Chapter 18
Ammonoids at the Triassic-Jurassic Transition: Pulling Back from the Edge of Extinction

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18.1 Introduction

The mass extinction at the end of the Triassic is one of the "big five" extinctions in the Phanerozoic and one of four that directly affected the evolutionary history of the ammonoids. At the Triassic-Jurassic (T-J) transition, approximately 22 % of marine families, 53 % of genera and 80 % of species became extinct (Pálfy 2003; Sepkoski 1996) but the event is of particular significance to the ammonoids because of their near demise. Left hanging by a thread, the group managed to pull back from the brink of extinction and, in spectacular fashion, re-establish itself as a dominant presence throughout the rest of the Mesozoic. As a result of the exceptionally low eustatic sea-level at the time, a situation that almost certainly contributed to the dynamics and severity of the extinction, there are only a very small number of marine stratigraphic sections that are reasonably continuous across the T-J boundary. The list includes an exposure in Austria that was recently designated Global Stratotype Section and Point for the base of the Jurassic (Hillebrandt et al. 2013). Studying the precise details of the T-J event horizon is therefore difficult, but a clear picture of the scale of the ammonoid near extinction and a sense of the dynamics of recovery can be obtained by considering high level taxonomic changes, broad patterns of generic diversity and differences in morphospace occupation across the entire Late Triassic to Middle Jurassic interval. This is the purpose of our brief review.

Interpreted environmental changes over the T-J interval include initial cooling, longer term global warming, widespread aridification, a global regression/transgression couplet, oceanic anoxia and a biocalcification crisis brought on by lower seawater pH (Hallam 1997, 2001; Hallam and Wignall 1997, 2000; Hesselbo et al.

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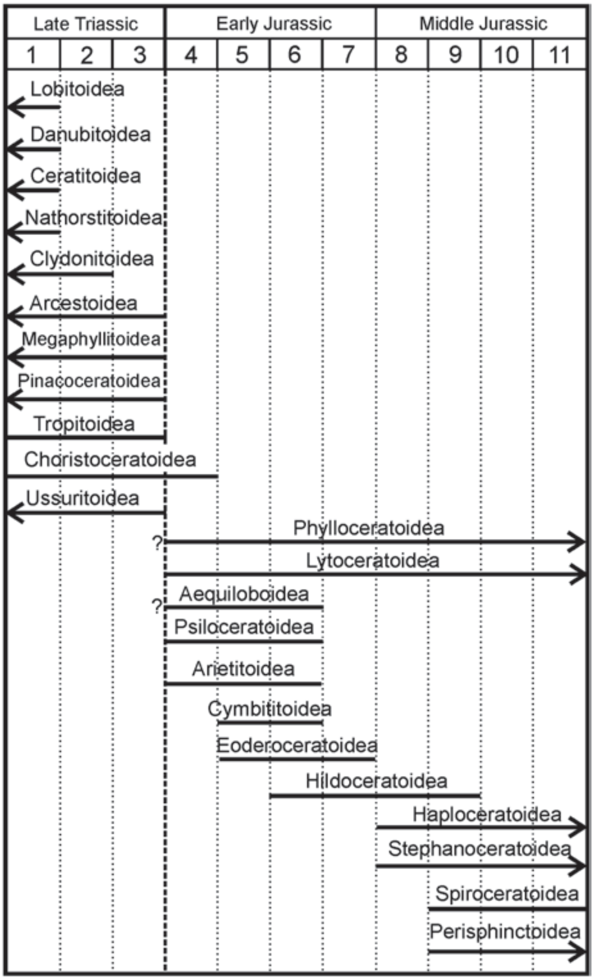
2004; Hillebrandt 2014; McElwain et al. 1999; Schootbrugge et al. 2007; Tanner et al. 2004; Tucker and Benton 1982). There was also a significant perturbation to the global carbon cycle with negative isotope anomalies identified in marine strata in British Columbia, Nevada, England, Austria, Italy, China and Hungary (Bachan et al. 2012; Galli et al. 2005; Guex et al. 2003, 2004, 2007; Hesselbo et al. 2002; Hillebrandt et al. 2013; Kuerschner et al. 2007; Lucas et al. 2007; McRoberts et al. 1997; Pálfy et al. 2001; Ward et al. 2001, 2004, 2007; Williford et al. 2007; Yin et al. 2006) and in terrestrial strata in Greenland and China (Hesselbo et al. 2002, 2006). Tanner et al. (2004) suggest that the T-J turnover may have been caused by a combination of gradual and catastrophic environmental changes. This could include long term ecological degradation from sea-level fluctuation or climate change in addition to more abrupt events such as flood basalt volcanism or possibly even bolide impact (Fowell and Olsen 1993; Fowell et al. 1994; Olsen et al. 1987, 2002a, b), although the latter is unlikely.

Flood basalt volcanism of the Central Atlantic Magmatic Province (CAMP) is currently considered the most likely cause of environmental perturbations and biotic crisis at the end-Triassic (Blackburn et al. 2013; Golonka 2007; Guex et al. 2004; Hesselbo et al. 2002, 2007; Hillebrandt et al. 2013; Knight et al. 2004; Marzoli et al. 1999, 2004, 2006, 2008, 2011; Pálfy 2003). These eruptions were caused by Pangean rifting prior to breakup producing basaltic lavas that extended over an area of 7×10^6 km^2 and had an estimated volume of $2–3 \times 10^6$ km^3 (Blackburn et al. 2013; Marzoli et al. 1999). The lavas were mostly produced by four major eruptive pulses in the first 600 Ka of extrusive activity, but the magmatic province as a whole had a duration of approximately 1.5 Ma or possibly longer in Morocco where volcanic activity began first (Blackburn et al. 2013; Nomade et al. 2007; Verati et al. 2007). The first of the four pulses probably triggered the extinction at 201.6 Ma (Blackburn et al. 2013; Schaltegger et al. 2008). Environmental change may have been caused by volcanic outgassing of CO_2 and SO_2, or perhaps more indirectly by the release of methane from shallow marine clathrate deposits, which acted as a positive feedback on global warming (Blackburn et al. 2013; Hesselbo et al. 2002; Pálfy et al. 2001).

18.2 Taxonomic Turnover

High level T-J ammonoid taxonomy is currently based principally on a stratophenetic rather than a cladistic approach. There are numerous stratophenetic phylogenies and taxonomic classifications, some that are more conservative and others that are less so (Dommergues and Meister 1999; Donovan et al. 1981; Page 1996, 2008; Tozer 1981, 1994; Venturi and Bilotta 2008). Figure 18.1 shows the ranges of 23 ammonoid superfamilies plotted at the resolution of age/stage. The superfamilies are based primarily on the approaches of Tozer (1981, 1994) for the Triassic and Page (2008) and Venturi and Bilotta (2008) for the Jurassic. A geographically restricted superfamily, the Aequiloboidea has recently been recognized by Bilotta

Fig. 18.1 Ammonoid superfamilies in the Late Triassic through Middle Jurassic. *1* = Carnian, *2* = Norian, *3* = Rhaetian, *4* = Hettangian, *5* = Sinemurian, *6* = Pliensbachian, *7* = Toarcian, *8* = Aalenian, *9* = Bajocian, *10* = Bathonian, *11* = Callovian. Resolution is at the stage level. Modified from Tozer (1981) and Page (2008) using data from Bilotta (2010), Hoffmann (2010), Howarth (2013), and Tozer (1994)



(2010). We include the Analytoceratoidea in the Lytoceratoidea following the work of Hoffman (2010).

Whatever classification is adopted, there is consensus that the order Phylloceratida is the only group to cross the T-J boundary and play a central role in the Early Jurassic recovery of the ammonoids. The Triassic phylloceratid superfamily Ussuritoidea is ancestral to the Early Jurassic phylloceratid superfamily Phylloceratoidea, although Pálfy and Dosztály (2000) have reported a very early occurrence of the Phylloceratoidea in the Rhaetian of Hungary. In addition, Bilotta (2010) speculates that the geographically restricted Aequiloboidea also had its origin in the latest Triassic but this is not proven and, anyway, the superfamily does not play a major role in the Early Jurassic radiation.

Of the nine superfamilies ranging upward from the Middle into the Late Triassic (Fig. 18.1), four are restricted to the Carnian with the Clydonitoidea ranging into the Norian and four ranging into the Rhaetian (Arcestoidea, Megaphyllitoidea, Pinacoceratoidea, Ussuritoidea). The Tropitoidea and the Choristoceratoidea are restricted to the Late Triassic ranging into the Rhaetian with rare Early Jurassic occurrences of Choristoceratoidea reported from the basal part of the Hettangian in North and South America (Guex 1995; Guex et al. 2012; Hillebrandt 2000a; Longridge et al. 2007). Basal Hettangian Choristoceratoidea have also been reported in Tibet (Yin et al. 2007) although Hillebrandt et al. (2013) recently questioned the Hettangian age of the co-occurring ammonoid based on his assessment of its septal suture. The long ranging Lytoceratoidea and Phylloceratoidea are present in the Hettangian together with the Psiloceratoidea (derived from the Phylloceratida), which gives rise to the Arietitoidea that is the source of much of the great Early Jurassic recovery. In addition, appearance of the Eoderoceratoidea, and, to a lesser extent, the Cymbitoidea in the Sinemurian add to the momentum of the recovery. In summary, at the superfamily level, the Carnian shows the greatest diversity followed by a decline through the Norian and Rhaetian with almost everything terminated at the T-J boundary. Although there may be some minor overlap of typically Triassic with typically Jurassic forms, it is negligible. The Psiloceratoidea was the rootstock of the Jurassic recovery which, at this taxonomic level, was relatively rapid such that the number of co-existing superfamilies from the Norian in the Late Triassic to the Callovian at the end of the Middle Jurassic was fairly consistent, averaging somewhat over six per stage with a Triassic minimum of six in the Rhaetian and a Jurassic minimum of four during the Toarcian.

At the lower end of the taxonomic hierarchy, we can consider generic data but, of course, estimates of the number of genera will contain errors based on synonyms and omissions. During the Late Triassic, which, according to Gradstein et al. (2012) had a duration of 35.7 million years, there existed in excess of 225 ammonoid genera whereas during the Early Jurassic, with a duration of 27.2 million years, there existed in excess of 325 genera. During the Middle Jurassic with a supposed duration of 10.6 million years there existed in excess of 325 genera (Smith et al. 2014).

When moving to a finer resolution, problems with time scale calibrations become significant. Gradstein et al. (2012) decided to abandon U-Pb dates based on Zr populations requiring that only single Zr crystal data be used in time scale calibration work. As a result, the 2012 Mesozoic time scale (Gradstein et al. 2012) is considerably less well constrained than the time scale produced in 2004 (Gradstein et al. 2004). The revised duration of Middle Jurassic ages seem particularly questionable but the problem can only be resolved by more field work integrating biochronology with samples for single crystal Zr analysis. However, if we accept the more recently produced time scale and plot the number of ammonoid genera per million years by geological age (Fig. 18.2), we see a steady decline during the Late Triassic followed by a significant jump in the Hettangian to levels exceeding those in the Late Triassic. A downward readjustment in the Sinemurian is followed by a steady increase in standing diversity throughout the rest of the Early and Middle Jurassic. The anomalously high value for the Bajocian (Fig. 18.2) could be an artifact

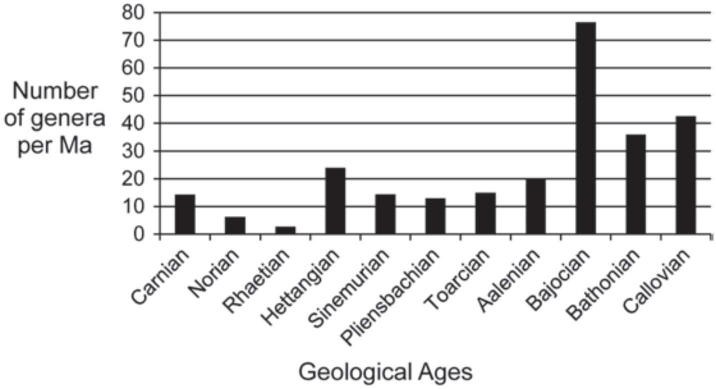


Fig. 18.2 Ammonoid genera per million years plotted at the level of geological age for the Late Triassic to Middle Jurassic interval. Diversity data from Smith et al. (2014); time scale data from Gradstein et al. (2012)

of time scale calibration problems, although the morphospace data discussed below also suggests that the Bajocian marked the time of full recovery for the ammonoids.

18.3 Changes in Morphospace Occupation

Another perspective on the magnitude of the T-J extinction and the dynamics of ammonoid recovery can be obtained by using a morphospace model. The advantage of this approach is that it is somewhat more objective than a taxonomic approach because it is not based on taxa definition and the interpretation of phylogenetic relationships. A recent study by Smith et al. (2014) employed Raup's accretionary growth model (Raup 1966, 1967) to develop a simple morphospace concept describing planispiral shell geometry and whorl shape using three variables to define a universal space. The occupation of this space before and after the event offers insights into the dynamics of the near extinction and the evolutionary, functional and ecological constraints that might have influenced recovery. The three variables of the Raup model, as used here, are based on six parameters which, using the terminology of Smith (1986), are defined as follows (Fig. 18.3a, b):

- 1. The expansion rate [$W=(r_2/r_1)^2$].
- 2. The relative distance between the generating curve and the axis of coiling [U=UD/D where UD is the umbilical diameter and D is the shell diameter].
- 3. The whorl width (WW) divided by whorl height (WH), which is a box model used to approximate the relative compression or depression of the specimen [WWWH = WW/WH].

The parameters W and U are used to generate a W-U coordinate system defining 'morphospace' for ammonoid shell geometry. Measurements from individual genera

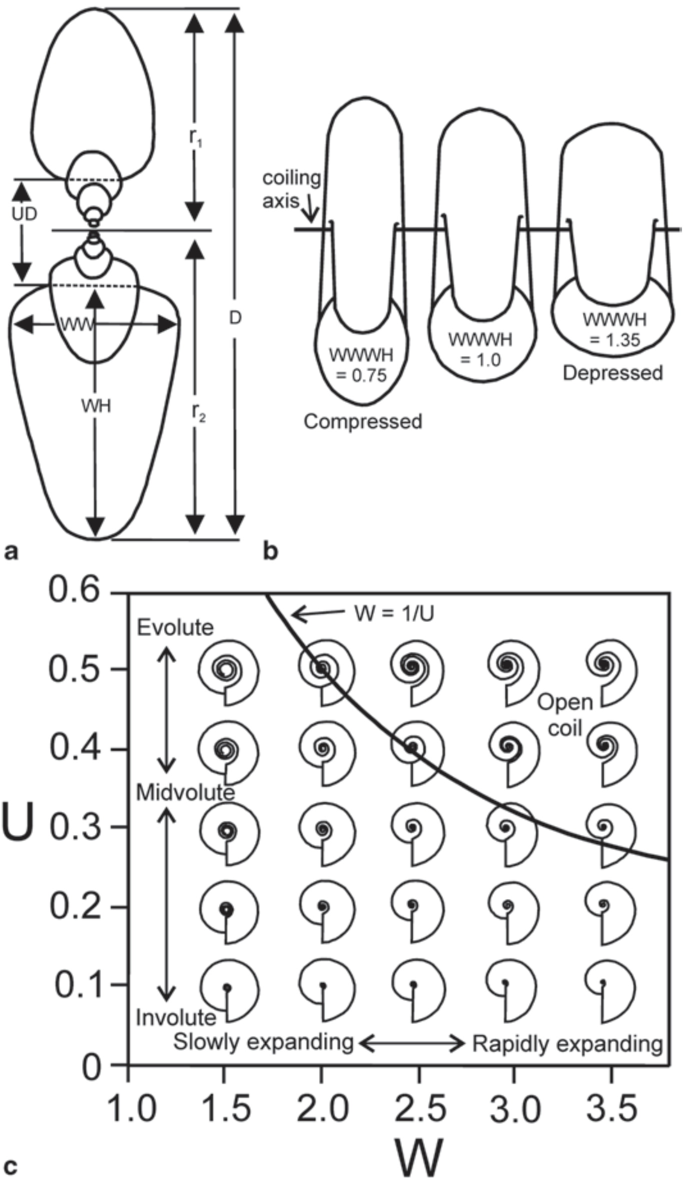


Fig. 18.3 **a** Linear dimensions used to characterize ammonoid shell morphology. *D* = shell diameter; *UD* = umbilical diameter; *WW* = whorl width; *WH* = whorl height. *Lower case letters* = shell radii. Ratios used are: relative width of umbilicus *U* = *UD*/*D* (equivalent to *D* of Raup 1966, 1967); expansion rate W = $(r_2/r_1)^2$; and whorl shape, *WWWH* = *WW*/*WH* (equivalent to S of Raup 1966, 1967). **b** Ventral view of ammonoids illustrating changes in whorl compression as measured by *WWWH*. **c** Schematic of ammonoid shell morphology in the *W*-*U* morphospace (modified from Raup 1967). Figure 1 and 2b of Smith et al. (2014); Figure was originally modified from Raup (1966), following the terminology of Smith (1986) and Liang and Smith (1997)

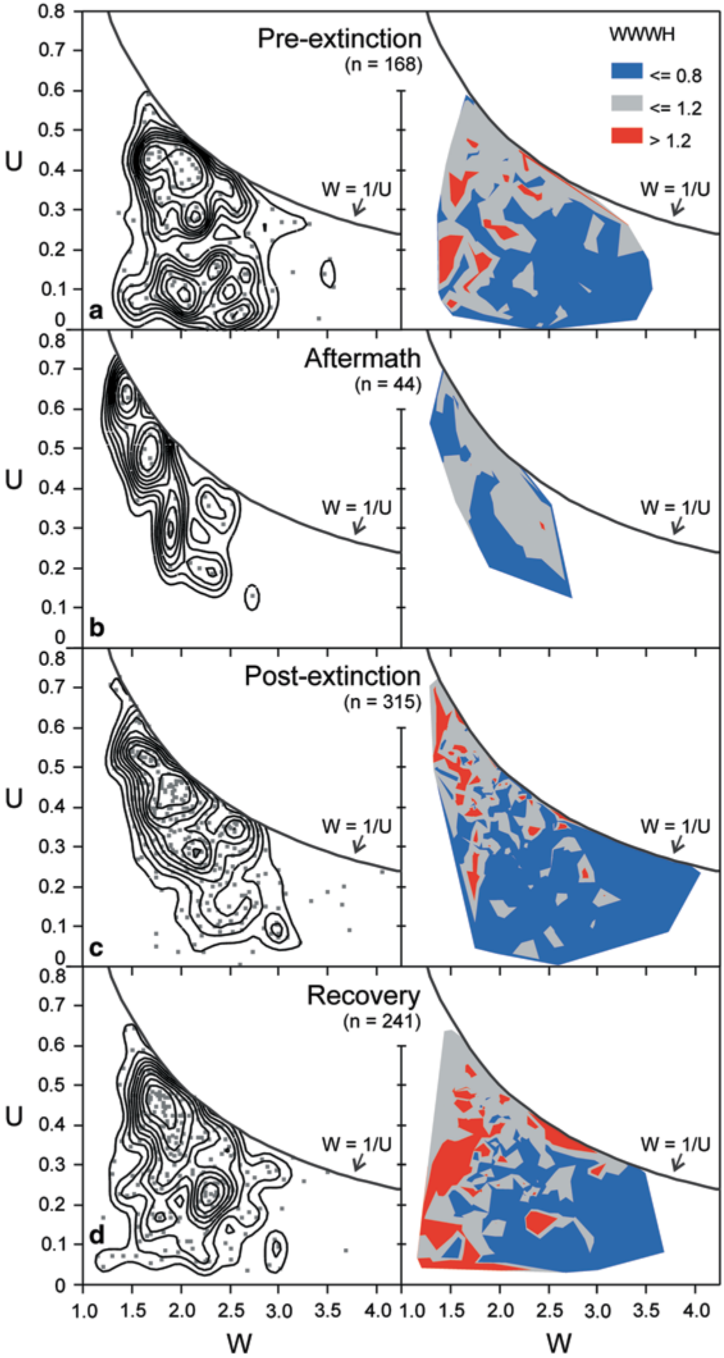
are plotted on the W-U graph and then contoured based on frequency of occurrence per unit area. Figure 18.3c provides illustrations of hypothetical shell geometries for several different W-U coordinates. The curved line on Fig. 18.3c, called the off-lap line (equation $W=1/U$), marks the boundary between coiled forms with whorl overlap and shells that have an open coil. These open coiled forms belong to the heteromorphs, which are part of a broader group the rest of which cannot be accommodated in the W-U Raup model. Consequently, the heteromorphs are commented upon separately. In the planispires, there is a persistent covariation between coiling geometry and whorl shape such that W-U morphospace can be used to explore all basic aspects of shell geometry. Different whorl shapes and their associated WWWH values are illustrated in Fig. 18.3b. Based on a stage-by-stage analysis across the T-J event, Smith et al. (2014) recognised four intervals, namely the pre-extinction (Carnian to Rhaetian), aftermath (Hettangian), post-extinction (Sinemurian to Aalenian) and recovery (Bathonian to Callovian) as shown in Fig. 18.4, which illustrates both shell coiling geometry and whorl shape. On the right side of Fig. 18.4, the same specimens are shown as for the contoured plot shown on the left side of the figure but the whorl shape is color coded. The blue color represents low WWWH values (less than 0.8) indicating the compressed end of the whorl shape spectrum. The red color represents high WWWH values (more than 1.2) indicating the depressed end of the whorl shape spectrum. The intermediate, more equidimensional whorl shapes are denoted by the silver-grey color.

It is clear that there is a core area of the W-U morphospace centred on the values $U=0.4$–0.45 and $W=1.75$–2.0 that remains occupied throughout the Late Triassic to Middle Jurassic interval. This represents midvolute forms that are slowly expanding and with whorl sections that are equidimensional to slightly depressed.

The Late Triassic pre-extinction interval (Fig. 18.4a) shows a W-U landscape that is broadly occupied in the planispire region and characterized by a multi-peaked density distribution. An overall linear correlation between W and U is not evident although rapidly expanding forms are consistently compressed. The pre-extinction interval is also characterized by the greatest diversity of heteromorph ammonoids with spherocone, open-coiled, straight, helicoid, and high-spired (gastropod-like) morphologies all represented.

There are two major changes in morphospace occupation that occur across the T-J boundary. Firstly, the Hettangian aftermath interval (Fig. 18.4b) is characterized by a significant contraction of morphospace occupation. This represents a significant loss of involute ammonoids including slowly and rapidly expanding forms and those that are compressed and depressed. Secondly, the aftermath witnesses the first appearance of very evolute, slowly expanding forms ($U>0.6$; $W<1.7$) with equidimensional (slightly compressed to slightly depressed) whorl sections. There is now a strong negative linear correlation between W and U. Apart from local, brief holdovers of open coiled ammonoids, there are no heteromorphs in the aftermath interval.

During the post-extinction interval (Fig. 18.4c) there is a partial reversal of the pattern established in the aftermath. The very evolute forms wane but there is a rapid reappearance of involute compressed forms (low U, high W, low WWWH).


Pre-extinction
(n = 168)
Aftermath
(n = 44)
Post-extinction
(n = 315)
Recovery
(n = 241)
WWWH
<= 0.8
<= 1.2
> 1.2
W = 1/U
U
W
a
b
c
d
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0

The linear correlation between W and U in the sample as a whole weakens and is less negative than in the aftermath landscape. Apart from sporadic and minor appearances of spherocones in the Sinemurian to Toarcian (Cymbitoidea and *Onychoceras*), there are no heteromorphs in the post-extinction interval.

The recovery interval (Fig. 18.4d) for the planispires sees a morphospace topography that is very similar to, but not exactly the same as the pre-extinction interval. The taxa are distributed broadly, and for the first time since the extinction, the area representing the involute, slowly expanding forms with equidimensional to depressed whorl sections ($U<0.2$; $W<1.7$) is also occupied. There are multi-peaks in the density distribution but a weak W-U covariation persists. All the heteromorph geometries have now reappeared except for the high-spired torticones, which are unknown throughout the Jurassic.

In his comprehensive summary of research on the modes of life and habitat of the ammonoids, Westermann (1996) makes the point that the majority seem to have been pelagic, divided equally amongst active swimmers (nekton), planktonic drifters and planktonic forms involved in vertical migration (Ritterbush and Bottjer 2012; Westermann 1996; Westermann and Tsujita 1999). All the remaining ammonoids he describes as demersal (benthopelagic or nektobenthonic). His conclusions concerning modes of life are based on a review of faunal associations and biofacies as well as shell architecture as it relates to poise, stability and mobility. Smith et al. (2014) pointed out that Westermann's correlation between shell shape and the habitats the ammonoids exploited could be plotted on the Raup morphospace model as shown in Fig. 18.5. Planktonic drifters are evolute, slowly expanding forms with subcircular to depressed whorl sections (high U, low W and $WWWH \geq 1$). Planktonic vertical migrants tend to be involute and slowly expanding with depressed whorl sections (low U, low W and $WWWH > 1$). Nektonic forms are involute and rapidly expanding with compressed whorl sections (low U, high W and $WWWH < 1$). Demersal forms occupy the area of overlap (Fig. 18.5) between nektonic and planktonic forms (average U values around 0.45, average W values around 2, and a range of WWWH values from somewhat compressed to somewhat depressed).

The demersal mode of life is at the core of the adaptive landscape, and it is this region that is never relinquished, including during the immediate aftermath of the T-J extinction (Fig. 18.4b). The demersals probably exploited a variety of food resources including bottom scavenging and predation of the lie-in-wait variety. The extinction aftermath is also characterized by a proliferation of ammonoids that were

Fig. 18.4 Contoured frequency of occupation of the *W* (expansion rate) and *U* (umbilical ratio) morphospace together with (*right panel*) the associated whorl shapes plotted for the following intervals: **a** Pre-extinction (Carnian-Rhaetian), **b** Aftermath (Hettangian), **c** Post-extinction (Sinemurian-Aalenian) and, **d** Recovery (Bajocian-Callovian). The $W=1/U$ lines indicated on the figure are the off-lap lines (Raup 1967). The morphospace defined by the shell expansion rate (W) and the looseness of coil (umbilical ratio U) shows points representing genera whose density of occurrence is contoured (increment is 10%, with 90% of the sample enclosed by the outer contour). Only planispiral, non-heteromorph shell occurrences are plotted. Colours in the *right panels* denote occurrences of compressed ($WWWH \leq 0.8$), equidimensional ($WWWH > 0.8 < 1.2$), and depressed ($WWWH \geq 1.2$) whorl shapes (see Fig. 18.3b). Modified from Fig. 4 of Smith et al. (2014)

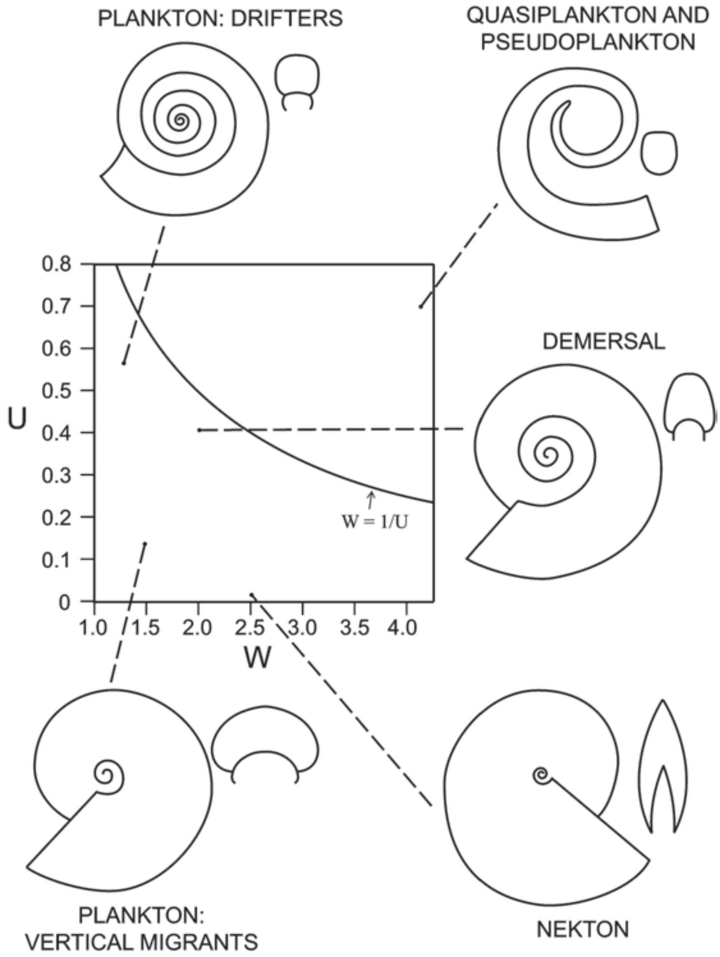


Fig. 18.5 Shell geometry related to the mode of life of ammonoids, as interpreted by Westermann (1996). Figure 9 of Smith et al. (2014)

planktonic drifters, a mode of life that assists with dispersal and recolonization. This dominance of demersal and planktonic forms in the Hettangian has also been pointed out by Ritterbush and Bottjer (2012). The evolute planktonic forms fade quickly during the Early Jurassic while at the same time the nektonic forms proliferate (Figs. 18.4b-c, 18.5). These were presumably the more active carnivores occupying roles at a higher level within the trophic structure. The Middle Jurassic saw a recovery of the involute, somewhat depressed, slowly expanding planispires, which were planktonic and may have migrated vertically in the water column (lower left parts of Figs 18.4c and 18.5). The open coiled planispire heteromorphs that reappeared in the Bajocian were probably drifters or pseudoplankton (very high W and U values in Fig. 18.5). The straight shelled heteromorphs that reappeared in the

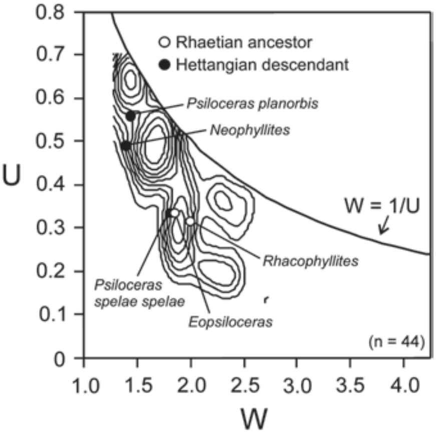


Fig. 18.6 The contoured occupation of W-U morphospace in the aftermath of the Triassic-Jurassic extinction (Hettangian) showing the prevalence of evolute, slowly expanding geometries, which dominate the succeeding, post-extinction interval. The Late Triassic genera *Eopsiloceras* and *Rhacophyllites* are indicated along with the oldest *Psiloceras, P. spelae spelae* and the slightly younger more evolute, more slowly expanding descendants *P. planorbis* and *Neophyllites*. Modified from Fig. 7 of Smith et al. (2014)

Bathonian were either planktonic or perhaps demersal with the ability to escape rapidly from benthic threats.

In summary, the T-J extinction resulted in the disappearance of nearly all planispiral ammonoid modes of life except the generalist demersals, which persist throughout the Late Triassic to Middle Jurassic interval. In the immediate aftermath of the extinction, the readily dispersed evolute drifters evolved for the first time but waned as the nektonic forms re-established themselves. It was not until the Bajocian and later that the full spectrum of modes of life was re-established. The greatest diversity of heteromorph ammonoids existed in the Late Triassic when partially uncoiled, open-coiled, straight-shelled, helicospires and torticones all existed. The aftermath and post-extinction intervals (Hettangian to Aalenian) are notable for the absence of heteromorphs. Minor exceptions include local occurrences of open coiled forms in the earliest part of the aftermath and the occurrence of partially uncoiled forms beginning in the Sinemurian. It was not until the recovery interval beginning in the Bajocian that a breadth of heteromorph shell geometry was established that was similar to the pre-extinction interval. An exception is the gastropod-like torticone geometry, which did not appear again until the Cretaceous (Arkell et al. 1957).

The consensus is that the Early Jurassic ammonoid genus *Neophyllites* and the significantly more important genus *Psiloceras* had their origins in the Late Triassic genera *Rhacophyllites* and *Eopsiloceras* (Fig. 18.6) (Guex 1982, 1987, 1995, 2006; Guex and Rakús 1991; Hillebrandt and Krystyn 2009). *Psiloceras spelae*, the very earliest species of *Psiloceras*, is similar in shell geometry to *Eopsiloceras* but subsequent species are considerably more evolute and slowly expanding (Fig. 18.6)

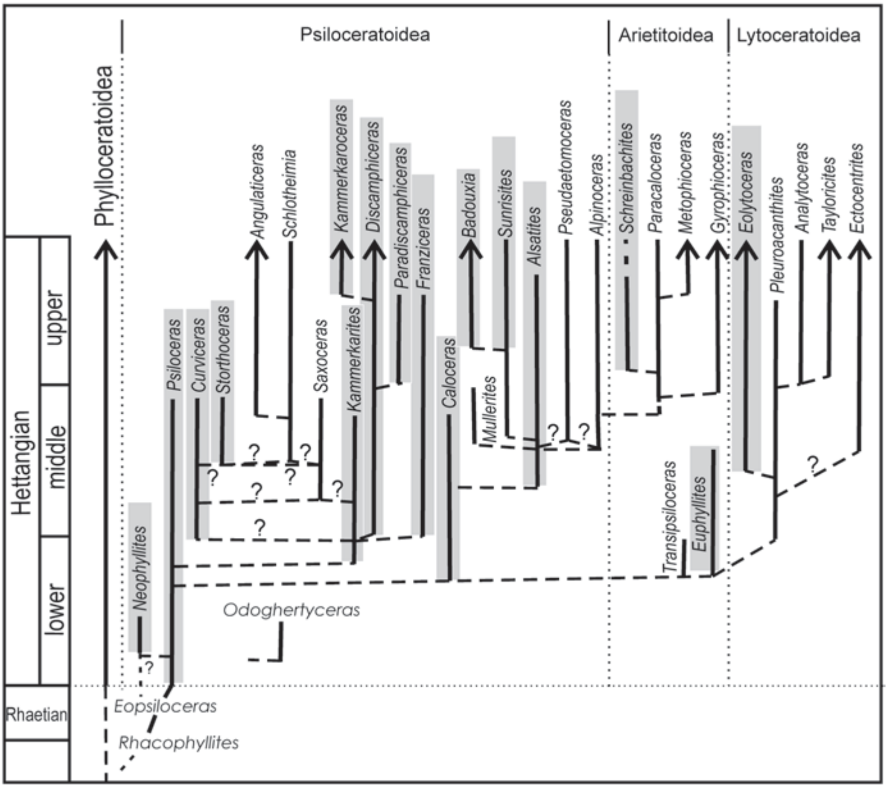


Fig. 18.7 Partial phylogeny of Hettangian ammonoids mostly including genera found in the Eastern Pacific. Genera where some or all species have an asymmetric siphuncle are indicated in *grey*. The *dashed* part of the range of Phylloceratoidea indicates an evolutionary relationship with the Ussuritoidea. Adapted from Guex (1995), Hillebrandt (2000a), Rakús (1993b); also including data from Bloos (1994), Efimova et al. (1968), Guex (1987, 2006), Guex et al. (1998, 2000), Hillebrandt (2000a-c), Longridge et al. (2006, 2007, 2008a, b), Meister et al. (2002) and Taylor (1998)

(Guex et al. 1998; Hillebrandt and Krystyn 2009; Smith et al. 2014). Similarly, *Neophyllites* is evolute and slowly expanding.

18.4 Siphuncle Offset and Septal Face Asymmetry

In most ammonoids the siphuncle runs ventrally along the shell's plane of bilateral symmetry but in many members of the Early Jurassic ammonoid radiation, individuals from groups that are not directly taxonomically related show asymmetry in the disposition of the siphuncle, which is offset from the venter (Fig. 18.7). This is accompanied by a corresponding asymmetry in the septa (Fig. 18.8a, b) whereby the septal suture line has the ventral lobe shifted to one side of the whorl as shown

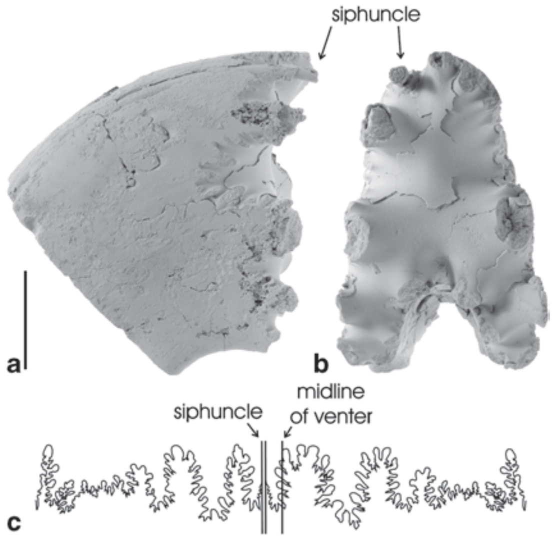


Fig. 18.8 Scanned fragment of *Badouxia columbiae*, **a**, Lateral view, **b**, Frontal view, scale bar = 2 cm, **c**, septal suture line from *B. columbiae*, scale bar = 4 cm. Modified from Fig. 1 of Longridge et al. (2009). © The Palaeontological Association

in Fig. 18.8c. There are no quantitative data but qualitative observations allow some general statements. Offset can be to the left or right of the line of symmetry but the magnitude remains consistent throughout ontogeny. Sometimes this general asymmetry (siphuncle offset and accompanying septal asymmetry) is characteristic of virtually all members of a species whereas in other cases it is only displayed in some individuals. The asymmetry is prevalent in many Hettangian genera including *Neophyllites*, *Psiloceras*, *Euphyllites*, *Eolytoceras*, *Caloceras*, *Alsatites*, *Sunrisites*, *Badouxia*, *Kammerkarites*, *Franziceras*, *Discamphiceras*, *Paradiscamphiceras*, *Kammerkaroceras*, *Curviceras* and *Storthoceras* (Bilotta 2010; Bloos 1981, 1994, 1996, 1999; Bloos and Page 2000; Böhm et al. 1999; Canavari 1882; Frebold 1951, 1967; Guérin-Franiatte 1990; Guex 1989, 1995; Guex and Rakús 1991; Hengsbach 1986a, b; Hillebrandt 2000a-c; Hillebrandt and Krystyn 2009; Lange 1941, 1952; Longridge et al. 2006, 2008a, b; Neumayr 1879; Rakús 1993b; Schlegelmilch 1976; Spath 1919, 1924; Taylor 1988; Wähner 1882–1898; Wiedmann 1970; Yin et al. 2007). Asymmetry is also recognized in some younger Early Jurassic genera such as *Arctoasteroceras*, *Aequilobus* and *Dudresnayiceras* in the Sinemurian, and *Sinuiceras* in the Pliensbachian (Bilotta 2010; Frebold 1960). We suspect that with close observation, the phenomenon will be discovered in additional Jurassic genera.

There are two main hypotheses for the cause of this asymmetry. The first, proposed by Hengsbach (1979, 1986a, b, 1991, 1996), favors a parasite infestation shortly after hatching. He suggests that parasites located in the soft body, at or near the siphuncle, caused a constant displacement of the root of the siphuncle and thus, of the ventral lobe of the suture. He claims that the degree and direction of offset were controlled by the location and size of the site of infestation and further suggests that after the death of the parasite, the asymmetry would have been too well established to be corrected in subsequent growth. The second hypothesis is that of Guex (2001, 2006) who suggests that environmental stress in the earliest Jurassic may have generated genetic changes in the ammonoid root stock, leading to offset of the siphuncle and corresponding asymmetry in the suture. Guex highlights work showing that in taxa other than ammonoids, external environmental stress can increase the rate of gene mutation and recombination as well as initiate asymmetries (Alméras and Elmi 1987; Hoffman and Parsons 1991; Williamson 1981). Furthermore he cites the work of Rutherford and Lindquist (1998) who show that external stresses can alter a protein that influences an organism's development thereby producing more morphological variants that, under the influence of natural selection, can accelerate evolutionary radiation. In sum, Guex argues that stress induced genetic or biochemical changes are potentially responsible for the offset siphuncle phenomenon.

Both hypotheses are plausible and it is difficult to decide which is correct based on the limited data currently available. Some of the evidence favors the hypothesis of Hengsbach. Offset is not consistently present even in closely related, contemporaneous genera. For example, siphuncle offset is only intermittently expressed at the generic level in the Psiloceratina (Fig. 18.7). It occurs in species of *Schreinbachites* (Bloos 1994, 1996) but has not been recognized in species of *Alpinoceras* or *Paracaloceras*, which are currently considered to be the ancestral genera (Fig. 18.7). Similarly, siphuncle offset is also sporadic at the species level whereby even contemporaneous species from a single genus may not consistently show asymmetry. Once again, if the cause of the offset was related to genetic changes, it seems reasonable to expect that all closely related forms would be affected. In contrast, it is easier to see how only some animals might be infested by a parasite.

Other evidence seems to better support the hypothesis of Guex. Firstly, single species often show siphuncle offset across extensive biogeographic ranges. For example, specimens of the Late Hettangian ammonoid *Badouxia canadensis* are found throughout the eastern Pacific and almost invariably have an offset siphuncle (Hall and Pitaru 2004; Hillebrandt 2000b; Longridge et al. 2006). It seems improbable that a parasite could cause siphuncle offset in virtually 100 % of individuals of a single species, spread over such a wide geographic range. Secondly, external influences can affect the position of the siphuncle. For example, in a specimen of *Eolytoceras* from Taseko Lakes (GSC 127429 in Longridge et al. 2008b), the external lobe and siphuncle switch sides from right to left of the median line between a shell diameter of c. 2.1 cm and 2.3 cm. The position then begins to 'correct' as growth continues and by the end of the preserved specimen, the siphuncle is nearly central. This disturbance was probably caused by an injury to the animal, but the fact that the position begins to correct suggests that it may have been influenced by genetics rather than an external influence such as parasites. This also suggests that the assertion of Hengsbach (1986a), that the siphuncle would continue to be displaced even after death of the parasite, could be incorrect.

Other patterns of siphuncle offset currently apparent in the fossil record could be equally well explained by either Hengsbach's hypothesis of parasite infestation or Guex's hypothesis of genetic influence. Triassic genera that are immediately ancestral to the Jurassic ammonoids (Tozer 1994; Yin et al. 2007) as well as the Hettangian Phylloceratoidea (Böhm et al. 1999; Hillebrandt 2000c; Longridge et al.

2008b; Neumayr 1879; Rakús 1993a, 1999; Wähner 1882–1898; Fig. 18.7) do not have the asymmetry. Furthermore, in many species where siphuncle offset occurs, the pattern of offset is not consistent. For example, over 40 specimens of *B. canadensis* come from a single locality in the Taseko Lakes area of British Columbia (Section D, bed 2 in Longridge et al. 2006). All members of this collection possess an offset siphuncle although the position varies. In some specimens, the siphuncle is shifted to the right of the plane of bilateral symmetry while in others it is shifted to the left. The degree of offset is also highly variable between individuals. Hengsbach (1996) claims that the side of the organism on which the malformation occurs should vary with a parasitic cause whereas it should not vary with a genetic cause. At the present time we do not have sufficient data to negate either the Hengsbach or the Guex hypothesis.

18.5 Discussion and Conclusions

According to Kauffman and Harries (1996), ecological generalists are one of the common survivors of mass extinctions. These groups tend to have broad geographical ranges, large niche sizes, relatively primitive morphology, and species with long stratigraphic ranges. Also, they usually occur consistently, but rarely, in great numbers over broad paleogeographic areas and often show limited post-extinction diversification (Kauffman and Erwin 1995; Kauffman and Harries 1996). An example is the Phylloceratina, a group that perhaps survived the end-Triassic mass extinction by persisting in the open oceans (Hillebrandt and Krystyn 2009). We suggest that the ammonoids generally follow a model of adaptive radiation whereby recovery represents a refilling of empty niches and a return to pre-extinction equilibrium (Erwin 2000, 2001; Sepkoski 1984). In the initial aftermath, biodiversity is low and geographically widespread taxa prevail. This survival interval is followed by the rapid appearance of new taxonomic groups that may show significant regional differences. Repopulation follows an exponential curve and the greater the extinction the longer the recovery interval. This pattern may be evident in the ammonoids where the earliest *Psiloceras* are widespread and morphologically variable. Later *Psiloceras* and descendant taxa show considerable regional differences (Hillebrandt and Krystyn 2009).

The T-J extinction occurred at 201.6 Ma (Blackburn et al. 2013; Gradstein et al. 2012; Schaltegger et al. 2008) and the effect on the ammonoids was profound. Demersal modes of life seem to be the most resistant to extinction. The immediate aftermath of the extinction is also characterized by forms interpreted to be planktonic drifters, which perhaps aided dispersal and recolonization. Determining the point at which full recovery was achieved is difficult and depends on the metric. Superfamilies proliferated and standing generic diversities increased fairly quickly but it was not until the Middle Jurassic that generic diversity per million years reached levels in excess of those seen in the Late Triassic. Similarly, by the Bajocian much of the planispire and heteromorph morphospace had been reoccupied, but it was not until the Bathonian-Callovian that shell disparity comparable to that of the Late Triassic was achieved. The Bajocian began at 170.3 Ma and the Callovian ended at 163.5 Ma. The time to full recovery of the disparity seen in Triassic ammonoid shell geometry was therefore between 30 and 40 million years (Smith et al. 2014).

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