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Fluctuations of the oxygen minimum zone at the end of Oceanic Anoxic Event 2 in the Gulf of Mexico and the response of ammonites

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Abstract The latest Cenomanian to basal middle Turonian (Late Cretaceous) section at Vallecillo, Mexico, contains a continuous and highly fossiliferous sedimentary record. It preserves a detailed insight into a pelagic ecosystem that recovered from Oceanic Anoxic Event (OAE) 2. The deposit formed during this period under the influence of an expanded, but fluctuating oxygen minimum zone, which also affected the fauna. In this section, the abundances of ammonites do not correlate with those of inoceramids; they not only rule out a preservational bias but also indicate that ammonites and their hatchlings populated shallower water depths than inoceramid larvae and planktic foraminifers, contrasting previous models. The most abundant species at Vallecillo, *Pseudaspidoceras flexuosum*, shows a response to these environmental changes. *Pseudaspidoceras flexuosum* clearly inhabited the open water column. It is among the first to reappear at the end of OAE 2 and may have been adapted to the layered water body. The improving conditions during the early Turonian led to a migration of *P. flexuosum* into other seas and oceans. Phases of a contracted OMZ are phases of immigration and changes in the ammonite faunas at Vallecillo, whereas phases of an expanded OMZ are phases of stagnation. Although the abundance of ammonites is independent of fluctuations of the OMZ, their dispersal and migration are related to them. This study is an example for the complexity of species-based analyses.

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Introduction

The Oceanic Anoxic Event (OAE) 2 was a palaeoceanographic event which caused a major global perturbation in the Cretaceous oceans ca. 95 Ma ago. It is related to one of the most extreme carbon cycle perturbations in Earth's history. Increased rates of organic carbon were buried in marine sediments at the height of the mid-Cretaceous greenhouse (Voigt et al. 2008). The OAE 2 is characterized globally by a major positive carbon isotope excursion in carbonates and organic matter (Arthur et al. 1987; Gale et al. 1993; Jenkyns et al. 1994; Tsikos et al. 2004; Sageman et al. 2006). It was accompanied by a rapid and profound warming of surface and shallow waters (Huber et al. 1999; Voigt et al. 2004, 2008; Forster et al. 2007), and the global occurrence of sediments indicating oxygen deficiency in the oceans. It has been shown that this oxygen deficiency did neither start nor end contemporaneously (Lüning et al. 2004; Tsikos et al. 2004; Voigt et al. 2008). This is why OAE 2 was defined to end with the cessation of the positive excursion of $\delta^{13}C$ values, which coincides with the FO of *Watinoceras* (Voigt et al. 2008). The oxygen-deficient conditions, however, are known to end in varying levels in the different Cenomanian-Turonian boundary sections (Lüning et al. 2004), indicating that the offset of anoxic conditions were not coeval globally.

These palaeoceanographic changes caused an intense faunal turnover in the marine faunas, and in part extinction (Kauffman et al. 1977; Elder 1991; Harries and Little 1999; Monnet 2009). Whereas the faunal turnover in microfossils is well-understood (Jarvis et al. 1988, e.g., Leary et al.

1989; Huber et al. 1999), the response of organisms higher in the food chains is less well known.

The Platy Limestone quarried near Vallecillo in the NE of Mexico (Fig. 1) contains a continuous and highly fossiliferous sedimentary record, which was deposited in the aftermath of OAE 2. The conditions at the sea-floor remained oxygen-deficient throughout the deposition of the platy limestone member (Ifrim 2006; Ifrim et al. 2007, 2008). At the same time, the OMZ repeatedly expanded and contracted in the open water column above. This shows that the OAE 2 conditions persisted on the shelf of the western Gulf of Mexico almost until the middle Turonian (Ifrim et al. 2011a).

The platy limestones are ca. 8-m thick and contain the fossil remains of a pelagic ecosystem during the latest Cenomanian to earliest middle Turonian. The Platy

Fig. 1 Map of Mexico with the state of Nuevo León shown in black, and zoom on Northeastern Mexico

Limestone was deposited on the outer shelf of the northwestern Gulf of Mexico, close to the entrance to the Western Interior Seaway (Fig. 2), and is a member of the Agua Nueva Formation (Ifrim 2006, and Fig. 3). The Vallecillo Platy Limestone provides insight into an early Turonian pelagic ecosystem with unique details (Ifrim 2006, 2013; Ifrim and Stinnesbeck 2007, 2008; Ifrim et al. 2005, 2007, 2008, 2010, 2011a, b; Schultze et al. 2010). The data presented here were published before (Ifrim 2006, 2013; Ifrim et al. 2011a, b), but are here interpreted in a new way from the perspective of ammonites.

The Vallecillo section and its fossils

The sediments of the Vallecillo section were deposited between the latest Cenomanian and the basal middle Turonian (Ifrim et al. 2007, 2011a; Ifrim and Stinnesbeck 2008; Ifrim 2013, summarized in Fig. 4), based on biozonation by ammonites, inoceramids, and planktic foraminifers. A series of excavations provided the data for a quantitative analysis of the fossil assemblage preserved at Vallecillo. Ca. 2100 findings throughout almost the whole section (Fig. 4) were registered and counted (Ifrim 2006; Ifrim et al. 2011a). The composition of the assemblage preserved at Vallecillo is thus well-known (Fig. 5): It is mainly composed of nekton (fishes, ammonites) and their dwelling traces (pellets, coprolites). Rare fossils such as marine reptiles are also known from Vallecillo (Ifrim 2006; Buchy 2007; Ifrim et al. 2008), but remains of them were not discovered on the limited excavation surfaces. They comprise turtles, several specimens of early mosasauroids, and the tooth of a pliosaurid. The latter two are potential predators for the ammonites, in addition to large fishes such as teleosts and latimeroids of >1 m length, and pycnodont sharks (Ifrim 2006, 2013; Giersch et al. 2010; Ifrim et al. 2010). The only benthic organisms at Vallecillo are inoceramid bivalves, not even benthic foraminifers are known. From the excavation dataset, the abundances of the different fossil groups, but also parameters of single species can be plotted against the section (Figs. 4, 6). The same can be done for foraminifers; these were counted from 1 cm^2 areas of thin sections.

The following quantitative analysis is from Ifrim et al. (2011a). Similar distributions of benthic inoceramids and planktic foraminifers during this period of an expanded, but fluctuating oxygen minimum zone (OMZ), were documented with a moderate positive correlation. It was assumed that the abundance of the benthic inoceramid bivalves was determined by the rate of larval recruitment, with the ecology of the larvae being similar to that of deeper-dwelling planktic foraminifers. With this positive correlation, four phases of expansion and contraction of the
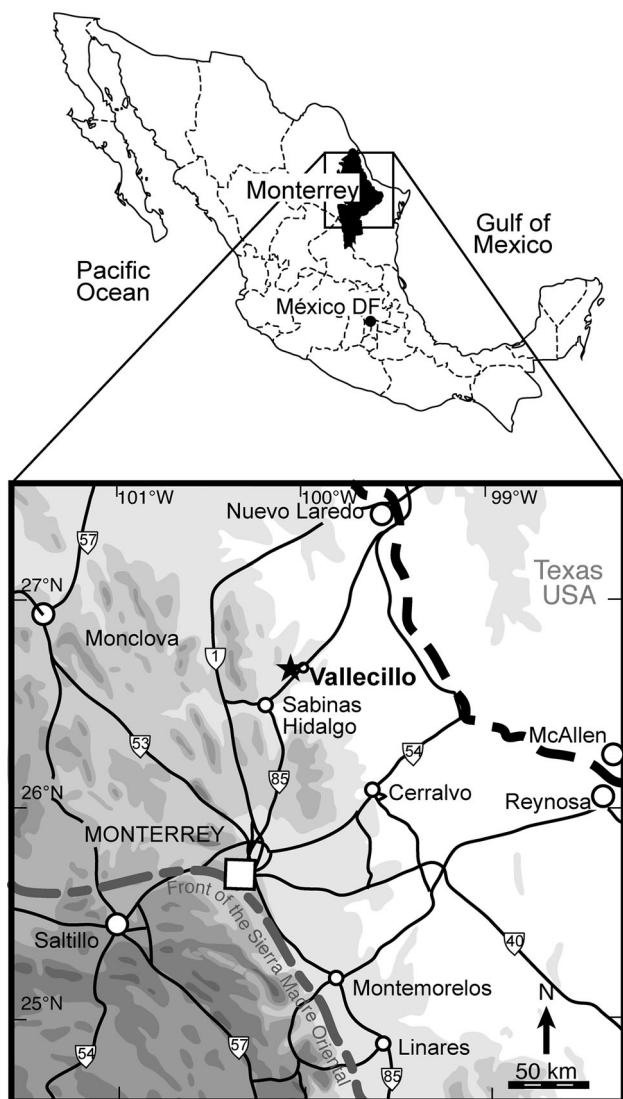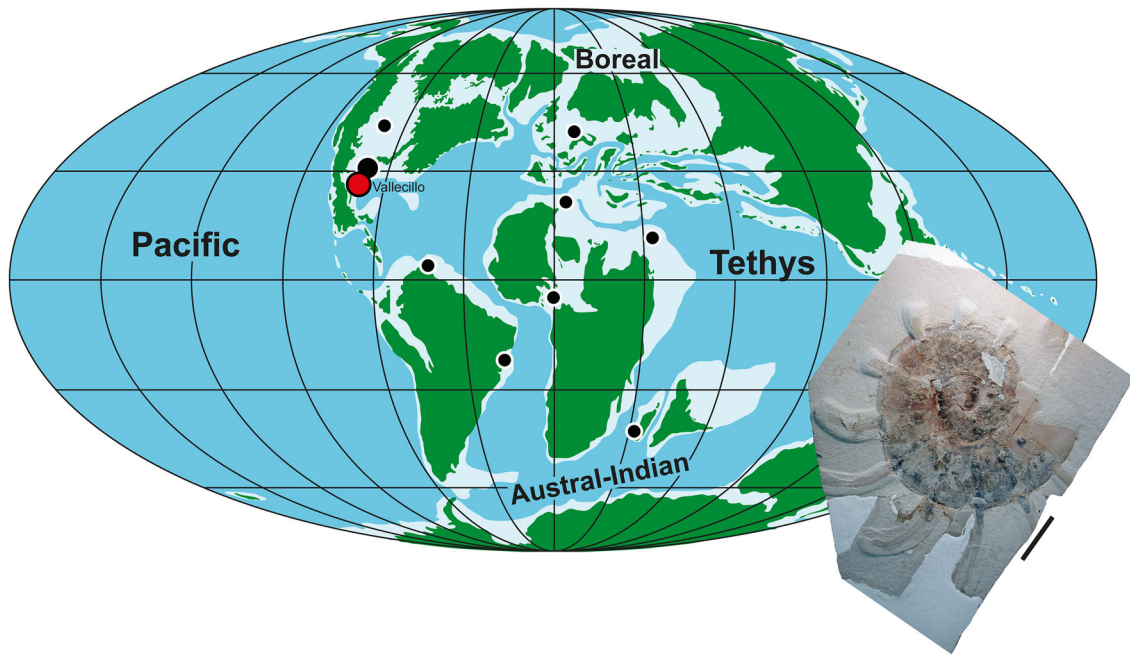
Fig. 2 Map of the Turonian world with occurrences of the ammonite *Pseudaspidoceras flexuosum*, shown in the lower right (*scale* 10 cm). The location of Vallecillo and the occurrence of this species in Texas are marked by larger dots because this seems to have been its main occurrence with the longest record. Map based on 95 Ma map of Blakey (2012), modified after Ifrim (2013)

OMZ were reconstructed over the Vallecillo section. The abundances of fish fossils and ammonites do not correlate, neither with each other nor with these two fossil groups, which indicates a primary distribution in the sediment. It is a proof that sedimentation rates were constant because the fossils are not equally concentrated in the same layers. Changes in the sedimentation rates do thus not play a role in the quantitative interpretation of the data.

A closer look at the ammonites

The size distribution of ammonites from Vallecillo, discussed by Ifrim (2006) and Ifrim (2013), shows the distribution of a living population. This is confirmed by the taphonomy of the ammonite shells: they show no sign of drifting (Ifrim and Stinnesbeck 2007; Ifrim et al. 2011b). The data are thus ideal to provide insight into the response of the ammonites to fluctuations of the OMZ.

The distributional mode of ammonites was interpreted to be similar to that of inoceramids, i.e., a dispersal by hatchlings or respectively larvae. At Vallecillo, the abundances of ammonites do not correlate with those of inoceramids (Fig. 4). Whereas planktic foraminifers and inoceramids show maxima in abundance in the same levels, there are no significant maxima or minima in the abundance of ammonites related to them. Inoceramid gametes and large, ornamented foraminifers were interpreted to inhabit deeper levels of the water column, whereas the data from Vallecillo indicate that ammonites and their hatchlings populated shallower water depths, because the seafloor at Vallecillo was very hostile to all organisms but inoceramids; no other benthic organisms was found, not even among benthic foraminifers (Ifrim et al. 2008, 2011a). The abundances of fossils over the Vallecillo section show thus that recruitment rates of ammonite hatchlings were independent of fluctuations of the OMZ. Despite the similar mode of distribution, strong differences in the extinction and recovery patterns of inoceramids and ammonites were documented during OAE 2 before (e.g., Elder 1991; Harries 1993). The data from Vallecillo provide a suitable explanation for this different response.

The overall survival rate of ammonite hatchlings, i.e., the "density" of ammonites observed a Vallecillo was thus independent of fluctuations of the OMZ. This is a rather surprising result, because it is well known that ammonites were strongly affected by OAE 2 (compare e.g., Elder 1991; Harries 1993; Gale et al. 2005; Kennedy et al. 2005; Monnet 2009; Kurihara et al. 2012): They became very rare and underwent a strong faunal turnover with a moderate extinction. The ammonite data thus need to be considered in more detail.

The size and abundance of the most abundant ammonite species at Vallecillo, *Pseudaspidoceras flexuosum*, are extracted from the database. The size refers to the diameter of the shell, abundance is given as number of specimens in

Fig. 3 Lithofacies map of Mexico (after Sohl et al. 1991; Goldhammer and Johnson 2001; Soegaard et al. 2003; Ifrim and Stinnesbeck 2007; and own data). The rectangle marks the area of the zoomed map in Fig. 1
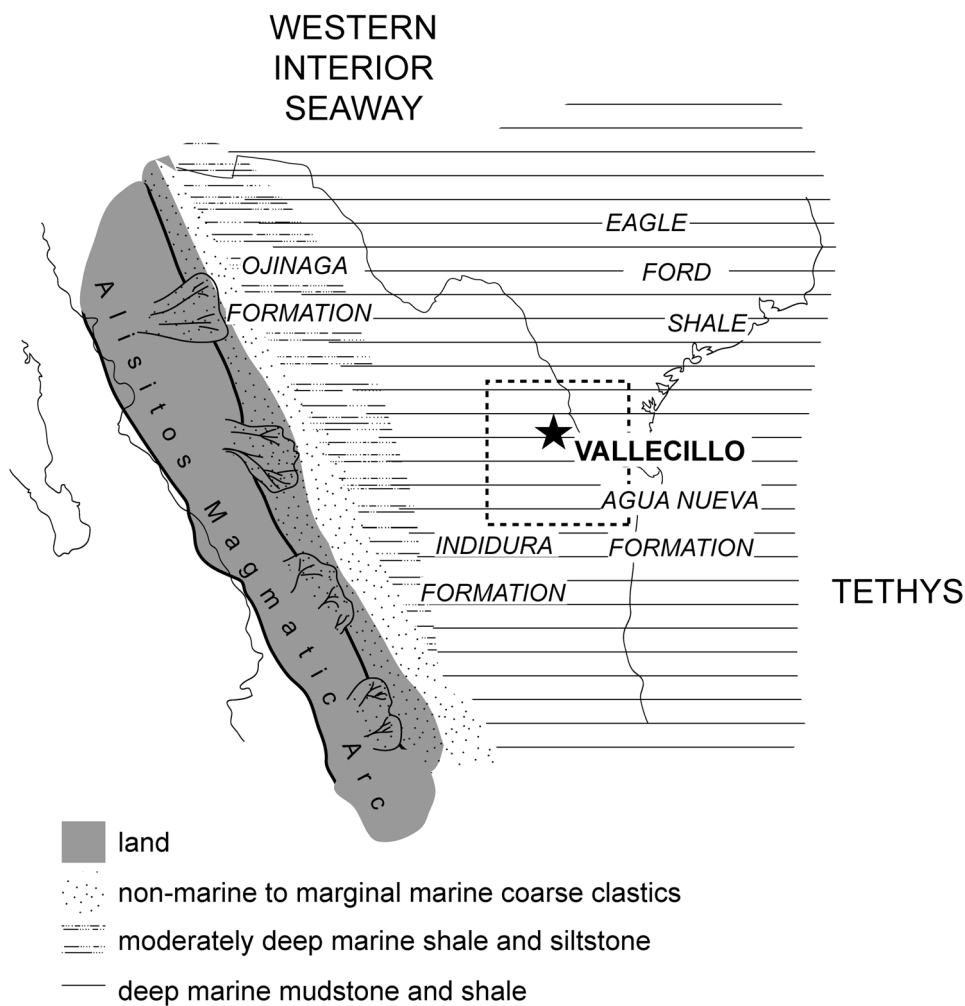
10 m^2 surface per 5-cm section (Fig. 6). This species was interpreted in palaeobiological and palaeoecological terms by Ifrim (2013). It was shown to have been covered with long spines on its outer whorl (e.g., Fig. 2, lower right). A demersal mode of life can be excluded for this species, based on scarcity of oxygen and prey at the sea-floor. Instead, this species is interpreted to have dwelled in the well-oxygenated upper surface waters, where there was a pelagic ecosystem with an active carbonate factory, and where it could have been colonized by stramentid epizoans (Ifrim et al. 2011b), at least for the final phase of its ontogeny. *P. flexuosum* clearly inhabited the open water column, supporting some (Schweigert and Dietl 1999; Westermann and Tsujita 1999) and contrasting others (Batt 1989; Monnet 2009) of the many different interpretations on the mode of life of spinose ammonite morphotypes.

At Vallecillo, this species is among the first to appear at the end of OAE 2 (Ifrim and Stinnesbeck 2007) and may have been adapted to the layered water body. The first specimens of this species occur during a phase with

contacted OMZ and improved conditions (Fig. 6). These are small but rapidly increase in size. The return of an expanded OMZ (middle *P. flexuosum* zone) leads to a stagnation in the diameters in this species. However, it seems to adapt to these conditions, indicated by a peak in abundance (due to scarcity of competing species?). Ca. 0.5 m upsection, shortly before the abundances of planktic foraminifers and inoceramids indicate a shrinking of the OMZ, *P. flexuosum* also increases in size. During the next phase of high oxygenation (upper *V. birchbyi* zone), *P. flexuosum* reaches its maximum diameters of >350 mm (e.g., the specimen in Fig. 2). It is noteworthy that this is about the biostratigraphic level where *P. flexuosum* occurs in other sections in the world, e.g., in Pueblo, Colorado, where the GSSP of the Cenomanian-Turonian boundary was defined (Kennedy et al. 2005), in Tunisia (Amédro et al. 2005, Robaszynski et al. 2010) or Nigeria (Zaborski 1995). During the following phases of expanded OMZ, *P. flexuosum* shows decrease in size and abundance. During the final improvement with a constantly contracted OMZ,
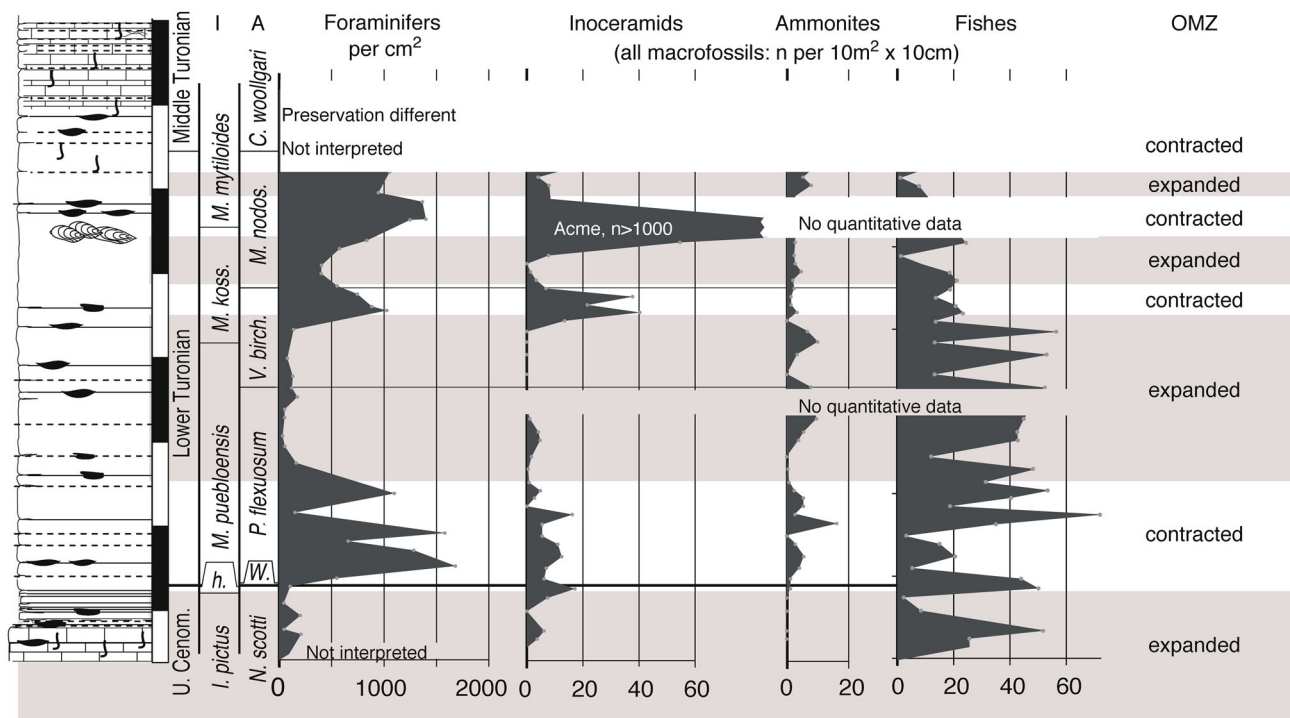
Fig. 4 The Vallecillo section with inferred expansion (*gray*) and contraction (*white*) of the oxygen minimum zone. *Left* the Vallecillo section and its biostratigraphic zonation, based on *I* inoceramids and *A* ammonoids. *Middle* abundances of planktic foraminifers, inoceramids, ammonites and fishes. *Right* interpreted expansion and contraction of the oxygen minimum zone (OMZ), indicating hostile or improved conditions in the deeper water column (modified from Ifrim 2006, 2013; Ifrim and Stinnesbeck 2007, 2008; Ifrim et al. 2011a)
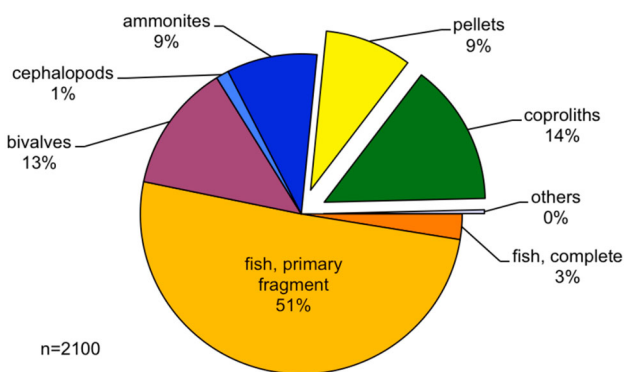

Fig. 5 Composition of the Vallecillo assemblage from all beds excavated. Note that apart from inoceramids only nektic organisms were identified. "Others" includes e.g., rare findings of driftwood, "cephalopods" includes cephalopods <100 mm, because these shells were dissolved and are only known from articulated siphos

this species disappears from the Vallecillo section above the 5.98 m level, 20 cm above the base of the middle Turonian, much later than in localities in the USA, central Europe, North Africa, Nigeria, or Brazil (Ifrim and Stinnesbeck 2008; Ifrim 2013). At Vallecillo, it shows the longest occurrence known worldwide. This species seems to have evolved in the NW Gulf of Mexico region during OAE 2 and dispersed into lower and middle latitudes when

the conditions became more favorable, but occurs there only for a short interval, whereas it had a stable population in the Vallecillo region. The on-going improvement of conditions during the early Turonian and the ultimate recovery of the marine ecosystem from the oceanic perturbation may then have led to increased ecologic pressure on *P. flexuosum*, causing its final disappearance (Ifrim 2013).

The response of *P. flexuosum* to the fluctuations of the OMZ is not reproduced when looking at the other ammonite species. Most first occurrences (FOs) take place during phases of a contracted OMZ, i.e., during improved conditions. Six FOs (*Quitmaniceras reaseri, Watinoceras* sp., *P. flexuosum, Paravascoceras* sp., *Phylloceras* sp., *P. pseudonodosoides,* cf. *Vascoceras*) are recorded during the first phase of improvement, in the second the FO of *Mammites nodosoides,* in the third the FOs of *Fagesia superstes, F. catinus* and *Neoptychites* sp. In the final improvement, *Collignoniceras woollgari* appears (Fig. 6). Beds which formed during improved conditions thus show phases of faunal changes and increased dispersal among ammonites. The only exceptions are *V. birchbyi* and a morphotype called "*Incertae sedis*" by Ifrim and Stinnesbeck (2007), which first occur during a phase of expanded OMZ. The FOs of *Watinoceras, Quitmaniceras reaseri,*
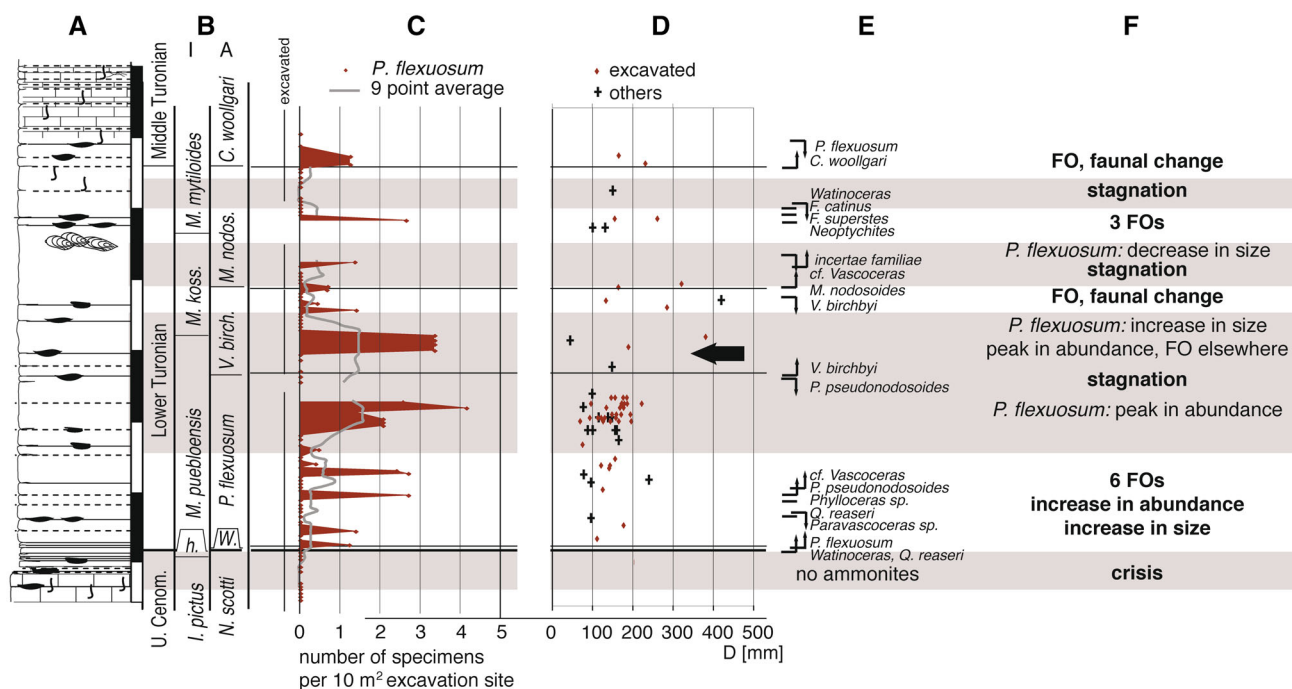
Fig. 6 The Vallecillo section with inferred expansion (*gray*) and contraction (*white*) of the oxygen minimum zone. *A* Litholog. *B* Biostratigraphic zonation based on *I* inoceramids and *A* ammonoids. *C* abundance of *P. flexuosum* over the section. *D* diameters of *P. flexuosum* plotted against the section. The *arrow* marks the approximate level, when *P. flexuosum* occurs in other sections, and when *V.* *birchbyi* first occurs within a phase of expanded OMZ. *E* first and last occurrences in the ammonoids. *F* interpreted bioevents in the ammonoid assemblage. *Bold* all-over response, *light* response of the species *P. flexuosum* (summarized from Ifrim 2006, 2013; Ifrim and Stinnesbeck 2007, 2008; Ifrim et al. 2011a)

Vascoceras birchbyi, and *Mammites nodosoides sp.* are more or less coeval at Vallecillo (Ifrim and Stinnesbeck 2008) within their palaeobiogeographic distribution. This was shown at larger scale for *Watinoceras* and *Mammites nodosoides* (Voigt et al. 2008). In contrast, the FO of *Fagesia superstes*, *F. catinus,* and *Neoptychites* were shown to be diachronous at Vallecillo; they immigrated into the region with a considerable delay, comparable to the planktic foraminifer *H. helvetica* and the inoceramid *M. kossmati* (Ifrim and Stinnesbeck 2008). Although the improvement of the conditions did not influence quantitatively the survival rates of ammonite hatchlings, it did affect their dispersal and migration patterns.

Last occurrences (LOs) of ammonites occur all over the section and do not seem to be related to the level of the OMZ (Fig. 6). They may rather represent changes in competition with other species such as immigrating ammonites, fishes of different types, or the early mosasauroids.

Comparison to other studies

A study similar to this was carried out by Reboulet et al. (2005) on the distribution of ammonoids across OAE 1d in southeast France. These Albian ammonoids also show little

evidence of post-mortem drift. The assemblages are mainly composed of Phylloceratidae, Lytoceratidae, and Ancyloceratidae. Although these groups persist throughout the Late Cretaceous, only a single specimen of *Phylloceras* was found at Vallecillo (Fig. 6) among the ca. 600 ammonites collected, and no Lytoceratid or Ancyloceratid was recorded. The absence or scarcity of these important ammonoid taxa at Vallecillo was interpreted to indicate an environment which was too hostile for them (Ifrim and Stinnesbeck 2007). Ammonitina found around the OAE 1d in south-eastern France were Desmoceratidae, also absent at Vallecillo. Here, the ammonoids belong to the families Acanthoceratidae and Muniericeratidae and some classified "incertae sedis", but none belongs to the taxa studied in south-eastern France. The overall changes in the Albian ammonoid communities were related to changes in the trophication of the water column, based on correlation to the abundance of indicative nannofossils, and to shifting of habitats from proximal to distal settings due to sea-level changes, but not to oxygenation of the water column as in Vallecillo.

Further studies exist which tried to relate morphotypes to palaeoenvironments, e.g., on their distribution in different facies (Batt 1989; Westermann 1996), or from quantitative analysis of the faunal turnover (Monnet 2009).

These studies, summarized by Ifrim (2013), do not interpret similar ecologies for the same morphotypes. The impact of environmental changes such as sea-level change, warming and the OAE1a on a persisting ammonoid population and related modifications in ornament and shell dimensions were described by Lehmann et al. (2015), but a response of the morphology to the environmental changes was not observed at Vallecillo. Other case studies deal with the interpretation of particular Upper Cretaceous species (Tanabe 1979; Tsujita and Westermann 1998; Wiese and Schulze 2005; Ifrim and Stinnesbeck 2010, Wilmsen and Mosavinia 2011), but they are not from stratigraphic levels coeval to those of Vallecillo. The only study from Cenomanian–Turonian boundary sediments is from a shallow-water environment in Nigeria (Courville 1992) and includes different species. In summary, none of the existing studies is comparable.

Conclusions

The quantitative data from the Vallecillo section show that ammonites did respond to fluctuations of the OMZ in the aftermath of OAE 2, although in a complex way.

Despite a similar mode of distribution through oceanic currents during early juvenile growth stages, the response of ammonites differs from that of inoceramids: The survival rate of ammonoid hatchlings is quantitatively independent of fluctuations of the OMZ (Ifrim et al. 2011a). They must have dwelled in higher water levels than inoceramid larvae. The hatchlings could not have dwelled in deeper parts of the water column because there the environment was too hostile for them to survive.

Whenever the OMZ contracted and the conditions improved in the deeper water column, although not at the sea-floor, ammonite species show FOs: six in the first phase of improvements (*Quitmaniceras reaseri*, *Watinoceras* sp., *P. flexuosum*, *Paravascoceras* sp., *Phylloceras* sp., *P. pseudonodosoides*, cf. *Vascoceras*), one in the second (*Mammites nodosoides*), three in the third (*F. catinus*, *F. superstes*, *Neoptychites* sp.), and another one in the final (*C. woollgari*). Exceptions are *Vascoceras birchbyi*, it has its FO in a phase of expanded OMZ, but at the level when also *P. flexuosum* disperses, and a morphotype described as "incertae sedis" by Ifrim and Stinnesbeck (2007). During phases of higher oxygenation, the ammonite species were thus able to disperse and reach the Turonian western Gulf shelf, although their total number did not increase. Phases of improvement thus represent phases of faunal changes at Vallecillo. During phases of expanded OMZ, however, the diversity seems to stagnate. LOs show no relation to the expansion and contraction of the OMZ.

The ammonite species *Pseudaspidoceras flexuosum* seems to have adapted to shallow oxygenated levels, or alternatively to levels of low oxygenation for part of the life cycle. This is shown by its increase in abundance, even during phases of an expanded OMZ. This peak in abundance coincides with a dispersals of *P. flexuosum* into other parts of the world, it occurs e.g., in sections of Colorado, Tunisia, or Nigeria. In a subsequent phase with improved conditions and a contracted OMZ in the upper *V. birchbyi* zone, *P. flexuosum* reaches its maximum in size. Upsection, the increased competition by newly immigrating species,s may have caused a considerable decrease in the abundance of *P. flexuosum* until its disappearance.

This study is another example for the complexity of species-based analyses. None of the existing studies on the palaeoecology of Cretaceous ammonoids is comparable to the results form Vallecillo. As already outlined by Ifrim (2013), this shows the complexity of analyses based on low taxonomic levels in ammonoids, and the necessity for more. It provides a further explanation, why the palaeoecology of ammonoids is still hard to access.

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