

Chapter 2

Evolutionary Trends of Triassic Ammonoids

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2.1 Introduction

This chapter is a review of the major evolutionary trends of Triassic ammonoids. During this period (ca. 252.2–201.3 Ma), global biota recovered, diversified and modernized after the end-Permian mass extinction, which was the most severe mass extinction of the Phanerozoic (Raup 1979; Raup and Sepkoski 1982; Hallam and Wignall 1997; Erwin 2006). Therefore, the Triassic is a key time interval for both Earth and Life history showing successive major biotic and abiotic events (see review of Ogg 2012). Ammonoids are well-known and have been used to date and correlate Triassic marine strata since the late nineteenth century (Mojsisovics et al. 1895). Their abundance and widespread distribution reflect that they constitute an appropriate group in the construction of the Triassic timescale (Tozer 1984; Balini et al. 2010; Jenks et al. 2015). Besides, all of the Triassic substages are currently defined by ammonoid bioevents. Triassic ammonoids are geographically widespread and their most important and complete records are in the Canadian Arctic (especially Ellesmere and Axel Heiberg islands), British Columbia, the western USA Basin (mainly Utah, Nevada, Idaho), the Germanic Basin, Western Tethys (the Alps from Italy to Turkey), Transcaucasia (Iran), Salt Range (Pakistan), Spiti (Himalayas), Tibet, South China (Guangxi and Guizhou provinces), and eastern Siberia (Balini

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et al. 2010). Despite this long history of biostratigraphic research and key evolutionary steps, the evolution of Triassic ammonoids still remains poorly studied. Nevertheless, during the last few decades, several publications have addressed this topic, especially in the context of the recovery after the end-Permian mass extinction (e.g., McGowan 2004; Brayard et al. 2009; Brühwiler et al. 2010; Brosse et al. 2013; Korn et al. 2013a).

The Triassic is a key interval in the evolutionary history of ammonoids and can be labeled as the “ceratite” world since it is characterized by the flourishing and the dominance of the Ceratitida with their typical suture line indented on the lobes only. Indeed, only a few ammonoid species crossed the Permian/Triassic mass extinction leading to a quasi-monophyletic group during the Triassic (Kummel 1973; Spinosa et al. 1975; Tozer 1980; Brayard et al. 2006; McGowan and Smith 2007; but for a few ambiguous cases, see, e.g., Glenister and Furnish 1980; Becker and Kullmann 1996; Brayard et al. 2007a). Following the end-Permian mass extinction, this time interval was one of the most interesting in the evolution of the Ammonoidea with an impressive succession of radiations and crises (Tozer 1980, 1982; Dagys 1988; Brayard et al. 2009; Balini et al. 2010; Brayard and Bucher 2015) and with the first experiment in heteromorphic coiling in the Late Triassic (e.g., Wiedmann 1973; Shevyrev 2005). The resulting impressive Triassic ammonoid record consists of three orders (Prolecanitida, Ceratitida, Phylloceratida), about 80 families, about 700 valid genera and an estimated 5000 valid species (Tozer 1980; Balini et al. 2010). A few Triassic ammonoid families (e.g., Sageceratidae, Sturiidae, Gymnitidae, Ptychitidae, Isculitidae, Cladiscitidae, Arcestidae, Sphingitidae and Joannitidae) consist of smooth, relatively long-ranging forms that are informally defined as “Leiostraca”, whereas the majority of families belong to the group “Trachyostraca”, which includes the ornamented, fast-developing and short-ranging forms. The Triassic ammonoids include a great variety of forms from evolute to involute, smooth to ribbed, tuberculated and spiny, and suture lines from ceratitic to ammonitic.

In biology and particularly in paleontology, evolutionary trends are a long standing theme. According to McNamara (2006), “*an evolutionary trend can be defined as a persistent, directional change in a character state, or set of character states, resulting in a significant change through time*” (see also Gould 1988; McNamara 1990; McShea 1994; Monnet et al. 2015). Commonly assumed examples of macroevolutionary trends include increasing adult body size (Cope’s rule) throughout the Cenozoic within horses coupled with a reduction in digit number (MacFadden 1986, 1992; Gould and MacFadden 2004), an increase in shell size in the Foraminifera (Gould 1988; Norris 1991), increasing complexity of life forms from eukaryotic cells to complex multicellular vertebrates (Gould 1996; McShea 1996), as well as, among many other, increase in suture indentation of ammonoids (Boyajian and Lutz 1992; Saunders et al. 1999). Most of the evolutionary trends described in the fossil record are macroevolutionary and large-scale (or long-term) in the sense that they occurred over several million years and among or above the species level. Since the works of Gould (1988, 1990) and McShea (1994, 2000), two basic patterns of evolutionary trends have been recognized: these may be either ‘passive’ or ‘driven’ (the absence of a trend characterizes a third pattern: stasis) (Monnet

et al. 2015). In a driven trend, not only the mean, but also the entire morphological range of an evolving lineage is shifted through time within its multidimensional morphological space. In a passive trend, the mean value of a character will increase and appear like a trend, but only because of a natural result of increase in variance (Gould 1988) constrained by a natural physiological/physical boundary in the morphological space of the studied organisms (so-called left-wall effect). For instance, if the species at the origin of a clade was small-sized, subsequent evolution could only be stasis or a shift towards larger sizes.

Large-scale macroevolutionary trends in fossils within their morphological space have usually been studied qualitatively or by the stratophenetic method (e.g., Raup and Crick 1981, 1982; Charlesworth 1984; Gingerich 1993; Roopnarine et al. 1999; Monnet et al. 2010), that is the distribution (or characteristic numbers of this distribution such as the mean) of some quantified morphological characters through successive stratigraphic strata or units (time slices). Recently, several authors developed quantitative methods to describe and assess statistically these trends: for details and example applications of these methods, see Monnet et al. (2011, 2015). With regard to quantified ammonoid shell characters, four of them commonly display long-term evolutionary trends through time: adult size, degree of involution (coiling), strength of ornamentation, and indentation of suture line (e.g., Haas 1942; Kennedy 1977, 1989; Bayer and McGhee 1984; Kennedy and Wright 1985; Dommergues 1990; Boyajian and Lutz 1992; Saunders et al. 1999; Guex 2003; Klug et al. 2005; Monnet et al. 2011, 2012; De Baets et al. 2012). Hence, the major goal of this chapter is to make a review of the rare studies analyzing the evolutionary trends of these ammonoid shell characters during the Triassic (for a review of processes generating evolutionary trends in ammonoids, see Monnet et al. 2011, 2015).

2.2 Adult Size

The most commonly observed evolutionary trends in the fossil record are probably those including adult body size, in particular the apparent frequency of size increase, which has been coined as Cope's rule (i.e. the widespread tendency of animal groups to evolve towards larger sizes). Different processes have been suggested to generate trends in body size evolution such as adaptiveness (or fitness), predator-prey relationships, energy intensiveness, life history strategies (r-K continuum), growth rates, external abiotic factors (e.g., temperature, food supply) (see Newell 1949; Stanley 1973; Vermeij 1987; McKinney 1990; Gould 1997; Jablonski 1997; Alroy 1998; Hone and Benton 2005; Novack-Gottshall and Lanier 2008). With regard to ammonoids, several authors have illustrated and discussed examples of increasing shell size (see Monnet et al. 2015 and references therein). However, very few studies focus on the Triassic (e.g., Klug et al. 2005; Monnet et al. 2012) and the sometimes large range of intraspecific variation of size at maturity is often overlooked (see De Baets et al. 2015). Several studies focusing on peculiar lineages have described evolutionary changes in adult shell size potentially compatible with

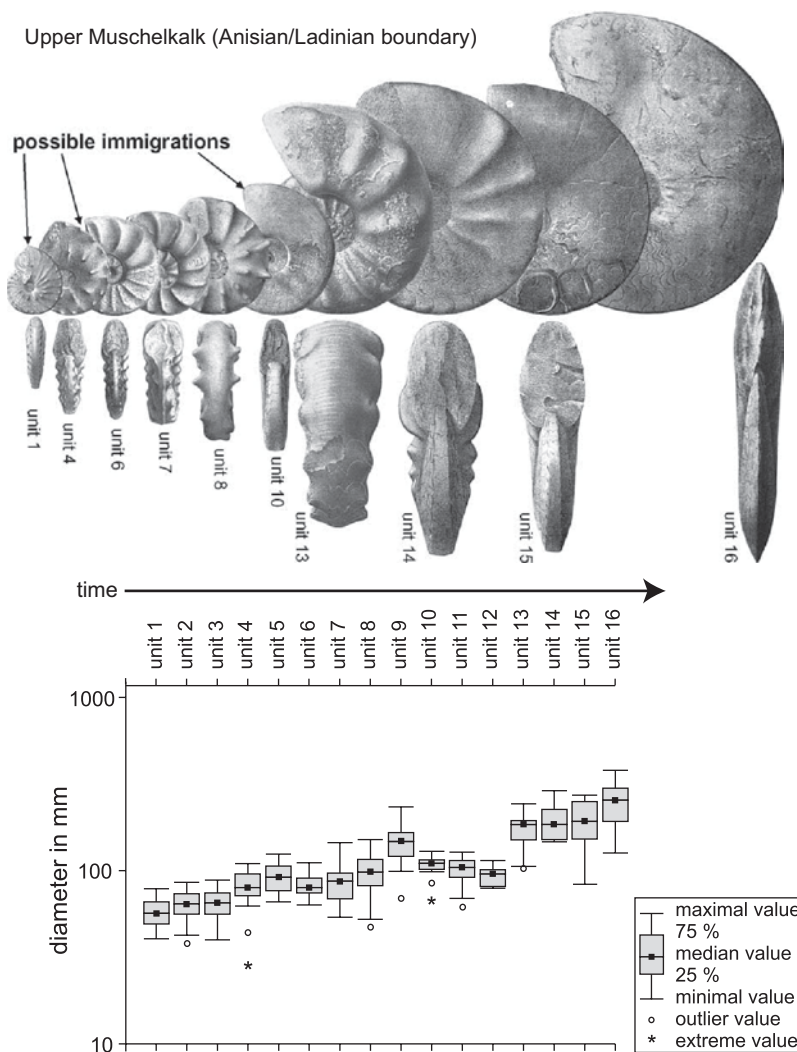


Fig. 2.1 Stratophenetic evolutionary trend of size increase of ammonoids during the deposition of the *Upper Muschelkalk* (Middle Triassic) of the Germanic Basin (modified after Klug et al. 2005)

Cope's rule. For instance, Klug et al. (2005) documented the stratophenetic evolution of Middle Triassic ammonoids from the German Muschelkalk for several morphological characters (Fig. 2.1). Interestingly, several of these (inclusive of adult shell diameter) show more or less regular changes in conch morphology through geological time, except for some intervals with abrupt and rather drastic transformations, which are synchronous with episodes of faunal immigrations.

The most recent and comprehensive study on adult ammonoid shell-size is from Dommergues et al. (2002) who documented in a large compendium (more than

1000 species) of Early Jurassic ammonoids that there are no statistically preponderant trends. This study highlighted that at a large taxonomic scale, there is no tendency in the evolution of conch size with a roughly equal number of cases of increase, decrease, and stasis. In contrast to Jurassic ammonoids, changes in shell size at a global scale have not yet been investigated for Triassic ammonoids. For Triassic ammonoids, only cases of size increase have been reported (see above). However, cases of conch size decrease are likely to have existed also in Triassic ammonoids. Indeed, Triassic ammonoids cover a large range of sizes (typically ranging between 5 to 500 mm), e.g., from the tiny *Paranannites dubius*, over the medium-sized *Rieppelites cimexianus*, to the large-sized *Churkites noblei* (Fig. 2.2). Therefore, evolutionary changes and trends in shell size can be expected within Triassic ammonoids, but a general study similar to that of Dommergues et al. (2002) still needs to be done in order to investigate dominance (or not) of one pattern among size changes of Triassic ammonoids. Guex (2001, 2006) argued that size decreases are more likely to be sudden and promoted by stressful abiotic events whereas size increases are more protracted during more stable environmental periods. Monnet et al. (2013) quantitatively described an example of this evolutionary hypothesis within the Triassic family Acrochordiceratidae. This family is characterized by a protracted morphological evolutionary trend during the early and middle Anisian (ca. 4 Myr) composed of classical increases in adult size, shell involution and suture indentation. This trend followed a sudden morphological change (e.g., drastic size reduction and uncoiling) at the Spathian/Anisian boundary between members of the family. This boundary is associated with several stressful environmental changes that may have triggered this evolutionary jump, which corresponds to a generalized morphological reset of long-term trends. This process differs from classic paedomorphic transformations since it is characterized by the reappearance of atavistic characters instead of paedomorphic characters (for further details, see Guex 2001, 2006).

Interestingly, ammonoids should have shown marked size decrease after the end-Permian mass extinction and during the successive Early Triassic oceanographic and climatic events (e.g., late Smithian; Brayard et al. 2006; Galfetti et al. 2007b; Romano et al. 2013). Indeed, a sharp size decrease of surviving taxa in the immediate aftermath of an extinction event is expected (the “Lilliput effect”) and has been suggested for other mollusks (see e.g., Payne 2005; Twitchett 2007; but see Brayard et al. 2010). However, although analyses remain qualitative for that time, the Early Triassic apparently records the highest abundance of the largest ammonoid specimens of the Triassic (see Brayard et al. 2013). Furthermore, the evolution of ammonoids is more complex as illustrated by a size decrease prior to the end-Permian mass extinction in some regions like Iran (compare Korn et al. 2013b).

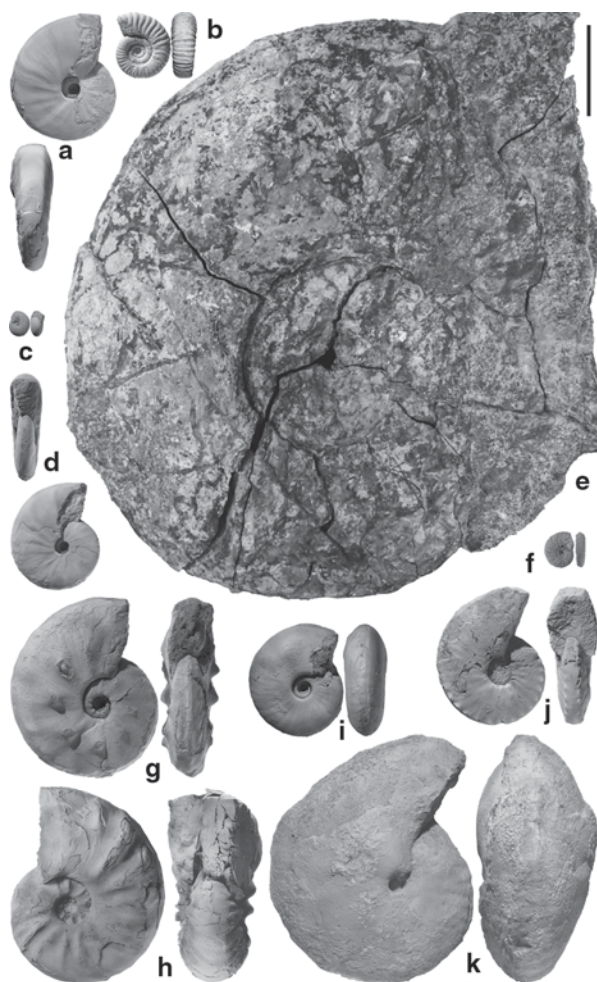


Fig. 2.2 The vast range of shell size in Triassic ammonoids. **a** *Billingsites cordeyi* (Anisian; after Monnet and Bucher 2005, pl. 7 Fig. 3). **b** *Paracrochordiceras americanum* (Anisian; after Bucher 2002, pl. 1 Figs. 1,2). **c** *Paranannites dubius* (Smithian; after Brayard and Bucher 2008, pl. 33 Fig. 13). **d** *Gymnotoceras mimetus* (Anisian; after Monnet and Bucher 2005, pl. 17 Fig. 1). **e** *Churkites noblei* (Smithian; after Brayard et al. 2013, Fig. 43a). **f** *Procurvoceratites pygmaeus* (Smithian; after Brayard and Bucher 2008, pl. 44 Fig. 4). **g** *Silberlingitoides cricki* (Anisian; after Monnet and Bucher 2005, pl. 26 Fig. 1). **h** *Acrochordiceras carolinae* (Anisian; after Monnet et al. 2010, text-Fig. 12). **i** *Paranannites ovum* (Smithian; after Brayard and Bucher 2008, pl. 34 Fig. 1). **j** *Rieppelites cimiganus* (Anisian; after Monnet et al. 2008, Fig. 11a, b). **k** *Globacrochordiceras transpacificum* (Spathian; after Monnet et al. 2013, Fig. 5). All specimens are at the same scale (scale bar = 5 cm)

2.3 Taxonomic Diversity

Fundamentally, paleontology focuses on past life and probably the most used synthesis of past changes have been the reconstruction of diversity curves. For paleontologists, diversity generally means taxonomic richness (i.e. the number of taxa present at a given time) and diversity trends have been studied since Phillips (1860). Reconstructing the trajectory of global diversity by compiling data from the fossil record has been a major research agenda for paleontologists for decades. The goal is to produce an accurate reconstruction of the pattern of global diversity that will ultimately allow understanding of the causes of diversity increases, decreases and transitions in the composition of the biota (Simpson and Kiessling 2010; Escarguel et al. 2011). Paleontologists attempt to document the history of biodiversity by tabulating fossil occurrences in large databases, especially for identifying large-scale evolutionary patterns (e.g., Raup and Sepkoski 1982; Sepkoski 1993; Alroy et al. 2008).

Ammonoids are well known for their high diversification and extinction rates and thus constitute a material of choice for diversity studies (Tozer 1980; House 1985; Page 1996). To build robust databases from which to extract reliable diversity patterns, a necessary prerequisite is having a homogeneous taxonomy complemented by up-to-date biostratigraphic data. During the last few decades (and still today), Triassic ammonoids have been thoroughly revised and documented, leading to more consistent taxonomic and biostratigraphic frameworks (see Jenks et al. 2015). This enabled Brayard et al. (2009) to provide a thorough quantitative analysis of ammonoid diversity trends during the entire Triassic, based on a database presently recording about 730 genera from 50 regions around the world. The major result of this study was that, although the ammonoids, which were abundant during the Permian, were nearly eradicated during the end-Permian mass extinction (only a few species survived), they recovered remarkably quickly taking only ~1 Myr after the extinction event (compared to the commonly suggested 10 million-year biotic recovery period for benthic organisms; Kirchner and Well 2000; Erwin 2006; but see e.g. Hofmann et al. 2011, 2014) and even had recovered to diversity levels higher than those seen in the Permian. For further details with regard to the recovery, see Brayard and Bucher (2015).

The diversity trends of Triassic ammonoids (Fig. 2.3) are characterized by four long-term successive diversity oscillations of declining magnitude, which are probably shaped by global climatic and oceanographic changes (Brayard et al. 2006; Galfetti et al. 2007b; Konstantinov 2008). As highlighted by Brayard et al. (2009), in the first oscillation, during the Olenekian, ammonoid generic diversity reached values (~110) higher than those for the Permian. This Early Triassic generic richness is unsurpassed during the Middle and Late Triassic, where diversity oscillated around an average value of ~70 sampled genera per time bin. This period also records a very rapid succession of new families and genera, echoed by the simultaneously high numbers and rates of origination and extinction. The Early/Middle Triassic transition was marked by a severe drop in ammonoid diversity, probably

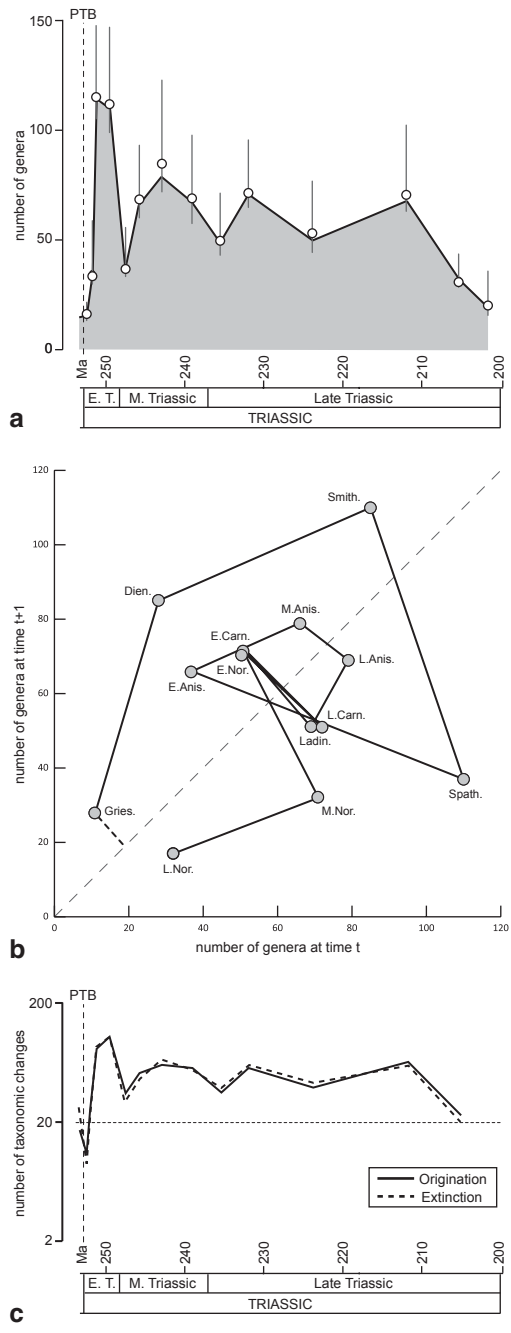


Fig. 2.3 Trends of taxonomic diversity of Triassic ammonoids (modified after Brayard et al. 2009). **a** Generic richness of Triassic ammonoids: black bold line: total generic richness (observed+inferred occurrences); large circles with vertical bars: mean Chao2 estimate of the overall generic richness with its 95% confidence interval. Triassic ammonoids actually reached

triggered by a fall in global sea level (Embry 1997); this interval also impacted ammonoid evolutionary trends (see Monnet et al. 2013). Middle and Late Triassic generic and family richness remained lower than in the late Early Triassic; they also appeared less variable, possibly because oceanic geochemical conditions stabilized during that time (Payne et al. 2004; Galfetti et al. 2007a, b). From the early Anisian onward, three successive diversity cycles are evident: Early Anisian–Early Carnian, Early Carnian–Early Norian, and Early Norian–Rhaetian. The latter ends with a marked diversity decline before the Jurassic. Additional studies have explored the diversity of Triassic ammonoids but with lower time resolution, smaller datasets and/or more restricted geographic scope (e.g., Yang and Wang 2000; Konstantinov 2008; Brühwiler et al. 2010; Zakharov and Abnavi 2013).

There appears to be a close relationship between changes in ammonoid diversity and climate, as reflected by the correlation between cosmopolitan to latitudinally restricted distributions of genera on the one hand and sea surface temperature gradient on the other hand (Brayard et al. 2006, 2007b, 2015). Also, these long-term trends in diversity were marked by shorter, but important disturbances, such as a diversity drop at the Smithian/Spathian boundary (Tozer 1982; Dagys 1988; Brayard et al. 2006) concomitant with a major perturbation of the global carbon cycle (Payne et al. 2004; Galfetti et al. 2007a, b, c). This end-Smithian global event did not markedly delay the explosive recovery of ceratitid ammonoids, although it was the most important one within the entire Triassic. Other significant extinction events for ammonoids occurred at the Spathian/Anisian boundary, in the early Ladinian, and at the Carnian/Norian boundary (Brayard et al. 2009).

2.4 Morphological Disparity

2.4.1 Shell Geometry

Quantitative analyses on diversity trends of fossil groups have usually and fruitfully focused upon taxonomic diversity (see above). However, there are multiple facets/metrics of biodiversity (e.g., genetic, morphological, ecological, phylogenetic, functional, body size). One of these considers morphological variation (or disparity), which is the raw material of biological evolution (Foote 1993) and the primary material of fossilized organisms. Disparity-based analyses supply relevant insights into biological evolution by the establishment of phenotypic spaces and

levels of diversity higher than in the Permian less than 1 million years after the PTB by an explosive and non-delayed diversification of the Ceratitida. Highest levels of diversity are reached in the Early Triassic, after which diversity slowly decreases, as well as the turnover rate, until the end of the Triassic. Note that the end-Smithian ammonoid extinction event discussed in the text is not illustrated here due to its short time duration. **b** Phase diagram of Triassic ammonoid diversity showing the rapid recovery of the Early Triassic, followed by a dynamic equilibrium during the Middle Triassic, and the final decrease of diversity in the Late Triassic. **c** Origination and extinction of Triassic ammonoid genera



Fig. 2.4 The vast range of shell geometry in Triassic ammonoids. **a** *Longobardites zsigmondyi* (Anisian; after Monnet and Bucher 2005, pl. 31 Fig. 13). **b** *Otoceras concavum* (Griesbachian; after Dagys and Ermakova 1996, pl. 2 Fig. 4; $\times 0.5$). **c** *Gymnites* sp. indet. (Anisian; after Monnet

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