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The last Cretaceous ammonites in Latin America

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Sections yielding late Maastrichtian ammonite assemblages are rare in Latin America and precise biostratigraphic correlation with European type sections remains difficult. In all, the extinction pattern of ammonites appears to differ between sites in southern high latitudes and those in the tropics to subtropics. In austral sections of Chile, and possibly also in southern Argentina, diverse assemblages range throughout most of the substage and then show a gradual decline prior to the Cretaceous–Paleogene (K–Pg) boundary. Further north, in northeast Brazil, only two genera (*Diplomoceras*, *Pachydiscus*) range into the uppermost Maastrichtian, but disappear within the last 0.3 Ma of the Cretaceous. In tropical sections of Columbia and Mexico, the decline of ammonites started earlier and *Sphenodiscus* is the last ammonite known to occur in the late Maastrichtian. In all sections revised here the disappearance of ammonites was completed prior to the end of the Maastrichtian and was thus independent of the asteroid impact at, or near, the end of the Cretaceous.

Key words: Ammonoidea, Cretaceous–Paleogene (K–Pg) boundary, Maastrichtian, Chile, Argentina, South America, Mexico.

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Introduction

Ammonites are characteristic and abundant components of Mesozoic invertebrate assemblages that disappeared at or near the end of the Cretaceous, during the Cretaceous–Paleogene (K–Pg) mass extinction. It is widely debated whether this extinction was catastrophic, precisely at the K–Pg boundary, or gradual, extending over several hundred thousands of years of the latest Maastrichtian, or whether some ammonites even extended into the earliest Paleogene (Wiedmann 1988; Kennedy 1989, 1993; Birkelund 1993; Surlyk and Nielsen 1999; Jagt et al. 2003; Machalski 2005a, b; Machalski and Heinberg 2005; Machalski et al. 2009; Jagt-Yazykova and Jagt 2006; Landman et al. 2007, 2010, 2012; Machalski et al. 2011).

The most diverse assemblages of late to latest Maastrichtian age are known from northern high-latitude sites in Denmark (Birkelund 1993), the Netherlands (Jagt 2002), Poland (Machalski 2005a, b), northern Greenland (Birkelund 1965), and New Jersey (Landman et al. 2004a, b, 2007, 2010, 2012). The Biscay area (southwest France, northern Spain) is characterised by intermediate-latitude to boreal environmental conditions. In this region, ammonites also reach up almost to the K–Pg boundary (Kennedy 1993; Ward and Kennedy 1993; Rocchia et al. 1999).

Diverse ammonite assemblages of latest Maastrichtian age are also known from southern high-latitude localities in South India (Kennedy and Henderson 1992a, b), Australia (Henderson and McNamara 1985; Henderson et al. 1992), New Zealand (Henderson 1970), Angola (Howarth 1965), South Africa (Kennedy and Klinger 1975, 1976, 1977, 1979, 1985, 2006; Klinger and Kennedy 1993, 1997, 2001, 2003, 2005), and Antarctica (Howarth 1966; Macellari 1986; Olivero and Zinsmeister 1989; Zinsmeister et al. 1989; Crame et al. 1991; Zinsmeister and Feldmann 1996; Olivero and Medina 2000).

Tropical or subtropical Tethyan localities with latest Maastrichtian ammonites, on the other hand, are scarce, the only exception known to us being El Kef in Tunisia (Goolaerts et al. 2004; Goolaerts 2010), the GSSP for the base of the Paleogene. At this site, an abundant and relatively diverse ammonite assemblage has been collected from a 5 m thick interval corresponding to a maximum flooding surface between 7 and 2 m below the K–Pg boundary iridium anomaly (Goolaerts et al. 2004; Goolaerts 2010). The top of this assemblage was dated as the middle of planktonic foraminiferal zone CF1 by (Li et al. 2000) and is thus 0.2 Ma older than the K–Pg boundary.

Latin American sections with late Maastrichtian ammonite assemblages are rare. Here we briefly revise the state of knowledge regarding these localities. Certainly, the Quiriquina Formation in central Chile contains the most diverse

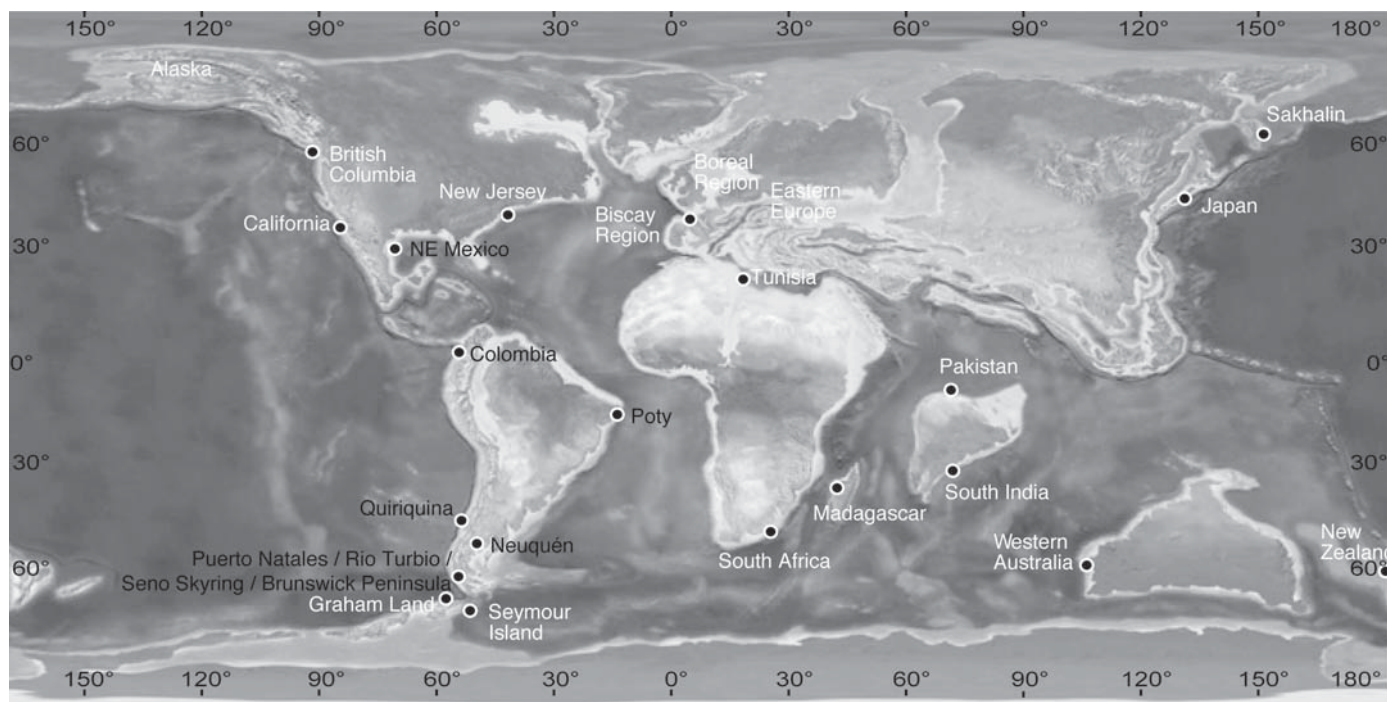


Fig. 1. Palaeogeographical map of the world during the Maastrichtian (after Blakey 2002), illustrating ammonite-bearing localities, with the Latin American sections mentioned in the text shown in black.

assemblage known to date (Stinnesbeck 1986, Salazar et al. 2010), but other southern high-latitude localities were described from southern Chile (Lahsen and Charrier 1972; Macellari 1988; WS and CS, personal observations) and the Argentinian Río Turbio (Hünicken 1965) and Neuquén areas (Keller et al. 2007). The Poty quarry in Pernambuco, Brazil (Stinnesbeck and Keller 1996) and upper Maastrichtian outcrops in northeast Mexico represent localities of intermediate to low latitudes.

Institutional abbreviations.—CPUC, Colección Paleontológica de la Universidad de Concepción, Chile; IMG, Instituto de Geología, Universidad Nacional Autónoma de México; IGH, Institute of Earth Sciences, University of Heidelberg, Germany.

Other abbreviations.—CF, foraminiferal zone; FO, first occurrence; GSSP, Global Stratotype Section and Point; LO, last occurrence; P1, Paleogene foraminiferal zone 1; UZA, cycle.

Geological setting

Subdivisions of the Maastrichtian

The Campanian–Maastrichtian boundary was dated 70.6 ± 0.6 Ma at Tercis, GSSP for that boundary in southwest France, based on the arithmetic mean of twelve biohorizons corresponding to the first or last occurrences (FO and LO, respectively) of stratigraphically important macro- and microfossil

taxa (Odin and Lamaurelle 2001; Gradstein et al. 2004). The FO of *Pachydiscus* (*Pachydiscus*) *neubergicus* is one of three ammonite markers used in this definition. The boundary between the early and late Maastrichtian, however, has not been defined formally yet (Ogg et al. 2004); its position has experienced many changes in definition. Suggestions included the placement of the boundary at the FO of the planktic foraminifer *Abathomphalus mayaroensis* (see Nederbragt 1991), but it is now known that this is diachronous, the species occurring earlier at high latitudes. Other authors have proposed a lower–upper Maastrichtian boundary based on the FO of another planktic foraminifer, *Rosita contusa*. The FO of this species also defines the base of biozone CF 6 of Li and Keller (1998a, b) and coincides with the FO of the Western Interior Seaway ammonite *Hoploscaphites birkelundae*, which was selected as boundary marker for this region (Walaszczyk et al. 2001). Numerically, the FO of *H. birkelundae* was placed at 69.5 Ma within the upper part of C31R (Gradstein et al. 1995), which corresponds to the FO of *Racemiguembelina fructifera* or the base of biozone CF 6. A third alternative is to equate the boundary with the FO of the planktic foraminifer *Racemiguembelina fructifera* at the base of CF 4 (Li et al. 1999), at 68.3 Ma. Here we follow the latter view.

Late Maastrichtian ammonites in Latin American sections

Patagonia.—Outcrops of uppermost Cretaceous to lower Paleogene sediments exist in the Austral basin of southern Patagonia on both sides of the border between Chile and Ar-

gentina, near Puerto Natales and Río Turbio, along the Seno Skyring Fjord and in Brunswick Peninsula (Malumian et al. 1983; Riccardi 1988; see Fig. 1). The Cerro Cazador Formation in this region, rich in invertebrates, has previously been studied by, among others, Wilckens (1905), Paulcke (1905), Cecioni (1956a), Macellari (1988), and Griffin and Hünicken (1994). Based on the ammonite assemblages, most authors have suggested the Cerro Cazador Formation to be of Campanian–Maastrichtian age (e.g., Riccardi 1988), but Macellari (1985, 1988) indicated that the uppermost fossil-bearing unit (above unit h) may reach the Paleocene, or even Eocene. The gastropod assemblage agrees with such an interpretation (Griffin and Hünicken 1994), showing close affinities with the Roca and Salamanca formations in northern and central Patagonia, as well as with the Wangaloa Formation in New Zealand. Among the ammonites, *Baculites rioturbioensis*, *Pseudophyllites peregrines*, *Diplomoceras austral*, *Maorites densicostatus*, *M. suturalis*, and *Grossouvrites gemmatus* (see Hünicken 1965) are closely related to or conspecific with taxa from central Chile.

In the Magallanes province of southern Chile, additional K–Pg boundary sections exist in the Seno Skyring region. The presence of both macro- and microfossils permits calibration of ammonite ages with foraminifer-based biozones. In this area, the Fuentes Formation has yielded *Pseudophyllites peregrines*, *Gaudryceras varagurense patagonicum*, *Polyptychoceras* sp., *Maorites densicostatus*, *Gunnarites* spp., and other ammonites (Charrier and Lahsen 1968a, b). Foraminifera such as *Abathomphalus mayaroensis* and *Bolivinoidea draco dorreeni* confirm a late Maastrichtian age (Lahsen and Charrier 1972). The Rocallosa Formation overlies the Fuentes Formation and also contains ammonites and foraminifera of a late Maastrichtian age (Charrier and Lahsen 1968a, b; Hünicken et al. 1975, 1980; Riccardi 1988). However, the position of the K–Pg boundary is a matter of dispute in this sedimentary sequence which reaches approximately 1000 m in thickness. On foraminiferal evidence, Natland et al. (1974) placed it within the upper Rocallosa Formation, while Charrier and Lahsen (1968a, b) and Lahsen and Charrier (1972) suggested that it was placed within the overlying Chorillo Chico or Tres Morros formations (see Lahsen and Charrier 1972: text-fig 3). This latter unit is rich in bivalves and gastropods but ammonites are characteristically absent.

The youngest Late Cretaceous assemblage from the Magallanes Basin, described by Macellari (1988), is dominated by *Maorites densicostatus*, with *Grossouvrites gemmatus* forming another characteristic element, albeit less common. This faunal assemblage is well established for the Cerro Cazador Formation in Argentina (Hünicken 1955, 1965), the Río Blanco Formation in Brunswick Peninsula, and the Río García Formation to the west of Lago Lynch, Tierra del Fuego, but confusion exists regarding the highest ammonite level in the Seno Skyring area. There *Gunnarites elegans* and *G. bhavaniformis* (Lahsen and Charrier 1972) are known from the upper Fuentes Formation, but *Maorites* is characteristically absent, thus differing from similar stratigraphic levels at

Río Turbio and in Seymour Island (Antarctic Peninsula). *Maorites* has never been identified in the Seno Skyring area, with the possible exception of Tres Morros in Brunswick Peninsula. The absence of the *Maorites* assemblage in the Seno Skyring area may thus be the result of erosion or non-deposition. This interpretation agrees with observations by Cecioni (1956a, b), who postulated that the boundary between the “lower Tertiary” Chorillo Chico and the Maastrichtian Rocallosa formations was an unconformity.

Neuquén Basin, Argentina.—Upper Cretaceous to lower Paleogene sediments are well exposed in the Neuquén Basin in central-south Argentina. These strata, assigned to the Jagüel Formation, consist of olive-green, friable calcareous claystone with relatively common exogyrine oysters, occasional pectinids and other bivalves (e.g., *Malletia*, *Nucula*, *Panopea*), gastropods and very rare baculitid ammonites.

A sequence (8 m thick) of the upper Jagüel Formation was sampled at Lomas Coloradas (LC), located 10 km northwest of Bajada de Jagüel and approximately 1 km east of provincial road No. 8. The section consists of 3.5 m of olive-green claystone and overlying 4.5 m of oyster-rich marls. A coquina layer at 1.5 m of the section contains abundant oysters and pectinid bivalves, as well as a single specimen of *Eubaculites* sp. (ex gr. *E. simplex*). This ammonite is of definite Maastrichtian age, and this can be constrained further as late Maastrichtian, based on correlation with the well-dated Bajada de Jagüel section. At Bajada de Jagüel, Keller et al. (2007) documented planktic foraminifera of zone CF 2 from the baculitid-bearing shale unit. The K–Pg boundary itself is not present, because a hiatus encompasses biozones CF 1 and P1a–b. However, ammonites are already extremely rare in biozone CF 2, which precedes the K–Pg transition by about 0.4 Ma (Keller et al. 2007).

Quiriquina Formation, Chile.—This unit, in central Chile, has long been known for its abundance of well-preserved and highly diverse ammonites. Monographic revisions of the assemblage by Stinnesbeck (1986) and Salazar et al. (2010) have documented 30 species in 17 genera. They are late Maastrichtian in age, based on the occurrence of *Hypophylloceras* (*Neophylloceras*) *surya*, *Zelandites varuna*, *Pachydiscus* (*P.*) *jacquoti*, *Diplomoceras cylindraceum*, *Baculites anceps*, *Eubaculites carinatus*, *Hoploscaphites constrictus*, *Menuites fresvillensis*, and other index taxa (Stinnesbeck 1996; Salazar et al. 2010). This fauna is exceptionally rich in phylloceratids and lycoceratids, which are rare in other Maastrichtian sections worldwide.

At Las Tablas, the type locality of the Quiriquina Formation in Quiriquina Island, ammonites are abundant in most of the 65 m thick section. *Eubaculites carinatus* is the commonest fossil in a unit of green siltstone with calcareous sandstone concretions. Co-occurring are *Gaudryceras kayei*, *Kitchinites darwini*, *Maorites densicostatus*, *Phyllopachyceras* (*Neophylloceras*) *ramosum*, *Pseudophyllites indra*, and *Zelandites varuna*, among others. In the uppermost 10 m of the Quiriquina Formation, however, *Eubaculites carinatus* is

characteristically absent in the calcareous sandstone concretions at Las Tablas and other sections in the area, even though other ammonites are still present. These last ammonites of the Quiriquina Formation are *Diplomoceras cylindraceum*, *Hypophylloceras* (*N.*) *ramosum*, *H.* (*N.*) *surya*, and *Hoploscaphites constrictus* (at Cocholgüe) (Stinnesbeck 1986, 1996; Salazar et al. 2010).

In the uppermost 5 m of the Quiriquina Formation trace fossils (*Teichichnus*, *Zoophycos*) are particularly abundant, but macrofossils are rare. No ammonites have been recovered by us or any other authors but detritus-feeding bivalves (e.g., *N.* [*Neilo*] *pencana*, *N.* [*N.*] *quiriquinae*, *Yoldia levitesta*, *Nuculana cocholguei*, *Tellina largillierti*) occur and indicate quiet-water conditions and an abundance of organic matter. Small pyrite concretions are also indicative of stagnant water and reducing environments. The marine sequence of the Quiriquina Formation is truncated by a massive unit of cross-bedded yellow sandstone with conglomeratic lenses (Curanilahue Formation of Paleogene age), reflecting brackish to fluviatile conditions. Charcoaled wood and an isolated shark tooth (*Isurus* sp., from Tomé) are the only megafossils recovered to date.

The decline of ammonites in the Quiriquina Formation of central Chile thus appears to be gradual in the uppermost 10 metres of the section and resulted in a total extinction within the uppermost Maastrichtian, prior to the K–Pg boundary. No ammonites were recovered from the uppermost 5 metres of the section.

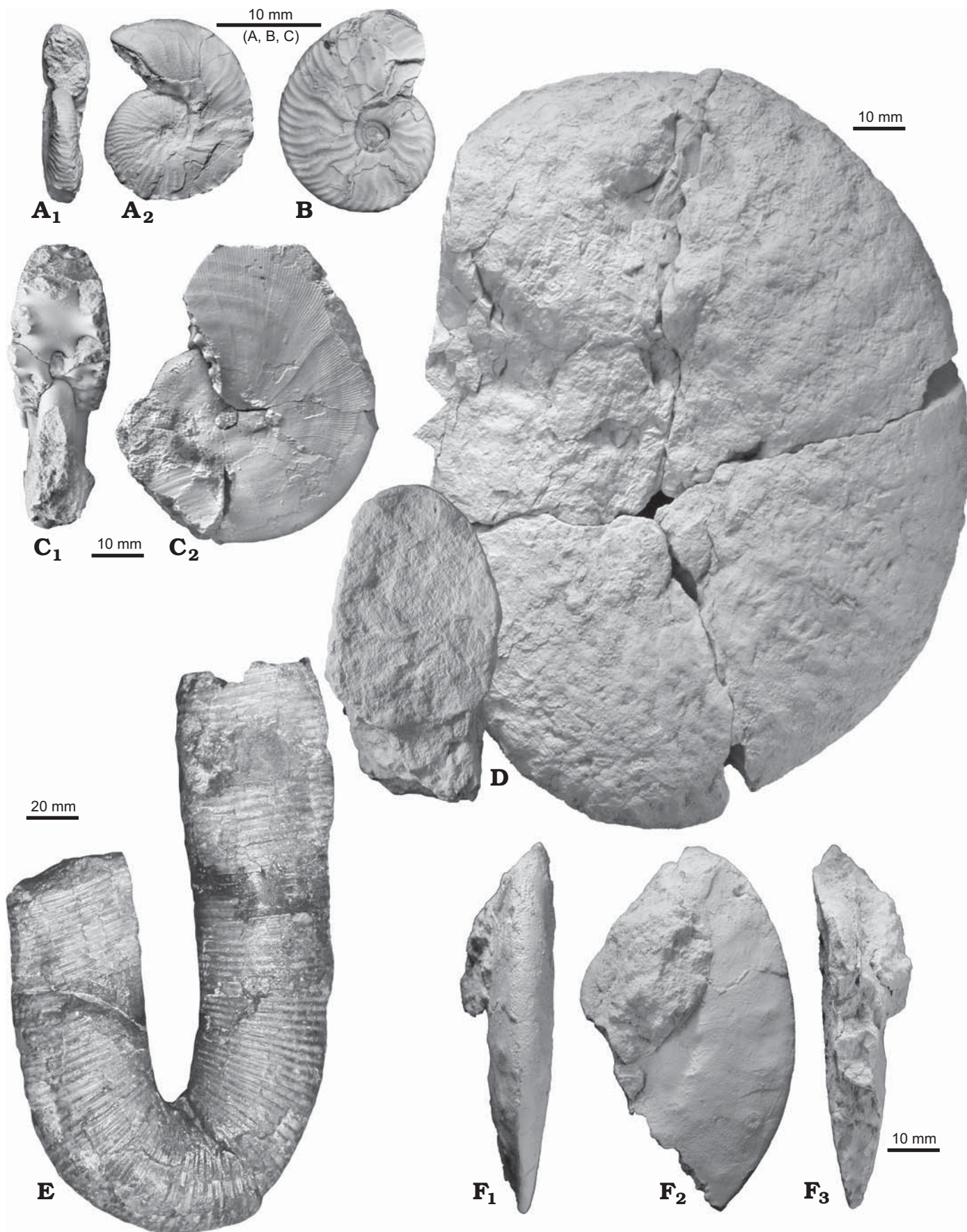
Poty, Brazil.—The Gramame Formation in the State of Pernambuco (northeast Brazil) is well known for its abundant megafauna (Maury 1936; Beurlen 1967; Mabesoone et al. 1968; Muniz 1993). Both the Maastrichtian and lower Paleogene are represented by marly limestone with abundant micro- and macrofauna (Stinnesbeck and Keller 1996). The Poty quarry, north of Recife, where the uppermost 9.5 metres of the Gramame Formation are mined, exposes a near-complete K–Pg boundary section. These Maastrichtian sediments contain typical late Maastrichtian calcareous nannofossil assemblages, such as *Watznaueria barnesae*, *Micula decussate*, and *Micula murus*. The planktic foraminiferal index marker of the last 0.3 Ma of the Maastrichtian, *Plummerita hantkeninoides*, has been noted in the uppermost 2 metres of this part of the section. Echinoids (*Hemiaster*), serpulids (*Hamulus*) as well as diverse planktic foraminifera are abundant and indicate a normal marine shelf environment with depths not exceeding 150 m (middle neritic). Ammo-

nites are rare, but *P.* (*Pachydiscus*) *neubergicus* and *Diplomoceras* sp. have been collected at 100 and 80 cm, respectively, below the K–Pg boundary, within the *P. hantkeninoides* planktic foraminiferal zone (CF 1 in Table 1). About 70 cm below the boundary, the marly limestone is capped by a layer of brecciated marl and limestone. This breccia unit also contains bones, phosphatic lumps, phosphatised foraminifera, glauconite and small pyrite concretions which indicate reworking and erosion from nearshore areas. Stinnesbeck and Keller (1996) suggested that this layer represented the latest Maastrichtian lowstand which in this region reduced water depth from the middle to an inner neritic environment, or by about 50 to 70 metres.

Pachydiscus and *Diplomoceras* are thus the last ammonite genera present and occur up to 100 and 80 cm below the K–Pg boundary, respectively. Both genera are also known to occur in the uppermost Maastrichtian sediments of Denmark (Birkelund 1979, 1993), the Bay of Biscay region of northern Spain and southwest France (Ward and Kennedy 1993) and the Antarctic Peninsula (Macellari 1986). In central Chile, *Diplomoceras* is a cosmopolitan generalist (sensu Ifrim et al. 2004) and one of the last surviving ammonites (Stinnesbeck 1986, 1996; Salazar et al. 2010). *Pachydiscus Neubergicus* is a proxy fossil for the base of the Maastrichtian (Gradstein et al. 2004). However, the presence of this species in upper Maastrichtian sediments of northeast Brazil, approximately 1 metre below the K–Pg boundary and in sediments containing well-defined latest Maastrichtian planktic foraminiferal assemblages (*Pachydiscus hantkeninoides* Zone), indicates that this ammonite taxon extended into the latest Maastrichtian. This fact has previously been noted by Kennedy and Henderson (1992b) and Ward and Kennedy (1993).

Columbia.—*Sphenodiscus pleurisepta* has recently been recorded from the La Tabla Formation in the Upper Magdalena Valley, in siliciclastic sediments deposited in regressive a lowstand system tracts (Patarroyo et al. 2010). This was a shallow-water taxon (e.g., Ifrim et al. 2005) which was widely distributed in northeast Mexico and the Western Interior Basin of North America where it ranged from the upper lower to the upper Maastrichtian (Ifrim and Stinnesbeck 2010). The Columbian specimens are associated with planktic foraminifera of late early Maastrichtian age (e.g., *Gansserina gansseri*). Towards the northern part of the Cretaceous Columbian Basin, i.e., towards Venezuela, a Maastrichtian unit known as the Mito Juan Formation contains *Sphenodiscus* and *Coahuilites*,

Fig. 2. The last ammonite species in Latin America. **A, B.** *Hoploscaphites constrictus quiriquiniensis* (Wilckens, 1904). **A.** CPUC/Q/CO/3260, in apertural (A_1) and right lateral (A_2) views. **B.** CPUC/Q/CO/3382H, in left lateral view. **C.** *Hypophylloceras* (*Neophylloceras*) *ramosum* (Meek, 1857), CPUC/Q/CO/2536, in apertural (C_1) and right lateral (C_2) views. **A–C** represent the last species recorded from the uppermost Maastrichtian of the Quiriquina Formation in Chile, ca. 6 m below the hiatus representing the K–Pg boundary (compare Salazar et al. 2010). **D.** *Pachydiscus* (*P.*) *neubergicus* (von Hauer, 1858), IMG 8671, from planktic foraminiferal zone CF 5, Cárdenas Formation (Maastrichtian), east-central Mexico. It was also recorded as one of the youngest species at the Poty quarry in Pernambuco, Brazil. **E.** *Diplomoceras cylindraceum* (Defrance, 1816), CPUC/Q/CO/2077 from the Quiriquina Formation (late Maastrichtian; Las Tablas bay, Quiriquina Island, Chile), but the taxon is cosmopolitan and among the last species recorded in many sections. **F.** *Sphenodiscus pleurisepta* (Conrad, 1857), IMG 8672, Cárdenas Formation (Maastrichtian), east-central Mexico, in ventral (F_1), left lateral (F_2), and apertural (F_3) views. This taxon is among the last species in many North American sections (Landman et al. 2004a, b; Ifrim and Stinnesbeck 2010).



but this has not yet been described in detail (Renz 1981, compare Patarroyo et al. 2010).

Northeast Mexico.—A large foreland basin developed north of the Sierra Madre Oriental (SMO) in an extended area of the Mexican states of Coahuila and Nuevo León. Sediment accumulation in this foreland reaches >6000 m in thickness and is known as the Difunta Group. The Difunta Group sediments accumulated in an enormous siliciclastic deltaic complex, fed by a river system located in Chihuahua and western Coahuila, and opened to the east into the ancient Gulf of Mexico. To the north, Difunta Group sediments gradually decrease in thickness and near the Río Grande, some 300 km north of Saltillo, only 100–200 m of coeval sediments are present, referred to as the Escondido Formation (Cooper 1971). The Difunta sedimentary complex is mostly Campanian to Maastrichtian in age, but it occasionally reaches the Paleogene (McBride et al. 1974; Vega-Vera et al. 1989; Soegaard et al. 2003; Vega et al. 2007). East and south of this sedimentary complex, the coeval Mendez Formation was deposited under open marine conditions and consists of marl and shale containing pelagic faunal assemblages. From the Difunta Group area, several ammonite assemblages have been described and interpreted, of different ages and facies (Wolleben 1977; Vega-Vera and Perrilliat 1990; Ifrim et al. 2004, 2005, 2010; Ifrim and Stinnesbeck 2010).

Nineteen ammonoid species, in 15 genera, and a single nautilid were described from the transition from pelagic (Mendez Formation) to neritic facies (Difunta Group) at the entrance to the Parras Basin during a sea level highstand. The assemblage consists of Tethyan (*Baculites ovatus*, *Brahmaites* [*Anabrahamites*] *vishnu*, *Fresvillia constricta*, *Hauericeras remba*, *Pachydiscus* [*P.*] ex gr. *neubergicus*, *Solenoceras reesidei*, *Tetragonites* cf. *superstes*), cosmopolitan (*Anagaudryceras politissimum*, *Desmophyllites diphylloides*, *Diplomoceras cylindraceum*, *Gaudryceras kayei*, *Phyllopachyceras forbesianum*, *Pseudophyllites indra*), and cold-water taxa (*Fresvillia teres*, *Hypophylloceras* [*Neophylloceras*] *surya*, *Hauericeras* [*N.*] *hetonaiense*, *Pachydiscus* [*P.*] cf. *egertoni*). *Eutrephoceras* sp. and *Menuites* juv. sp. could not be identified to species level. A similar assemblage was described from the Méndez Formation at Cerralvo, Nuevo León, 100 km to the east. This assemblage consists of >1000 specimens referred to 23 species in 18 genera. It is early Maastrichtian in age (biozone CF 7) and similar to the La Parra assemblage in composition and preservation. Zone CF 7 documents a short sea level lowstand. The Cerralvo fauna was interpreted to represent an ingress of cool- or even cold-water faunal elements into the warm-water environment of the ancient Gulf of Mexico during CF 7, which caused a mixing of cephalopod assemblages from different latitudes and thus an increase in faunal diversity (Ifrim et al. 2004).

Of the twenty taxa described from La Parra, 20 km north of Saltillo, seventeen also occur in Cerralvo. *Eutrephoceras* sp., *Pachydiscus* (*P.*) cf. *egertoni* and *P.* (*P.*) juv. sp. are known only from La Parra, whereas *Saghalinites cala*, *Zelandites*

varuna, *Solenoceras texanum*, *Nostoceras* (*N.*) *colubriformis*, *Nostoceras* (*N.*) *alternatum*, *Nostoceras* (*N.*) *rugosum* and the ?coleoid *Naefia neogaeia* were recorded exclusively from Cerralvo. The diversity and abundance of cold-water species are higher in the open-shelf palaeoenvironment exposed near Cerralvo than at the entrance to the Parras and La Popa basins. Apparently, ammonites flourished around the lower–upper Maastrichtian boundary.

The precise biostratigraphic data allow for the reconstruction of migratory pathways of some ammonite species. *Baculites ovatus* migrated into the La Popa Basin as a result of the sea level highstand documented at La Parra during CF 5. Coeval with the Difunta Group, shallow-water deltaic complexes developed near the border with Texas and in central-east Mexico. The Escondido Formation of northeast Mexico and southern Texas contains shallow-water ammonites such as *Coahuilites sheltoni*, *Sphenodiscus aberrans*, *S. lobatus*, and *S. pleurisepta* (Böse 1928; Cooper 1970; Ifrim et al. 2005). *Pachydiscus colligatus*, a species with a Tethyan (sensu lato) distribution, is also present (Böse 1928).

To the south, shallow-water sediments exist on the Late Cretaceous San Luis Potosí carbonate platform of central-east Mexico. These sediments, known as the Cárdenas Formation, were interpreted as wave-dominated, shoreface-delta system and show response to sea level changes similar to the Difunta Group (Schafhauser et al. 2007). In the lower Cárdenas Formation, *Coahuilites sheltoni*, *Pachydiscus* (*P.*) *neubergicus* and *Sphenodiscus pleurisepta* have been identified (Ifrim et al. 2005). *Pachydiscus* (*P.*) *neubergicus* is a warm-water species with a Tethys (sensu lato)-wide distribution; the other species are considered shallow-water species, consistent with the sedimentary facies in which they were found. With the exception of *Pachydiscus*, the above assemblage corresponds to the shallow-water assemblages widely known from the Difunta Group.

Nostoceras (*N.*) *alternatum*, *N.* (*N.*) *colubriformis* and *N.* (*N.*) *rugosum* are known from Cerralvo, but not from La Parra. These taxa were described exclusively from mid- to outer-shelf facies of the northern-northwestern Gulf of Mexico (Stephenson 1941; Cobban and Kennedy 1991a, b, 1993, 1995; Ifrim et al. 2004) and the Atlantic Coast (Cobban 1974; Kennedy and Cobban 2000). Individuals of these three species are abundant at Cerralvo (28.0%), and their absence at La Parra may be a result of palaeobathymetry; water depth at La Parra was considerably less than at Cerralvo. However, during that time nostoceratids became extinct worldwide (Goolaerts 2010), with a single exception recorded from the upper Maastrichtian of the Netherlands (Jagt et al. 2006).

Sphenodiscus pleurisepta is the last ammonite in northeast Mexico; it occurs throughout the Maastrichtian up to 3 m below the K–Pg boundary in the La Popa Basin (Lawton et al. 2001). Sphenodiscids dispersed and radiated during the latest Campanian and Maastrichtian, until they went extinct at or near the Cretaceous–Paleogene boundary. *Sphenodiscus* was the last remaining taxon in Mexico; its shallow-water environment was subject to many short-term changes before terminal

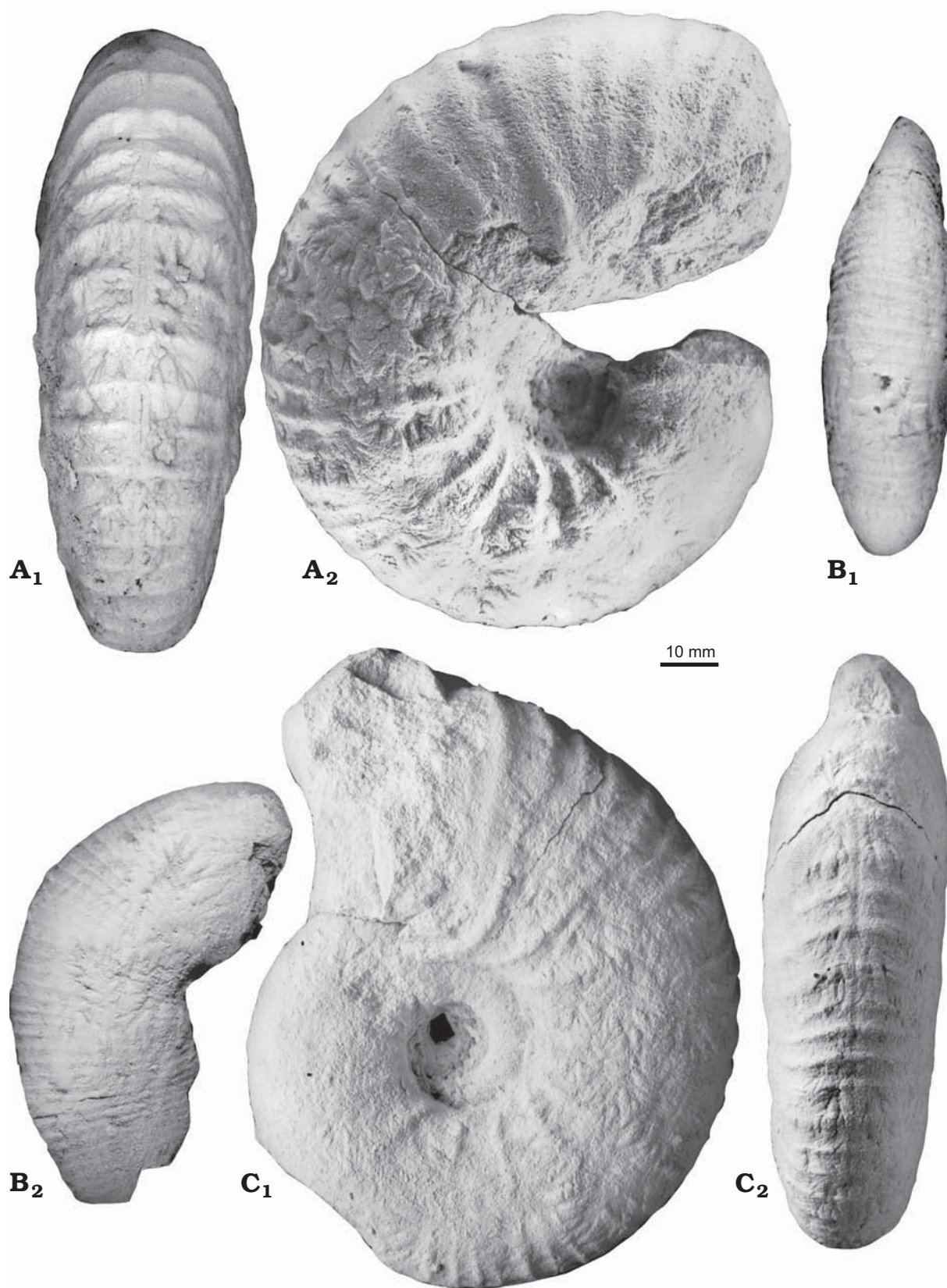


Fig. 3. The last ammonites in Brazil. **A, C.** *Pachydiscus* (*Pachydiscus*) *neubergicus* (von Hauer, 1858). **A.** IGH 1010, in ventral (**A₁**) and left lateral (**A₂**) views. **C.** IGH 1012, in right lateral (**C₁**) and ventral (**C₂**) views. **B.** *Diplomoceras cylindraceum* (Defrance, 1816), IGH 1011, in ventral (**B₁**) and left lateral (**B₂**) views. The three specimens were collected at Poty in the State of Pernambuco, where they occur in marly limestone approximately 5.5 m (**A, B**) and 1 m (**C**) below the K–Pg boundary.

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Table 1. Occurrences of the last ammonites in Latin America. Where possible, the foraminiferal zone (see Li et al. 1999) is shown, or the last appearance is given in metres below the K–Pg boundary. The palaeobiogeographical subdivision is from Ifrim et al. (2004) and Salazar et al. (2010). Abbreviations: CF, Cretaceous foraminiferal zone (see Li et al. 1999); LM, lower Maastrichtian; UM, upper Maastrichtian.

Faunal province	Species	Magellanes Basin, Patagonia	Quiriquina Fm., central Chile	Neuquén Basin, central Argentina	Poty, Brazil	Columbia	Northeast Mexico
Southern Indo-Pacific	<i>Baculites huenickeni</i>		UM				
	<i>Baculites rioturbensis</i>	+					
	<i>Baculites vicentei</i>		LM				
	<i>Diplomoceras australe</i>	+					
	<i>Gaudryceras varagurense patagonicum</i>	+					
	<i>Grossouvrites gemmatus</i>	+	UM				
	<i>Grossouvrites joharae</i>		UM				
	<i>Grossouvrites spinosissimus</i>		UM				
	<i>Gunnarites bhavaniformis</i>	+	?LM				
	<i>Gunnarites elegans</i>	+					
	<i>Hypophylloceras (Neophylloceras) inflatum</i>			UM			
	<i>Kitchinites darwini</i>			UM			
	<i>Kitchinites ifrimae</i>			UM			
	<i>Kitchinites vicentensis</i>			LM			
	<i>Kosmaticeras (Natalites) erbeni</i>			UM			
	<i>Maorites densicostatus</i>	+	UM				
	<i>Maorites suturale</i>	+					
	<i>Maorites tenuicostatus</i>	+					
	<i>Menuites gerardoii</i>			UM			
	<i>Pachydiscus (P.) gutierrezii</i>			UM			
<i>Pseudophyllites peregrinus</i>	+						
Cold-water, both hemispheres	<i>Anagaudryceras sublineatum</i>		UM				
	<i>Fresvillia teres</i>						CF 5
	<i>Hypophylloceras (N.) hetonaiense</i>		UM				CF 5
	<i>Hypophylloceras (N.) ramosum</i>		5–7 m				
	<i>Hypophylloceras (N.) surya</i>		5–7 m				?CF 7
	<i>Pachydiscus (P.) egertoni</i>						?CF 5
<i>Zelandites varuna</i>			UM			CF 7	
North American	<i>Coahuilites sheltoni</i>						+
	<i>Nostoceras (N.) alternatum</i>						CF 7
	<i>Nostoceras (N.) colubriiformis</i>						CF 7
	<i>Nostoceras (N.) rugosum</i>						CF 7
Low-latitude and boreal	<i>Baculites anceps</i>		LM				
	<i>Baculites ovatus</i>						CF 3
	<i>Brahmaïtes (Anabrahmites) vishnu</i>						CF 5
	<i>Fresvillia constricta</i>						CF 5
	<i>Hauericeras rembda</i>						CF 5
	<i>Hoploscaphites constrictus</i>		5–7 m				
	<i>Pachydiscus (P.) neubergicus</i>				CF 1		CF 5
	<i>Solenoceras reesidei</i>						?CF 7
	<i>Solenoceras texanum</i>						CF 7
	<i>Sphenodiscus pleurisepeta</i>					CF 5	CF 3
<i>Tetragonites superstes</i>						CF 7	
Cosmopolitan	<i>Anagaudryceras politissimum</i>		UM				CF 5
	<i>Desmophyllites diphyloides</i>						CF 5
	<i>Diplomoceras cylindraceum</i>		5–7 m				CF 5
	<i>Eubaculites carinatus</i>		UM				
	<i>Gaudryceras kayei</i>		UM				CF 5
	<i>Menuites fresvillensis</i>		UM				
	<i>Pachydiscus (P.) jacquoti</i>		UM				
	<i>Phyllopachyceras forbesianum</i>		UM				CF 5
	<i>Pseudophyllites indra</i>		UM				CF 5

Faunal province	Species	Magellanes Basin, Patagonia	Quiriquina Fm., central Chile	Neuquén Basin, central Argentina	Poty, Brazil	Columbia	Northeast Mexico
Undefined	<i>Diplomoceras</i> sp.				CF 1		
	<i>Eubaculites</i> ex gr. <i>simplex</i>			CF 2			
	<i>Menuites</i> juv. sp.						CF 5
	<i>Phylloptychoceras</i> sp.		UM				
	<i>Polyptchoceras</i> sp.	+					
	<i>Saghalinites cala</i>						CF 7

Maastrichtian events, and it may thus have been able to endure pre-K–Pg environmental changes.

Migratory pathways of *Sphenodiscus lobatus* and *S. pleurisepta* in North America were reconstructed from the precise dating of many occurrences throughout this continent. During the latest Campanian and early Maastrichtian, the two species immigrated into northeast Mexico coming from the south. Subsequently, *S. lobatus* disappeared from the fossil record in this region, whereas *S. pleurisepta* persisted, as indicated by numerous Maastrichtian records from the region. Both species used changes of the sea level to migrate or disperse over the continent. They entered shallow-marine basins including the Western Interior Seaway during an early Maastrichtian sea level highstand (UZA 4.5) and characterise shallow-water settings during the final stages of this epicontinental sea. After the loss of this habitat, both species migrated along the Atlantic Coast, where their highest occurrences in New Jersey are close to the Cretaceous–Paleogene boundary. The dispersal route of *Sphenodiscus* during the Maastrichtian does not reflect a general dispersal pattern for ammonites in North America, as indicated by the opposing north-to-south migration trend of *Baculites ovatus* (Ifrim and Stinnesbeck 2010).

Discussion and conclusions

Some of the uncertainties regarding the timing and course of ammonite extinction relate to the fact that localities containing latest Maastrichtian ammonites are relatively scarce on a global scale. This paucity, or absence, of ammonites in marine sediments was also observed for Latin America, but may in part be the result of less detailed geoscientific research in this area. In addition, the Maastrichtian was a time of great changes in climate (Li and Keller 1998b), and thus in sea level and marine facies. These changes hamper a direct comparison of faunal assemblages from different stratigraphic levels within the Maastrichtian. In northeast Mexico, for instance, the abundant and diverse ammonite assemblage of La Parra relates to a sea level highstand in an otherwise shallow-marine deltaic environment, unsuited for ammonites other than sphenodiscids and occasional baculitids. This high sea level corresponds to the terminal stage of the Western Interior Seaway further to the north. The following drop in sea level at the end of UZA 4.5 (early late Maastrichtian) led to a halt in marine sedimentation in the Western Interior Seaway

and thus to the final and complete disappearance of this major epicontinental habitat (Ifrim and Stinnesbeck 2010).

In part, the paucity of latest Maastrichtian faunas is also an artifact of biostratigraphic age control. Correlation with European type localities is still difficult to achieve based solely on ammonites; faunal provincialism and the frequent absence of age-diagnostic microfossils (coccolithophorids, planktic foraminifera) in sediments containing ammonites aggravate the problem. This is particularly true for the southernmost Latin American faunas described here, i.e., the Patagonian ammonites.

It is thus unclear at present whether the absence, or scarcity, of ammonites is a primary signal due to gradual extinction of taxa during the late Maastrichtian, e.g., illustrated by nostoceratids, or whether this is the result of a preservational bias related to the drop in sea level. However, in all sections described here, the abundance of ammonites decreases considerably in the last few metres below the boundary, even when the preservation potential remains the same, e.g., in the Gramame Formation of Brazil or the uppermost Maastrichtian of Mexico.

Another question is a possible climate-related component in the disappearance of ammonites. Their pattern of extinction appears to be different and diachronous between low- and high-latitude regions, initiating in the tropics and subtropics and progressively expanding towards high latitudes. In Latin America, the most abundant and diverse ammonite assemblages of unequivocally late Maastrichtian age are present in the austral sections of Chile and possibly southern Argentina. Diversity remained high throughout most of the substage and then declined rapidly, albeit prior to the K–Pg boundary. This may explain why ammonites generally disappear before the K–Pg boundary in lower latitudes, including the Latin American localities, even when a change in preservation potential cannot be observed. While sections in Neuquén may have been too shallow to allow for an abundant occurrence of ammonites, the subtropical Poty section in northeast Brazil was located in a middle-neritic environment. Despite this, only *Diplomoceras* and *Pachydiscus* range into the uppermost Maastrichtian and according to planktic foraminiferal data disappear within the last 0.3 Ma of the Cretaceous.

In consequence, many questions about the onset and progress of the global faunal crisis remain open. The current database indicates that the terminal decline and extinction of ammonites, commonly attributed to an asteroid or comet impact at the K–Pg boundary, began earlier, several hundreds

of thousand years prior. By the time of the boundary, tropical and subtropical elements had almost gone. All terminal Maastrichtian Latin American populations described here were characterised by severely reduced species populations. These last survivors were either taxa specialised to changing environments, such as *Sphenodiscus*, or cosmopolitan species which occurred in a wide range of latitudes and environments during the Maastrichtian already, e.g., *Diplomoceras* and *Pachydiscus* in Brazil. Other more specialised taxa such as *Nostoceras* had already gone extinct. No single sudden kill mechanism, such as a bolide impact, can account for this gradual, progressive extinction pattern.

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