

Chapter 19

Ammonites on the Brink of Extinction: Diversity, Abundance, and Ecology of the Order Ammonoidea at the Cretaceous/Paleogene (K/Pg) Boundary

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19.1 Introduction

Ammonite shells are common fossils in marine Mesozoic deposits. Their disappearance in Cenozoic strata has intrigued naturalists from the early nineteenth century onward, and the cause of their extinction has been the subject of lively debate. Following the seminal publication of Alvarez et al. (1980), paleontologists have considered that the most plausible explanation for their disappearance was the impact of an asteroid, and its ensuing consequences (Gould 1995; Ward 1996). Today, the evidence for the Chicxulub impact in the Yucatán Peninsula, Mexico, is overwhelming (Schulte et al. 2010). Indeed, the stratigraphic layer of debris associated with the

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impact serves as the official base of the Danian Stage (= base of Cenozoic Erathem) (Molina et al. 2006). Yet, the diversity and geographic distribution of ammonites just prior to and at the moment of impact are still not well documented. Kiessling and Claeys (2002) provided an overview of localities where ammonites occur near or at the K/Pg boundary (KTBase project). However, only a handful of sections were described, leaving many blind spots. Thanks to renewed collecting efforts during the past decade to recover ammonites from close to the boundary, it is now possible to assemble a much more detailed picture of the health of this group at the brink of extinction.

19.2 Methods

We examined the stratigraphic distribution of ammonites at a total of 29 sites encompassing 14 regions around the world to tabulate the generic and specific diversity of these animals just prior to and at the K/Pg boundary. These sites include the Atlantic Coastal Plain of North America (New Jersey and Maryland); the Gulf Coastal Plain of North America (Missouri, Mississippi, and Texas); the La Popa Basin, northeastern Mexico; Denmark (Stevns Klint, Kjølby Gård, and the “*Dania*” Quarry); the Maastrichtian type area (the Netherlands and northeast Belgium); Poland (Nasiłów, Mełgiew, and Lechówka); Kyzylsai, Kazakhstan; the Sumbar River, Turkmenistan; the Bay of Biscay (Zumaya, Hendaye, and Bidart); Bjala (= Byala), Bulgaria; Tunisia (Kalaat Senan, El Kef, and Garn Halfaya) and Egypt (Dababiya Quarry Corehole); the Naiba River Valley, Sakhalin, Far East Russia; the Poty Quarry, Brazil; Lomas Colorados, Bajada de Jagüel, the Neuquén Basin, Argentina; and Seymour Island, Antarctica (Fig. 19.1, Appendix). We have arbitrarily focused on the last 0.5 million years of the Maastrichtian at each site (our target interval) because this is the shortest interval of time that still yields enough ammonite data from different environmental settings and geographic areas. However, it is worth noting that taphonomic bias and collection failure play a much larger role in the recovery of ammonite data than they do in the assembly of, for example, microfossil data.

We demarcated our target interval using biostratigraphy, magnetostratigraphy, and cyclostratigraphy, as well as data on fossil occurrences in relation to the K/Pg boundary in sections without any physical sign of a sedimentary break between the highest ammonites and the K/Pg boundary. In terms of biostratigraphy, many of our sites belong to, or can be correlated with, Calcareous Nannofossil Zone CC26b of Perch-Nielsen (1985), which is approximately equivalent to Zone UC20dTP of Burnett (1998), and extends from the FO of *Micula prinsii* to the LO of unreworkeed, non-survivor Cretaceous taxa, which starts 750 kyr (Hennebert 2012) to 530 kyr (Dinarès-Turell et al. 2013) before the end of the Cretaceous (see also Gardin et al. 2012). This interval is approximately equivalent to geomagnetic polarity Chron 29r, which starts 0.3 myr prior to the K/Pg boundary according to recent calculations (e.g., Husson et al. 2011). For planktic foraminifera, our 0.5 myr interval corresponds to the combined *Plummerita hantkeninoides* CF1 Zone, *Pseudoguembelina*

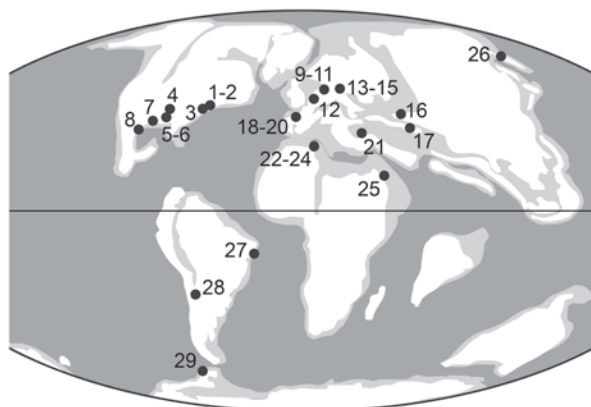


Fig. 19.1 Distribution of localities described in the text plotted on a paleogeographic map of the Earth at the K/Pg boundary (after Blakey 2011). 1 Central Monmouth County, New Jersey, 2 Northeastern Monmouth County, New Jersey, 3 Anne Arundel County, Maryland, 4 Stoddard and Scott Counties, Missouri, 5 Tippah County, Mississippi, 6 Chickasaw County, Mississippi, 7 Falls County, Texas, 8 Northeastern Mexico, 9 Stevns Klint, Denmark, 10 Kjølbj Gård, Denmark, 11 Dania Quarry, Denmark, 12 Maastricht, the Netherlands, 13 Nasilów, Poland, 14 Mełgiew, Poland, 15 Lechówka, Poland, 16 Kyzylsaiy, Kazakhstan, 17 Sumbar River, Turkmenistan, 18 Zumaya, Spain, 19 Hendaye, France, 20 Bidart, France, 21 Bjala, Bulgaria, 22 Kalaat Senan, Tunisia, 23 El Kef, Tunisia, 24 Garn Halfaya, Tunisia, 25 Dababiya Quarry core, Egypt, 26 Sakhalin Island, Russia, 27 Poty Quarry, Brazil, 28 Bajada de Jagüel, Argentina, 29 Seymour Island, Antarctica. (See Appendix for a description of the localities)

palpebra CF2 Zone, and possibly also the upper part of the *Pseudoguembelina fructicosa* CF3 Zone. The base of CF1 is approximately 0.23 myr prior to the K/Pg boundary, according to Hennebert and Dupuis (2003).

In evaluating the record of ammonites at the K/Pg boundary, it is important to distinguish between complete and incomplete sections. For example, in complete sections, e.g., in Tunisia, all of the impact markers are present, including a layer of fine clay (the so-called K/Pg boundary clay) with elevated concentrations of iridium. In such sections, the timescale of deposition is constrained by two points: the impact layer, which represents the same moment everywhere (isochronous), and the base of the highest biostratigraphic zone, which is possibly diachronous. This timescale can be further refined using cyclostratigraphic data, as in the Bay of Biscay, the Tunisian Trough Basin, and the Maastrichtian type area. In incomplete sections, e.g., at Nasilów, central Poland, in contrast, the fallout layer (boundary clay) is not preserved, although it was undoubtedly deposited, and instead the boundary is marked by an erosional unconformity. The amount of time this unconformity represents is difficult to estimate using biostratigraphic indices and can include parts of the latest Maastrichtian and earliest Danian.

The authors of the ammonite species mentioned in the text are listed in Table 19.1. Some of the ammonites documented are in open nomenclature because the specimens are worn or consist of only fragments. For example, specimens of

Table 19.1 (continued)

Taxon/Site number:	ATLANTIC COAST			GULF COAST			DEN-MARK			POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA		AN					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29		
<i>Pachydiscus (P.) neubergicus dissinus</i> Henderson and McNamara, 1985																	1														
<i>Pachydiscus (P.) gollevillensis</i> (d'Orbigny, 1850)																				1											
<i>Pachydiscus (P.) ultimus</i> Macellari, 1986																				1											1
<i>Pachydiscus (P.) jacquoti jacquoti</i> (Seunes, 1890)											1						1														
<i>Pachydiscus (P.) armenicus</i> Atabekian and Akopian, 1969																				1											
<i>Pachydiscus (P.) noetlingi</i> Kennedy in Fatmi and Kennedy, 1999											1									1											
<i>Pachydiscus (P.) flexuosus</i> Matsumoto, 1979																															1
<i>Pachydiscus (P.)</i> sp. A of Goolaearts, 2010																															

Table 19.1 (continued)

Taxon/Site number:	ATLANTIC COAST			GULF COAST				DEN-MARK			MA			POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	FER	SOUTH AMERICA			AN	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29			
<i>Diplomoceras cylin-</i> <i>draceum</i> (Defrance, 1816)								1																		1						
<i>Diplomoceras lambi</i> Spath, 1953									1										1	1												1
<i>Diplomoceras</i> sp. of Stinnesbeck et al., 2012																																
<i>Phylloptychoceras</i> cf. <i>P. sipho</i> (Forbes, 1846) of Jagt et al., 2006											1																					
<i>Phylloptychoceras</i> cf. <i>P. sipho</i> (Forbes, 1846) of Goolaerts, 2010																																
<i>Phylloptychoceras</i> sp. of Birkelund, 1993								1																								
BACULITIDAE																																
<i>Baculites anceps</i> Lamarck, 1822											1																					
<i>Baculites ovatus</i> Say, 1821								1																								
<i>Baculites vertebralis</i> Lamarck, 1801								1			1																					
<i>Baculites</i> cf. <i>B. verte-</i> <i>bralis</i> Lamarck, 1801																																

Table 19.1 (continued)

Taxon/Site number:	ATLAN-TIC COAST			GULF COAST					DEN-MARK			POLAND			KA	TR	BISCAY REGION			BU	TUNISIA			EG	SOUTH AMER-ICA		AN							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14			15	16	17		18	19	20		21	22		23	24	25	26	27	28	29
<i>Discoscaphites</i> cf. <i>D. gulosus</i> (Morton, 1834) of Kennedy et al., 2001								1																										
<i>Discoscaphites iris</i> (Conrad, 1858)	1	1	1	1	1	1	1																											
<i>Discoscaphites</i> cf. <i>D. iris</i> (Conrad, 1858) of Landman et al., 2004a			1																															
<i>Discoscaphites jerseyensis</i> Landman et al., 2007	1																																	
<i>Discoscaphites minardi</i> Landman et al., 2004a	1			1																														
<i>Discoscaphites</i> cf. <i>D. minardi</i> Landman et al., 2004a of Landman et al., 2004a			1																															
<i>Discoscaphites sphaeroidalis</i> Kennedy and Cobban, 2000	1			1																														

Geographic distribution of ammonite species at 29 sites in the last 0.5 myr of the Cretaceous. Abbreviations: MA: Maastrichtian type area, The Netherlands and Belgium; KA: Kazakhstan; TR: Turkmenistan; BU: Bulgaria; EG: Egypt; FER: Far East Russia; AN: Antarctica; * = the two species may be synonymous, but further research is required.

Phylloptychoceras from Tunisia are small pyritic fragments of shafts and can, therefore, only be referred to as *Phylloptychoceras* cf. *P. siphon*. Similarly, specimens of *Baculites* from this region are too incomplete and lack details of ornamentation and suture to permit species identification. On the Atlantic and Gulf Coastal plains, the poor state of preservation of some specimens of *Glyptoxoceras* and *Discoscaphites* also precludes their identification to species level. Even in sections that have been studied for decades, such as those in Denmark, some material is too crushed or incomplete to be assigned to a particular species with any certainty (e.g., *Saghalinites* n. sp. of Birkelund 1993).

19.3 Results

19.3.1 Atlantic Coastal Plain of North America

(Sites 1–3: New Jersey and Maryland). The *Discoscaphites iris* Zone, the highest ammonite zone in North America, is present in this area and has yielded nine species, four (sub)genera, and four families distributed among the Ammonitina (*Pachydiscus* (*Neodesmoceras*) and *Sphenodiscus*) and Ancyloceratina (*Eubaculites* and *Discoscaphites*) (Landman et al. 2004a, b, 2007; Figs. 19.2, 19.3; Tables 19.1, 19.2). This zone corresponds to Calcareous Nannofossil Zone CC26b, representing approximately the last 0.5 myr of the Maastrichtian. At offshore sites (~100 m deep) containing ammonites, the section is demonstrably incomplete with an unconformity at the K/Pg boundary. At more nearshore sites (~40 m deep) containing ammonites, the sequence is apparently more complete. The upper part of the section consists of a very fossiliferous unit (called the *Pinna* Layer) that yields numerous specimens of *Discoscaphites* and *Eubaculites*. The *Pinna* Layer is overlain by the Burrowed Unit, which bears many fewer ammonites, almost all of which are *Eubaculites*. However, the *Pinna* Layer occurs above a horizon with a weak iridium anomaly (520 pg/g). The crucial question is whether this iridium anomaly represents the record of the bolide impact and, if so, whether it is in place or has migrated downward (Landman et al. 2007, 2012b; Miller et al. 2010; for additional discussion about the remobilization of iridium, see Racki et al. 2011). For example, if the iridium anomaly is in place, then the ammonites in the *Pinna* Layer and the Burrowed Unit may have been short-term survivors of the bolide impact, possibly persisting into the earliest Danian. However, even if the iridium anomaly has migrated downward from the top of the *Pinna* Layer, a more conservative interpretation favored here and elsewhere (Landman et al. 2014), the species of *Eubaculites* in the Burrowed Unit are still Danian survivors (see 19.4.1).

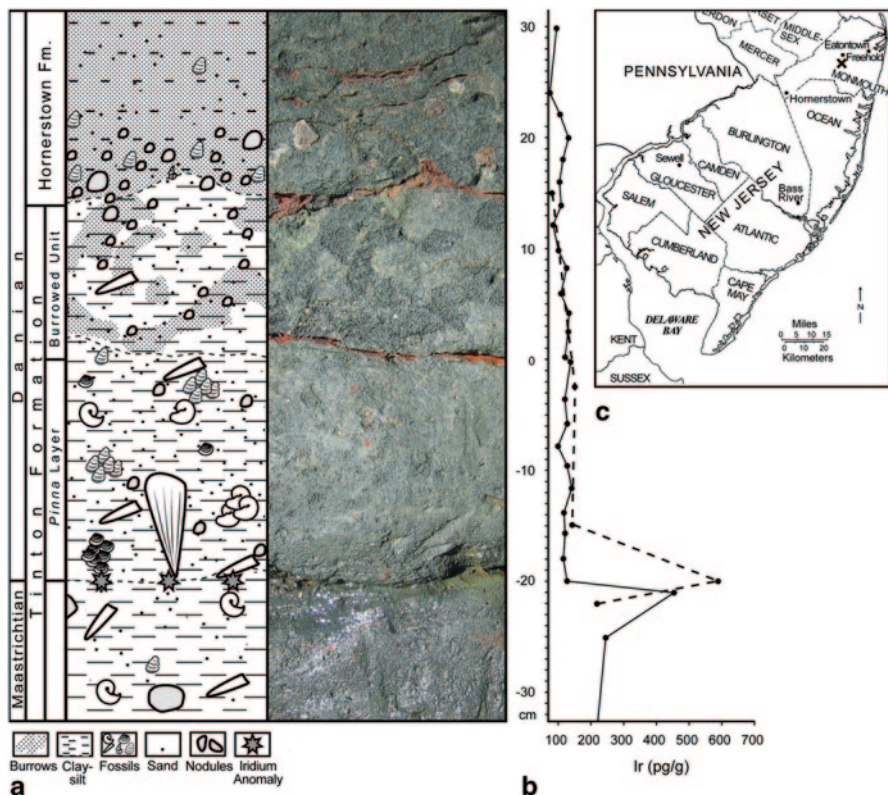


Fig. 19.2 Stratigraphic section of the upper Maastrichtian and lower Danian in Monmouth County, New Jersey, Atlantic Coastal Plain, USA. **a** The top of the Tinton Formation consists of the *Pinna* Layer overlain by the Burrowed Unit, which is overlain, in turn, by the Hornerstown Formation. An enriched concentration of iridium occurs at the base of the *Pinna* Layer (indicated by the stars). The position of the K/Pg boundary is based upon the assumption that the enriched concentration of iridium has been remobilized. **b** Iridium profile from two sites (represented by the solid and dashed lines) (Landman et al. 2007). **c** Map of part of New Jersey with the locality marked by an X

19.3.2 Gulf Coastal Plain of North America

(Sites 4–7: Missouri, Mississippi, and Texas). The *Discoscaphites iris* Zone is present on the Gulf Coastal Plain in Missouri (Stephenson 1955), Mississippi (Cobban and Kennedy 1995; Kennedy and Cobban 2000), and Texas (Kennedy et al. 2001) and contains as many as 15 species, although not all of them are present at every site (Fig. 19.4; Tables 19.1, 19.2). In Stoddard and Scott Counties, southeastern Missouri, the Owl Creek Formation consists of clayey sands, which were probably deposited at depths of less than 100 m, and is unconformably overlain by the Clayton Formation (Campbell et al. 2008). In Tippah County, northeastern Mississippi, the Owl Creek Formation consists of micaceous clays, which were probably deposited at similar depths. The Owl Creek Formation at this site is also unconformably

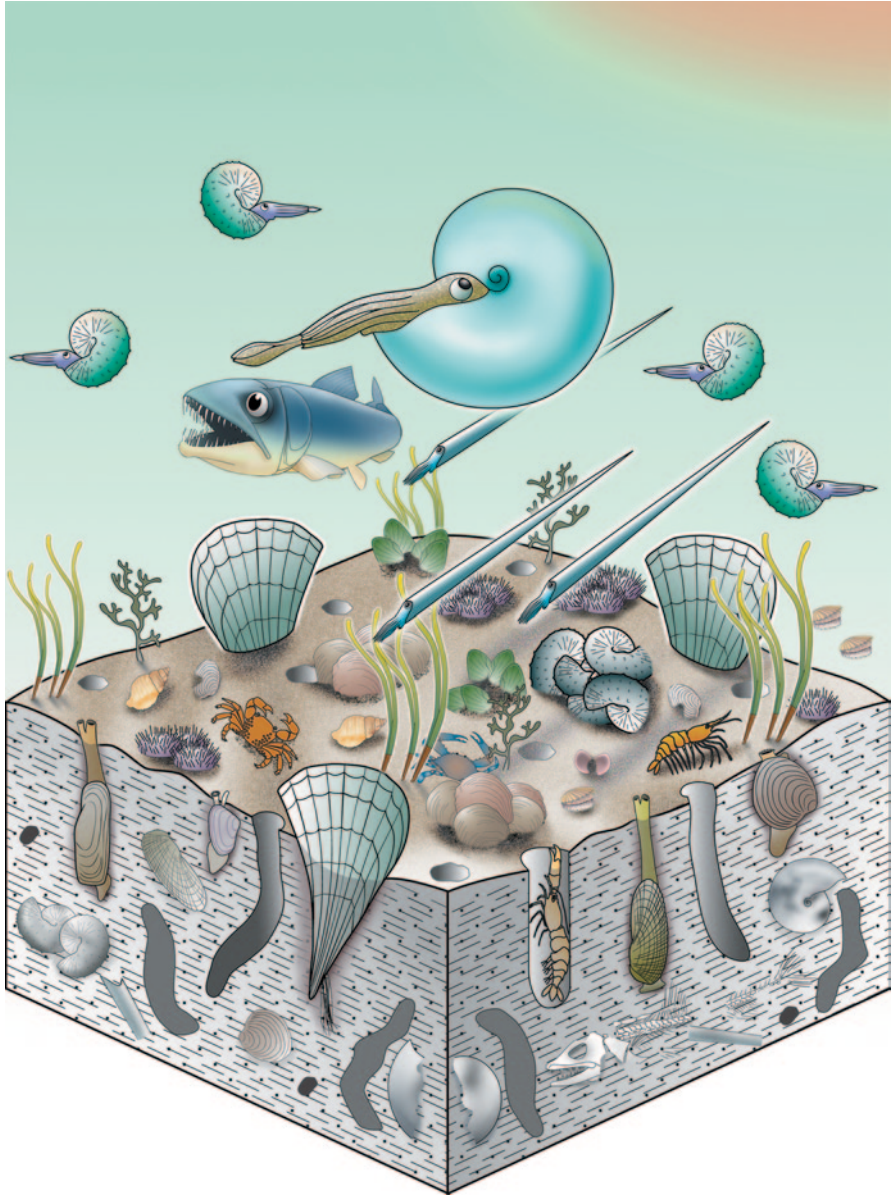
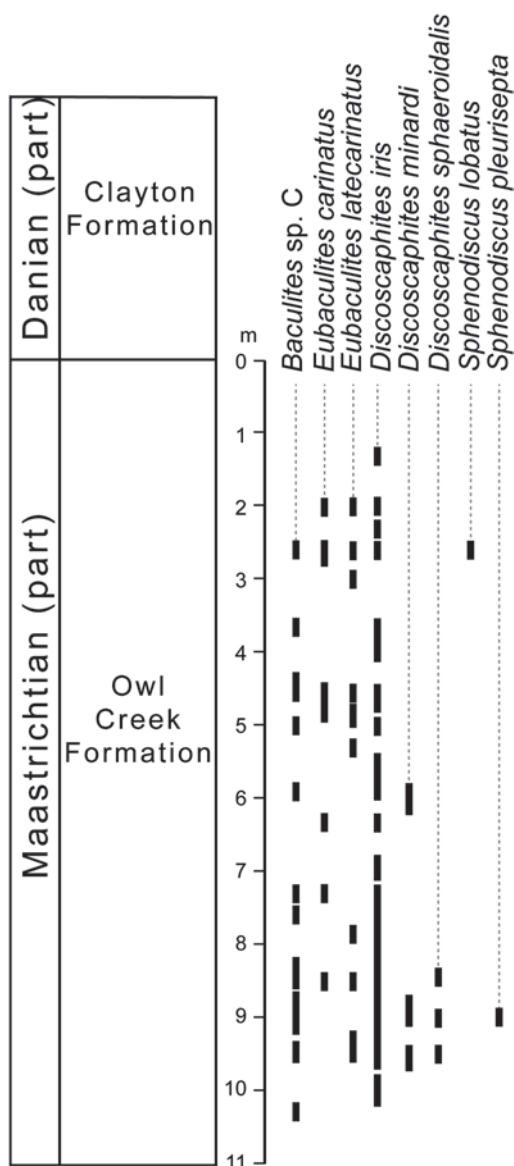


Fig. 19.3 Hypothetical reconstruction of the sea bottom on the Atlantic Coast at the end of the Maastrichtian just before the meteor impact, as inferred from sections in Monmouth County, New Jersey. The ammonites include *Sphenodiscus lobatus*, *Discoscaphites iris*, and *Eubaculites latecarinatus* (from Landman et al 2007)

Table 19.2 Geographic distribution of 31 ammonite genera at 29 sites in the last 0.5 my of the Cretaceous

	ATLAN- TIC COAST		GULF COAST							DEN- MARK		MA		POLAND			KA	TR	BISCAY REGION			BU	TUNISIA					EG	FER	SOUTH AMER- ICA		AN	
Taxon/Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N	occur- rences		
1 <i>H. (Neophyl- loceras)</i>									1		1							1	1	1		1				1				7			
2 <i>Phyllopachy- ceras</i>																		1	1	1		1								4			
3 <i>Gaudryceras</i>																		1								1				2			
4 <i>Anagaudry- ceras</i>																		1	1	1	1	1				1			1	7			
5 <i>Vertebrites</i>																					1									1			
6 <i>Zelandites</i>																		1								1			1	5			
7 <i>Tetragonites</i>																						1	1							2			
8 <i>Saghalinites</i>									1	1										1		1								4			
9 <i>Pseudophyl- lites</i>																				1	1	1	1	1				1	6				
10 <i>Desmophyl- lites</i>																		1											1				
11 <i>Hauericeras</i>																														3			
12 <i>Pseudokoss- maiceras</i>																				1										1			
13 <i>B. (Brahmaites)</i>											1											1	1	1						5			
14 <i>Grossou- reites</i>																													1	1			

Fig. 19.4 Stratigraphic range chart of the ammonites in the Owl Creek Formation in Tippah County, north-eastern Mississippi, Gulf Coastal Plain, USA (Larina et al. 2012). The Owl Creek Formation is unconformably overlain by the Clayton Formation, with no evidence of impact debris. Ammonites extend to approximately 1 m below the unconformity, which presumably contains the K/Pg boundary



overlain by the Clayton Formation, without any evidence of impact debris. Ammonites extend to approximately 1 m below the unconformity, which presumably contains the K/Pg boundary, and the absence of ammonites above this level may be due to dissolution (Larina et al. 2012). Towards the southeast in Chickasaw County, Mississippi, the Owl Creek Formation passes into the Prairie Bluff Chalk, which contains the same assemblage of ammonites. However, the base of the Clayton Formation in this area consists of a 30-cm-thick unit filled with impact spherules and reworked Maastrichtian fossils (Boas et al. 2013a, b).

On the other side of the Mississippi Embayment, ammonites are present in the upper Corsicana Formation along the Brazos River, Falls County, Texas. The erosional surface at the top of this formation has been interpreted as the K/Pg boundary (Hansen et al. 1987; for further discussion of this interpretation see Hart et al. 2012). The ammonites are the same as those in Mississippi with the addition of *Pachydiscus (P.) j. jacquoti* and *Glyptoxoceras* cf. *G. rugatum*. Two ammonite species (*Eubaculites carinatus* and *Discoscaphites* cf. *D. gulosus*) extend into the uppermost 1 m of the formation (Kennedy et al. 2001). In addition, Keller et al. (2009, p. 54) reported a single specimen of *D. iris* at the base of the *Pseudoguembelina palpebra* CF2 Zone in the Brazos River Mullinax-1 Core.

19.3.3 *La Popa Basin, Northeastern Mexico*

(Site 8). In northeastern Mexico, Stinnesbeck et al. (2012: table 1) reported *Sphenodiscus pleurisepta* and *Baculites ovatus* from Planktic Foraminifera Zone CF3. The highest occurrence of *S. pleurisepta* is 3 m below an erosional unconformity marking the K/Pg boundary.

19.3.4 *Denmark*

(Sites 9–11: Stevns Klint, Kjølbj Gård, and the “*Dania*” Quarry). The ammonite record in Denmark has been extensively studied because these sections exhibit nearly continuous deposition across the K/Pg boundary (Birkelund 1979, 1993; Schiøler et al. 1997; Machalski 2005a, b; Machalski and Heinberg 2005; Rasmussen et al. 2005; Surlyk et al. 2006; Hart et al. 2011; Damholt and Surlyk 2012; Gravesen and Jakobsen 2013). The environment is interpreted as a shelf sea ranging from the euphotic zone to several hundred meters deep (Surlyk 1997; Surlyk et al. 2006; Schulte et al. 2010). The stratigraphy along the 14.5 km long classic section at Stevns Klint is complex, with the upper, but not uppermost, Maastrichtian Sigerslev Member separated by one or two closely spaced hardgrounds from the uppermost Maastrichtian Højerup Member (Fig. 19.5). These hardgrounds were probably produced by early diagenetic cementation during shallowing events (Hansen 1990; Surlyk 1997; Surlyk et al. 2006). Correlation of these events with those in the upper part of the Nekum and Meerssen members in the Maastricht area (Hart et al. 2011) suggests that the hardgrounds developed in the last 240 kyr of the Maastrichtian (Schiøler et al. 1997). The Højerup Member corresponds to the uppermost Maastrichtian *Stensioeina esnehensis* Foraminifera Zone.

The Højerup Member is internally organized into a series of low asymmetrical bryozoan bioherms alternating with basins, producing a relief of as much as 4 m. The K/Pg transition is continuous in the basins with the Højerup Member conformably overlain by the basalmost Danian Fiskeler Member (Fish Clay), which is overlain, in turn, by the Cerithium Limestone Member (Rødvig Formation; Surlyk et al. 2006). The uppermost Højerup Member is rich in ammonites, especially on

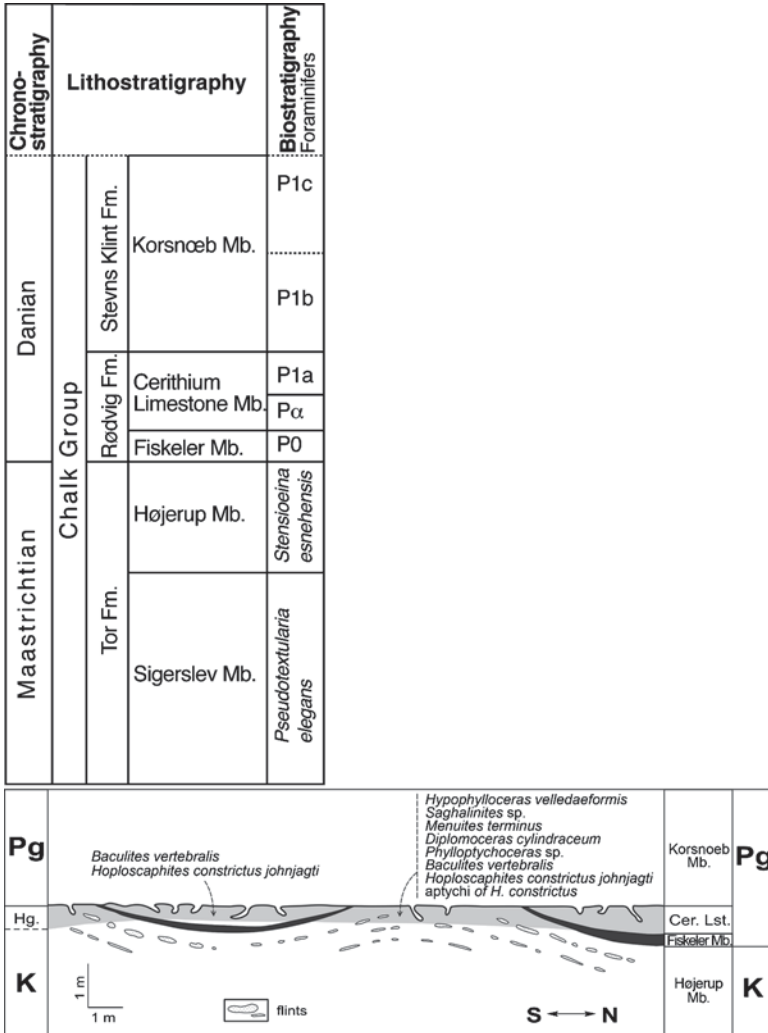
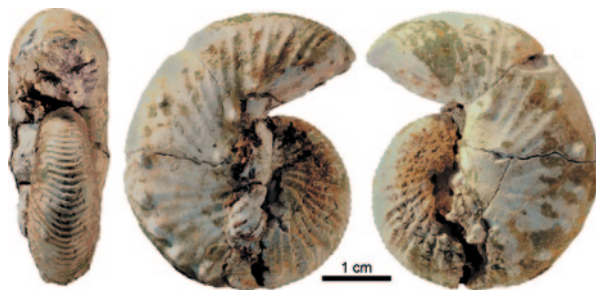


Fig. 19.5 *Top.* Stratigraphic chart of the K/Pg section at Stevns Klint, Denmark (modified from Surlyk et al. 2006). *Bottom.* Diagram of the boundary interval. Hg=Hardground (modified from Machalski and Heinberg 2005)

the crests of the bioherms, which are incorporated into a Danian hardground that truncates both the Højerup Member and Cerithium Limestone (Birkelund 1993; Machalski 2005a). In total, the fauna consists of eight species, seven genera, and six families distributed among the Phylloceratina (*Hypophylloceras* (*Neophylloceras*)), Lytoceratina (*Saghalinites*), Ammonitina (*Menuites*), and Ancyloceratina (*Phylloptychoceras*, *Diplomoceras*, *Baculites*, *Hoploscaphites*) (Tables 19.1, 19.2). Specimens of *B. vertebralis* and *H. constrictus johnjagti* also occasionally occur in the basal Danian Cerithium Limestone Member (Birkelund 1979, 1993; Surlyk and Nielsen 1999; Machalski 2002). These specimens have generally been interpreted

Fig. 19.6 *Hoploscaphites constrictus johnjagti* from the Cerithium Limestone Member at Stevns Klint, Denmark (modified from Machalski and Heinberg 2005)



as reworked material, but Machalski and Heinberg (2005) argued that they may represent early Danian survivors (Fig. 19.6).

At Kjølbj Gård, ammonites occur up to 20 cm below the K/Pg boundary (Birkelund 1993). The “*Dania*” Quarry, northern Denmark, has also been thoroughly studied and represents the *stevensis-chitoniformis* brachiopod Zone, which correlates with the *Palynodinium grallator* dinoflagellate Zone (Hansen 1977; Håkansson and Hansen 1979; Birkelund 1993; Machalski 2005a, b; Gravesen and Jakobsen 2013). The sequence at “*Dania*” is unique among Danish graveyard sequences in containing the uppermost Maastrichtian zonal species *Micula prinsii*. This nannofossil is present in one of the marl layers low in the sequence (Håkansson and Hansen 1979), which implies that the “*Dania*” succession occurs within Calcareous Nannofossil Zone CC26b of Perch-Nielsen (1985).

19.3.5 Maastrichtian Type Area

(Site 12: the Netherlands and northeast Belgium). Several outcrops and quarries near Maastricht on both sides of the border between the Netherlands and Belgium that expose the uppermost Maastrichtian are treated together. This area has been extensively studied because of its importance for biostratigraphy (Zijlstra 1994; Smit and Brinkhuis 1996; Schiøler et al. 1997; Jagt 1996, 2002; Jagt et al. 2003, 2006; Jagt and Jagt-Yazykova 2012; Mai 1998). The clay beds just above the Berg en Terblijt Horizon at the base of the IVf-7 interval (Meerssen Member) are assigned to Planktic Foraminifera Zone P0. Our targeted interval of 0.5 myr was bracketed by reference to this horizon and by using the cyclostratigraphic interpretation of Zijlstra (1994) and Schiøler et al. (1997) to define the lower part of our interval. According to them, the Nekum and Meerssen members (upper part of the Maastricht Formation) represent the last 300 kyr of the Maastrichtian. This part of the formation is interpreted as having been deposited on a shallow carbonate platform (Kennedy and Jagt 1998; Jagt 1996, 2002, 2005, 2012; Jagt et al. 2006).

We examined the record of ammonites from the Meerssen and Nekum members. In terms of dinoflagellate zonation, this interval (upper Nekum and Meerssen members) corresponds to the *Palynodinium grallator* dinoflagellate Zone, and the Meerssen Member to the *Thalassiphora pelagica* dinoflagellate Subzone (e.g., Mai 1998). A total of 19 species, 12 genera, and seven families of ammonites are present

near or at the K/Pg boundary distributed among the Ammonitina (*Brahmaites*, *Pachydiscus*, *Menuites*, and *Sphenodiscus*) and Ancyloceratina (*Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Phylloptychoceras*, *Baculites*, *Eubaculites*, *Hoploscaphites*, and *Acanthoscaphites*?) (Fig. 19.7; Tables 19.1, 19.2). The most common ammonites are *Baculites* and *Hoploscaphites*.

Several scaphitids and baculitids have also been recorded from Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon in the section exposed at the former Curfs quarry near Geulhem, southern Limburg, southeast Netherlands (Jagt et al. 2003; Machalski et al. 2009; Jagt 2012; Fig. 19.8). As stated above, this horizon is generally interpreted as marking the K/Pg boundary (although there is no evidence of impact debris) and these specimens are assigned to Planktic Foraminifera Zone P0. Because the species of *Baculites* are different from those below this

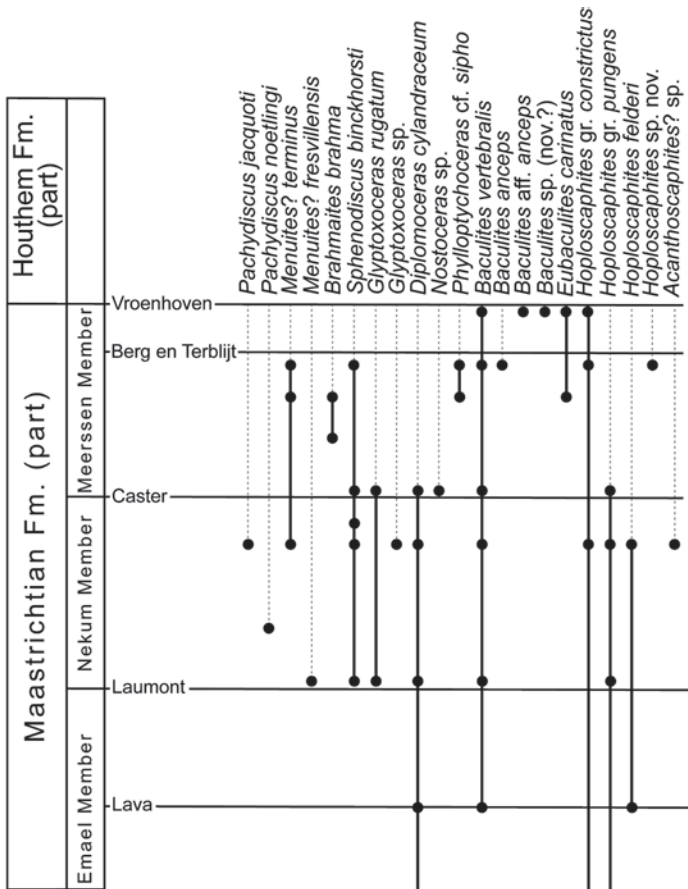


Fig. 19.7 Stratigraphic range chart of the ammonites at the K/Pg section in the Maastrichtian region, the Netherlands and northeast Belgium (modified from Jagt et al. 2006). The Berg en Terblijt Horizon, which forms the base of section IVf-7, is interpreted as the K/Pg boundary. The dots indicate isolated occurrences and the lines indicate “more or less” complete ranges

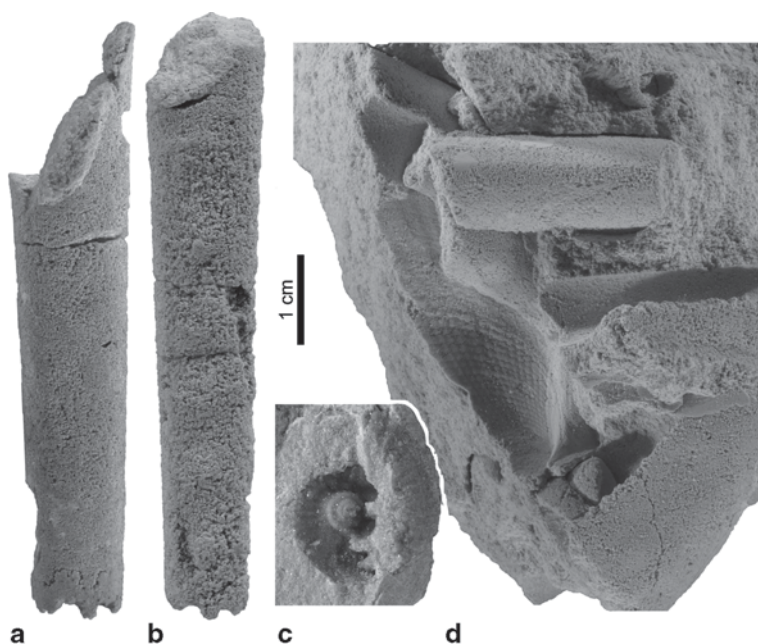


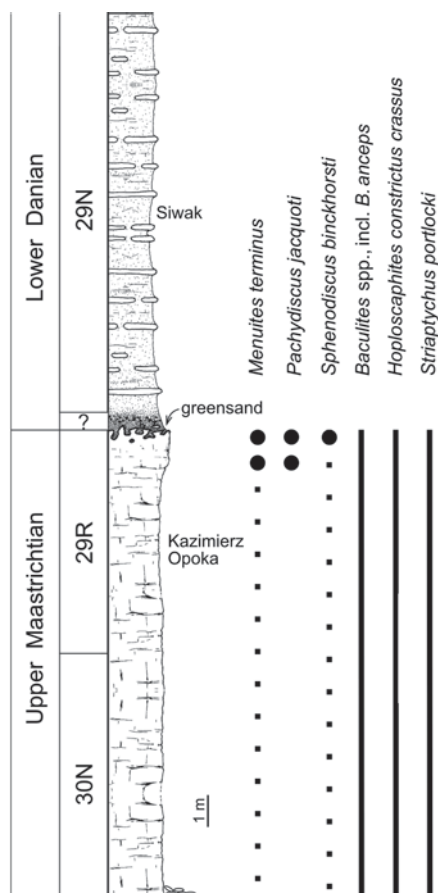
Fig. 19.8 Ammonites from the top of Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon in the section exposed at the former Curfs quarry near Geulhem, southern Limburg, southeast Netherlands (Jagt et al. 2003; Jagt 2012; Machalski et al. 2009). **a, b, d** *Baculites* aff. *anceps* (Jagt Collection, NHMM). The mature apertures are preserved in **a** and **b**. The empty spaces in **d** are voids left by dissolution of the original aragonite. **c** *Hoploscaphites constrictus*, with incomplete filling of the phragmocone (Jagt Collection, NHMM). All of these features indicate that the ammonites in this unit were buried with their shells intact without significant reworking or transport, which would have otherwise destroyed the delicate apertural features. In addition, the shells must have been buried rapidly enough to prevent complete infilling of the phragmocones

horizon and because many of them are preserved with their apertures intact, they may represent early Danian survivors (Smit and Brinkhuis 1996; Jagt et al. 2003).

19.3.6 Poland

(Sites 13–15: Nasiłów, Mełgiew, and Lechówka). The K/Pg boundary is exposed in Nasiłów in the Kaziemierz Dolny area, Poland (Hansen et al. 1989; Machalski 2005a). According to Abdel-Gawad (1986), the upper part of the section represents deposition in an inner shelf environment. However, the section is incomplete with a hiatus that spans the topmost Maastrichtian and the lowermost Paleocene encompassing as much as 500 kyr, but possibly much less. This inference is based in part on the absence of *H. constrictus johnjagti*, the terminal Maastrichtian chrono-subspecies of the *H. constrictus* lineage, which characterizes the uppermost Maastrichtian of Denmark (Højerup Member) and the Netherlands and northeast

Fig. 19.9 Stratigraphic range chart of the ammonites at the K/Pg section in Nasiłów, Poland (Machalski and Walaszczyk 1987, 1988; Machalski 2005a). Reworked specimens are present in the greensand



Belgium (top Nekum-Meerssen members) (Machalski and Walaszczyk 1987, 1988; Machalski 2005a).

Ammonites occur in the *Belemnella kazimiroviensis* belemnite Zone, Magnetic Chron 29r, and lower part of the *Palynodinium grallator* dinoflagellate Zone. They are preserved in a hard limestone layer at the top of the Kazimierz Opoka (silicious chalk) (Figs. 19.9, 19.10). This unit passes into a thin layer of soft opoka, with both layers penetrated by crustacean burrows filled with sediment derived from the overlying Danian glauconitic sandstone. A total of six species, five genera, and four families are present (Tables 19.1, 19.2). The fauna is dominated by *Baculites* spp., including *Baculites anceps*, followed by *Hoploscaphites constrictus crassus*. The rest of the ammonite fauna consists of *Menuites terminus*, *Pachydiscus* (*P.*) *j. jacquoti*, and *Sphenodiscus binckhorsti*.

A K/Pg boundary interval similar to that of Nasiłów is exposed nearby, on the opposite side of the Wisła River at Bochoznica. The section at Mełgiew, Poland, is more complete than that at Nasiłów with a hiatus of only a few thousand years at the K/Pg boundary (Machalski 2005a), as indicated by the presence of the chrono-subspecies *Hoploscaphites constrictus johnjagti*. The only additional ammonites include *Baculites* spp., but this section has not been as thoroughly studied

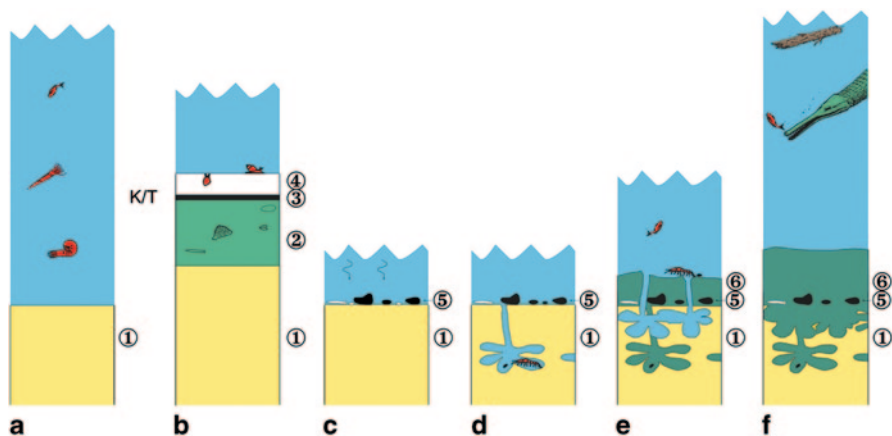


Fig. 19.10 Depositional and erosional history at the K/Pg boundary in the Kazimierz Dolny region, Poland (from Machalski 1998). Stage **a**: Sedimentation of the siliceous chalk (Kazimierz Opoka) of late Maastrichtian age (1). Stage **b**: Sedimentation of a slightly glauconitic carbonate mud unit (2) of late Maastrichtian age, followed by a clay layer (3) and a carbonate unit (4), both of Danian age. Stage **c**: Erosion or dissolution (?) episode in early Danian leading to the destruction of the top of unit 1 and total destruction of units 2–4, and to the formation of a residual lag (5) composed of reworked nodules, early diagenetic molds, and other fossils of Maastrichtian and Danian age. Stage **d**: Omission conditions on the sea floor and the development of burrowing leading to the formation of the first generation of visible burrows during the Danian. Stage **e**: Start of sandy-glauconitic sedimentation (6) of Danian age, filling of earlier burrows and formation of the next generation, origin of pseudobreccia at the top of the Kazimierz Opoka, and additional reworking of the residual lag. Stage **f**: Continuation of Danian sedimentation

as the Nasiłów section. At Lechówka, Poland, ammonites occur just below the iridium spike in the top of the *Guembelitra cretacea* planktic foraminifera Zone *sensu* Peryt (1980) (Racki et al. 2011).

19.3.7 Kyzylsai, Kazakhstan

(Site 16). The uppermost Maastrichtian of the Mangyshlak Peninsula contains rare and poorly preserved specimens of *Baculites* sp. and *Hoploscaphites constrictus* (see Naidin 1987; Herman et al. 1988; Jeffrey 1997; Tables 19.1, 19.2). They occur in white chalks that were deposited at depths of less than 100 m. The specimens of *H. constrictus* occur in the *Belemnella kazimiroviensis* belemnite Zone immediately below the boundary clay, which is marked by an anomalous concentration of iridium, with no signs of any sedimentary breaks.

19.3.8 Sumbar River, Turkmenistan

(Site 17). An apparently complete boundary section occurs in the Sumbar River area, western Kopet Dag, southwest Turkmenistan (Machalski et al. 2012). The

boundary is marked by a clay layer with an anomalous iridium concentration. The area is interpreted as a relatively deep-water environment on the outer shelf, based on the high percentage of planktic species in the foraminiferal assemblages. Two ammonite species, *Hoploscaphites constrictus johnjagti* and *Baculites* cf. *B. vertebralis*, have been recovered from the *Pseudotextularia elegans* Planktic Foraminiferal Zone as high up as 5 cm below the boundary clay (Moskvin 1959; Alekseev et al. 1988; Machalski et al. 2012; Tables 19.1, 19.2). These records represent the southeasternmost extent of these two (sub)species, which are otherwise known from northwest and central Europe. In addition, a single specimen of what appears to be *H. constrictus* is present in the Danian part of the section in an interval 22–24 cm above the base of the boundary clay. However, it is currently unclear if this specimen is reworked from the Maastrichtian or dates from the Danian.

19.3.9 Bay of Biscay

(Sites 18–20: Zumaya, Hendaye, and Bidart). This region of southwestern France and northeastern Spain encompasses many K/Pg sections that are apparently continuous and complete (Wiedmann 1987, 1988a, b; Kennedy 1993; Ward and Kennedy 1993; Ten Kate and Sprenger 1993; Rocchia et al. 2002). The strata consist of massive marls with rare turbidites deposited in an outer-shelf setting with water depths of 100–500 m (Mathey 1982; Schulte et al. 2010). In Zumaya, using the cyclostratigraphic studies of Batenburg et al. (2012) and Dinarès-Turell et al. (2013), our targeted interval (last 0.5 myr of the Maastrichtian) appears to correspond to the top few meters of Member IV and the entire Member V of Ward and Kennedy (1993). This is a conservative estimate as due to small differences in measured thicknesses between Ward and Kennedy (1993), Dinarès-Turell et al. (2013), and Batenburg et al. (2012), the exact position of the base of our 0.5 myr interval cannot be situated more precisely than 1 m. The base of Member V is approximately 15 m below the K/Pg boundary in Ward and Kennedy (1993), 12 m below the K/Pg boundary in Batenburg et al. (2012), and 10.2 m below the K/Pg boundary in Dinarès-Turell et al. (2013). The base of our 0.5 myr interval thus equates to approximately 20 and 18 m below the K/Pg boundary on the Batenburg et al. (2012) and the Dinarès-Turell et al. (2013) logs, respectively. Thus, being conservative, only ammonite records from Member V and the top few meters of Member IV were included in our tally. Unit V of Ward and Kennedy (1993) falls within the *Micula prinsii* Zone (= Calcareous Nannofossil Zone CC26b of Perch-Nielsen 1985).

Ammonites are rare throughout most of the section in the Bay of Biscay (Fig. 19.11). They are present in the uppermost few meters of Member IV and the entire Member V of Ward and Kennedy (1993). In total, they consist of 13 species, representing 11 genera belonging to the Phylloceratina (*Phylloceras*, *Phyllopachyceras*), Lytoceratina (*Anagaudryceras*, *Zelandites*, *Pseudophyllites*), Ammonitina (*Desmophyllites*, *Brahmaites*, *Pachydiscus*, *Pseudokossmaticeras*, *Menuites*), and Ancyloceratina (*Diplomoceras*). The top 1.5 m in the combined sections at Zumaya, Hendaye, and Bidart contain approximately 40 specimens representing ten species, although only one of these specimens is present in the highest 10–15 cm of the section (Ward

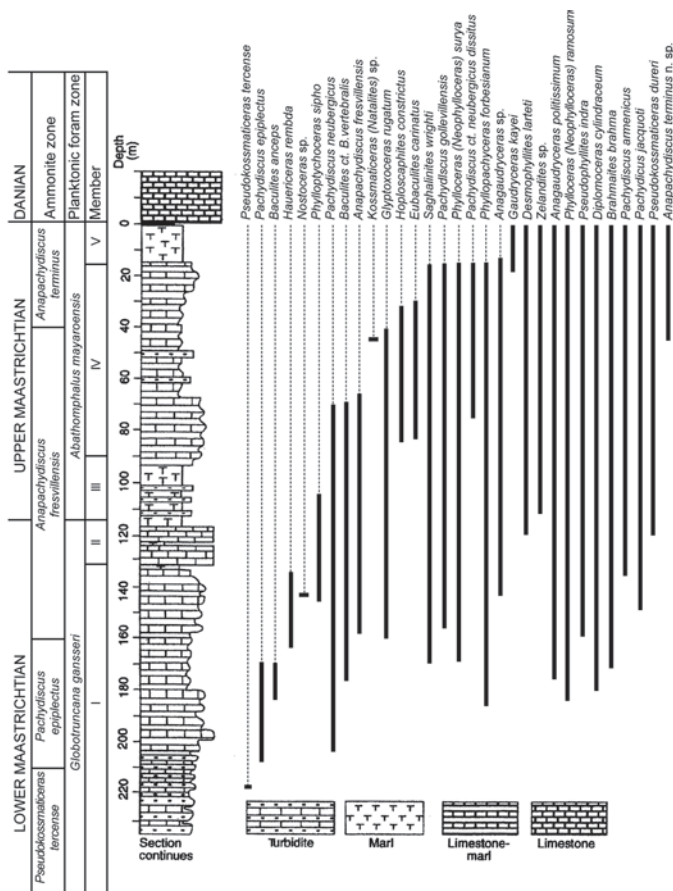


Fig. 19.11 Composite stratigraphic range chart of the ammonites at the K/Pg section in the Bay of Biscay plotted on the measured section at Zumaya, Spain (modified from Marshall and Ward 1996)

and Kennedy 1993). In addition, Rocchia et al. (2002) reported the occurrence of a poorly preserved specimen from 5 cm below the boundary clay at Bidart, which contains Ni-rich spinel crystals and an anomalously high concentration of iridium.

Marshall and Ward (1996) also used statistical methods (confidence intervals) to examine the ranges of ammonite species in the top 1.5 m of the composite section in the Bay of Biscay to determine the likelihood that the actual ranges extended above the observed ranges. Using a 50% confidence range interval, they concluded that at least two of these species could have persisted to the K/Pg boundary, even though they are not actually preserved at this level.

19.3.10 Bjala (= Byala), Bulgaria

(Site 21). In the area of Bjala (= Byala), eastern Bulgaria, along the shores of the Black Sea, several sections of the Bjala Formation contain a complete K/Pg

boundary succession (Preisinger et al. 1993; Ivanov and Stoykova 1994; Ivanov 1995; Stoykova and Ivanov 2004, 2005). The formation consists of marls in the lower part of the section and marls alternating with marly limestones in the upper part, which were deposited on the outer shelf and inner slope. The section is capped by a 1–3-cm thick clay bed marked by an anomalous concentration of iridium. Five species occur in Calcareous Nannofossil Zone CC26b (Preisinger et al. 1993; Ivanov and Stoykova 1994; Ivanov 1995; Stoykova and Ivanov 2004, 2005): *Pseudophyllites indra*, *Anagaudryceras politissimum*, *Vertebrites kayei*, *Menuites terminus*, and *Pachydiscus* sp. indet. (Tables 19.1, 19.2). Two of these species (*P. indra* and *A. politissimum*) occur 40 cm below the iridium enriched layer of clay.

19.3.11 Tunisia and Egypt

Tunisia (Sites 22–24: El Kef, Kalaat Senan, and Garn Halfaya); Egypt (Site 25: Dababiya Quarry Corehole). Several of the most complete K/Pg boundary sections are located in the Tunisian Trough Basin (Goolaerts et al. 2004; Goolaerts 2010a). Indeed, the reddish layer at the base of the Boundary Clay near El Kef (the KS locality) is the Global Stratotype Section and Point (GSSP) for the K/Pg boundary (Molina et al. 2006). Ammonites occur as high as 1–2 m below the boundary at El Kef (GSSP section), Kalaat Senan (Aïn Settara, Tabet Zaara, and Oued Raïne sections), and Garn Halfaya (Garn section), although almost all of the specimens occur as surface float and may have moved slightly downslope. The highest ammonite occurs 1 m below the boundary at Garn Halfaya, which is approximately equivalent to 50 kyr prior to the end of the Cretaceous based on the cyclostratigraphic data of Hennebert and Dupuis (2003). All of the reported ammonites occur in the highest ammonite zone, the *Indoscaphites pavana* Assemblage Zone, which represents approximately the last 420 kyr of the Maastrichtian based on the cyclostratigraphy of Hennebert and Dupuis (2003) and Hennebert (2012). In the Dababiya Quarry Corehole, specimens occur within Calcareous Nannofossil Zone CC26b (Goolaerts and Dupuis 2012; Berggren and Ouda 2013; Berggren et al. 2012).

The ammonite assemblage in the ultimate 0.5 myr of the Maastrichtian in the Tunisian Trough Basin consists of 22 species, 17 genera, and 10 families (Fig. 19.12; Tables 19.1, 19.2). This assemblage is the taxonomically most diverse terminal Maastrichtian fauna discovered to date. However, because the specimens consist of small septate inner whorls less than 20 mm in diameter, they are sometimes difficult to identify to species or even genus level. They are distributed among the Phylloceratina (*Neophylloceras* and *Phyllopachyceras*), Lytoceratina (*Anagaudryceras*, *Zelandites*, *Tetragonites*, *Pseudophyllites*, and *Saghalinites*), Ammonitina (*Hauericeras*, *Brahmaites*, *Menuites*, *Pachydiscus*, *Neodesmoceras*, and *Desmoceratoidea* gen. indet.), and Ancyloceratina (*Diplomoceras*, *Phylloptychoceras*, *Fresvillia*, *Baculites*, and *Indoscaphites*) (Tables 19.1, 19.2).

The ammonite fauna is dominated by scaphitids (*Indoscaphites*), baculitids (*Baculites*), and pachydiscids. The environment is interpreted as outer neritic to bathyal (Schulte et al. 2010), but the variation in the abundance of *Indoscaphites* suggests a depth gradient. The abundance increases from a minimum of 48% at El

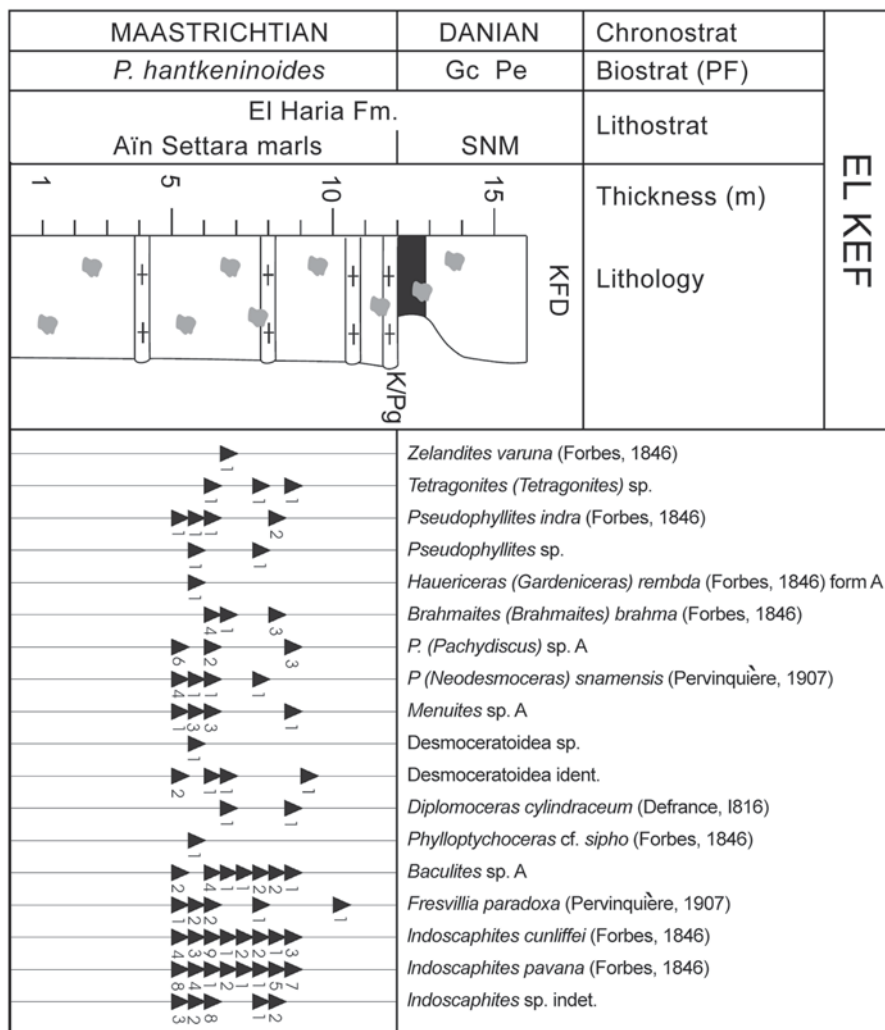


Fig. 19.12 Stratigraphic distribution of ammonite species by number of specimens in the upper part of the El Haria Formation at the El Kef GSSP section for the base of the Paleogene Period (modified from Goolaerts 2010a)

Kef to 60% at Garn Halfaya to a maximum of 76% at Kalaat Senan. Correlatively, the abundance of Lytoceratina decreases along this same transect. Phylloceratina are extremely rare, and have only been found at Kalaat Senan, which is probably due to the greater number of specimens collected at this site (643) compared to that at El Kef (145) and Garn Halfaya (108). The dominant elements of the fauna, the scaphitids and baculitids, are also reported from the uppermost Maastrichtian of Egypt (Dababiya Core; Berggren et al. 2012; Goolaerts and Dupuis 2012). The absence of other species in this region is probably due to the paucity of specimens collected from this site (10).

19.3.12 *Naiba River Valley, Sakhalin, Far East Russia*

(Site 26). The latest Maastrichtian ammonites at this site are not very well constrained in terms of biostratigraphy. Numerous well-preserved specimens of *Zelandites*, and a few specimens of *Gaudryceras* and *Hypophylloceras* (*Neophylloceras*) have been recovered from a concretionary horizon approximately 2 m below a 20-cm-thick green clay marking the K/Pg boundary (Yazykova in Zonova et al. 1993; Yazikova 1994; Yazykova 1991, 2004; Jagt-Yazykova 2011, 2012; *contra* Kodama et al. 2000; Kodama 2003; Hasegawa et al. 2003). The next lower concretionary horizon is 4–5 m below the K/Pg boundary and contains seven ammonite (sub)genera: *Hypophylloceras* (*Neophylloceras*), *Zelandites*, *Gaudryceras*, *Anagaudryceras*, *P.* (*Pachydiscus*), *P.* (*Neodesmoceras*), and *Diplomoceras*.

19.3.13 *South America*

(Site 27: Poty Quarry, Brazil; Site 28: Lomas Colorados, Bajada de Jagüel, Neuquén Basin, Argentina). In the Poty quarry in northeastern Brazil, ammonites are rare but *Pachydiscus* (*P.*) *neubergicus* and *Diplomoceras* sp. have been collected in the *Plummerita hantkeninoides* CF1 Zone at 100 and 80 cm, respectively, below the erosional unconformity containing the K/Pg boundary (Stinnesbeck and Keller 1996; Stinnesbeck et al. 2012; Tables 19.1, 19.2). In the Neuquén Basin, near Bajada de Jagüel (Argentina), a single specimen of *Eubaculites* sp. (ex gr. *E. simplex*) is present in the *Pseudoguembelina palpebra* CF2 Zone (Stinnesbeck et al. 2012).

19.3.14 *Seymour Island, Antarctica*

(Site 29). The section at Seymour Island has been extensively studied (Macellari 1986, 1988; Elliot et al. 1994; Zinsmeister and Feldmann 1996; Zinsmeister 1998; Zinsmeister et al. 1989; Tobin et al. 2012). The sequence consists of mid-shelf clastic to inner-shelf concretionary siltstones and silty sandstones of the López de Bertodano Formation. The K/Pg boundary is defined as the first occurrence of Paleogene dinocyst fossils, which coincide with the presence of an enhanced concentration of iridium. The *Pachydiscus* (*P.*) *ultimus* Zone is the highest ammonite zone and contains the lower part of Magnetic Chron 29r. It contains nine species, eight genera, and six families distributed among the Lytoceratina (*Zelandites*, *Anagaudryceras*, *Pseudophyllites*), Ammonitina (*Maorites*, *Grossouvrites*, *Kitchinites*, and *Pachydiscus*), and Ancyloceratina (*Diplomoceras*) (Fig. 19.13; Tables 19.1, 19.2). According to Zinsmeister (1998), five ammonite species are present at 50 cm below the K/Pg boundary: *Zelandites varuna*, *Pseudophyllites loryi*, *Maorites densicostatus*, *Kitchinites* (*K.*) *laurae*, and *Diplomoceras maximum* (for a discussion of the taxonomy of *Diplomoceras lambi*, *D. maximum*, and *D. cylindraceum*, see Machalski 2012).

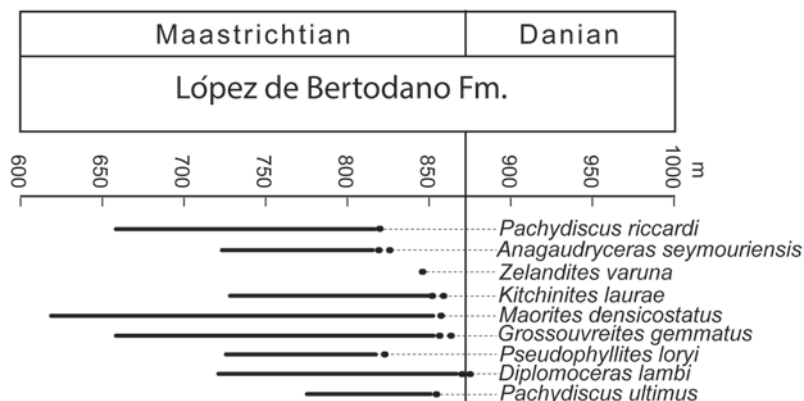


Fig. 19.13 Stratigraphic range chart of the ammonites at the K/Pg section in Antarctica (modified from Tobin et al. 2012). The solid bars indicate actual ranges (Zinsmeister et al. 1989). The dots indicate 20% range extensions based on a statistical analysis of confidence intervals. (Wang and Marshall 2004)

Wang and Marshall (2004) used statistical methods to examine the stratigraphic ranges of the highest ammonite species on Seymour Island. Using 50% range extensions, they estimated that the fossil record is consistent with the possibility that all of the species actually extended to the K/Pg boundary. More recently, Tobin et al. (2012) analyzed additional occurrence data using the same techniques as those of Wang and Marshall (2004) and reached a similar conclusion.

19.4 Discussion

19.4.1 Ammonite Diversity at the K/Pg Boundary

Based on the above compilation, ammonites are abundant and diverse in the last 0.5 million years of the Maastrichtian. They are distributed across all four Cretaceous suborders, the Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, comprising six superfamilies (Phylloceratoidea, Tetragonitoidea, Desmoceratoidea, Acanthoceratoidea, Turrilitoidea, and Scaphitoidea) and 31 (sub)genera (*Hypophylloceras* (*Neophylloceras*), *Phyllopachyceras*, *Gaudryceras*, *Anagaudryceras*, *Zelandites*, *Vertebrites*, *Tetragonites*, *Saghalinites*, *Pseudophyllites*, *Desmophyllites*, *Hauericeras*, *Kitchinites*, *Pseudokossmaticeras*, *Brahmaites* (*Brahmaites*), *Grossouvreites*, *Maorites*, *P.* (*Pachydiscus*), *P.* (*Neodesmoceras*), *Menuites*, *Sphenodiscus*, *Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Phylloptychoceras*, *Baculites*, *Eubaculites*, *Fresvillia*, *Indoscaphites*, *Hoploscaphites*, *Acanthoscaphites*, and *Discoscaphites*) (Table 19.2). They comprise 57 species (Figs. 19.14, 19.15, 19.16, 19.17; Table 19.1). If the specimens in open nomenclature are also included in the count, the tally increases to 93 species.

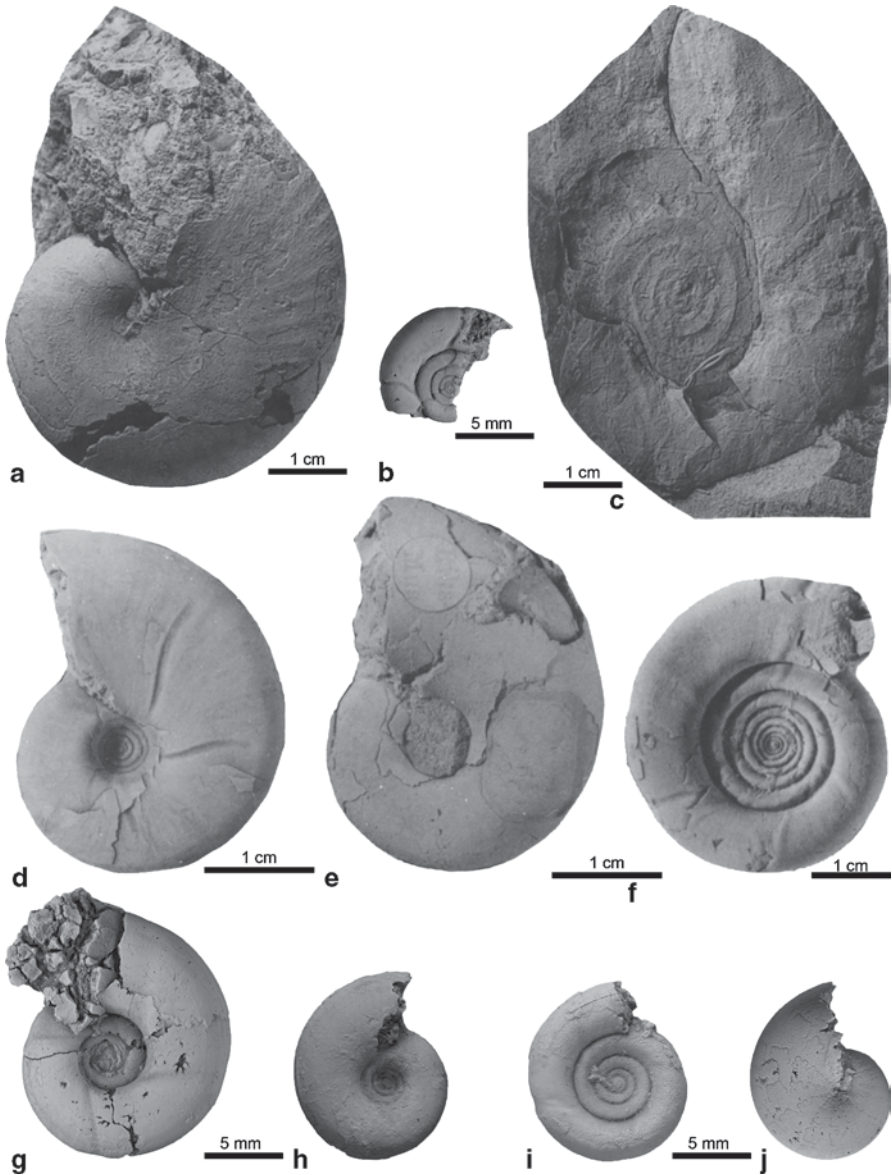


Fig. 19.14 Illustration of some of the youngest ammonites belonging to the Phylloceratina and Lytoceratina at the close of the Maastrichtian. **a** *Phyllopachyceras forbesianum*, Bay of Biscay (Ward and Kennedy 1993, Fig. 18.6). **b** *Saghalinites cala*, Tunisia (Goolaerts 2010b, pl. 1, Fig. 24). **c** *Anagaudryceras politissimum*, Bay of Biscay (Ward and Kennedy 1993, Fig. 17.12). **d** *Zelandites varuna*, Antarctica (Macellari 1986, Fig. 11.11). **e** *Pseudophyllites loryi*, Antarctica (Macellari 1986, Fig. 11.1). **f** *Anagaudryceras seymouriense*, Antarctica (Macellari 1986, Fig. 9.3). **g** *Tetragonites* sp., Tunisia (Goolaerts 2010b, pl. 2, Fig. 4). **h** *Pseudophyllites indra*, Tunisia (Goolaerts 2010b, pl. 2, Fig. 18). **i** *Anagaudryceras* cf. *A. politissimum*, Tunisia (Goolaerts 2010b, pl. 1, Fig. 20). **j** *Phyllopachyceras forbesianum*, Tunisia. (Goolaerts 2010b, pl. 1, Fig. 9)

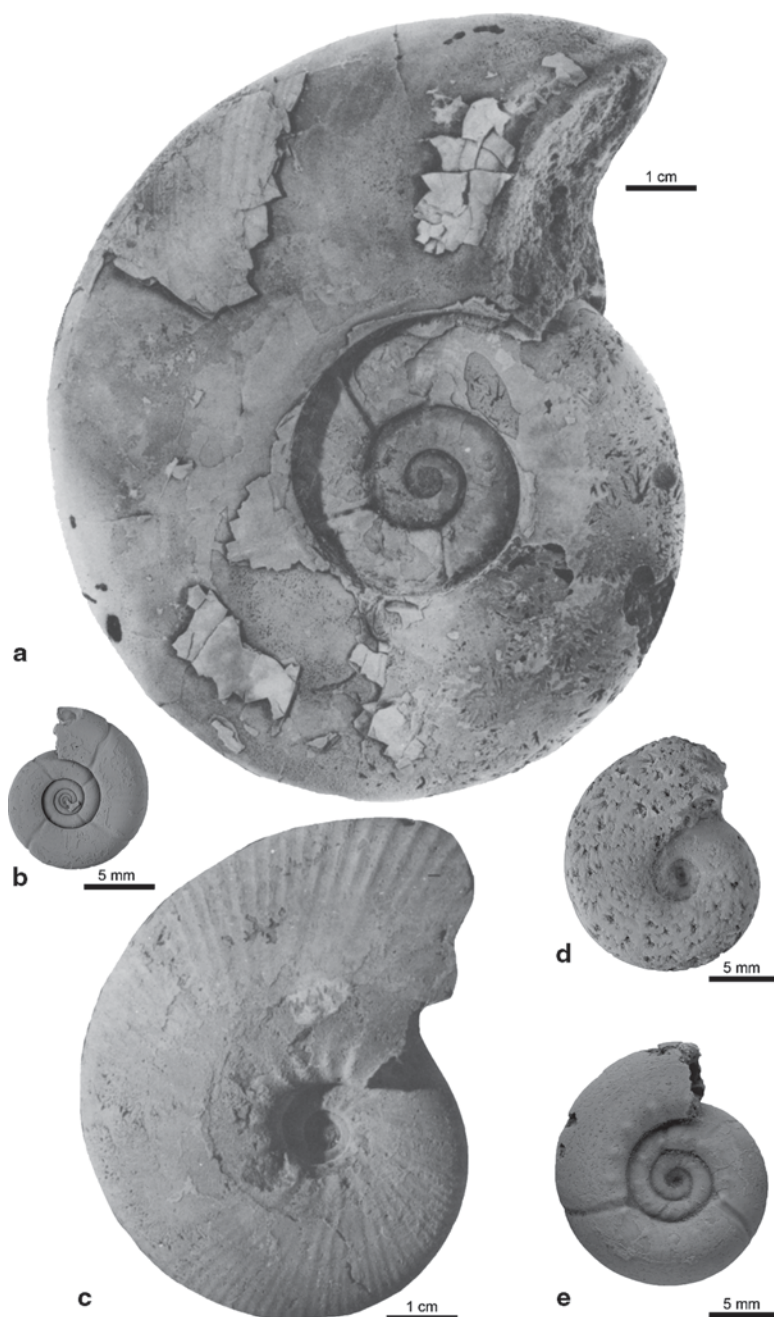


Fig. 19.15 Illustration of some of the youngest ammonites belonging to the Ammonitina at the close of the Maastrichtian. **a** *Kitchinites laurae*, Antarctica (Macellari 1986, Fig. 20.3). **b** *Hauericeras rembda*, Tunisia (Goolaerts 2010b, pl. 3, Fig. 19). **c** *Pachydiscus (P.) riccardi*, Antarctica (Macellari 1986, Fig. 37.4). **d** *Pachydiscus (Neodesmoceras) snamensis*, Tunisia (Goolaerts 2010b, pl. 7, Fig. 16). **e** *Brahmaites brahma*, Tunisia. (Goolaerts 2010b, pl. 4, Fig. 14)

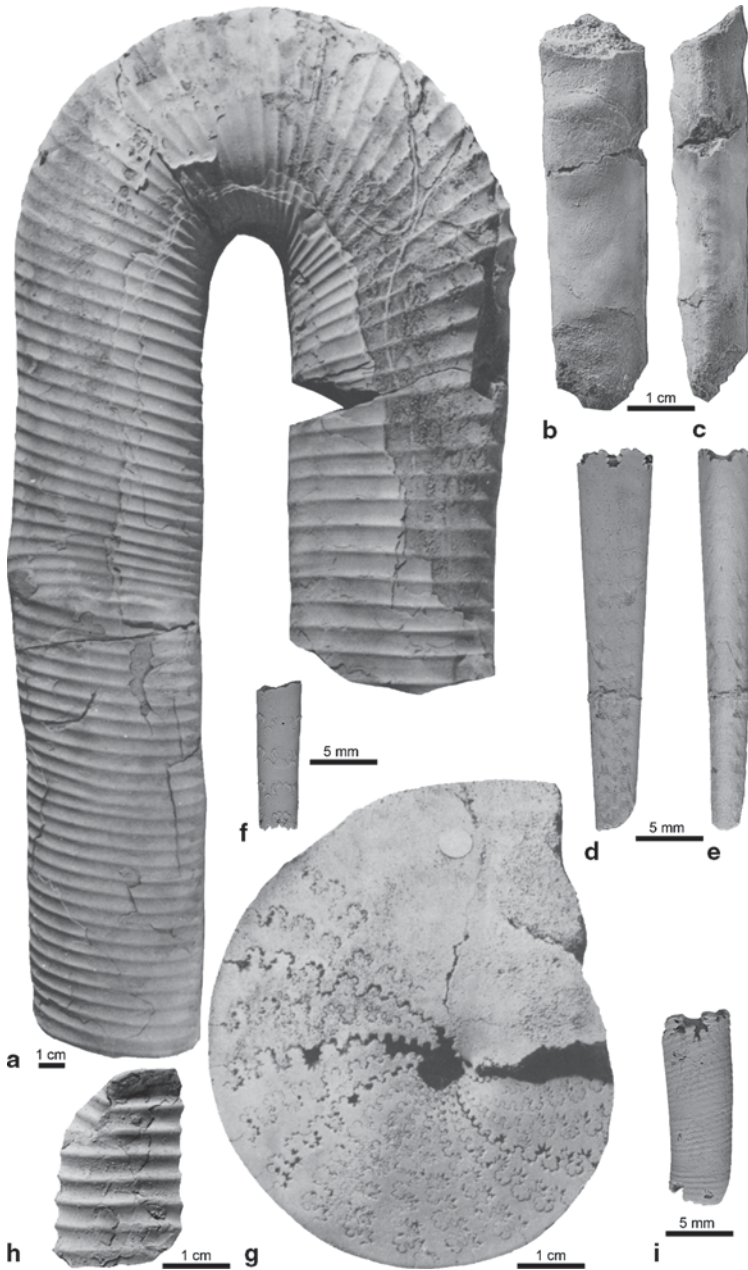


Fig. 19.16 Illustration of some of the youngest ammonites belonging to the Ammonitina and Ancyloceratina at the close of the Maastrichtian. **a** *Diplomoceras lambi*, Antarctica (Macellari 1986, Fig. 14.1). **b, c** *Eubaculites carinatus*, lateral and dorsal views, New Jersey (Landman et al. 2007, Figs. 320, Q). **d, e** *Baculites* sp. A, lateral and dorsal views, Tunisia (Goolaerts 2010b, pl. 9, Figs. 2, 3). **f** *Fresvillia paradoxa*, Tunisia (Goolaerts 2010b, pl. 8, Fig. 22). **g** *Sphenodiscus binckhorsti*, the Netherlands (Kennedy 1986, Fig. 9C). **h** *Glyptoxoceras* cf. *G. rugatum*, Texas (Kennedy et al. 2001, Fig. 4d). **i** *Diplomoceras cylindraceum*, Tunisia (Goolaerts 2010b, pl. 8, Fig. 11)

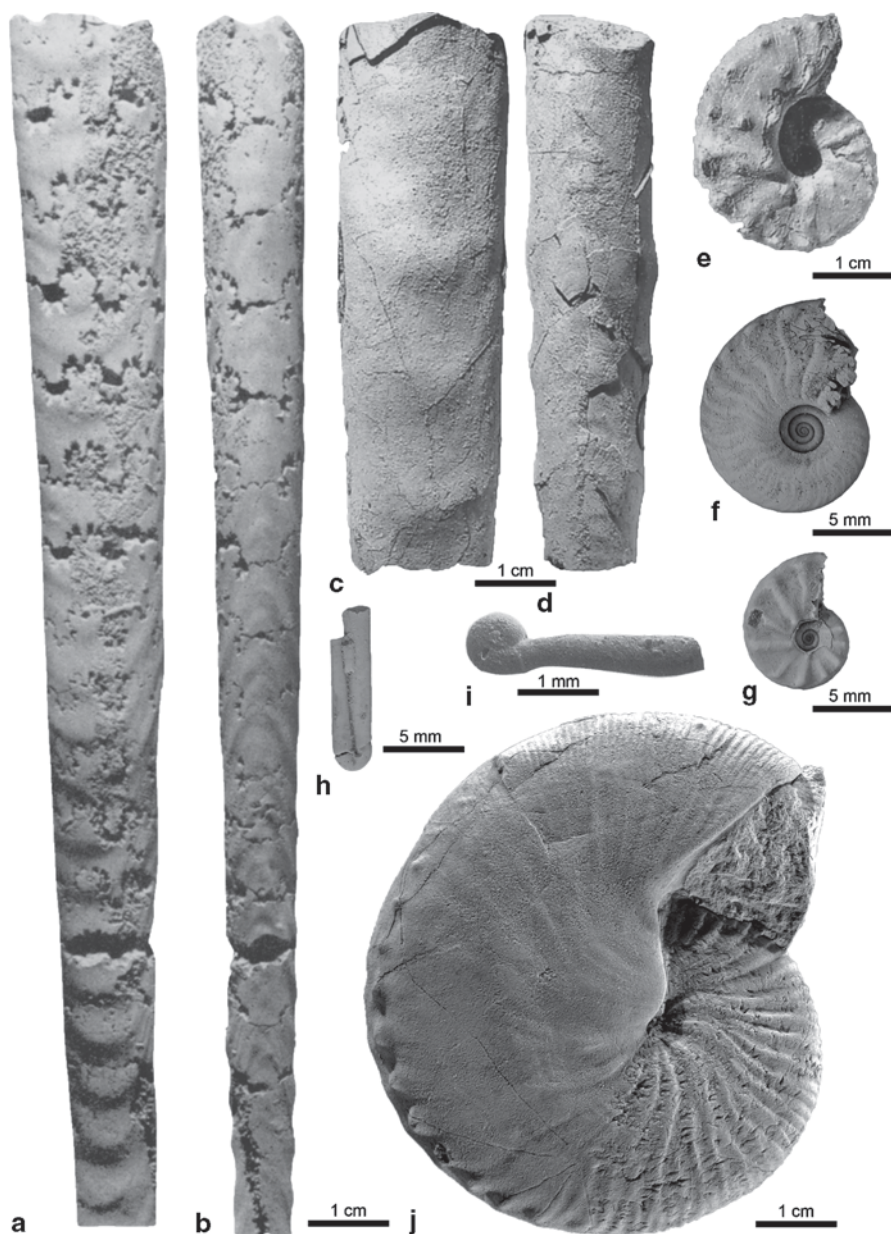


Fig. 19.17 Illustration of some of the youngest ammonites belonging to the Ancyloceratina at the close of the Maastrichtian. **a, b** *Baculites anceps*, lateral and dorsal views, the Netherlands (Kennedy 1986, Figs. 10N, O). **c, d** *Baculites* cf. *B. undatus*, lateral and dorsal views, Mississippi (Kennedy and Cobban 2000, pl. 2, Figs. 29, 30). **e** *Discoscaphites iris*, microconch, Mississippi (Kennedy and Cobban 2000, pl. 3, Fig. 14). **f** *Indoscaphites pavana*, Tunisia (Goolaerts 2010b, pl. 15, Fig. 10). **g** *Indoscaphites cunliffei*, Tunisia (Goolaerts 2010b, pl. 14, Fig. 19). **h** *Phylloptychoceras* cf. *P. siphon*, Tunisia (Goolaerts 2010b, pl. 8, Fig. 15). **i** *Baculites vertebralis*, early ontogenetic stage, Denmark (Birkelund 1993, Fig. 6A). **j** *Hoploscaphites constrictus crassus*, Poland (Machalski 2005a, Fig. 8D)

The stratigraphic distribution of these species demonstrates that ammonites are present in the uppermost part of the Maastrichtian just below or at the K/Pg boundary. For example, in northeastern Mississippi, eight species extend to approximately 1 m below an unconformity, which presumably encompasses the K/Pg boundary. The absence of ammonites above this level may be due to dissolution (Larina et al. 2012). In Denmark, eight species occur in the upper part of the Maastrichtian Høj-erup Member (Birkelund 1979, 1993; Surlyk and Nielsen 1999), and two of *them* extend into the overlying Danian Cerithium Limestone Member (Machalski and Heinberg 2005). In Turkmenistan, two species have been recovered from as high up as 5 cm below the boundary clay and a single specimen is present in the Danian part of the section (Machalski et al. 2012). In Bulgaria, Ivanov and Stoykova (1994) and Ivanov (1995) recorded five specimens comprising at least two species at 40 cm below the boundary clay, which is marked by an anomalous concentration of iridium. In northeastern Brazil, two species have been collected in the uppermost 1 m of the section below an erosional unconformity encompassing the K/Pg boundary (Stinnesbeck et al. 2012). In Antarctica, five species are present in the López de Bertodano Formation at 50 cm below the K/Pg boundary, as indicated by an enriched concentration of iridium (Zinsmeister 1998). In addition, based on a statistical analysis of the range data of these five species, they may even have persisted into the early Danian (Wang and Marshall 2004). In Sakhalin, Jagt-Yazykova (Yazikova 1994; Jagt-Yazykova 2011, 2012) reported three species from a concretionary horizon approximately 1.5 m below a 20-cm-thick green clay marking the K/Pg boundary.

How does stratigraphic distance below the K/Pg boundary translate into years before the asteroid impact? In stratigraphically complete K/Pg sections, the time can be estimated by taking into account the thickness between the impact layer (time zero) and the base of the highest biostratigraphic zone (estimated, for example, at 300 kyr before impact), assuming a constant rate of sedimentation. A better approach is to use cyclostratigraphy, which permits the construction of a high-resolution time scale that takes into account variation in the rate of sedimentation and the degree of completeness of the section. For example, in the Tunisian Trough Basin, the highest ammonites occur 1 m below the boundary (Goolaerts 2010a). Based on a cyclostratigraphic study of the alternation of limestones and marls at this site (Hennebert and Dupuis 2003), these ammonites were probably deposited at approximately 50 kyr prior to the K/Pg boundary. In the Bay of Biscay, ten species are present in the top 1.5 m of the section, and one species is present in the top 10–15 cm of the section (Ward and Kennedy 1993). Rocchia et al. (2002) also noted the occurrence of a poorly preserved specimen filled with iridium debris at 5 cm below the boundary clay. Based on the temporal interpretation of the alternation of limestone and marl beds in this area, the two highest specimens were buried at less than 500–800 years prior to the boundary (Rocchia et al. 2002). Near Maastricht, in the Netherlands and northeast Belgium, 19 species are present near or at the K/Pg boundary in the upper part of the Nekum Member and overlying Meerssen Member. According to interpretations of the short-term cyclicity (centimeter-meter scale) of the beds in this area, the highest Maastrichtian ammonites were deposited at less than 20 kyr before the K/Pg boundary (Zijlstra 1994; Schiøler et al. 1997).

The stratigraphic distribution of ammonites at or near the K/Pg boundary has been examined using statistical methods (confidence intervals) to estimate the degree to which their observed ranges underestimate their actual ranges. In Antarctica, the highest ammonite zone contains nine species, five of which extend to 50 cm below the K/Pg boundary. Using 50% range extensions, Wang and Marshall (2004) estimated that five of these species actually persisted to the K/Pg boundary. Using a more conservative approach (20% range extensions), they estimated that only one of these species persisted to the boundary. In the Bay of Biscay, ten species are present in the top 1.5 m of the section. Using a statistical method employing 50% confidence intervals, Marshall and Ward (1996) argued that at least two of these species persisted to the boundary. Indeed, in both areas, recent, intense collecting has yielded additional specimens in the uppermost Maastrichtian, consistent with the previously noted statistical predictions (Rocchia et al. 2002; Olivero 2012; Tobin et al. 2012).

The paucity of specimens in the uppermost Maastrichtian in some sections, and their absence altogether in the uppermost Maastrichtian of other sections, is probably due to taphonomic bias, collection failure, or local environmental changes rather than to their actual disappearance. For example, in the Tunisian Trough Basin, the species that occur in the highest levels are the most common species, suggesting that the likelihood of fossilization correlates with species abundance. The best explanation for the observed decrease in species richness in the uppermost Maastrichtian in this area is either collection failure or local environmental change rather than extinction (Goolaerts 2010a). In addition, as noted for the Bay of Biscay, Antarctica, and the classic area of Maastricht, ongoing research has yielded additional specimens in the uppermost part of the section, emphasizing the importance of renewed collecting efforts even in well-studied areas (Machalski et al. 2009; Jagt 2012). Thus, it is likely that the commonly cited decline in ammonite diversity at the end of the Maastrichtian (Stinnesbeck et al. 2012) is related more to local environmental changes or collection failure rather than to global extinction.

It is possible that ammonites not only persisted to the K/Pg boundary, but survived for days to tens of thousands of years later, according to various estimates. Most of this evidence comes from shallow-water settings. In New Jersey, nine ammonite species are present in a 20-cm-thick unit (the *Pinna* Layer) above a horizon with a weak iridium anomaly (Landman et al. 2012b; Figs. 19.2, 19.3). The mode of occurrence of the fossils in this layer indicates an autochthonous accumulation with little or no time-averaging. Fewer ammonites are present above this layer in the so-called Burrowed Unit and consist of broken specimens of *Eubaculites carinatus* associated with isolated jaws (aptychi) of this species. Because such jaws are absent in the underlying *Pinna* Layer, it suggests that these fossils were not reworked from below but were fossilized during the deposition of the Burrowed Unit. If the horizon with iridium marks the K/Pg boundary, it implies that ammonites persisted and perhaps even initially thrived in the early Danian (as shown by the ammonites in the *Pinna* Layer), followed by a brief appearance of a more impoverished fauna (as shown by the ammonites in the Burrowed Unit). Even if the iridium anomaly was displaced downward from the top of the *Pinna* Layer, as previously noted, it still implies that the ammonites in the Burrowed Unit would have survived. In the

Maastrichtian type region, Jagt et al. (2003) reported several dozen specimens of *Baculites* and *Hoploscaphites* in Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon, which is generally interpreted as marking the K/Pg boundary, rather than the overlying Vroenhoven Horizon. The fact that many of the baculitids are preserved with their apertures intact suggests that they may have survived into the early Danian (Planktic Foraminiferal Zone P0) (Fig. 19.8). In Denmark, Machalski and Heinberg (2005) reported *B. vertebralis* and *H. constrictus johnjagti* in the lower Danian Cerithium Limestone Member (Fig. 19.6). These specimens have generally been interpreted as reworked material. However, the mode of occurrence of these specimens suggests that they were fossilized at the same time as the deposition of the Cerithium Limestone Member. In addition, the most common fossils in the underlying Maastrichtian chalk are virtually absent in the Cerithium Limestone, which is inconsistent with a hypothesis of reworking. Thus, both these lines of evidence suggest that the ammonites in the Cerithium Limestone Member represent early Danian survivors (Machalski and Heinberg 2005).

19.4.2 Depth Distribution of Ammonites at the K/Pg Boundary

At the end of the Maastrichtian, shallower water settings (< 100 m) are represented by deposits in northern and central Europe and North America. In northern and central Europe, the most abundant ammonites are *Baculites* followed by *Hoploscaphites* (Figs. 19.16, 19.17). In addition, the fauna contains a few species of desmoceratoids, including *Menuites terminus*, and a few species of diplomoceratids including *Glyptoxoceras rugatum* and *Diplomoceras cylindraceum*. In North America, the most abundant ammonites are also baculitids, represented by *Eubaculites* and *Baculites*, followed by scaphitids, represented by *Discoscaphites*. Sphenodiscids are relatively common but desmoceratoids and diplomoceratids (e.g., *Glyptoxoceras*) are rare, and phylloceratids and lytoceratids are absent.

Deeper-water settings (> 100 m) at the end of the Maastrichtian are represented by deposits in the Bay of Biscay, the Tunisian Trough, Antarctica, and Sakhalin. In the Bay of Biscay, the fauna is characterized by several species of phylloceratids and lytoceratids, many of which are endemic to the area (Fig. 19.14). In addition, the fauna contains a high diversity of desmoceratoids. In contrast, only one species of *Diplomoceras* is present and *Eubaculites* and *Hoploscaphites* are absent in the upper part of the section. Several of the same species of phylloceratids and lytoceratids (*Hypophylloceras* (*Neophylloceras*) *ramosum* and *Anagaudryceras politissimum*) are present in Bulgaria. The fauna in the Bay of Biscay also has several species in common with the fauna in Tunisia, including phylloceratids and lytoceratids (e.g., *Phyllopachyceras forbesianum* and *Pseudophyllites indra*) and desmoceratoids (e.g., *B. (Brahmaites) brahma*). The most distinctive elements of the Tunisian fauna, however, are species of *Indoscaphites*, suggesting a strong connection with southern India. In Antarctica, phylloceratids are absent but lytoceratids are present, including *A. seymouriense* and *Pseudophyllites loryi*, both of which are endemic to the area. The fauna is also characterized by five endemic

species of desmoceratoids including *Maorites densecostatus*, *Kitchinites laurae*, and *Pachydiscus (P.) riccardii*. Surprisingly, few species are shared with South America, especially with the slightly older Quiriquina Formation in central Chile (Salazar et al. 2010), which contains two species of phylloceratids but no lytoceratids. In Sakhalin, the fauna is dominated by phylloceratids and lytoceratids, with a few genera and species in common with Tunisia, Bulgaria, and the Bay of Biscay. It is also characterized by two species of pachydiscids that are endemic to the area.

19.4.3 Ecology of Ammonites at the K/Pg Boundary

The phylloceratids and lytoceratids, although never abundant in terms of individuals, are well represented in deeper-water settings (>100 m deep) at the end of the Maastrichtian (Fig. 19.14). A total of seven genera are each present in Tunisia and the Bay of Biscay, and three each in Bulgaria and Antarctica. They are characterized by relatively compressed shells without much ornament, and comprise the traditional Leiostroaca, and are restricted to the distal shelf and upper continental slope based on paleoenvironmental data. This habitat is consistent with depth estimates based on studies of the strength of the siphuncular tube and septa (Hewitt 1996). The buccal apparatus of these forms is different from other ammonites at the end of the Cretaceous in featuring a calcareous deposit at the apical end of the lower jaw, possibly permitting them to feed on hard material, like crustacean carapaces (Tanabe and Landman 2002; Tanabe et al. 2013). Depending on the genus, Westermann (1996) interpreted the mode of life of these forms as demersal swimmers, planktic vertical migrants, or nekctic swimmers. However, an analysis of the isotopic composition of the outer shell of several species of Late Cretaceous *Hypophylloceras*, *Phyllopachyceras*, and *Gaudryceras* from Japan suggests that these forms lived close to the sea floor (Moriya et al. 2003).

The desmoceratoids at the end of the Maastrichtian also favored deeper-water settings, with five genera each in Tunisia and the Bay of Biscay, and four in Antarctica (Fig. 19.15). With their relatively thick septa, narrow but thick-walled siphuncular tubes, and long septal necks, desmoceratoids are well adapted to deeper-water settings. They possess moderately compressed, involute shells with a rounded venter and relatively smooth surface. The hydrodynamic properties of desmoceratoids are, thus, similar to those of other Mesozoic ammonites with low shell-thickness ratios (Seki et al. 2000). These forms are considered to have been demersal swimmers, which lived on the distal shelf and upper continental slope (Westermann 1996). This interpretation is consistent with isotopic analyses of the outer shell, which suggest a mode of life near the bottom (Moriya et al. 2003). It is notable that desmoceratoids appear to have modified their aptychus-type jaw, reducing the aptychus to only a thin covering (Tanabe and Landman 2002; Tanabe et al. 2013). This may have permitted them to broaden their diet to include carrion from the sea floor.

Scaphitids at the close of the Cretaceous occur in shallow-water settings such as the Gulf and Atlantic Coastal Plains of North America and northern and central Europe, although they occasionally occur in deeper-water settings such as

Turkmenistan (Fig. 19.17). In terms of numbers of individuals, they are probably the most abundant ammonites after baculitids. The mode of life and habitat of Late Cretaceous scaphitids has been investigated by Landman et al. (2012a) based on analyses of the functional morphology of the shell and buccal apparatus, light stable isotopes, facies distributions, faunal associations, and the mechanical strength of the septa, shell, and siphuncle. Based on this evidence, scaphitids were probably sluggish swimmers that preferred well-oxygenated water just above the bottom. They may have exploited a low-energy lifestyle, remaining at a single site for an extended period of time. As members of the Aptychophora Engeser and Keupp 2002, scaphitids possessed an aptychus-type lower jaw and may have preyed upon small organisms in the water column, such as decapod crustaceans, copepods, and newly hatched ammonites.

Sphenodiscids were also relatively common in the same facies as scaphitids in North America and northern and central Europe at the end of the Maastrichtian (Fig. 19.16). Based on their streamlined, oxyconic shells and distribution in nearshore facies, sphenodiscids have been interpreted as inhabitants of shallow-water environments ranging from around wave base to slightly below (Ifrim and Stinnesbeck 2010). They may have been capable of brief spurts of relatively rapid swimming permitting ambush predation (Westermann 1996). However, they are equipped with aptychus-type lower jaws without sharp cutting edges, precluding the likelihood of a diet of hard-shelled prey.

The diplomoceratids (*Glyptoxoceras*, *Diplomoceras*, and *Phylloptychoceras*) and baculitids are nearly cosmopolitan at the end of the Cretaceous, suggesting that they were facies-independent. The diplomoceratids occur at eight regions ranging from deeper-water (Bay of Biscay) to shallower-water settings (the Netherlands and northeast Belgium) (Fig. 19.16). The baculitids (*Baculites*, *Eubaculites*, and *Fresvillia*) are even more widespread than the diplomoceratids and occur in ten regions (Figs. 19.16, 19.17). Indeed, baculitids are probably the most abundant ammonites at the end of the Cretaceous in terms of number of individuals. The wide distribution of these forms with respect to environmental settings suggests that they may have lived high in the water column, well above the bottom. This is consistent with the fact that they are occasionally preserved even in areas with dysoxic bottom water that excluded benthic fauna. Baculitids have generally been interpreted as sluggish swimmers (Klinger 1981) hovering in the water column at an inclined angle to the vertical (Fig. 19.3), but this requires a counterbalance at the adapical end. Based on studies of the morphology of the radula and the presence of prey remains in the buccal apparatus, it is possible that baculitids preyed on small micro-organisms in the water column, such as tiny crustaceans (Kruta et al. 2011). This interpretation may also have applied to the diplomoceratids with their upturned aperture at maturity, which is also consistent with a microphagous mode of life.

19.4.4 Causes of Ammonite Extinction

Following the Alvarez hypothesis, it is now generally accepted that the disappearance of ammonites in the latest Maastrichtian/earliest Danian was due to the

asteroid impact. However, the exact killing mechanism is still unknown. The most plausible explanation is perhaps a transient episode of surface water acidification on the heels of the asteroid impact (Alegret et al. 2012; Arkhipkin and Laptikhovsky 2012; Hönisch et al. 2012). According to these arguments, the gypsum-rich deposits at the impact site would have vaporized, producing sulfuric acid. In addition, the heating of the atmosphere would have generated nitric acid due to the oxidation of N_2 , resulting in acid rain. The alternative hypothesis of a global collapse in primary productivity (called the Strangelove Ocean) or export productivity (called the Living Ocean) lacks support because the benthic foraminifera in the deep sea did not suffer a severe extinction at the time, unlike the planktic foraminifera (Alegret et al. 2012). Darkness due to the fine dust in the atmosphere following the collision may also have been a contributing factor, blocking solar radiation and leading to a short-lived cold spell (Vellekoop et al. 2014).

Surface ocean acidification would have had disastrous consequences for planktic calcifiers, including calcareous nannofossils, planktic foraminifera, and ammonites. All the ammonites at the end of the Cretaceous, irrespective of their mode of life at maturity, probably followed a planktic mode of life immediately after hatching (Landman et al. 1996; Westermann 1996; Arkhipkin and Laptikhovsky 2012). This hypothesis is based on two functional arguments: the small size of the embryonic shell (ammonitella), which ranges from 0.5 to 1.5 mm in diameter, and its near-spherical shape, both of which are presumably adaptations to life in the plankton (Fig. 19.18). The newly hatched ammonites may have been passive vertical migrators, drifting with surface currents. This interpretation is consistent with a number of observations on the mode of occurrence of ammonites preserved at this stage of development. For example, the Late Cretaceous Sharon Springs Member of the Pierre Shale in Wyoming contains small specimens of newly hatched ammonites. These sediments are interpreted to have been deposited on an anaerobic bottom with oxygenated water above, implying that the newly hatched ammonites were planktic or at least nektic (Landman 1988). This mode of life may have been very 'effective' during background times, but it may have proved to be an Achilles Heel for ammonites during stressful times (Arkhipkin and Laptikhovsky 2012).

Variation in the degree of surface ocean acidification can help explain the fact that all of the evidence for the short-term survival of ammonites in the early Danian is from relatively shallow-water settings (the Atlantic Coastal Plain, the Netherlands and northeast Belgium, and Denmark). The ammonites in these areas may have survived for days to tens of thousands of years after the impact. It is possible that these coastal areas may have been buffered from transient surface water acidification due to the burning of plants on the land, and the resultant increase in riverine run-off. As a consequence, some planktic organisms that secreted calcium carbonate, including ammonites, may have persisted for a brief interval of time in these regions. Ironically, this kill mechanism apparently favored scaphitids and baculitids, which are characterized by short-term species longevities, rather than phylloceratids and lytoceratids, which are characterized by long-term species longevities (for a discussion of the evolutionary mode and tempo of Cretaceous ammonites, see Ward and Signor 1983). Thus, this kill mechanism was independent of the evolutionary success of particular ammonites, at least as measured by their species longevity.

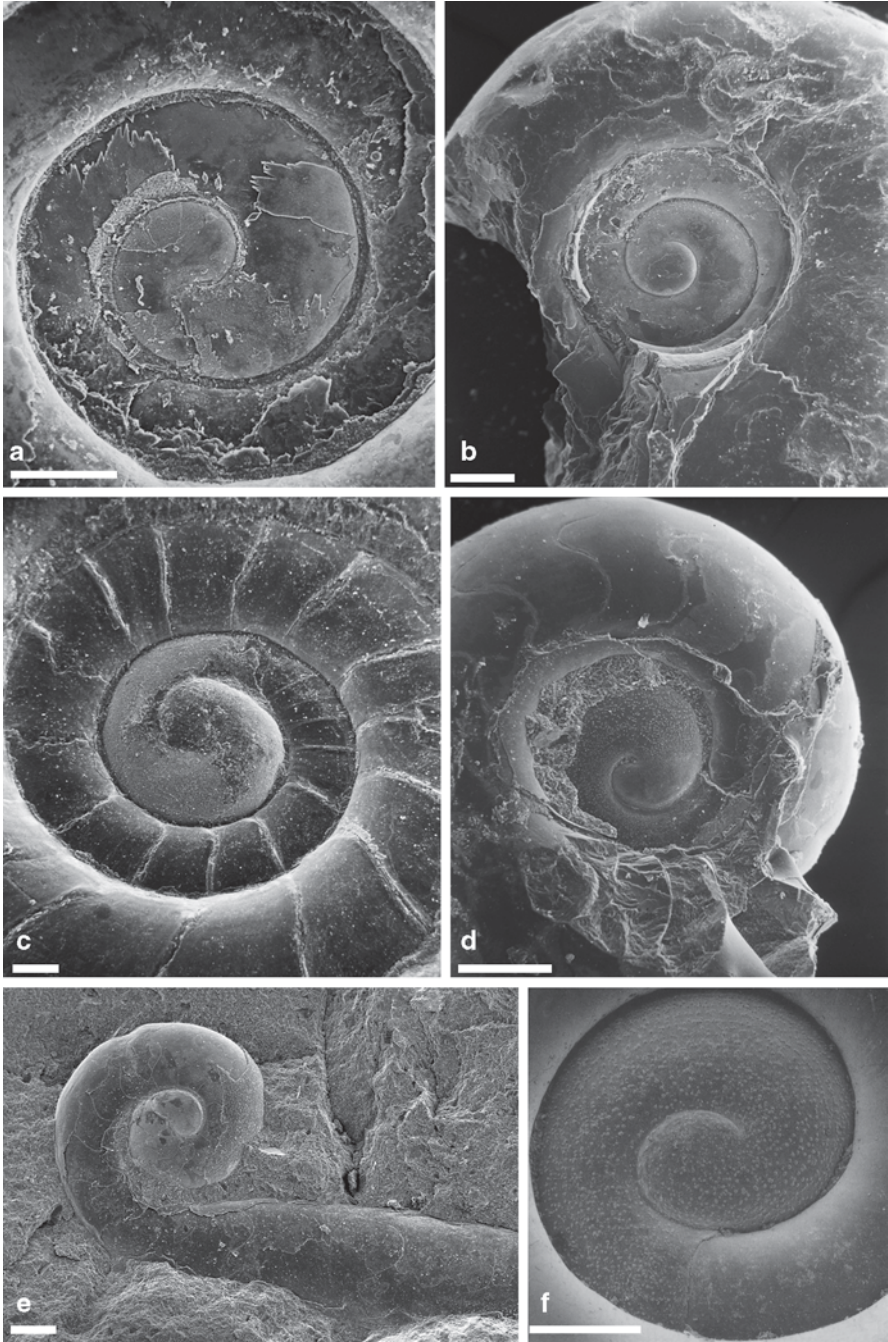


Fig. 19.18 Illustration of the embryonic shells of six species of Late Cretaceous ammonites (a–e, with kind permission of K. Tanabe, University of Tokyo). The embryonic shell consists of the protoconch and approximately one whorl ending in the primary constriction, and is ornamented

The geographic distribution of ammonite genera may also have played a role in their pattern of extinction. Landman et al. (2014) compiled a database of all ammonite genera in the last 0.5 myr of the Maastrichtian. They also incorporated data on ammonite genera that appear to have briefly survived into the Paleocene (Jagt et al. 2003; Jagt 2012; Machalski and Heinberg 2005; Machalski et al. 2009; Landman et al. 2012b). Using two metrics to evaluate the geographic range of each genus (first, a convex hull encompassing all of the occurrences of each genus and, second, the maximum distance between occurrences for each genus), they documented that most ammonite genera at the end of the Maastrichtian were restricted in their geographic distribution, possibly making them vulnerable to extinction. However, the geographic distribution of those genera that may have briefly survived into the Paleocene is significantly greater than that of ‘non-surviving’ genera, implying that more broadly distributed genera were more resistant to extinction. Similar geographic patterns of survivorship have been observed in other molluscs at the K/Pg boundary. For example, Jablonski (2008) noted that in terms of marine bivalve genera, survivors were significantly more broadly distributed than victims. However, even the most widely distributed ammonites eventually succumbed to extinction. Evidently, a broad geographic distribution may have initially protected some ammonites against extinction, but it did not guarantee their survival.

19.5 Conclusions

Ammonites are abundant and diverse in the last 0.5 million years of the Maastrichtian. They are distributed across all four Cretaceous suborders, the Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, comprising six superfamilies, 31 (sub)genera, and 57 species. The distribution of ammonites is dependent on the environmental setting. In shallow-water environments (< 100 m deep), almost all of the ammonites are ancyloceratines, including scaphitids, baculitids, and diplomoceratids. In fact, baculitids and diplomoceratids are the most widespread ammonites at the end of the Cretaceous. In deeper-water settings (> 100 m deep), almost all taxa comprise phylloceratids, lytoceratids, and ammonitids (especially desmoceratoids). The commonly cited decline in ammonite diversity at the end of the Maastrichtian is related more to local environmental changes or collection failure rather than to global extinction. Indeed, ongoing research has yielded additional specimens even in well-studied areas. In addition, recent data from shallow water settings (Atlantic Coastal Plain, the Netherlands and northeast Belgium, and Denmark) suggest

with a microtuberculate ornamentation. **a** *Hypophylloceras subramosum* (Phylloceratina), middle Campanian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2D). **b** *Phyllopachyceras ezoense* (Phylloceratina), middle Campanian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2C). **c** *Gaudryceras denseplicatum* (Lytoceratina), Coniacian, Hokkaido, Japan (refigured from Tanabe 1989, Fig. 2A, B). **d** *Menuites* sp. (Ammonitina), middle Campanian, Hokkaido, Japan (refigured as *Anapachydiscus* sp. in Tanabe 1989, Fig. 1A, B). **e** *Baculites compressus* (Ancyloceratina), late Campanian, South Dakota, USA. **f** *Hoploscaphites* sp. (Ancyloceratina), upper Maastrichtian, South Dakota (Refigured from Landman and Waage 1993, Fig. 13D). Scale bar=200 μm

that not only did ammonites persist to the boundary, but some species may even have survived for as much as tens of thousands of years afterward. The most likely explanation for ammonite extinction is a brief episode of surface water acidification immediately following the Chixculub impact, which caused the decimation of the calcareous plankton including, possibly, the planktic post-hatching stages of ammonites. However, the geographic distribution of ammonites may also have played a role in the events at the end of the Cretaceous, with more broadly distributed genera more resistant to extinction.

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Appendix of Localities

- 1: Manasquan River Basin, Monmouth County, New Jersey, U.S.A., 40°12'30"N, 74°17'30"W
- 2: Northeastern Monmouth County, New Jersey, U.S.A., 40°17'30"N, 74°7'14"W
- 3: Round Bay, Anne Arundel County, Maryland, U.S.A., 39°2'13"N, 76°33'28"W
- 4: Stoddard and Scott counties, Missouri, U.S.A., 37°00'17"N, 89°51'02"W
- 5: Tippah County, Mississippi, U.S.A., 34°44'55"N, 88°54'47"W
- 6: Chickasaw County, Mississippi, U.S.A., 33°58'04"N, 89°00'05"W
- 7: Brazos River, Falls County, Texas, U.S.A., 31°8'11"N, 96°49'40"W
- 8: La Popa Basin, Northeastern Mexico, 26°12'44"N, 101°4'25"W
- 9: Stevns Klint, Denmark, 55°16'45"N, 12°26'47"E
- 10: Kjølbj Gård, Denmark, 57°3'15"N, 8°44'55"E
- 11: "Dania" Quarry, northern Denmark, 56°39'42"N, 10°1'56"E
- 12: Maastrichtian Type Area, The Netherlands and Belgium, 50°49'18.41"N, 5°41'39.54"E
- 13: Nasilów, Poland, 51°20'39"N, 21°57'35"E
- 14: Mełgiew, Poland, 51°13'30"N, 22°47'8"E
- 15: Lechówka, Poland, 51°10'17"N, 23°14'43"E
- 16: Kyzylsai, Kazakhstan, 44°20'1"N, 52°26'10"E
- 17: Sumbar River, Turkmenistan, 38°27'18"N, 56°12'41"E
- 18: Zumaya, Bay of Biscay Area, 43°17'54"N, 2°16'16"W
- 19: Hendaye, Bay of Biscay Area, 43°23'1"N, 1°49'26"W
- 20: Bidart, Bay of Biscay Area, 43°26'25"N, 1°35'41"W
- 21: Bjala (=Byala), Bulgaria, 42°52'44"N, 27°53'57"E
- 22: Kalaat Senan, Tunisia, 35°47'15"N, 8°27'21"E
- 23: El Kef, Tunisia, 36°9'15"N, 8°38'55"E
- 24: Garn Halfaya, Tunisia, 36°0'40"N, 8°33'23"E

- 25: Dababiya Quarry Corehole, Egypt, 25°30'10"N, 32°31'27"E
 26: Naiba River Valley, Sakhalin, Far East Russia, 47°28'34"N, 142°24'10"E
 27: Poty Quarry, Brazil, 7°53'95"S, 34°51'14"W
 28: Lomas Colorados, Bajada de Jagüel, Neuquen Basin, Argentina, 37°59'24"S, 68°47'38"W
 29: Seymour Island, Antarctica, 64°16'50"S, 56°43'23"W

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