

The Upper Campanian – lower Maastrichtian cephalopod fauna of Botellos, Nuevo León: a key to understand faunal turnover across the Campanian–Maastrichtian boundary in NE Mexico

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ABSTRACT:

Ifrim, C., Lara de la Cerda, J.E., Peña Ponce, V.H. and Stinnesbeck, W. 2017. The Upper Campanian – lower Maastrichtian cephalopod fauna of Botellos, Nuevo León: a key to understand faunal turnover across the Campanian–Maastrichtian boundary in NE Mexico. *Acta Geologica Polonica*, **67** (1), 145–162. Warszawa.

A new cephalopod collection from the Campanian-Maastrichtian boundary interval of NE Mexico, consisting of 1076 individuals assigned to 29 species and 22 genera is presented. This collection is a mix of ammonoids, one coleoid and one nautilid, which originate from at least three ammonoid biozones: The upper Campanian *Exiteloceras jenneyi* and *Nostoceras* (*Nostoceras*) *hyatti* zones, and the lower Maastrichtian *Pachydiscus* (*Pachydiscus*) *neubergicus* Zone. The age of the collection is thus middle late Campanian to late early Maastrichtian, and it closes a stratigraphic gap between faunas described formerly from this region. The specimens are nuclei collected from the desert pavement. The abundance of specimens allows for a comparison to other Campanian–Maastrichtian ammonoid records from Mexico, North America and Europe.

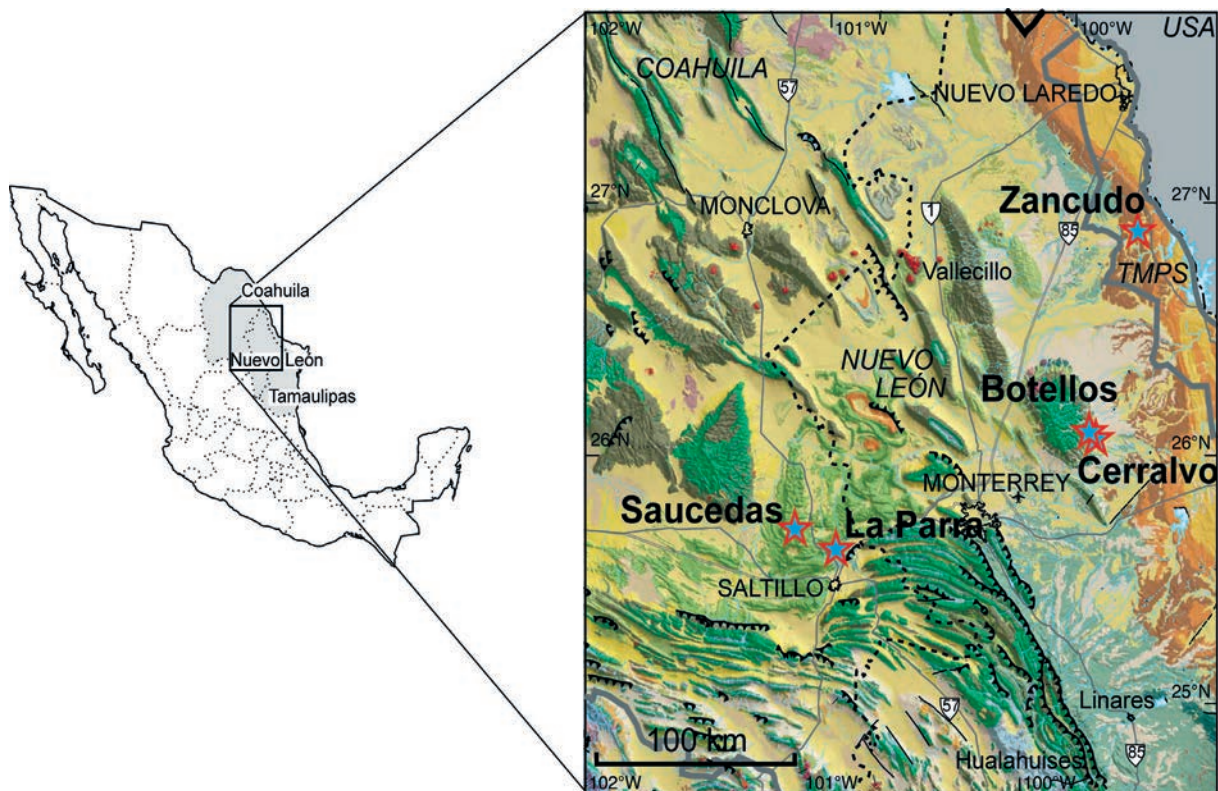
Key words: Ammonoids; Campanian; Maastrichtian; Mexico; Faunal turnover.

INTRODUCTION

In the last decade, five Campanian–Maastrichtian-aged cephalopod assemblages were described from NE Mexico, originating from lithostratigraphic units that were formerly described to be almost devoid of body fossils, such as the Méndez and the Parras formations. Each assemblage provided insight into faunal dynamics during isolated time slices of the late Campanian and early Maastrichtian of NE Mexico. The Upper Cretaceous of the region turned out to be

a “crossroad” between major ammonite provinces (Ifrim *et al.* 2004, 2005, 2010, 2013, 2015b; Ifrim and Stinnesbeck 2007, 2008) and regarding other marine organisms (Ifrim and Stinnesbeck 2007; Vega *et al.* 2007; Ifrim *et al.* 2008; Fuchs *et al.* 2010; Giersch *et al.* 2010; Giersch *et al.* 2011; 2014).

The fossils described here were discovered by EL and VH northwest of Botellos, a quarter of the town Cerralvo, Nuevo León (Text-fig. 1). An early Maastrichtian ammonite collection of 1002 specimens was reported from the south of Cerralvo by Ifrim *et al.*



Text-fig. 1. Overview map of Mexico with the three states covered in this study marked (left) and zoom on the working area (right) with geological map (Servicio Geológico de México 2007). The localities mentioned in the text are marked by asterisk

(2004). With 1076 specimens, the new Botellos collection is the richest ever found in this region. Its faunal composition and biostratigraphic relevance are here discussed under the aspect of the Campanian–Maastrichtian boundary transition.

Similar to Cerralvo, no section could be logged at Botellos. The few outcrops in gullies and dry river beds, located at $26^{\circ} 8'51.03''\text{N}$, $99^{\circ}44'31.69''\text{W}$, expose grey mudstone assigned to the Mendez Formation of Campanian–Maastrichtian age. The majority of specimens were collected loose from the desert pavement. All specimens are preserved as Fe-oxide internal moulds, comparable to Maastrichtian molluscan assemblages described earlier from the Méndez Formation (Ifrim *et al.* 2004; 2010; Ifrim and Stinnesbeck 2013).

PALEONTOLOGICAL RECORD

A formal description of most of the Botellos taxa can be found in earlier publications on late Campanian–Maastrichtian cephalopods with similar preservation (Ifrim *et al.* 2004; 2010; 2013; 2015b; Ifrim and Stinnesbeck 2013) and is therefore not repeated

here. Instead, the systematic palaeontology is abbreviated to a list of species and the numbers of specimens found and their occurrence, summarized in Text-fig. 2 and Appendix: Table 1.

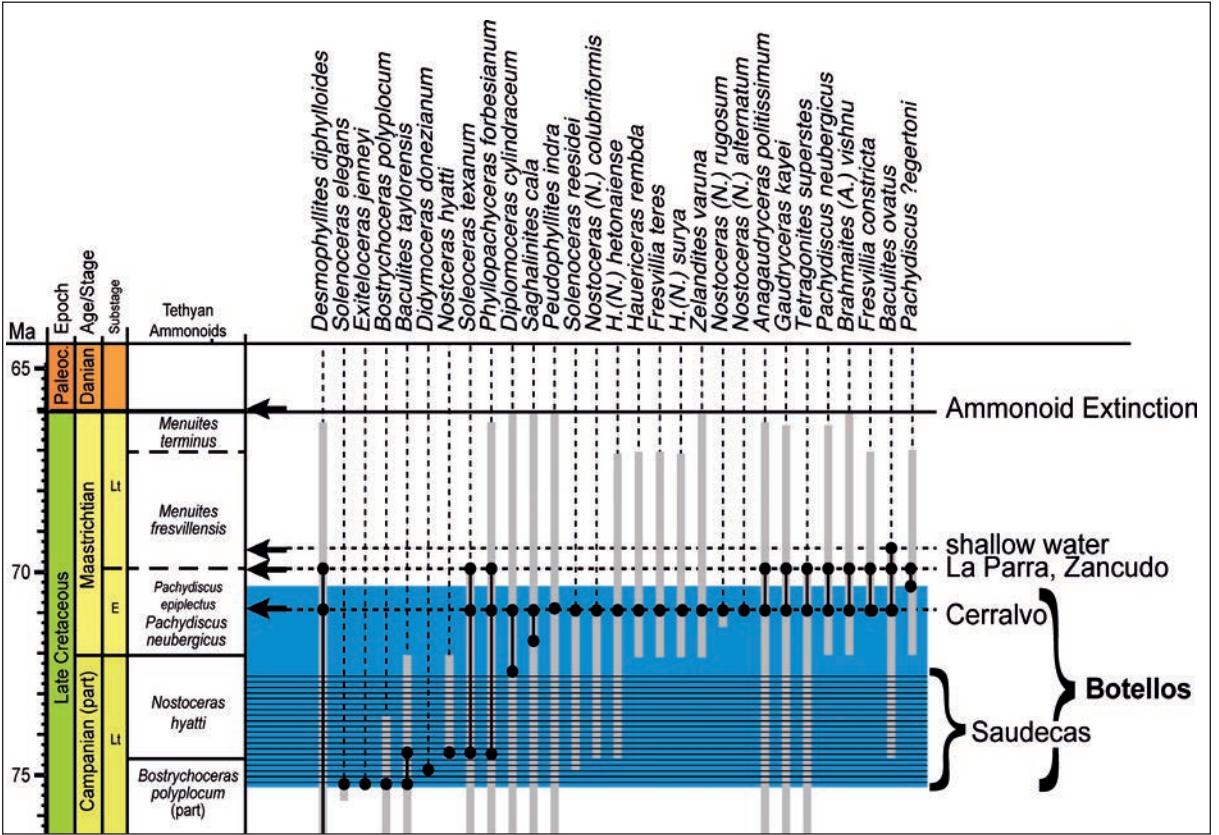
The specimens are registered in the Colección de Paleontología (CPC), housed in the Museo del Desierto, Saltillo, Coahuila. Some of them were analyzed with grinding tomography (e.g. in Text-fig. 3.5–13.14 and Pl. 1, Figs 81–87) in the Heidelberg Grinding Tomography Lab (for the method see Pascual-Cebrian *et al.* 2013); the datasets are then available there instead of the fossils. One advantage of this method is the visibility of whorl sections by a cross section through the digital fossil.

The faunal composition of the Botellos cephalopod collection is as follows (*Asterisks refer to an abbreviated systematic description):

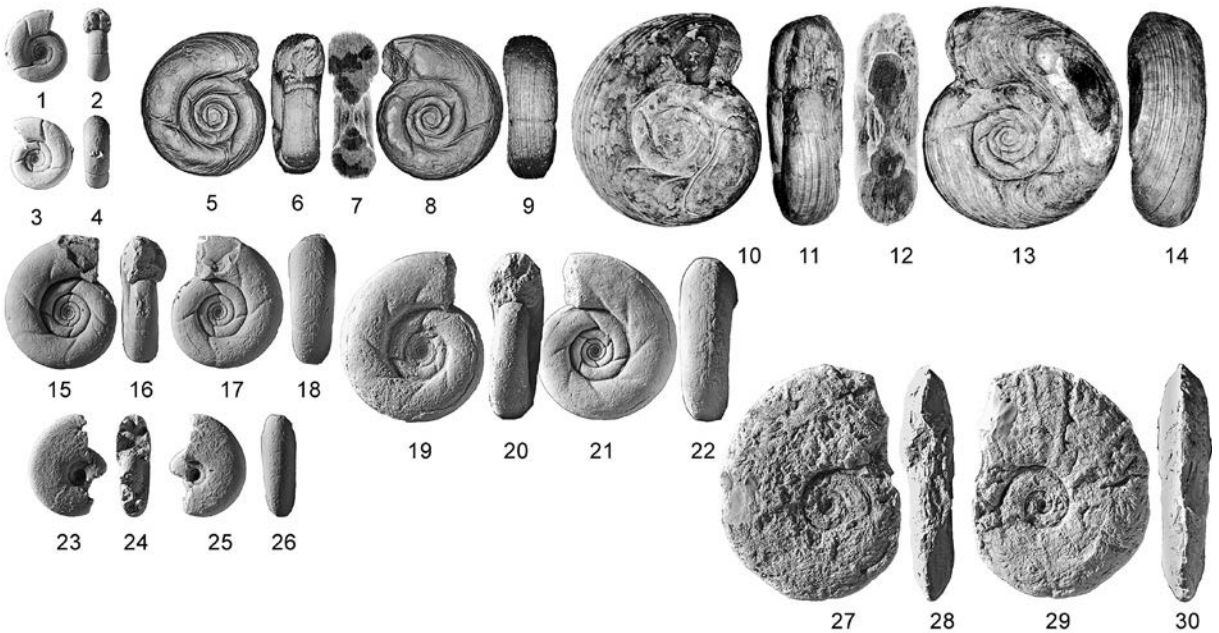
Order Coleoidea Bather, 1888

Longibelus sp., (= *Naefia neogaeia* by Ifrim *et al.* 2004, re-discussed by Fuchs *et al.* 2013)

Order Ammonoidea von Zittel, 1884



Text-fig. 2. Stratigraphic ranges of species collected at Botellos and stratigraphic comparison with other NE Mexican assemblages (black, data from Ifrim *et al.* 2004; Ifrim *et al.* 2005; Ifrim *et al.* 2010; Ifrim and Stinnesbeck 2013; Ifrim *et al.* 2015b) and worldwide (grey) in localities mentioned in the text. The ranges of the Botellos taxa are marked in blue, the one of the upper Campanian Saucedas assemblage in streaks. Time scale from Gradstein *et al.* (2012)



Text-fig. 3. *Saghalinites* and *Pachydiscus* from Botellos. 1-22 – *Saghalinites cala* (Forbes 1846); 1-4 – CPC-974; 5-9 – CPC-983; 10-14 – CPC-984; 15-18 – CPC-975; 19-22 – CPC-977. 23-30 – *Pachydiscus* (*Pachydiscus*) *neubergicus* von Hauer, 1858; 23-26 – CPC-980; 27-30 – CPC-981. All × 1

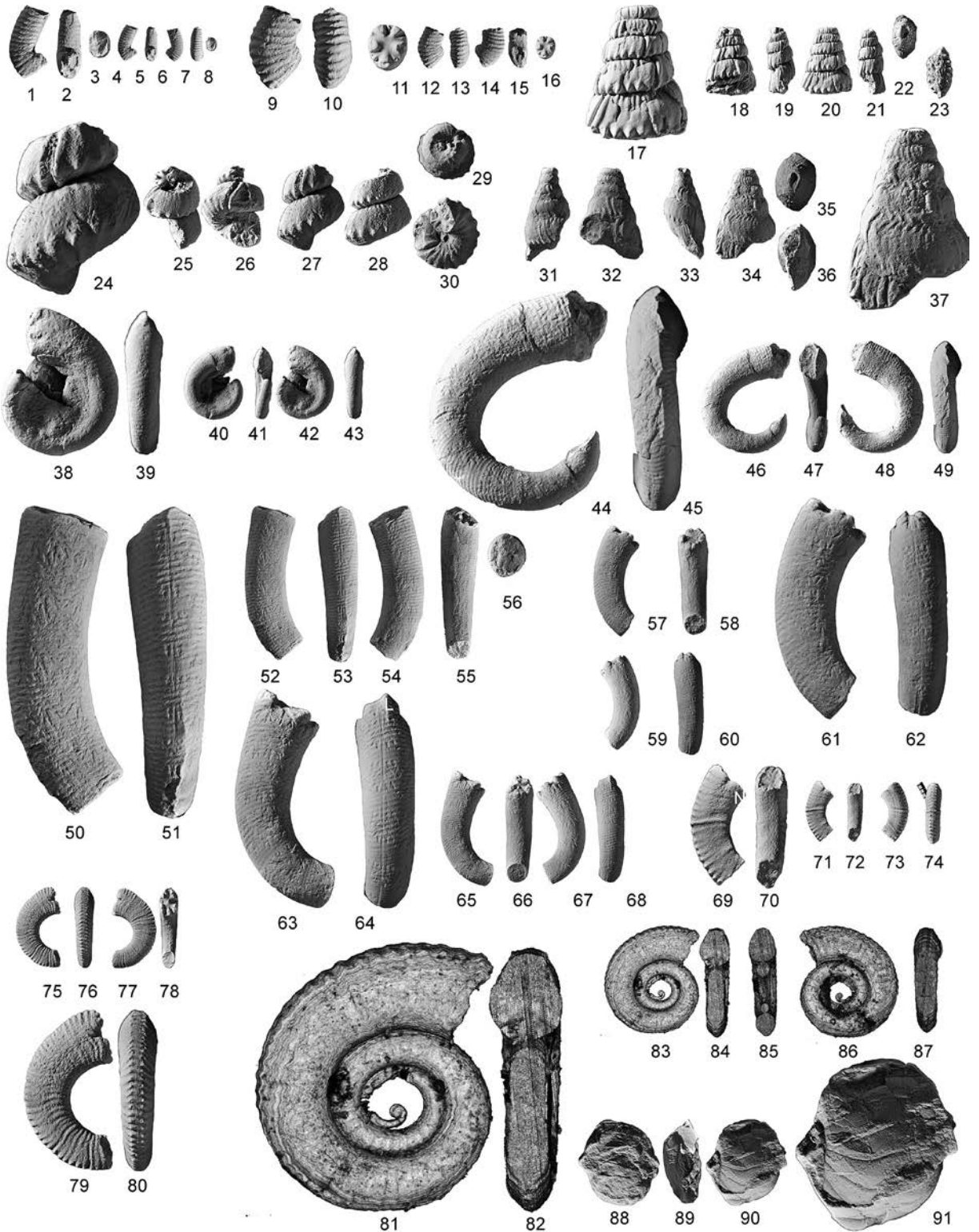


Plate I. Heteromorph ammonoidea and *Eutrephoceras* sp. indet from Botellos. 1-16 – *Parasolenoceras* sp.; 1-8 – CPC-968; 9-16 – CPC-967. 17-37 – *Nostoceras* (*Nostoceras*) *hyatti* Stephenson, 1941; 17-23 – CPC-971; 24-30 – CPC-9973; 31-37 – CPC-972. 38-68 – *Didymoceras* juv. sp.; 38-43 – CPC-965; 44-49 – CPC-962; 50-56 – CPC-964; 57-62 – CPC-966; 63-68 – CPC-963. 69-87 – *Exiteloceras jenneyi* (Whitfield 1877); 69-74 – CPC-959; 75-80 – CPC-961; 81-97 – CPC-985. 88-91: cf. *Eutrephoceras*; CPC-982. Specimens in natural size except 1-2, 9-10, 17, 24, 37-39, 44-45, 50-51, 61-64, 69-70, 79-82, 91 which are $\times 2$

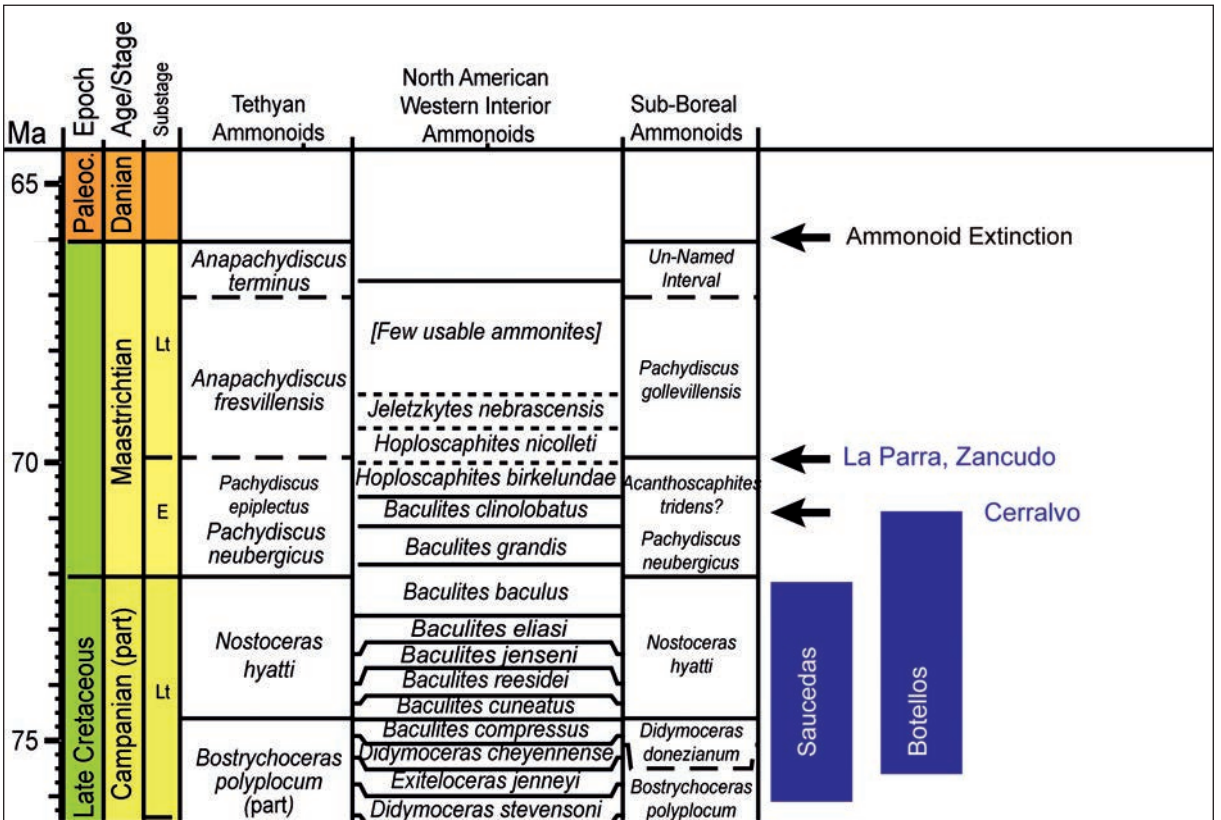
Hypophylloceras (*Neophylloceras*) *hetonaiense* (Matsumoto 1942); *Hypophylloceras* (*Neophylloceras*) sp. cf. *H. (N.) surya* (Forbes 1846); *Phyllopachyceras forbesianum* (d'Orbigny 1850); *Tetragonites superstes* van Hoepen, 1921; *Saghalinites cala* (Forbes, 1846), Pl. 1, Figs 1–22; *Pseudophyllites indra* (Forbes 1846); *Gaudryceras kayei* (Forbes 1846); *Anagaudryceras politissimum* (Kossmat 1895); *Zelandites varuna* (Forbes 1846); *Desmophyllites diphylloides* (Forbes 1846); *Hauericeras rembda* (Forbes 1846); *Pachydiscus* (*Pachydiscus*) *neubergicus* (von Hauer, 1858)*; *Pachydiscus* (*Pachydiscus*) cf. *egertoni* (Forbes, 1846); *Brahmaites* (*Anabrahmaites*) *vishnu* (Forbes 1846); *Baculites ovatus* Say, 1820; *Fresvillia constricta* Kennedy, 1986; *Fresvillia teres* (Forbes 1846); *Diplomoceras cylindraceum* (Defrance, 1816); *Parasolenoceras* sp. (Pl. 1, Figs 1–16); *Solenoceras elegans* Kennedy, Landman, Cobban and Scott, 2000b; *Solenoceras reesidei* Stephenson, 1941; *Solenoceras texanum* (Shumard 1861); *Nostoceras* (*Nostoceras*) *hyatti* Stephenson, 1941*, (Pl. 1, Figs 17–37); *Nostoceras* (*Nostoceras*) *alternatum* (Tuomey 1854); *Nostoceras* (*Nostoceras*) *rugosum* Cobban, 1991; *Didymoceras* juv. sp.*, Pl. 1, Figs 38–68; *Exiteloceras jenneyi* (Whitfield 1877), Pl. 1, Figs 69–87).

Order Nautiloidea Agassiz, 1848
cf. *Eutrephoceras*, Pl. 1, Figs 88–91

BIOSTRATIGRAPHY

The range of the taxa described from Botellos is shown in Text-fig. 2. The material collection is a mixture of several ammonite biozones. This is indicated by the co-occurrence of the biostratigraphic index fossils non-overlapping elsewhere (from Cobban *et al.* 2006, for Western Interior zonation; and Gradstein *et al.* 2012, for Tethyan zonation). These are, from youngest to oldest: *Pachydiscus* (*Pachydiscus*) *neubergicus* (Tethyan, FO base of the Maastrichtian); *Nostoceras* (*Nostoceras*) *hyatti* (Tethyan); *Exiteloceras jenneyi* (Western Interior).

Nostoceras hyatti is a widely used zonal index for the uppermost Campanian in lower and middle latitudes (Gradstein *et al.* 2012), with the original record from Texas (Stephenson 1941) and numerous ones from North America (Anderson 1958; Cobban and Kennedy 1993b; Kennedy and Cobban 1993c; Kennedy *et al.* 2000a; Larson 2012), Europe (Hancock and Kennedy 1993; Kennedy 1993; K uchler



Text-fig. 4. Ammonoid zonation of the Campanian–Maastrichtian (Gradstein *et al.* 2012), with correlation of localities mentioned in the text

2000b; Summesberger *et al.* 2007; Niebuhr *et al.* 2011; Machalski 2012), the Levant (Lewy 1967; Kennedy and Lunn 2000), North Africa (Hennebert *et al.* 2010), as far South has Southwest Africa (Howarth 1965). It is also present at Botellos.

Nostoceratid species are thus useful for trans-Atlantic correlation, but only *Solenoceras elegans* allows for correlation with the Western Interior Seaway, notably with the *Didymoceras stephensoni* and *Exiteloceras jenneyi* biozones of this region. *D. stephensoni* was not identified at Botellos, but *E. jenneyi* is present and correlates to the lower-middle *E. jenneyi* Zone of the upper Campanian in the Western Interior (Cobban *et al.* 2006).

The arithmetic mean of twelve horizons with particular bioevents marks the base of the Maastrichtian (Odin and Lamaurelle 2001). Of those twelve events, FO of *Pachydiscus (P.) neubergicus*, which occurs in Botellos, is a good proxy of the base of the Maastrichtian at Tercis, France. *Diplomoceras cylindraceum*, another form reported from Tercis as a good proxy of this boundary, and also reported from Botellos, was meanwhile recognised to appear distinctly earlier (Remin *et al.* 2015). Another two species from Botellos, *Nostoceras (N.) rugosum* and *N. (N.) alternatum*, characterize two successive early Maastrichtian biozones of US Gulf Coast area (Cobban and Kennedy 1991b, a) and confirm that a considerable part of the lower Maastrichtian is present in the Botellos assemblage.

The Botellos material is thus late Campanian through early Maastrichtian in age. It is a mix of successive faunal assemblages which developed across the Campanian–Maastrichtian boundary (Text-fig. 4), and may be derived from a condensed level within the Méndez Formation.

COMPARISON OF UPPER CAMPANIAN AND LOWER MAASTRICHTIAN ASSEMBLAGES

An ammonite faunal turnover can be demonstrated when comparing the Botellos assemblage quantitatively with the upper Campanian assemblage from Saucedas (Ifrim *et al.* 2015b) and the lower Maastrichtian assemblage from south of Cerralvo (Ifrim *et al.* 2004). The palaeobiogeographic terminology is based on Westermann (2000), and palaeobiogeographic assignments of the species on Ifrim *et al.* (2004), Ifrim and Stinnesbeck (2013), and Ifrim *et al.* (2015a).

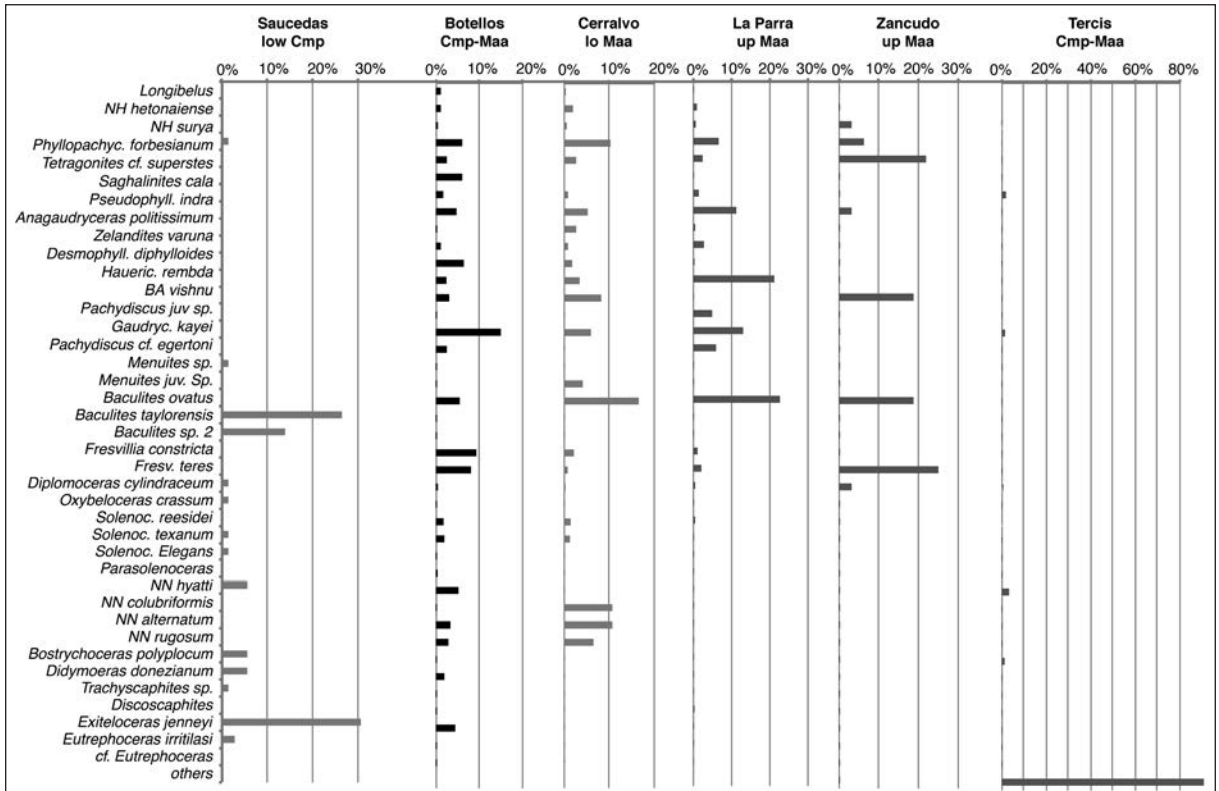
Comparison within Mexico

The quantitative compositions of the assemblages of late Campanian Saucedas, Campanian–Maastrichtian Botellos and the lower Maastrichtian Cerralvo assemblages are given in Table 1 (in Appendix). Additionally included are two upper Maastrichtian assemblages from the same region: Zancudo in northern Nuevo León (after Ifrim and Stinnesbeck (2013), and La Parra in central-south Coahuila (after Ifrim *et al.* (2010). The quantities are illustrated in Text-fig. 5.

In contrast to the upper Campanian Saucedas assemblage, *Phyllopachyceras forbesianum* is much more abundant at Botellos (6% instead of 1% of the assemblage), whereas *Exiteloceras jenneyi* is much rarer at Botellos (3% instead of 31 %) than at Saucedas. All other species which occur in both localities have comparable shares in the two assemblages.

Some of the species have a lower abundance at Botellos than in younger assemblages, e.g. the cosmopolitan species *Phyllopachyceras forbesianum* (Botellos 6%, 10% in the upper lower Maastrichtian Cerralvo assemblage, 6–7% in the two youngest assemblages Zancudo and Parras) or Maastrichtian species such as *Anagaudryceras politissimum* (>1% to 3%), *B. vishnu* (3% to 8%), *B. ovatus* (5% to 17%), *Nostoceras (N.) alternatum* (3 to 11%), and *N. (N.) rugosum* (3 to 7%). The share of *Zelandites varuna* remains low and about the same at Botellos and Cerralvo. It increases to 3% at La Parra but is absent from Zancudo. The latter three are entirely Maastrichtian species in southern North America.

Six Maastrichtian species are characteristically absent from Saucedas, but more abundant at Botellos than in the younger Cerralvo collection. These are *Saghalinites cala* (6% to <<1%), *Desmophyllites diphylloides* (6% to 2%), *Fresvillia constricta* (9% to 2%), *F. teres* (8% to 1%), *P. (P.) neubergicus* (15% to 6%), and *Solenoceras reesidei* (2 to 1 %). The coleoid *Longibelus* is a rare species in both collections; it was interpreted to have been a short-term immigrant into the area from the Pacific (Fuchs *et al.* 2013). The share of cosmopolitan *Pseudophyllites indra* is generally low and decreases from 2% at Botellos to 1% in younger assemblages. *D. diphylloides*, although not present at Saucedas, was previously documented from the lower Campanian of south-central Coahuila (Ifrim *et al.* 2013). *Saghalinites cala*, *P. indra*, *A. politissimum* and *T. superstes* have similar ranges at a global scale; their absence in NE Mexico in beds older than the latest Campanian, or even at the base of the Maastrichtian, is explained by endemism as discussed by Ifrim *et al.* (2013). *Saghalinites cala*, particularly



Text-fig. 5. Percentage of the species in the Mexican localities and Tercis

abundant at Botellos, first occurs in the Campanian of South Africa (Kennedy and Klinger 1977), but is also known from the Maastrichtian of Europe (Ward and Kennedy 1993); in North America it was only documented from the Maastrichtian of Mexico.

These seven abundant Botellos species may have played a great role after their immigration into the Gulf of Mexico, and then they become less frequent, although they all range into the Upper Maastrichtian.

Comparison with the Gulf Coast, Western Interior Seaway and Atlantic Coast

Comparison with three other palaeobiogeographic areas of North America is not possible quantitatively. Here, they are based on species richness presented in detail in Table 2 (in Appendix).

In the Campanian, species richness is highest in the northern Gulf Coast province (incl. Arkansas), whereas the Western Interior and the Atlantic Coast show a species richness of 11 and 13 species, respectively, comparable to NE Mexico. However, they all share only $\leq 25\%$ of their species with NE Mexico, which clearly justifies a palaeobiogeographic separation of this latter province. Species with a range crossing the Campanian–Maastrichtian boundary

have only been documented from NE Mexico, and these are: *D. diphyloides*, *D. cylindraceum*, *P. forbesianum*, and *S. texanum*. They also have a wider geographic occurrence (see Ifrim *et al.* 2004, 2010).

Within NE Mexico, only six species are restricted to the lower Maastrichtian. Of those, *N. (N.) alternatum* and *N. (N.) rugosum* are Gulf Coast heteromorphs, the latter with a further record from the Atlantic Coast. *N. (N.) colubriformis* was not recorded from Botellos, but is known from the nearby Cerralvo locality.

The other sixteen species from Botellos have a longer stratigraphic range and were also recorded from the Upper Maastrichtian of NE Mexico. Two of them were recorded in the Maastrichtian of the Atlantic Coast, four in the Gulf Coast province (the planispiral morphotypes only as isolated specimens), and none in the Western Interior. However, shallow water specialists, such as *Sphenodiscus lobatus* (Tuomey, 1854), *S. pleurisepta* (Conrad, 1857) or *Coahuilites sheltoni* Böse, 1928 (Ifrim *et al.* 2005; Ifrim and Stinnesbeck 2010) are not present at Botellos. Apparently, bathymetric dependence played a role in the exchange, because the numbers increase when taking shallow water species into account. Nine of the Maastrichtian species from NE Mexico are also present in the Maastrichtian of the Gulf Coast province,

three are in common with the Maastrichtian of the Western Interior Seaway, and four with the Atlantic Coast. Faunal interchange between NE Mexico, the southern Western Interior, the Gulf Coast and the Atlantic Coast was seemingly more restricted in deeper waters. For the Western Interior Seaway, the reason is obviously its shallowing and final disappearance during the Maastrichtian (e.g. Ifrim and Stinnesbeck 2010), but this pattern is less easily explained for the Northern Gulf and the Atlantic Coast.

Comparison with the Tercis section (France)

The Global Boundary Stratotype Section and Point (GSSP) for the base of the Maastrichtian was assessed at Tercis, SE France, and quantitative data are present (Odin and Lamaurelle 2001). 43 ammonoid taxa were documented across the Campanian–Maastrichtian boundary of this well-documented section (Hancock and Kennedy 1993; and further material summarized in Odin *et al.* 2001) that comprises the *B. polyplacum*, *N. hyatti* and *P. neubergicus* biozones. Seven of the 43 species documented at Tercis also occur in NE Mexico. These are *B. polyplacum* (only from Saucedas, Ifrim *et al.* 2015b), *D. cylindraceum*, *Hypophylloceras* (*Neophylloceras*) *surya*, *N. (N.) hyatti*, *P. (P.) neubergicus*, *P. indra*, and *Solenoceras reesidei*. Together they comprise 9% of individuals in the overall Tercis collections. Most of these species occur in the late Campanian of Tercis, with the exception of *D. cylindraceum* that first occurs ca. 2 m below the boundary, and *H. (N.) surya* and *P. (P.) neubergicus* that appear at the boundary. Of the remaining 36 taxa, *Hoploscaphites pumilus*, *Nostoceras (N.) approximans*, and *Nostoceras (N.) helicinum* are among the most abundant species in Tercis; these have not been recorded from Mexico, but from the Atlantic seaboard and the Western Interior.

Pseudophyllites indra is documented in North America from near the base of the Maastrichtian and above, but the species occurs much earlier in Europe and the southern hemisphere (Wiedmann 1962; e.g. Kennedy and Klinger 1977; Kaplan *et al.* 2005). *H. (N.) surya* is considered to be an entirely Maastrichtian species, its FO at the base level in Tercis is thus very early.

Comparison with Central Europe

The comparison of NE Mexico with Central Europe is also based on species richness (Appendix: Table 2). The upper Campanian of NE Mexico has only the Tethyan biostratigraphic index species *B. poly-*

placum and *N. hyatti* in common with Central Europe. *Didymoceras donezianum*, which characterizes a zone between the zones of *Bostrychoceras polyplacum* and *Nostoceras (N.) hyatti*, was not recorded from Botellos, but is known from Saucedas.

Diplomoceras cylindraceum ranges across the Campanian–Maastrichtian boundary on both continents, but with an earlier occurrence in central Europe (Remin *et al.* 2015). *Phyllopachyceras forbesianum* and *S. texanum* are restricted to levels either above or below the boundary in the European sections.

In the Maastrichtian, three cosmopolitan species (*P. indra*, *G. kayei* and *A. politissimum*), and three species with a wide distribution, in lower and middle latitudes (*B. (A.) vishnu*, *B. ovatus* and *H. rembda*), are shared between Europe and NE Mexico, although with much shorter stratigraphic ranges in Europe. In addition, *F. constricta* is only known from one locality in Europe but has a longer range and wider distribution in NE Mexico. *S. reesidei* is a Maastrichtian species in NE Mexico but has only one Campanian record in Tercis. *P. (P.) neubergicus* is well-represented in NE Mexico and throughout Europe.

CONCLUSIONS

The Botellos collection represents a mixture of assemblages that range from the late Campanian (Saucedas) to the late early Maastrichtian (Cerralvo). It thus closes the stratigraphic gap between these two (Text-figs 2, 3 and Appendix: Table 1). In the late Campanian, heteromorph ammonoids dominated the faunas (94% of individuals and 79 % of species in Saucedas), but the share of planispiral forms increases considerably with the transition to the Maastrichtian. From then on, planispiral morphotypes have a much higher share (53% of individuals/50% resp. 63% of species in Botellos and Zancudo, 49% of individuals/58% of species in Cerralvo, and 73% of individuals/67% of species in La Parra).

The unusually rich Botellos collection provides an important insight into the faunal dynamics on the shelf of the Gulf of Mexico and indicates a restricted faunal exchange between NE Mexico and North America in the late Campanian and early Maastrichtian. The NE Mexico has the highest share of common species with the Biscay region (31%), higher than with other North American provinces with which it shares around 25% of species. At first sight this may be related to an ongoing circum-equatorial current which distributed species in lower latitudes. During the Campanian, the most widely distributed species were nostoceratids,

a very diverse group which includes many species with a narrow geographic range. The widely distributed species were restricted to the Northern hemisphere, but not restricted to low latitudes. They also occur in the middle latitudes of Europe and in part of the North American Atlantic Coast. Only *Didymoceras donezianum*, *Nostoceras (N.) helicinum* and *N. (N.) hyatti* reached the North American Western Interior Seaway.

The Atlantic Province was established throughout the Late Cretaceous due to the widening of the Atlantic Ocean (Ifrim *et al.* 2015a). However, during the Campanian, this province seems to have differentiated further into latitudinal zones, expressed in a latitude-dependant interchange between both continents. Maastrichtian species shared between the Biscay region and NE Mexico are rather cosmopolitan or with a wide distribution in lower and middle latitudes, including the southern hemisphere, although they have few or no records in central Europe or the Western Interior. Interchange with the southern latitudes thus seems to have increased around the Campanian-Maastrichtian boundary at the coasts along the open oceans, but it was restricted with the epicontinental seas of Europe and North America.

SYSTEMATIC PALEONTOLOGY

The taxa discussed here have either been determined differently before as in the case of *P. (P.) neubergicus*, or they are recorded here for the first time in NE Mexico.

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Wiedmann, 1966

Superfamily Desmocerataceae Zittel, 1895

Family Pachydiscidae Spath, 1922

Genus *Pachydiscus* Zittel, 1884

Subgenus *Pachydiscus (Pachydiscus)*

Matsumoto, 1947

Pachydiscus (Pachydiscus) neubergicus

(von Hauer, 1858)

(Text-figs 3.23–3.30)

2004. *Pachydiscus (Pachydiscus)* juv. sp.; Ifrim *et al.*, p. 1598, text-figs 8i–j, 10a–e

2011. *Pachydiscus (Pachydiscus)* juv. sp. sp. ex gr. *Pachydiscus (Pachydiscus) neubergicus*; Ifrim *et al.*, p. 606, figs 5r–s, 7m–ff, 8

MATERIAL: 161 internal moulds, no body chamber was identified.

REMARKS: Ifrim *et al.* (2004) discussed comparable growth stages of various species of *Pachydiscus* and came to the conclusion that the specimens from their Cerralvo locality, ca. 50 km SSE of the Botellos locality, relate to the group of *P. (P.) neubergicus* (von Hauer, 1858). The species *P. (P.) neubergicus* sensu stricto displays smooth early growth stages up to a diameter of about 25 mm (Henderson and McNamara 1985). Its whorl section is very similar to that of the Botellos specimens with respect to whorl dimension. *Pachydiscus (P.) gollevillensis* (d'Orbigny, 1850), a species closely related to *P. (P.) neubergicus*, is more compressed at a comparable state of growth than our specimens. The same is true for closely related *P. (P.) armenicus* Atabekian and Akopian, 1969, but the early juvenile growth stages of these two species are very similar. The smaller specimens in the Botellos assemblage correspond to the Cerralvo specimens in every detail, but the Botellos assemblage yields four larger specimens, which already bear ornament consisting of six primary ribs per half whorl. These characteristics, the initial diameter and the number of ribs, are similar to the juvenile ornament of the specimens described in detail by Henderson and McNamara (1985). Secondaries are intercalated from a quarter whorl later on. They number eight per quarter whorl in the Botellos specimens, which also matches the density described by Henderson and McNamara (1985). The larger Botellos specimens thus close a gap in documented growth stage between the small ones preserved in other localities of the region (Ifrim *et al.* 2005; Ifrim *et al.* 2010) and known growth stages of *P. (P.) neubergicus* (von Hauer, 1858).

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Turrilitoidea Gill, 1871

Family Nostoceratidae Hyatt, 1894

Genus and Subgenus *Nostoceras* Hyatt, 1894

Nostoceras hyatti Stephenson, 1941

(Pl. 1, Figs 17–37)

1941 *Nostoceras hyatti* Stephenson, p. 410, pl. 81, figs 9–12.

1974 *Nostoceras hyatti* Stephenson; Cobban, p. 10, pl. 5, figs 1–21; pl. 6, figs 1–12; pl. 7, figs 1–10; pl. 8, figs 1–30, text-fig. 12 (with synonymy).

1986 *Nostoceras hyatti* Stephenson; Kennedy, p. 90, pl. 20, figs 7–9.

1993 *Nostoceras hyatti* Stephenson; Cobban and Kennedy, p. B3, pl. 1, figs 10–12, 16, 17, 20, 21, 25–27; pl. 2, figs 7–10, 12–15; pl. 3, figs 4, 5, 9–11 (with additional synonymy).

- p.1993 *Nostoceras hyatti* Stephenson; Hancock and Kennedy, p. 162, pl. 9, figs 1, 4; pl. 14, figs 2–4; pl. 16, figs 2, 3; pl. 17, figs 10, 11; pl. 18, figs 4, 5, 7, 8; pl. 19, figs 1–4, 8–10 only.
- 1993 *Nostoceras hyatti* Stephenson; Kennedy and Cobban, p. 417, figs 9.2, 11.1–11.27.
- 2000 *Nostoceras hyatti* Stephenson; Kennedy *et al.*, p. 12, figs 6, 7g–i.
- 2000 *Nostoceras hyatti* Stephenson; Küchler, p. 480, pl. 17, figs 2–6.
- 2012 *Nostoceras hyatti* Stephenson; Larson, p. 22, pl. 7, figs 8, 9; pl. 9, figs 1–7.
- 2012 *Nostoceras hyatti* Stephenson; Machalski, p. 108, pl. 8, figs 4, 5 (with additional synonymy).
- 2015 *Nostoceras hyatti* Stephenson; Ifrim *et al.*, p. 241, fig. 11m–x, 12a–g.

MATERIAL: 56 fragments, internal whorls of juvenile phragmocones.

REMARKS: *N. hyatti* is widely distributed and a zonal index for the uppermost Campanian. The species shows a wide range in morphology, with the moderately irregular, coarse ornamentation being the most conspicuous feature. The juvenile growth stages of the other three species of *Nostoceras* are described in detail by Ifrim *et al.* (2004). The 56 specimens differ from the juveniles of these three species regarding whorl section, ribbing and tuberculation. *N. colubriformis* has a rounded whorl section and finer ribs at comparable stages, whereas *N. hyatti* has a ventrolateral ridge formed by moderately distant tubercles. *N. alternatum* has a wider apical angle than the specimens of *N. hyatti*. *N. rugosum* has a more regular ornament and conspicuous tubercles forming a ridge at comparable growth stages, instead of a rather irregular ornament.

Genus *Didymoceras* Hyatt, 1894

REMARKS: This genus has been discussed in detail by Kennedy *et al.* (2000b).

Didymoceras juv. sp.

MATERIAL: Four short fragments of the juvenile phragmocone.

DISCUSSION: The specimens of *D. donezianum* (Michailov 1951) described by Kennedy and Cobban (1993b) are all from later ontogenetic stages, with

juvenile ornament consisting of ribs much stronger than in the Botellos specimens. The same applies to the specimen shown by Kennedy and Summesberger (1984) and even the holotype (Michailov 1951, pl. 5, figs 23, 24). A specimen of Błaszkiwicz (1980) is of comparable size but with coarser ribs. Our specimens are thus not comparable to *D. donezianum*, but rather to the juvenile stage of *D. varium* (Błaszkiwicz 1980) from Poland in their fine ribbing and absence of tubercles at comparable growth stages (Błaszkiwicz 1980, pl. 7, fig. 21), or to *D. nebrascense* of the Western Interior (Kennedy *et al.* 2000b, fig. 8a–c, 11a, b). This latter species has juvenile whorls which coil at later stages, and the coiled whorls are thicker (higher WB/D and WH/D). In summary, the juvenile stages preserved do not allow unequivocal assignment to a species, and are thus determined as *Didymoceras* juv. sp.

Acknowledgements

CI thanks student assistants Christoph Wollny, Sandra Rybakiewicz, Julian Wüstner for their help in the production of tomographies, and Hüseyin Çilingir, Hanna Brück and Michael Zech for digital processing of the tomographies. Klaus Will, Heidelberg, is thanked for photography of the other specimens. Financial support by the German Science Foundation (DFG fund IF61/4-1) is gratefully acknowledged. Two anonymous reviewers and the editor, Ireneusz Walaszczyk, are thanked for their careful reviews and comments.

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Manuscript submitted: 30th March 2016

Revised version accepted: 15th March 2017

APPENDIX: Table 1. Upper Campanian and Maastrichtian species from North-eastern Mexico and from Tercis, the type section for the Campanian-Maastrichtian boundary, with number of specimens found and share of individuals in the assemblage, sorted after locality and age (data from Tercis from Odin *et al.* 2001; data from Mexican localities other than Botellos from Ifrim *et al.* 2004, 2005, 2010, 2015b; Ifrim and Stinnesbeck 2013)

	SAU	BOT		CE	LP	ZC	Tercis	
	upper Cmp	upper Cmp-lower Maa		lower Maa	upper Maa	upper Maa	Cmp/Maa boundary	
specimens	72	1076		1008	604	32	455	
species richness	14	31		24	21	8	43	
shared with NE Mexico	N/A	N/A		N/A	N/A	N/A	9	
Upper Campanian								
<i>Menuites</i> sp.	1 (1%)							
<i>Baculites taylorensis</i>	19 (26%)							
<i>Baculites</i> sp. 2	10 (14%)							
<i>Oxybeloceras crassum</i>	1 (1%)							
<i>Solenoceras elegans</i>	1 (1%)	2	0%					
<i>Parasolenoceras</i>		4	0%					
<i>N. (N.) hyatti</i>	4 (6%)	56	(5%)				15	(3%)
<i>Bostrychoceras polyplacum</i>	4 (6%)						6	(1%)
<i>Didymoceras</i> juv. sp.	4 (6%)	21	(2%)					
<i>Trachyscaphites</i> sp.	1 (1%)							
<i>Exiteloceras jemeyi</i>	22 (31%)	48	(4%)					
<i>Eutrephoceras irritilasi</i>	2 (3%)							
Upper Campanian–Maastrichtian								
<i>Phyllopachyceras forbesianum</i>	1 (1%)	65	(6%)	104 (10%)	40 (7%)	2 (6%)		
<i>Diplomoceras cylindraceum</i>	1 (1%)	5	0%)	3 (<1%)	3 (<1%)	1 (3%)	4	(1%)
<i>Solenoceras texanum</i>	1 (1%)	21	(2%)	13 (1%)				
<i>Desmophyllites diphylloides</i>		69	(6%)	18 (2%)	2	0%		
other species from Tercis							412	(91%)
Lower Maastrichtian								
<i>Longibelus</i>		12	(1%)	4	0%			
<i>Saghalinites cala</i>		65	(6%)	1	0%			
<i>N. (N.) alternatum</i>		36	(3%)	108	(11%)			
<i>N. (N.) rugosum</i>		31	(3%)	66	(7%)			
<i>N. (N.) colubriformis</i>				108	(11%)			
<i>Menuites</i> juv. sp.				42	(4%)			
Maastrichtian								
<i>N. (H.) hetonaiense</i>		12	(1%)	20 (2%)	6	1%)		
<i>N. (H.) surya</i>		5	(<1%)	6 (1%)	4 (1%)	1 (3%)	1	(<1%)
<i>Tetragonites</i> cf. <i>superstes</i>		27	(3%)	27 (3%)	15 (2%)	7 (22%)		
<i>Pseudophyllites</i> <i>indra</i>		18	(2%)	9 (1%)	9 (1%)		9	(2%)
<i>Gaudryceras kayei</i>		51	(5%)	53 (5%)	68 (11%)	1 (3%)		
<i>Anagaudryceras politissimum</i>		3	(<1%)	27 (3%)	3	0%		
<i>Zelandites varuna</i>		12	(1%)	9 (1%)	17 (3%)			
<i>Hauericeras rembda</i>		26	(2%)	35 (3%)	128 (21%)			
<i>B. (A.) vishnu</i>		33	(3%)	83 (8%)	1	0%	6	(19%)
<i>P. (P.) neubergicus</i>		161	(15%)	60 (6%)	79 (13%)		7	(2%)
<i>P. (P.) jacquoti</i>								
<i>P. (P.)</i> cf. <i>egertoni</i>		27	(3%)		36 (6%)			
<i>Baculites ovatus</i>		59	(5%)	167 (17%)	137 (23%)	6 (19%)		
<i>Fresvillia constricta</i>		100	(9%)	22 (2%)	7 (1%)			
<i>Fresvillia teres</i>		87	(8%)	8 (1%)	13 (2%)	8 (25%)		
<i>Solenoceras reesidei</i>		19	(2%)	15 (1%)	3	0%	1	(<1%)
cf. <i>Eutrephoceras</i>		1	(<1%)		1	0%		
Upper Maastrichtian								
<i>Pachydiscus</i> juv. sp.					30 (5%)			
<i>Discoscaphites</i>					2	0%		

APPENDIX: Table 2. Upper Campanian and Maastrichtian species occurrences from NE Mexico, US Western Interior, US Gulf and Atlantic coasts, and Europe [Biscay region, Tercis (the type section for the Campanian-Maastrichtian boundary) and central Europe], with number of specimens found and share of individuals in the assemblage, sorted after locality and age. Data from Mexico after Ifrim *et al.* (2004); (2005; 2010; 2015b); Ifrim and Stinnesbeck (2010, 2013), and herein; Biscay region from Ward and Kennedy (1993) and Küchler (2001a, 2001b); northern Gulf Coast from Cobban and Kennedy (1991a, 1991b, 1995), Kennedy and Cobban (1993a, 1993d, 1993b, 2000, 2001); Western Interior from Kennedy *et al.* (1996; 2000b), Hancock and Kennedy (1993); Kennedy and Cobban (1993c, 1999) and Landman and Cobban (2003); Atlantic Coast from Kennedy and Cobban (1994a); Kennedy and Cobban (1994b, 1997); Kennedy *et al.* (1997); Kennedy *et al.* (2000a); Tercis from Hancock and Kennedy (1993); Hancock *et al.* (1993) and Odin *et al.* (2001); Central Europe from Błazskiewicz (1980); Kennedy (1993); Jagt (2002); Niebuhr (2003, 2004); Jagt and Neumann (2006). Every species is listed once. When it occurs in a different stratigraphic unit, this is mentioned (Cmp: Campanian, Maa: Maastrichtian). Species richness for substages or stratigraphic units were calculated using occurrences within units, even when the species is listed in a different unit

	NE Mexico	Northern Gulf Coast	Western Interior	Atlantic Coast	Biscay region	Tercis	central Europe
No of specimens	2856	-	-	-	-	455	-
Total species richness	43	75 (14 not listed)	20 (5 not listed)	40 (10 not listed)	51 (19 not listed)	43 (9 not listed)	77 (31 not listed)
Shared with NE Mexico	N/A	19 (25%)	5 (25%)	7 (18%)	16 (31%)	9 (21%)	13 (17%)
Upper Campanian species richness	12	42	11	13	11	27	22
<i>Menuites</i> sp.	x			<i>portlocki</i> ; <i>complexus</i>		sp.	<i>wittekindi</i> ; <i>portlocki</i>
<i>Pachydiscus</i> spp.		<i>arkansanus</i>			<i>haldemisis</i> , <i>colligatus</i> ; <i>oldhami</i> ; <i>launayi</i> ; cf; <i>complanatus</i>	<i>oldhami</i> , <i>colligatus</i> , <i>haldemisis</i> , <i>launayi</i> , <i>perfidus</i> , <i>subrobustus</i> , <i>perfidus</i>	<i>haldemisis</i> , <i>subrobustus</i> , <i>oldhami</i> , <i>colligatus</i>
<i>Pseudokosmatice-ras galicianum</i>		x	x			<i>colligatus</i>	
<i>Baculites taylo-rensis</i>	x	x					
<i>Baculites</i> sp. 2	x						
<i>Baculites</i> spp.		<i>claviformis</i> , <i>crickmayi</i> , <i>undatus</i>		<i>undatus</i>	<i>leopoliensis</i>		indet., <i>knorrianus</i> ; <i>baculus</i> ; <i>aquilaensis</i>
<i>Oxybeloceras crassum</i>	x	x	x				x
<i>Solenoceras elegans</i>	x		x				
<i>Parasolenoceras</i>	x	<i>pulcher</i>			cf. <i>interruptum</i>		<i>phaleratum</i>
<i>N. (N.) hyatti</i>	x	x		x	x	x	x
<i>N. (N.)</i> spp.		<i>archiancianum</i> , <i>approximans</i> , <i>arkansanum</i> , <i>danei</i> , <i>draconis</i> , <i>helicinum</i> , <i>monotuberculatum</i> , <i>pauper</i> , <i>platycostatum</i> , <i>pleuricostatum</i> , <i>pulcher</i> , <i>stantoni</i>	<i>monotuberculatum</i>	<i>approximans</i> , <i>draconis</i> , <i>monotuberculatum</i>	<i>archiacia-num</i>	sp. 1, sp. 2, <i>helicinum</i> , <i>approximans</i> ,	<i>junior</i>
<i>Bostrychoceras polyplocum</i>	x	x			x	x	x
<i>Didymoceras</i> spp.	juv. sp., <i>donezianum</i>	<i>aurarium</i> , <i>binodosum</i> , <i>cochleatum</i> , <i>donezianum</i> , <i>hornbyense</i> , <i>mortoni</i> , <i>navarroense</i> , <i>tortum</i>	<i>nebrascense</i> , <i>stephensoni</i> , <i>cheyennese</i>	<i>platycostatum</i> , <i>binodosum</i> , <i>stevensoni</i> , <i>draconis</i>		<i>varium</i> , sp. 1, sp. 2, <i>attenuatum</i> , <i>postremum</i> , <i>densecostatum</i> ,	<i>postremum</i> , <i>varium</i>

	NE Mexico	Northern Gulf Coast	Western Interior	Atlantic Coast	Biscay region	Tercis	central Europe
<i>Trachyscaphites</i> sp.	x	<i>redbirdensis</i> Maa only: <i>alabamensis</i> , <i>yorkensis</i>	<i>redbirdensis</i>		<i>spiniger</i> ; <i>pulcherrimus</i>	sp., <i>pulcherrimus</i>	<i>pulcherrimus</i> , <i>spiniger</i>
<i>Exiteloceras jenneyi</i>	x		x	<i>rude</i>			
<i>Eutrephoceras irritilasi</i>	x						
Upper Campanian–Maastrichtian species richness	4	1	0	0	1	9	1
<i>Phyllopachyceras forbesianum</i>	x				Maa only		Maa only
<i>Diplomoceras cylindraceum</i>	x				Maa only	x	x
<i>Solenoceras texanum</i>	x	upper Cmp only					upper Cmp only
<i>Desmophyllites diphylloides</i>	x	upper Cmp only					
Lower Maastrichtian	6	3	0	1	4	see below	3
<i>Longibelus</i>	x						
<i>Saghalinites cala</i>	x						
<i>N. (N.) alternatum</i>	x	x		x			
<i>N. (N.) rugosum</i>	x	x					
<i>N. (N.) colubriformis</i>	x	upper Cmp only					<i>schloenbachi</i>
<i>Menuites</i> juv. sp.	x						<i>A. tridens</i>
Maastrichtian species richness	19	17	5	14	12	6	19
<i>N. (H.) hetonaiense</i>	x						
<i>N. (H.) surya</i>	x				x	x	
<i>Tetragonites</i> cf. <i>superstes</i>	x						
<i>Saghalinites wrighti</i>					x	upper Cmp	x
<i>Pseudophyllites. indra</i>	x	x		x	also upper Cmp	also upper Cmp	x
<i>Gaudryceras kayei</i>	x				upper Maa only		x
<i>Anagaudryceras politissimum</i>	x				x		<i>lunenburgense</i>
<i>Zelandites varuna</i>	x						
<i>Desmophyllites larteti</i>					x	upper Cmp	
<i>Hauericeras rembda</i>	x	x			lower Maa only		Cmp only: <i>sulcatum</i> , <i>pseudogadani</i>
<i>B. (A.) vishnu</i>	x	indet., lower Maa only			upper Maa only		
<i>B. (B.) brahma</i>					lower Maa only		x
<i>P. (P.) neubergicus</i>	x			x	x	x	x
<i>P. (P.) jacquoti</i>		x			x		x
<i>P. (P.)</i> cf. <i>egertoni</i>	x	x					
<i>P. (P.)</i> spp.		<i>macoensis</i> , cf. <i>gollevillensis</i>			<i>armenicus</i> , <i>epipectus</i>	<i>lindei</i> , <i>epipectus</i>	<i>gollevillensis</i> , <i>epipectus</i>
<i>P. (N.)</i>				<i>mokotibensis</i>			<i>mokotibense</i>

	NE Mexico	Northern Gulf Coast	Western Interior	Atlantic Coast	Biscay region	Tercis	central Europe
<i>Menuites fresvillensis</i>					x		x
<i>Sphenodiscus lobatus</i>	x	x	x	x			
<i>Sphenodiscus pleurisepta</i>	x up to K/Pg	x	x	x		upper Cmp: sp.	upper: binckhorsti
<i>Coahuilites sheltoni</i>	x	x	x				
<i>Baculites anceps</i>					lower Maa only		x
<i>Baculites ovatus</i>	x	upper Cmp – lower Maa		upper Cmp only			x
<i>Baculites vertebralis</i>	?	<i>undatus</i>		x	x		x
<i>Eubaculites</i>		<i>carinatus claviformis</i>		<i>carinatus</i> , cf. <i>labyrinthicus</i>			<i>lyelli</i>
<i>Fresvillia constricta</i>	x						lower Maa only
<i>Fresvillia teres</i>	x						
<i>Solenoceras reesei</i>	x	upper Cmp only				upper Cmp	
<i>Hoploscaphites</i>		<i>brevis</i> , <i>binodosus</i>	<i>birkelundae</i> , <i>dorfi</i> , Cmp: <i>nododosus</i> ; <i>brevis</i> ; <i>landesi</i>	<i>compressus</i> , <i>nebrascensis</i> , <i>pumilus</i> , <i>nododosus</i> ; cf. <i>plenus</i> ; <i>criptonodosus</i>	lower Maa: <i>tenuistriatus</i>	<i>constrictus</i>	<i>crassus</i> ; <i>felderi</i> ; <i>pungens</i>
<i>Eutrephoceras</i>	cf.	<i>planoventer</i>					