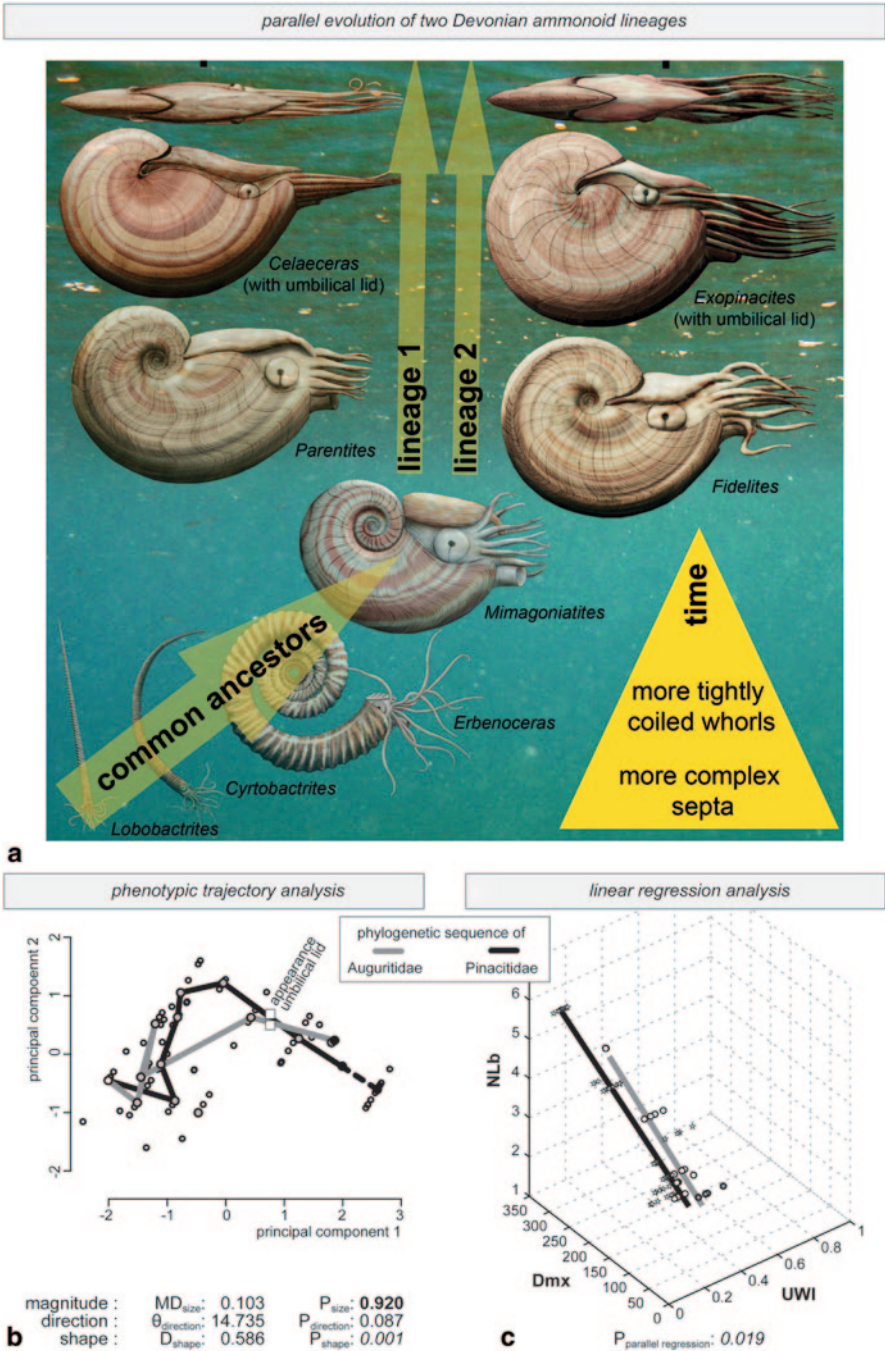
Fig. 5.10 Parallel evolution of two Devonian ammonoid families (Auguritidae and Pinacitidae) during the most intense phase of the "Devonian Nekton Revolution" (modified after Monnet et al. 2011). **a** Illustration of this parallel evolution with reconstructions of the loosely coiled ancestors

by permutation of species. If the two studied lineages evolved in parallel, the original test statistic should not be an outlier in the permutation distribution of summed squared distances (Mitteroecker et al. 2005; Monnet et al. 2011). In other words, the affiliation of permuting specimens does not increase the residuals of the multivariate regressions and this is possible only if specimens of both families are close together in the studied morphological space. The major constraint of this method is that it assumes a linear trajectory of the evolution of studied lineages in the phenotypic space, but evolutionary steps are not required to be comparable and of the same quantity as opposed to the first method (Adams and Collyer 2009).

For ammonoids, the multivariate phenotypic trajectory analysis and permutation test were applied by Monnet et al. (2011) for the first time by investigating the evolution of eight shell characters for two Devonian lineages (Auguritidae, Pinacitidae). This period was a time of major changes in the marine ecosystems with the major diversification of several important nektonic groups such as jawed fishes and ammonoids (Klug et al. 2010). In time and through phylogenetic order of appearance, both lineages display morphological directed trends toward more involute coiling, larger adult body size, more sutural elements, and the development of an umbilical lid in the most derived taxa (Figs. 5.8, 5.10a).

The hypothesis of parallel evolution of the quantified characters under consideration has been tested by the two previously described permutation methods based on the character subset including UWI, Dmx and NLb (Fig. 5.10b). These three characters were selected because they were previously demonstrated to follow directed trends and not just random walks (see above; Fig. 5.8). Using the phenotypic trajectory analysis approach of Adams and Collyer (2009), it appears that there are no significant differences in the magnitude ($MD_{size}=0.103$, $P_{size}=0.920$) and in the direction ($\theta_{dir}=14.735$, $P_{dir}=0.087$) of phenotypic evolution between the two lineages (Fig. 5.10b). However, there are significant differences in the shape of the two evolutionary trajectories ($D_{shape}=0.586$, $P_{shape}=0.001$). This difference is, however, expected because the taxa in each lineage are not truly equivalent and do not necessarily represent the same evolutionary steps. Using the linear regression approach of Monnet et al. (2011), it appears that the hypothesis of parallel trajectories of the two studied lineages cannot be rejected ($p=0.019$), but the value is low (Fig. 5.10c). Hence, it appears likely that auguritids and pinacitids evolved in parallel with respect to increasing involution, adult size, suture indentation and construction of an umbilical lid.

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and two representatives of the two lineages under consideration. **b** Statistical evaluation of the parallel evolution by means of the trajectory approach of Adams and Collyer (2009). Plot of the first and second principal components estimated from the correlation matrix for auguritids and pinacitids based on the three standardized characters UWI, Dmx, and NLb. There are no significant differences in magnitude and direction of the trajectories, but they are different in shape. **c** Statistical evaluation of the parallel evolution by means of the regression approach of Monnet et al. (2011). The phylogenetic trajectory of each lineage is fitted by a linear total least square regression. The *p*-value of the test is low, but the hypothesis of parallel trajectories could not be rejected by the permutation test

5.5 Discussion

5.5.1 Adaptation (Functional Constraints)

Among the documented morphological evolutionary trends of ammonoids, the trends of increasing involution, increased adult shell diameter, and increased suture indentation are the most frequent. In the context of the neo-Darwinian theory of evolution, all these phenotypic trends have been and still can be interpreted as reflecting increasing adaptation of shell morphology to environmental factors and/ or inter-/intra-specific competition. The various forms of the ammonoid shell have thus been interpreted in terms of functional needs, mostly in order to reconstruct the modes of life and habitats of this extinct group (see e.g., Kennedy and Cobban 1976; Westermann 1996; Westermann and Tsujita 1999; Ritterbush and Bottjer 2012; Lukeneder 2015). Opposite trends also have been documented for each shell character (see above).

   With regard to increasing adult body size, several advantages have been enumerated, such as increased defense against predation, increased food competition, increased success in mating and reproduction, increased individual longevity, and better energy use (e.g., Newell 1949; Kurten 1953; Simpson 1953; Rensch 1959; Gould 1966; Stanley 1973; Brown and Maurer 1986; Hone and Benton 2005; Korn and Klug 2007; Monnet et al. 2011; De Baets et al. 2012). Hence, trends toward larger shell diameter have traditionally been interpreted to reflect persistent adaptive selection within long-ranging lineages. Trends toward smaller size, often interpreted by paedomorphosis, are also documented (e.g., Wright and Kennedy 1979; Kennedy and Wright 1985; Korn 1995b; Korn et al. 2013b).

   With regard to trends of increasing involution, their abundance and recurrence among numerous and distantly related ammonoid clades suggest that it may have an adaptive significance due to functional constraints (Dietl 1973, 1978; Westermann 1996; Klug and Korn 2004; Saunders et al. 2004, 2008). Although hydrodynamic capabilities of these extinct animals are impossible to measure, it appears reasonable to assume that they were no enduring high-speed swimmers (Chamberlain 1980; Jacobs 1992). This interpretation is corroborated by mechanical experiments on shell models and analytical calculations of shell hydrodynamics (Chamberlain 1976, 1980; Saunders and Shapiro 1986; Elmi 1991, 1993; Jacobs 1992; Jacobs and Chamberlain 1996; Seki et al. 2000; De Blasio 2008; Naglik et al. 2015), as well as by analogy with recent nautilids (the only extant cephalopod with a chambered external shell; Ward 1988; Jacobs and Landman 1993). It has been widely demonstrated that, for shells with oxyconic shell shapes (involute and compressed), the energy consumption for swimming is the lowest and potential maximal swimming speed is the highest (decreasing drag, increasing streamlining, etc.; Schmidt 1930; Raup 1967; Chamberlain 1976, 1980; Chamberlain and Westermann 1976; Jacobs 1992; Jacobs and Chamberlain 1996; Hassan et al. 2002; Klug and Korn 2004; Klug et al. 2008; Naglik et al. 2015). Increased involution of the shell therefore appears to represent an adaptation toward improved hydrodynamic properties of the shell
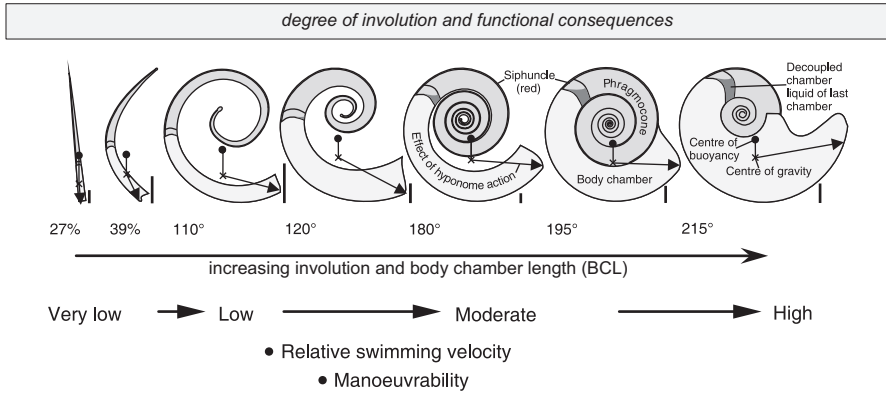
Fig. 5.11 Degree of involution of the ammonoid conch and functional interpretation. Phylogenetic change in orientation of the conchs and swimming velocity of Bactritida and primitive Ammonoidea during the Devonian (modified after Klug and Korn 2004; Klug et al. 2008). Outlines of the conchs with body chamber lengths (BCL), orientation of the aperture (OA), and relative swimming speed. Centre of gravity is indicated by a cross and the centre of buoyancy by a circle

(Fig. 5.11; but for alternative interpretations including sea-level changes and predatory pressure, see, e.g., Bayer and McGhee 1984, 1985; McGhee et al. 1991; Neige et al. 1997; Olóriz et al. 1997, 1999; Kröger 2005; Wilmsen and Mosavinia 2011). For example, the gradual shift during the Devonian from marine communities dominated by organisms with openly-coiled shells to communities dominated by tightly coiled shells in distantly related organisms (e.g., nautilids, ammonoids, gastropods) was probably caused by predatory selective forces (Nützel and Frýda 2003; Kröger 2005; Klug et al. 2010), assuming that open coiling makes shells weak and vulnerable to attack and force but also, they are simply larger (this selection pressure is also linked with swimming abilities).

With regard to trends of increasing suture frilling, the function of septal folding is subject of much debate (e.g., Kennedy and Cobban 1976; Saunders 1995; Hewitt and Westermann 1997; Daniel et al. 1997; Westermann and Tsujita 1999; Lewy 2002; Checa 2003; Klug and Hoffmann 2015). The classic morpho-functional interpretation is that increasing suture frilling reduces the risk of implosion by providing buttressing against hydrostatic pressure on the phragmocone (Pfaff 1911; Westermann 1971, 1975; Hewitt and Westermann 1986, 1997; Seilacher 1988; Jacobs 1990; Hewitt 1996; Daniel et al. 1997; Hassan et al. 2002; De Blasio 2008). By contrast, available quantitative analyses of the ammonoid fossil record reveal no correlation between suture frilling and supposed water depths (Olóriz and Palmqvist 1995; Olóriz et al. 1997, 1999). The evidence for paleobathymetric reconstruction is, however, commonly poor, thus making the hypothesis of depth-controlled suture frilling difficult to test. Ammonoids were mostly epipelagic organisms inhabiting the uppermost part of the marine water column (<300 m; Westermann 1996; Westermann and Tsujita 1999; Lukeneder 2015). Wells (1999) even thought that this payed a role in their extinction, because nautilids (simple septa) can sustain pressures in depths up to 700 m (e.g., Ward 1988; Dunstan et al. 2011). In any case, septum shape

has also a strong developmental component (suture frilling increases through growth and is significantly correlated with the space available; Klug and Hoffmann 2015).

5.5.2   Iterative Evolution and Evolutionary Jumps

Numerous examples of morphological long-term trends have been described in the literature within ammonoid cephalopods (see above). These repeated trends in phenotypic traits are commonly regarded as evidence of adaptation under common selection pressures (Simpson 1953; Endler 1986; Schluter 2000), therefore illustrating natural selection's major role in shaping morphological evolution and repeatability of evolutionary processes.

In this context, repetitive sedimentary sequences reflecting cyclic environmental changes (e.g., sea level, climate) have been suggested as a major trigger of morphological evolutionary trends of the ammonoid shell by means of similar morphofunctional adaptive responses. For instance, Bayer and McGhee (1984, 1985) studied the morphological evolution of several ammonoid lineages during the Jurassic and they identified *"iterative repetition of identical evolutionary courses"* in the ammonite faunas (Fig. 5.4b). They argued that these iterative morphological changes were in response to cyclic changes in the physical marine environment: "*similar environments were inhabited by ammonite faunas of similar morphology, and moreover, similar directional changes in the physical environment are mirrored by similar morphological changes in the ammonite faunas*" (Bayer and McGhee 1984). Both endemic forms, which evolved *in situ* and migrant forms from the Tethyan realm were equally affected. The phenomenon of iterative evolution in ammonoids is well known and several authors noted that these morphological sequences are repeated in groups separated both in time and taxonomy (e.g., Schindewolf 1940, 1950; Haas 1942; Arkell et al. 1957; Wiedmann 1973; Kennedy and Cobban 1976). However, most discussions in the literature concern taxonomic and biostratigraphic consequences of the implied homeomorphies. This view of iterative evolution led to the concept that ammonoids repeatedly evolved from long-lived generalist lineages mainly inhabiting distal environments toward short-lived opportunistic lineages inhabiting shallower environments (e.g., Wiedmann 1973; Jacobs et al. 1994).

In contrast, Guex (1992, 2001, 2003, 2006) qualitatively examined these iterative patterns for Mesozoic ammonoids. He argued that during stable periods, ammonoid lineages experience classic long-term evolutionary trends of their shell (e.g., increase of shell size, involution, compression, as well as increase of suture frilling) and that during extinction periods, relatively tightly coiled ammonites can give rise to highly evolute forms or heteromorphs with simple ornamentation and almost ceratitic suture line. He dubbed this sudden evolutionary change, which is at variance with previous long-term changes, an "*evolutionary jump*". He pointed out that these evolutionary jumps are characterized by the appearance of forms, which are partly homeomorphic with remote ancestors of their own lineage and interpreted these newly evolved homeomorphic taxa as being atavistic. He called also this

phenomenon "*proteromorphosis*" because it cannot be explained by normal pae-
domorphic transformations. Monnet et al. (2013) recently described such a poten-
tial evolutionary jump within a lineage of Triassic ammonoids. Guex (1992, 2001,
2006) also argued that episodes of strong environmental stress are at the origin of
many new ammonoid lineages by promoting the abrupt appearance of significantly
different forms by means of such evolutionary jumps.

The most extreme case of iterative evolution is probably the recurrent appear-
ance of loosely coiled, uncoiled and trochospirally coiled heteromorph ammonoids,
which have not only been linked to periods of environmental stress (Guex 2006),
but also to advantageous trophic conditions (Nesis 1986; Cecca 1997) or sea-level
changes (Keupp 2000). Such heteromorphic ammonoids were long seen as evolu-
tionary dead ends and irreversible, phylogenetic end-forms (for a review, see Wied-
mann 1969). Before this time, the belief in Dollo's law of irreversibility was deeply
entrenched in the thoughts of natural scientists, stating that the re-evolution of any
complex character like the coiled ammonoid shell was considered unlikely or im-
possible. Besides methodological problems with interpreting uncoiled as less com-
plex than coiled shells (Urdy and Chirat 2006), there are additional reasons to see
heteromorphic ammonoids as anything but evolutionary dead ends. Heteromorphs
were highly successful (diverse and abundant) during some periods (Cretaceous),
and diverse heteromorphic lineages gave rise to coiled representatives, which
counter-act these ideas (e.g., Wiedman 1969; Cecca 1997; Bert and Bersac 2013).
Contra-intuitively involute forms have also been seen as phylogenetic end-forms.
For instance, this seems to be the case of the Devonian Auguritidae and Pinacitidae
(Monnet et al. 2011), Triassic Sagecerataceae and Pinacocerataceae (Diener 1917;
McGowan and Smith 2007; Korn 2012), and Jurassic Amaltheidae (Meister 1988),
among others. However, some lineages with oxyconic forms have also successfully
given rise to less coiled descendants.

The major characteristic of all these models of macroevolution of the ammonoid
shell is that they rely on two widespread views among ammonitologists: (i) the am-
monoid conch is shaped by its functional needs only and thus reflects environmen-
tal changes, and (ii) ammonoids evolved toward particular morphologies, which
correspond to adaptive peaks in the ammonoid phenotypic landscape. By contrast,
the widespread adaptive interpretations of the ammonoid conch are *ad hoc* expla-
nations in many cases, partially because their behavior cannot be observed (e.g.,
swimming speeds, habitat depths, vertical movements; compare Ritterbush et al.
2014, Naglik et al. 2015). This is a common problem in paleontology (Ebbighausen
and Korn 2013), strongly limiting the range and number of falsifiable hypotheses.
In some cases, iterative intricate evolutionary patterns or morphological character-
istics allow speculations with a certain degree of plausibility, which justifies their
description and discussion.

Moreover, natural selection is one possible and important, although commonly
over-rated, trigger and driver among several others in the fabric of evolutionary
trends. Interestingly, evolutionary trends are never global and opposite patterns are
also common: usually, they occur only in specific clades, while other coexisting
clades still retain or evolve very different shell morphologies. For instance, crioconic,

serpenticonic and platyconic forms coexisted with the highly involute auguritids and pinacitids (see Klug 2002; Korn and Klug 2003). Representatives with very complex and very simple suture lines were found together (e.g., *Beloceras* and *Archoceras*: Korn et al. 2013b; *Metoicoceras* and *Euomphaloceras*; Cobban et al. 1989). Micromorphic and large-sized ammonoids also co-occured (e.g., *Nannometoicoceras* and *Metoicoceras*; Kennedy 1989), and very involute and compressed forms coexisted with evolute and/or depressed forms (e.g., *Oxylongobardites*, *Tropigastrites* and *Proarcestes*; Monnet and Bucher 2005). Furthermore, quantitative analyses of the correlation between the supposed adaptive shell characters and environmental factors produced variable results (Bayer and McGhee 1985; Donovan 1985; Cariou and Hantzpergue 1988; Batt 1989; Jacobs et al. 1994; Westermann 1996; Neige et al. 1997; Olóriz et al. 1997, 1999, 2002; Westermann and Tsujita 1999; Vörös 2002; Kawabe 2003). But it must be acknowledged that environmental parameters (e.g., bathymetry, temperature) are usually difficult to assess and quantify in the past and in most cases, evidence for the ammonoids' actual habitats is weak because they might have lived anywhere in the water column above where they are found (De Baets et al. 2015) and their shells could easily be transported (Wani and Gupta 2015). Nevertheless, some indication of their habitat can be constrained by combining multiple lines of evidence (Ritterbush et al. 2014; Naglik et al. 2015), including predator–prey interactions (e.g., Keupp 2006; Kruta et al. 2011; Hoffmann and Keupp 2015; Tanabe et al. 2015) and stable isotopes of their shells (e.g., Lécuyer and Bucher 2006; Lukeneder et al. 2010; Lukeneder 2015). Interestingly, the co-occurrence in time of different evolutionary trends leading to very disparate co-existing morphologies may reflect the existence of multiple adaptive peaks in the ammonoid phenotypic landscape and/or that the triggers of these trends are not global and not only adaptive. The model of Guex (2001, 2006) assumed that trends are reset during periods of high environmental stress. This remains to be tested but enables us to ask about the distribution, influence and frequency of trends within/among space, time, taxonomy, and phylogeny, as well as the proportion of adaptation, covariation and chance generating these trends. Furthermore, rates of morphological change depend on the observed time interval, so that these first need to be quantified to speak about evolutionary jump as opposed to normal evolutionary trends.

### 5.5.3   Covariation (Constructional Constraints)

Evolution of shell shape driven by adaptation, although reasonable from a mechanical point of view, is certainly not the sole driving mechanism behind long-term evolutionary trends in ammonoids. To explain how certain organisms have evolved certain features, evolutionary biologists emphasized the role of constructional/developmental constraints on evolution (Williamson 1981; Alberch 1982; Charlesworth and Lande 1982; Holder 1983; Maynard-Smith et al. 1985; Raff 1987; Goldsmith 1990; Arnold 1992; Tabin 1992). Maynard-Smith et al. (1985, p. 266) defined a developmental constraint as "*a bias on the production of various phenotypes caused*

by the structure, character, composition, or dynamics of the developmental system".
Correlations between characters belong to the most common patterns attributed to
developmental constraints. Such correlations may result from interactions between
tissues during the development or the involvement of the same genes or develop-
mental pathways in multiple morphogenetic processes. Although it is difficult to
rule out selective (functional) constraints (adaptation), constructional, developmen-
tal and/or genetic constraints can also explain common evolutionary patterns (e.g.,
Morita 1993, 2003; Wagner and Erwin 2006).

In this context, it is here suggested that many of the described long-term mor-
phological evolutionary trends of ammonoids can be explained, in part, by other
constraints than selective ones. Indeed, some of the documented trends of the am-
monoid shell can be produced by constructional constraints (Seilacher 1973; Urdy
et al. 2010a, 2010b; Monnet et al. 2011) referred to as covariation. In other words,
some morphological trends of specific characters of the ammonoid shell can result
from trends in other traits because the way the shell is constructed (morphogenesis)
involves the covariation (scaling, usually by means of allometric rules) of several
shell characters. It is important to identify such aspects of covariation, because in
this case, it is unnecessary to search for an adaptive explanation.

Covariation of shell characters is well known from ammonoids. For instance, the
intraspecific variation of an ammonoid species is usually expressed by the follow-
ing gradient: the more evolute the shell, the thicker the whorl shape (large whorl
width to whorl height ratio), and the more robust the ornamentation. It is referred to
as Buckman's first rule of covariation (e.g., Reeside and Cobban 1960; Westermann
1966; Dagys and Weitschat 1993; Morard and Guex 2003; Yacobucci 2004; Ham-
mer and Bucher 2005; Monnet et al. 2010, 2015b; Bert and Bersac 2013; De Baets
et al. 2013a, De Baets et al. 2015). This covariation pattern concerns intraspecific
variability and differs from the type of covariation discussed below. Among phe-
notypic directed evolutionary trends of ammonoids, the concept that some of these
trends can be due to scaling effects is discussed below for the two most frequent
morphological trends: increasing involution and increasing suture indentation.

A striking pattern of ammonoid evolution is that trends of increasing adult shell
diameter are commonly, but not systematically, associated with trends of increas-
ing involution and increasing suture indentation. These trends in size are usually
interpreted to exemplify Cope's rule. However, these trends concern the adult shell
diameter, not the volume of the soft tissues. Soft tissues of ammonoid cephalopods
are insufficiently known and consequently also their relation with conch size. Nev-
ertheless, we can reasonably assume that their soft body scales with the volume of
the body chamber (Arkell et al. 1957; Doguzhaeva and Mutvei 1991; De Baets et al.
2012, De Baets et al. 2015). Yet, from a morphogenetic point of view, what would
happen if a studied ammonoid clade followed a size-increase of its soft body? It
appears that increasing body size (volume of soft tissues in the body chamber) can
be accommodated in several ways (Guex 2001, 2003): increasing arc length of the
body chamber, increasing whorl width, or increasing whorl height, which can result
in increasing shell diameter and/or involution (Fig. 5.12). We stress that several
trends in ammonoid shell geometry can be explained by increasing adult body size
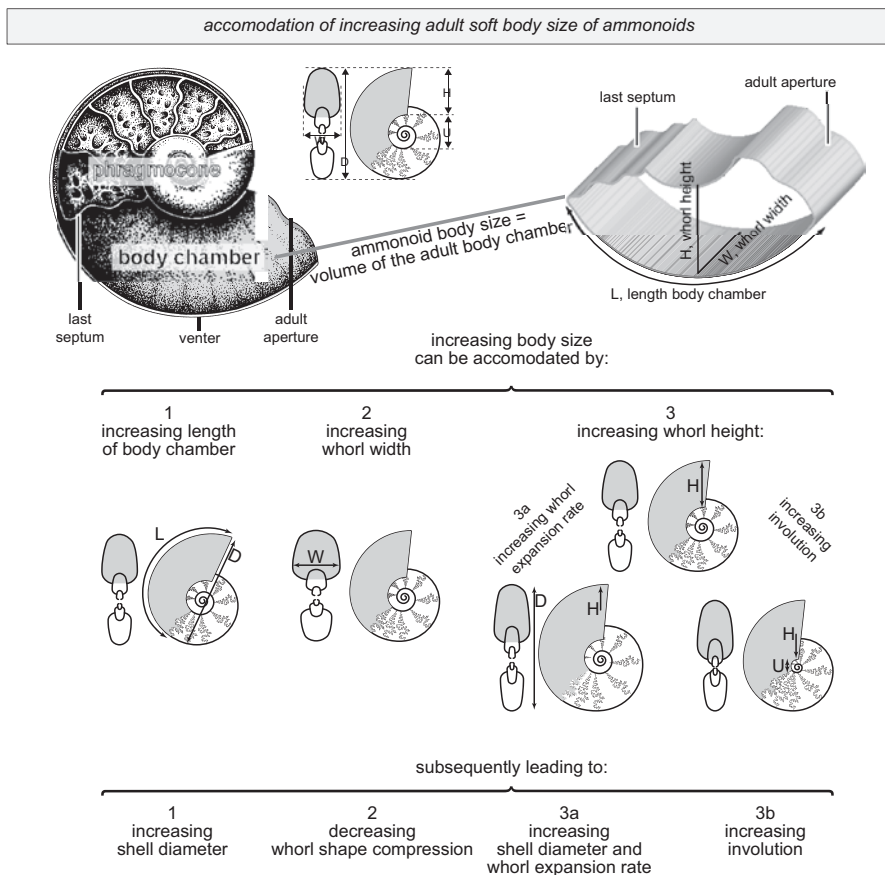
Fig. 5.12 Scheme illustrating the various ways that an increase of adult soft body size of ammonoids can be accommodated by the geometry of their external shell. Increase in ammonoid soft body size can be expressed in terms of three basic alternatives, which are not mutually exclusive and can be accumulated in various combinations and proportions: increasing arc length of body chamber, increasing whorl width, and increasing whorl height. These three accommodating changes can lead to four increasing phenotypic trends of shell geometry: in shell diameter, in whorl shape depression, in whorl expansion rate, and in involution (compare with Figs. 5.5, 5.8)

as an alternative to functional explanations (Guex 2003), because both changes in shell diameter and shell involution are two possible paths for ammonoids to accommodate soft body size increase. Although shell diameter is usually assumed to reflect body size, it does not suffice and even is not required to identify a case of body size increase for ammonoids. For example, increasing whorl width or increasing involution without changes in shell diameter still can be induced by an increasing adult body size (Fig. 5.12). Therefore, an evolutionary increase of ammonoid soft body size can indirectly trigger several trends in ammonoid geometry.

Bearing this distinction in mind is essential because morphological trends of the ammonoid shell are quite often interpreted by more or less *ad hoc* adaptive and

morpho-functional explanations. With regard to trends of increasing involution, it may well result solely from an increase in body size, and not directly from a selection pressure on the coiling itself and its associated swimming advantage; increase in body size may itself be a swimming-related factor, because it provides the possibility for a larger volume of propulsive muscles and hydrodynamic properties change with body size as well (Naglik et al. 2015). Therefore, some conclusions on improved hydrodynamics of the shell may be speculative and represent secondary adaptations (Gould and Lewontin 1979; but see Levinton 2001). The role of hydrodynamic efficiency in ammonoid shell shape, argued by several authors, may have been overestimated (Weitschat and Bandel 1991). This is also supported by large intraspecific variability in shell shape in several ammonoid lineages (Dagys and Weitschat 1993; De Baets et al. 2015). With regard to trends of increasing suture indentation, it may also result from an increase in body size, and not directly from selection pressure on the suture frilling. Although knowledge of the morphogenesis of ammonoid septa remains incomplete (Klug and Hoffmann, 2015), septal patterns display similarities with structures that developed under a "*domain effect*" by a "*viscous fingering*" phenomenon (see also review of Checa and García-Ruiz 1996). In this morphogenetic model, details of the suture pattern depend on the space and shape available for the suture during its formation (septa are secreted after the surrounding shell). This is supported by the widely documented significant increase in suture indentation throughout ontogeny of the ammonoid shell (the number of suture elements increases with whorl height of the shell; e.g., Swinnerton and Trueman 1917; Erben 1966; Korn and Klug 2003; Pérez-Claros et al. 2007). In this context, as for involution, folding and fluting of the septal mantle are an additional means to accommodate body size increase (Guex 2003; compare Illert and Reverberi 1988). Interestingly, even if some trends in ammonoid shell geometry can be triggered by an increase of ammonoid soft body size and thus result from constructional constraints as stressed above, adaptive pressure can still operate indirectly: An increase in soft body size coupled with a constant shell diameter will induce a loss of buoyancy, which can be compensated in several ways (e.g., decrease of body chamber length or decrease of shell thickness, which both influence shell orientation). Hence, positive or negative adaptive feedback can enhance or minimize the impact of constructional constraints.

The comparison of these theoretical investigations with the previously described long-term evolution of Triassic acrochordiceratids and Devonian auguritids and pinacitids (Figs. 5.5, 5.8) is striking. The three lineages are characterized by directed trends toward increasing involution and suture indentation concomitant with increasing adult shell size (Monnet et al. 2011, 2012). Following the previous reasoning, it appears that these trends can be induced by covariation (constructional constraints) with evolutionary changes in soft body volume. They may be secondary trends and as such their interpretation in terms of adaptation should be cautious. Notably, these trends in the three studied ammonoid lineages are not associated with any trend in whorl shape compression whereas it is one of the possible ways of accommodating increased soft body volume (compare Figs. 5.5, 5.8, 5.12). This observation highlights the view that the relative influence of these different possible

covariation patterns remain to be elucidated and investigated, as well as why certain evolutionary trajectories are favored or not (possibly by means of adaptive feedbacks induced by some constructional constraints). Therefore, it is stressed that long-term phenotypic trends in ammonoid shell form must be tested rigorously and conjointly. This remains to be done, but such an effort is crucial because it is not really possible to interpret the adaptive value of trends in ammonoid shell form without accounting for such possible constructional constraints. An additional problem is that there may be other constructional or even adaptive constraints that are not yet understood because of missing data, non-preservation or simply the historic aspect (i.e. behavior). In the case of the degree of septal frilling, it has to be understood that not all aspects of septal growth and construction are fully understood yet. This situation strongly limits the scientifically correct approaches to identify potential evolutionary drivers triggering the evolution of ammonoid septa.

In conclusion, from a theoretical point of view, long-term phenotypic evolutionary trends of the ammonoid shell can result from adaptation (selective constraints),from covariation (constructional constraints) or a combination of these and other factors. For instance, both increasing involution and suture indentation can just be scaling effect of within-lineage size-increase (if soft body volume is considered and not shell diameter); similarly, seeming simplification of sutures might have originated in size-reduction or changes in whorl cross section or development. The respective relative role of these non-mutually exclusive, possible drivers of evolutionary trends in shaping ammonoid evolution has not been investigated sufficiently yet. Furthermore, morphogenesis of the ammonoid shell (and other mollusk shells) is still insufficiently known. More and new information on mollusk shell morphogenesis could provide crucial insights on patterns and processes of mollusk evolution. In this context, it is not surprising that previous studies trying to evaluate the prevalence of Cope's rule or increasing complexity of life resulted in unclear and controversial results. Indeed, such studies have to differentiate between adaptive trends and covariation, be it driven by scaling effects or other factors.

5.5.4   Developmental Constraints and Heterochrony

Constraints on evolutionary trends are not limited to adaptive selection and constructional covariation. Naturally, there are also developmental and genetic constraints. The latter cannot be assessed in ammonoid cephalopods since it is an extinct group and DNA of that age is unknown, but these factors may have an important role. For instance, the repeated evolution of a shell character may speculatively result from the repetitive loss of the expression of regulatory Hox-genes (Averoff and Patel 1997; Prud'homme et al. 2006) or the repeated recruiting of developmental genes (Lindsey 1962; Colosimo et al. 2005). Sudies on extant shell-bearing mollusks such as gastropods are one of the only ways to provide clues about this kind of constraints on the evolution of ammonoids.

Major evolutionary changes in a trend are often constrained by morphological and functional trade-offs, with one structure improving at the expense of another.
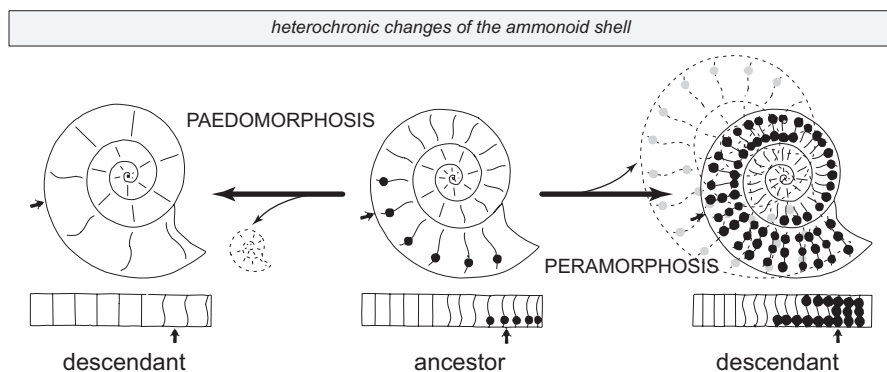
Fig. 5.13 Scheme illustrating the paedomorphosis and peramorphosis of an ancestral ammonoid with regard to the presence and number of rows of tubercles (modified after Landman and Geyssant 1993)

Many such trade-offs have a developmental basis and have arisen from heterochrony (McNamara 1997). Heterochrony (i.e. developmental change in the timing of events, leading to changes in size and shape) is a fundamental aspect of evolution, supported by a vast biological and paleontological literature. It has been argued that heterochrony plays an important role in evolutionary trends (McNamara 1982, 1990), including both anagenetic and cladogenetic trends, and both micro- and macro-evolutionary trends (McNamara and McKinney 2005). Briefly, heterochrony can be described in the form of paedomorphosis and peramorphosis that occur between an ancestor and its descendant: on the one hand, paedomorphosis can be observed when a descendent retains in its reproductive, adult stage the juvenile traits of its ancestor taxon, and on the other hand, peramorphosis is delayed maturation and extended periods of growth (Fig. 5.13). It must, however, be kept in mind that in fossil organisms like ammonoids only size and shape is available, while the duration (age) and the rate of growth are mostly unknown (Landman and Geyssant 1993; allometric heterochrony *sensu* McKinney 1988). A relationship between evolutionary trends and heterochrony arises because evolutionary trends are, like ontogenetic trajectories, unidirectional. For trends to develop, in addition to the intrinsic factor of heterochrony, extrinsic factors are also critical. Selection of either progressively more paedomorphic or more peramorphic traits must take place along an environmental gradient, such as in the aquatic environment from deep to shallow water, or from coarse to fine-grained sediments (McNamara 1982, 2006). An evolutionary trend from ancestors to descendants that show increasingly more paedomorphic characters is called a paedomorphocline. If the trend shows increasing peramorphic descendants, it is called a peramorphocline (McNamara 1982, 1990). Collectively these are called heterochronoclines. Many examples of heterochronoclines have been described in ammonoids and for various characters and in various directions in their shell morphospace (e.g., Gould 1977; Dommergues et al. 1986, 1989; Landman 1988, 1989; Meister 1988; Dommergues and Meister 1989; McNamara 1990; Dommergues 1990; Korn 1992, 1995a, 1995b; Landman and Geyssant 1993; Gerber 2011; Korn et al. 2013b; Fig. 5.4). Hence, not

only developmental constraints play a significant role in ammonoid evolution, but also this role can be evaluated thanks to the accretionary mode of growth of mollusk shells, which provides an invaluable access to individual ontogenetic development in individual ammonoids. In this context, the recurrence of morphological evolutionary trends within ammonoids can be seen as the repetitive and preferential selection of the same heterochronic process because of similar environmental conditions/gradients and intrinsic constraints that canalize the evolution of ammonoid clades (Dommergues et al. 1989; McNamara 1990).

Heterochronoclines *ipso facto* induce a rough parallel trend between phylogeny and ontogeny that has been frequently described in ammonoid evolution. However, within the same lineages, the chronocline evolution of the different ammonoid shell characters is a mosaic pattern characterized by various trends and stases that are often at variance. For instance, in the case of the previously discussed Triassic acrochordiceratids, one important ontogenetic pattern is that several shell characters show significant and persistent shift during ontogeny (Monnet et al. 2012, Fig. 5.11). Members of this lineage became more involute, developed more compressed whorl sections, and reduced the number of ribs during development. Interestingly, while the ontogenetic trends in coiling and ribbing density mirror their long-term stratophenetic trend (this can be described as a size-based or allometric peramorphocline; McKinney 1988; Dommergues et al. 1989; McKinney and McNamara 1991), no ontogenetic trend in whorl shape compression could be found in the evolution of this group during the Anisian. Hence, evolutionary trends of the Anisian Acrochordiceratidae parallel their ontogenetic developments in part only. This partial concordance between the evolution of the group and its ontogenetic changes poses the question whether the direction of evolutionary change at the phenotypic level may be a product of the within-individual dynamics of development and/or of the within-population dynamics of natural selection. In other words, was the morphological evolutionary trend of increasing coiling of ammonoids driven by natural selection, by a developmental constraint, or by a combination of both (Arthur 2001, 2004)? Paleontologists and neontologists sometimes underestimate developmental constraints in the shaping of anagenetic morphological trends (McKinney 1990). Since the evolution of organisms is an equilibrium between various mutually interacting processes (Waddington 1941), what is the relative influence of the various constraints (selective, constructional, developmental, chance, etc.) on the evolution of the ammonoid shell? The exact contribution of each type of constraints remains to be investigated and also requires a better understanding of the morphogenesis of the ammonoid shell. Crucial information may come from the ongoing development of quantitative and theoretical modeling of the mollusk shell (e.g., Raup 1966; Ubukata et al. 2008; Monnet et al. 2009; Urdy et al. 2010a; Parent et al. 2010, 2012; Moulton et al. 2012, 2015; Chirat et al. 2013), as well as from the comparison with growth-monitored individuals in the wild or in aquaria (Urdy et al. 2010b).

5.5.5   *Prospects on Long-Term Phenotypic Trends*

Understanding the patterns of evolution requires identifying the processes that shape these patterns and in which context they apply. Currently, the knowledge and

understanding of the fabrics and dynamics of long-term morphological evolutionary trends is complicated by two major sources of bias.

Natural selection as a driver of phenotypic evolution tends to be overrated, or, in the words of Graffin and Olson (2010), there is a "*false idol of natural selection*". Although adaptation has been historically overestimated, the existence of adaptation and selection as drivers of evolution with a much smaller role than originally thought appears reasonable. A fundamental epistemological problem of both is the near impossibility to prove the causal relationship between, e.g., an ecological factor and a morphological change. However, it is legitimate and stimulating to seek correlations between evolutionary change in ammonoid morphology and other factors such as ecological factors, paleogeography, predation patterns, and particular evolutionary patterns. At some degree of correlation between evolutionary patterns and ecological processes, randomness of evolutionary change becomes increasingly implausible, allowing near-hypothetical speculations on aspects of adaptation and selection influencing evolution.

A first example has been discussed in great detail above, namely the parallel evolution of two distantly related lineages of Devonian Auguritidae and Pinacitidae (Monnet et al. 2011). It appears unlikely that several morphological traits including highly unusual ones such as the umbilical lid evolve in parallel over millions of years without the slightest aspect of adaptation or selective mechanism as evolutionary driver. It is undoubted that covariation explains a significant part of the evolutionary change, but explaining the entire course of this case of parallel evolution would mean circular reasoning. At some point, adaptation or selection must have a played a role, even if only gently. Sexual selection is well-known to play an important role in extant organisms, but is hard to prove for extinct ones; it is well conceivable that sexual selection is also responsible for some evolutionary trends in ammonoid evolution (compare Knell et al. 2013).

A second example is a number of distinct evolutionary trends (although a left wall effect cannot be entirely ruled out in these cases) in early ammonoid evolution (Korn and Klug 2003; Klug and Korn 2004; De Baets et al. 2012, 2013b; Klug et al. 2015a), which are well documented for the embryonic shell (De Baets et al. 2012). These include a reduction in ammonitella size, increase in coiling of the ammonitella (Erben 1964, 1965, 1966; House 1996; De Baets et al. 2012, 2013b) but also of post-embryonic whorls (Klug and Korn 2004), the decrease of the size of the umbilical window until its closure (House 1996; De Baets et al. 2012) as well as an increase of the whorl expansion and soft-part volume (Korn and Klug 2003; Klug and Korn 2004). Several alternative explanation for these trends present themselves: (i) ammonitella-size decreased simultaneously with increasing soft-body size, suggesting increasing reproductive rates (and reduced survivorship of offspring) (discussion in De Baets et al. 2012); (ii) in the Early Devonian, an increase in coiling is documented from several clades (Ammonoidea, Dacryoconarida, Orthocerida) synchronous with a decrease in embryonic or larval shell size (Gastropoda, Ammonoidea)—a random coincidence appears less likely than selective pressure from profound macroecological pressures (Klug et al. 2010); (iii) with increasing coiling, the orientation of the aperture changed from vertically downward *via* oblique to horizontally upward (Korn and Klug 2003; Klug and Korn

2004)—a random evolutionary change appears, again, unreasonable, since it makes perfect sense from a hydrodynamic point of view (a more or less horizontal aperture enhances maneuverability and swimming; see discussion in Klug and Korn 2004); and (iv) increased coiling and improved swimming capabilities do make sense in the light that more or less synchronously the gnathostome fish underwent an explosive radiation, thus suggesting a selective pressure from evolving mobile predators, probably progressively occupying the same habitats as the ammonoids (compare Klug et al. 2010, 2015a).

Therefore, it appears easier and reasonable to keep hands off adaptive explanations for evolutionary change among ammonoids, but selection and adaptation must have played a role of unknown proportion in ammonoid evolution. Its denial is of no help in under-standing ammonoid evolution, but great care and openness towards criticism and discussion is essential.

A major second source of biases in the analysis of long-term trends is rooted in the data available and the approaches used to these analyses. Most studies are partly biased by one or a combination of the following aspects: absence of a rigorous phylogenetic framework, insufficient consideration of anagenetic and ontogenetic changes, insufficient taxonomic coverage, insufficient consideration of morphogenetic constraints, absence of comparison with simulated evolutionary patterns (especially to evaluate the impact of chance alone), among others. For instance, evolutionary changes in size were documented to apply to several ammonoid groups, but there are no quantitative data covering all ammonoid taxa (rather than specific-clades) of a distinct time interval, with a robust phylogenetic framework and with integration of covariation patterns of the diverse shell characters (compare Hallam 1975 and Dommergues et al. 2002). In this context, several questions on evolutionary patterns and processes remain to be investigated. What is the proportion between adaptive (selective constraints) and scaled (constructional constraints) morphological long-term evolutionary trends among ammonoids? Under which conditions did these trends occur? Are trends (be it adaptive and/or a secondary effect) restricted in time and space and clades? What is the influence of origination and extinction events on the fabrics of evolutionary trends (see Guex 2006)? All these questions among many others remain to be investigated and await adequate data collection and subsequent quantitative analyses.

Finally, the impact of chance on the frequency of ammonoid evolutionary trends remains also to be assessed. Theoretically, evolutionary trends in involution and suture indentation can be adaptive and/or scaling effects of size changes. Since apparent trends in evolutionary series can be produced randomly (Raup and Gould 1974; Raup and Crick 1981; Bookstein 1987, 1988; Raup 1997; Roopnarine et al. 1999; Hunt 2006), are these documented trends more frequent than what can be expected just by sheer random evolution? All morphological characters have lower and upper viable limits. Hence, the location of origination of a clade or taxon in its phenotype space directly influences the chance of having a trend among its descendants. Indeed, the chance of a taxon having a larger descendant (or with a more involute shell, or with a more indented suture, etc.) may be related to the distance from the limits of the considered character in the morphological space of the studied group.

Hence, it remains to be seen whether documented evolutionary trends of the ammonoid shell are caused (and in which proportion) by random evolution constrained by the constructional limits of the shell (left-wall effect).

Now, if we consider shell characters in the biological concept of adaptive landscapes (Wright 1932; McGhee 1999, 2007; Wilson 2013), shell form can be expected to exhibit repeated trends in some characters given the functional properties of the ammonoid shell (buoyancy device containing soft-tissues). In this case, is the distribution in time and space of trends concordant with adaptive hypotheses? Can we derive a morphological adaptive landscape of the ammonoid shell? Finally, in this context of evolutionary trends and morphological landscapes, several questions remain to be investigated. Are kinds of trends randomly distributed among shell characters (for instance, are cases of size trends restricted to particular morphologies)? Do trends originate at random locations in the morphospace of the studied group? New data delivering answers to these questions will provide insights on patterns and processes of long-term phenotypic trends of the ammonoid conch such as convergence, divergence, and parallel evolution.

5.6   Conclusions

Long-term morphological evolutionary trends of ammonoid cephalopods are numerous and suggest the existence of common processes acting regularly to mold their macroevolution. Although ammonoid cephalopods are extinct, their high evolutionary rates and the excellent fossil record of their shells make them superb study objects to reveal insights into patterns and processes of long-term phenotypic evolutionary trends. Unfortunately, quantitative studies are still rare and often lack a phylogenetic framework. As acknowledged by Jablonski (2000): "*only a few studies have met the necessary protocols for the analysis of evolutionary tempo and mode at the species level, and so the distribution of evolutionary patterns among clades, environments, and modes of life remains poorly understood*".

From the few existing studies, it appears that constructional (covariation) and adaptive constraints are not mutually exclusive. Both can contribute to the fabrics of evolutionary trends for ammonoid lineages. This underlines that evolutionary and developmental morphogenesis, and the controls upon them, can never be truly understood in separation from functional adaptation and constructional covariation. Distinction between covariation and adaptation in evaluating evolutionary trends is essential in order to avoid over-interpretation of the evolutionary patterns. For instance, the frequent increase in suture indentation is probably not a primary adaptation to water depth against implosion, but likely represents a secondary trend caused partly by an increase of adult shell size and shape due to covariation (constructional constraints). Hence, recurrence of particular combinations of morphology, which are commonly regarded as strong arguments for functional constraints, can also represent "fabricational noise" (Seilacher 1970, 1973). It is thus crucial for

evolutionary analyses to understand the driving factors behind evolutionary morphological modifications.

Selective (adaptation) and constructional (covariation) constraints do occur in the evolution of the ammonoid shell. Taken separately, they do not explain every evolutionary trend, and their respective contribution to ammonoid evolution remains to be quantified. Understanding the underlying processes of directed evolution still require further research. Answers to such questions strongly needs adequate quantitative datasets framed with robust phylogenies, comparison against simulated random evolution (to evaluate the prevalence of constraints or chance in generating trends), a better knowledge of shell morphogenesis (to precisely quantify the expectable covariation between measured shell characters), and accounting for both anagenetic and cladogenetic changes.

We expect that further discoveries and the application of quantitative methods and better knowledge of mollusk shell morphogenesis will continue to reveal information on the evolutionary history of this major marine extinct group, the ammonoids, and contribute to the understanding of patterns and processes in macroevolution. If ammonitologists do so, they can become nomothetic scientists, which Stephen Jay Gould would probably have appreciated.

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