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The first record of sauropod dinosaurs from a palaeotopographical upland environment and its implications for megaherbivorous dinosaur faunal turnover in the Early Cretaceous of northwestern Europe

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Abstract

A fragmentary centrum of a dorsal vertebra and a manual ungual phalanx of eusauropod dinosaurs from the Upper Barremian – Lower Aptian of Balve in western Germany are described. The dorsal centrum shares potential synapomorphies with the enigmatic genus *Ornithopsis* and can probably be referred to a titanosauriform. The Balve record is of significance as it represents the only known direct evidence of this clade from an upland environment in Europe, which is assumed to have reached palaeoelevations of several hundred meters above sea level. Taphonomic signatures at some of the material from this site indicate prolonged surface exposure plus various stages of wear caused by water transport. The remains were finally deposited in sediment traps within a karst cave or fissure system.

The fossil record suggests a retreat or shift of sauropod habitat range from coastal plains and lowlands to hinter- and uplands during the Early Cretaceous in northwest Europe. It is hypothesized that this was linked to the faunal replacement of low- and mid-level browsing sauropods (e.g. diplodocoideans) by iguanodontian ornithopods near the Jurassic-Cretaceous boundary in this region. High-browsing titanosauriform sauropods had small overlap in the trophic niche with the ornithopods, facilitating a sympatric coexistence of both groups. However, their range was dependent on high-canopy vegetation that was probably more abundant in uplands. The previously observed "mid-Cretaceous bottleneck" in sauropod diversity may therefore be a result of partial extinction and/or a sampling bias, as the preservation of upland faunas are very exceptional. However, it is be cautioned to interpolate these regional observations to global sauropod diversity patterns.

Keywords: sauropod, faunal change, Rhenish Massif, Westphalia, Balve, Barremian-Aptian, fissure-filling

Kurzfassung

Ein fragmentarisches Centrum eines Rückenwirbels und ein Unguale aus der Hand eusauropoder Dinosaurier werden aus dem Ober-Barremium/Unter-Aptium von Balve, Nordrhein-Westfalen beschrieben. Das Centrum weist mögliche Synapomorphien mit der wenig bekannten Gattung *Ornithopsis* auf und wird hier mit Vorbehalt zu den Titanosauriformes gestellt. Es handelt sich um den ersten direkten Nachweis von Sauropoden aus einem Hochlandhabitat in Europa, welches vermutlich eine paläotopographische Höhe von mehreren Hundert Metern über dem damaligen Meeresspiegel erreichte. Taphonomische Indikatoren weisen auf eine längere subaerische Exposition, sowie auf verschiedene Abrasionstufen durch Wassertransport, zumindest bei einem Teil des Materials aus dieser Fundstelle, hin. Es wurde schließlich in Sedimentfallen innerhalb eines Karsthöhlensystems abgelagert.

Der Fossilbericht für die Unterkreide Nordwesteuropa, weisen auf einen graduellen Rückzug oder eine Verlagerung des Verbreitungsgebiets der Sauropoden aus Küsten-ebenen und Tiefländern in Hinter- und Hochlandregionen hin. Es wird die Hypothese aufgestellt, dass diese Veränderung mit dem ökologischen Ersatz von niedrigweidenden Sauropoden (z.B. Diplodocoiden) durch iguanodonte Ornithopoden bis zur Jura/Kreidegrenze in Verbindung steht. Hochweidende titanosauriforme Sauropoden hatten dagegen nur eine geringe Überlappung ihrer trophischen Nische mit den Ornithischiern, was eine sympatrische Koexistenz erleichterte. Allerdings war ihre Verbreitung an das Auftreten von Pflanzentaxa mit hohen Baumkronen gebunden, welche wahrscheinlich vor allem im Hochland vorkamen. Der „mittelkretazische Flaschenhals“ der Sauropodendiversität dürfte daher nur teilweise auf Aussterben und ebenso auf die geologischen Überlieferungslücken zurück zu führen sein, da Hochlandfaunen nur sehr selten überliefert sind. Gleichzeitig muss eine globale Verallgemeinerung dieser in Nordwesteuropa beobachtbaren Muster kritisch gesehen werden.

Schlüsselwörter: Sauropoden, Faunenwechsel, Rheinisches Massiv, Westfalen, Balve, Barremium-Aptium, Spaltenfüllung

Introduction

Although sauropod dinosaurs became replaced by ornithischians as dominant megaherbivores in the fossil record at the Jurassic/Cretaceous transition, they remained an important constituent of the global dinosaur fauna well to the end of the Cretaceous (e.g. Upchurch et al. 2004, Poropat et al. 2022). However, especially in Europe their record is rather sparse and incomplete. A notable exception, however, are the Iberian Peninsula, southern France, and Romania, where more abundant and diverse dinosaur material was recovered from Cretaceous strata (e.g. Nopcsa 1915; Lapparent & Zbyszewski 1957; Sanz et al. 1987; LeLoeuff 1993, 1995, 2005; Csiki 1999; Canudo et al. 2002, 2008; Garcia et al. 2010; Pereda Suberbiola et al. 2012; Vila et al. 2012; Castanera et al. 2014; Santos et al. 2015; Ősi et al 2017; Royo-Torres et al. 2017; Figuereido et al. 2021; Poropat et al. 2022).

The Cretaceous sauropod record in northwestern Europe is represented by tracks and scanty skeletal remains from the Berriasian of England (Ensom 1987, 2002), Germany (Hendricks 1981, Fischer 1998, Lockley et al. 2004, Hornung et al. 2012, Hornung 2013), and Denmark (Bonde & Christiansen 2003, Bonde 2012). Recently, substantial remains of embryonic sauropods, adult turiasaurs and basal macronarian sauropods have been found in the Berriasian of Angeac-Charente, western France (Barrett et al. 2016; Allain et al. 2022). The Wealden Supergroup (upper Berriasian through lower Albian) and the Cambridge Greensand (Upper Albian) of England yielded a rather diverse but very incompletely known sauropod assemblage (e.g. Mantell 1850, 1852; Seeley 1869, 1870, 1871, 1876; Owen 1875, 1876; Lydekker 1888, 1889 1890; LeLoeuff 1993: Blows 1995; Naish & Martill 2001a, 2007; Taylor & Naish 2007; Mannion 2009; Mannion et al. 2011; Upchurch et al. 2011; 2015; Taylor 2018). More comprehensive material is known from Albian strata of the Normandy region in northwestern France (*Normanniasaurus genceyi* Le Loeuff, Suteethorn & Buffetaut, 2013). Additional isolated elements have been recovered from Albian and Cenomanian deposits of northern France (Gervais 1852, Lapparent 1946, Buffetaut 1984, Le Loeuff 1993, Martin et al. 1993, Buffetaut & Nori 2012).

Here we report new sauropod skeletal remains (a manual ungual phalanx and a dorsal vertebral centrum) from northwestern Germany. This material expands the known palaeogeographical range of Lower Cretaceous (Upper Barremian – Lower Aptian) sauropods. More importantly, however, the remains, which derive from an upland locality formed in a palaeokarst environment, represent, to our knowledge, the first sauropod skeletal elements ever described from this palaeoenvironmental setting in Europe.

Geological Setting

The northern Sauerland (Fig. 1) shows multiple structures across its east-west range which are interpreted as paleo-deep karst. Comparable structures can also be observed in the western extensions of the Rhenish Massif, beyond Wuppertal to Wülfrath and west of the

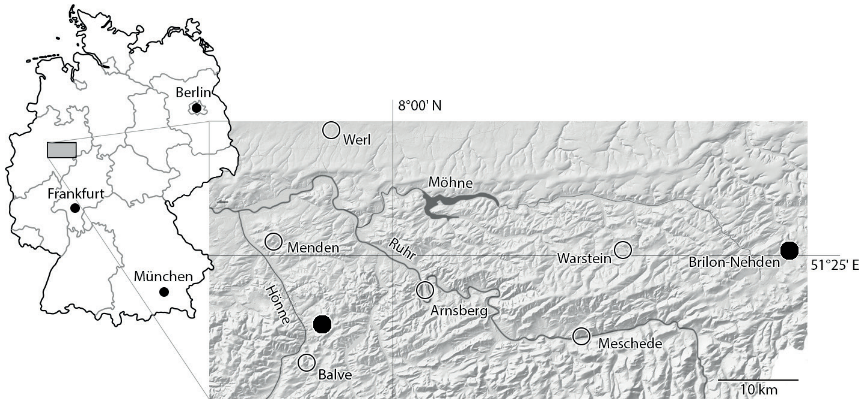


Fig. 1: Location of the Busche quarry at Balve-Beckum.

Lower Rhine Bight, in the northern Eifel (Drozdzewski et al., 1998, 2017). The opening of endokarst cavities to the surface occurred from the Lower Cretaceous onward. Thus, Lower Cretaceous or younger fillings are found at various sites in the northern Sauerland (Wirth 1970, Richter et al. 2014, Huckriede 1982, Schudack 1987, Lanser & Heimhofer 2013). Partially, the karstified carbonates have been inundated by the Aptian or Cenomanian transgressions (e.g Clausen & Leuteritz 1989, Ribbert & Skupin 2009).

The quarry discussed here is located in Balve-Beckum, in the area of the Remscheid-Altena Anticline (Fig. 1). The fossil site belongs to a NW-SE striking fault in the area of the quarry. The filling of the cavity has been cut by quarry operations at the level of 300, and 290 m above mean sea level (MSL), respectively, about 15 to 25 m below the original ground level before limestone quarrying began. Three horizontal cuts of infilled cavities are known from the 290 m above MSL. The largest has an approximately circular shape of 30 by 35 m ("Balve I", Lanser & Heimhofer 2013), a second one is also circular with a diameter of ca. 8 m ("Balve III"), and a third is more elongate, 4 m wide and more than 10 m long ("Balve II"). As far as known at the current state of excavations, the walls of all cavities are very steeply to vertically dipping.

In 2000, the first fossils identified as dinosaur teeth and bone fragments were found in the filling of the largest cavity (Balve I), and since then a highly diverse and abundant vertebrate assemblage has been recovered, including mammals, dinosaurs, pterosaurs, crocodyliforms, chelonians, squamates, lissamphibians, and selachians (e.g. Lanser & Heimhofer 2013, Lanser 2015, Schwermann et al. 2018, Skutschas et al. 2020, Martin et al. 2020, 2021; Sachs et al. 2022; AHS pers. obs., Figs. 2-3). The fossiliferous sediments consist of grey clays and silts, intercalated with coarser boulders (Lanser & Heimhofer 2013). In the course of the excavations, a complex depositional pattern of primarily fine-grained sediments was revealed. In most cases, the sediments are very clayey silts. Charcoal particles of small size occur regularly in these grey silts. They also contain vertebrate fossils, usually isolated fragments with varying degrees of mechanical wear. In addition, clasts occur which are, on the one hand, well rounded allochthonous clasts of different rocks (lydite of Carboniferous age, quartz, sandstone of as yet undetermined age) and, on the other hand, components of more autochthonous character (more or less weathered blocks of Devonian limestone, calcite as sharp-edged fragments and in larger blocks, calcarenite, and isolated fossils from Devonian limestone; Püttmann 2013, Hübner 2016). The sedimentary texture shows layered structures, indicating successive accumulation of filling. There are also distinct slump structures in the sedimentary succession. In some places, the sediments have subsided to such an extent that the strata dip nearly vertical, parallel to the fissure wall.

The sediments of the cavity filling at Balve have been palynostratigraphically dated to the Late Barremian to Early Aptian by Lanser & Heimhofer (2013). An Aptian age has also been assumed based on palynostratigraphy for the Brilon-Nehden locality (Schultz & Noll 1987), but the characean record indicates a correlation to the Barremian (Schudack 1987). The Saint Barbe Clays Formation at Bernissart was palynologically dated to the mid-Barremian to Early Aptian (Yans et al. 2006), and the co-occurrence of the iguanodontians *Iguanodon bernissartensis* Boulenger in van Beneden, 1881 and *Mantellisaurus atherfieldensis* (Hooley, 1925) in Barremian strata of England (Norman 2011, 2012), at Bernissart (Norman 1980, 1986, 2012), and Brilon-Nehden (Norman 1987), supports a Late Barremian age of all these localities. The iguanodontian remains of Balve have not yet been identified at genus or species level, but the overall evidence points to a stratigraphically similar position close to the Barremian-Aptian boundary. At this time, the site belonged to the Central European Rise, which includes, from West to East, the London-Brabant Massif, the Rhenish Massif, and the Bohemian Massif (Fig. 4).

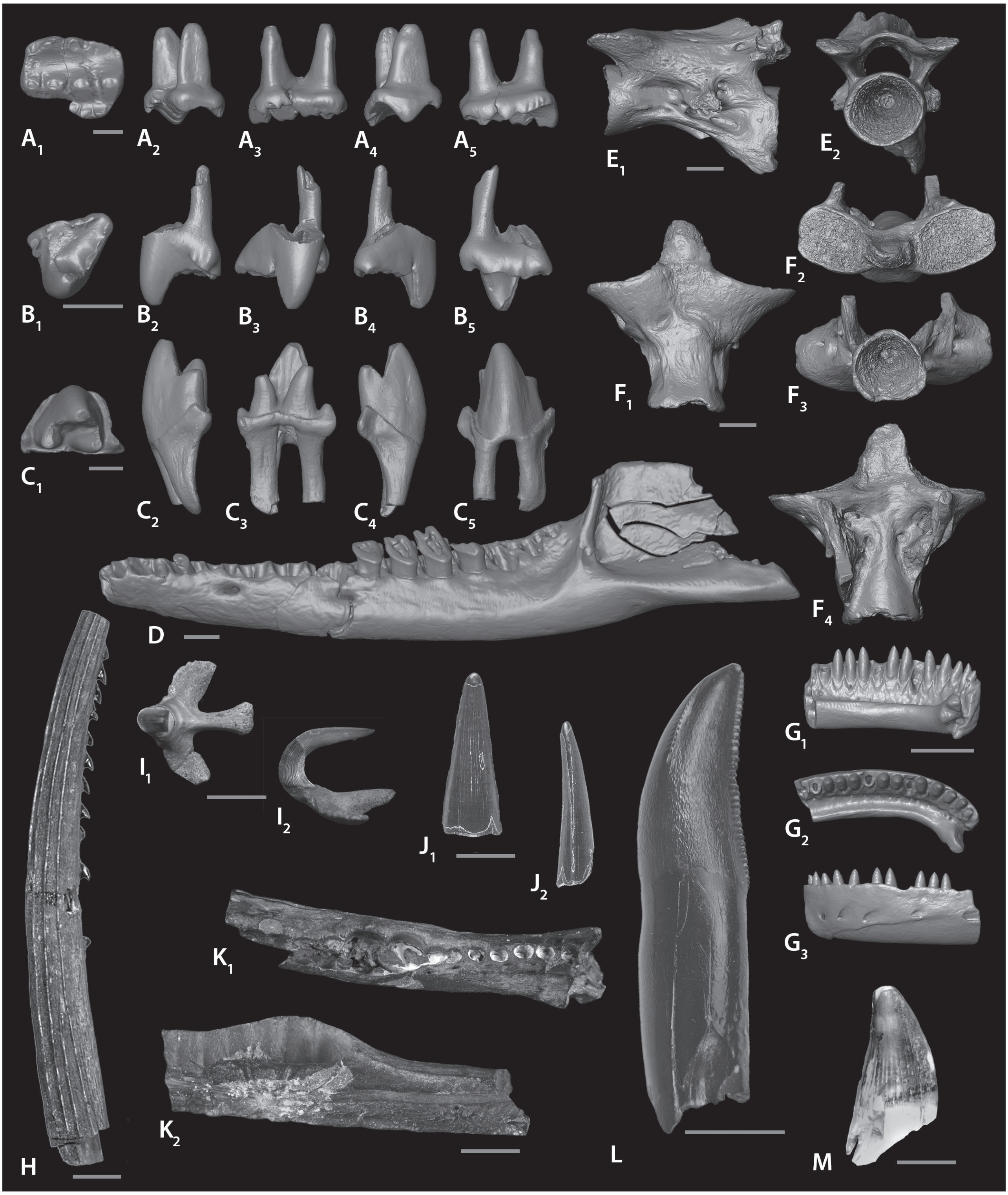


Fig. 2 Microvertebrate remains, Balve cave deposits, Upper Barremian – Lower Aptian, Balve. A-D Mammalia: **A** *Bructerodon alatus* Martin, Averianov, Schultz & Schwermann, 2021, WMNM P79403 (holotype), left upper M2 in A1 occusal, A2 mesial, A3, lingual, A4 distal, and labial views; **B** *Minutolestes submersus* Martin, Averianov, Schultz, Schellhorn & Schwermann, 2022, WMNM P82306 (holotype), right upper molar in B1 occusal, B2 mesial, B3 lingual, B4 distal, and labial views; **C** *Cifellitherium suderlandicum* Martin, Averianov, Schultz, Schellhorn & Schwermann, 2022, WMNM P82305 (holotype), right lower molar in C1 occusal, C2 mesial, C3 lingual, C4 distal, and C5 labial views; **D** *Beckumia sinemeckelia* Martin, Averianov, Schultz, Schellhorn & Schwermann, 2022, WMNM P82301 (holotype), dentary in buccal view; E-G Lissamphibia: **E** *Balveherpeton hoennetalensis* Skutschas, Kolchanov & Schwermann, 2020, WMNM P76320, anterior caudal vertebra in E1 left lateral and E2 posterior view; **F** *B. hoennetalensis*, WMNM P76315, atlas vertebra in F1 ventral, F2 anterior, and F3 posterior view; **G** Albanerpetontidae indet., WMNM uncat.,, left dentary in G1 lingual, G2 occusal, and G3 buccal view; H-I Selachii: **H** Hybodontiformes indet., WMNM uncat., dorsal fin spine in left lateral view. **I** Hybodontiformes indet., WMNM uncat., cephalic spine (photographic composite) in I1 dorsal and I2 left lateral views; J-M: Archosauria: **J** Pterosauria indet, WMNM uncat., tooth in J1 lingual and J2 mesial/distal views; **K** Crocodyliformes: Mesoeucrocodylia indet., WMNM uncat., left dentary in K1 occusal and K2 lingual views; **L** Dinosauria: Theropoda indet., WMNM uncat., tooth crown in lingual view; **M** Crocodyliformes: Goniopholididae indet., WMNN uncat., tooth in lingual view. A-C, E-G: Digital images of 3D models. Scales: A-C, E-G 0,5 mm, D 1mm, H-M 5 mm

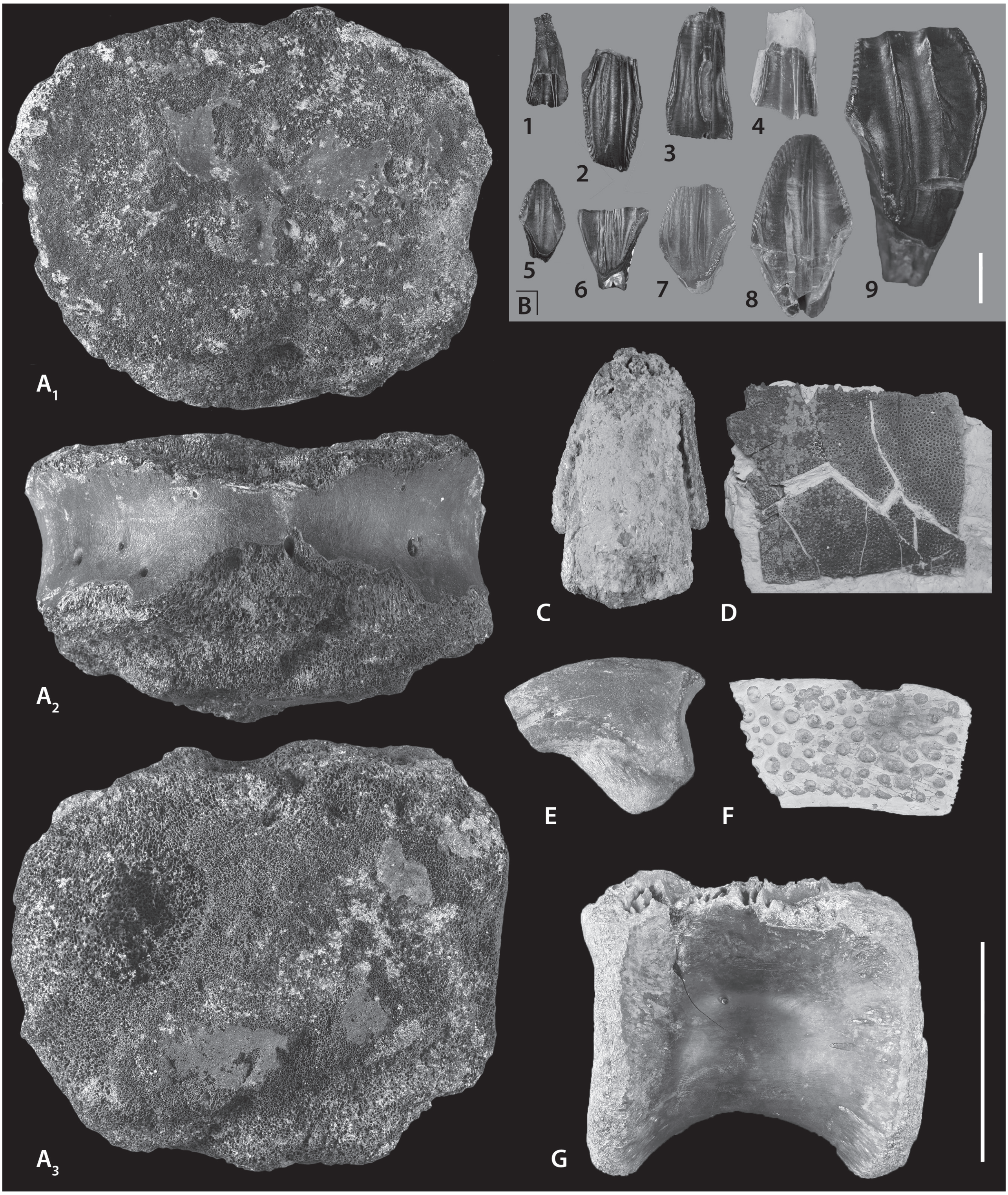


Fig. 3: Vertebrate remains, Balve cave deposits, Upper Barremian – Lower Aptian, Balve. A-C Dinosauria: Iguanodontia indet. **A** WMNM P48300, centrum of anterior caudal vertebra, in A1 anterior, A2 ventral, and A3 posterior view, **B** isolated teeth crowns in labial view, B1-B4 maxillary tooth crowns, B1 WMNM P48222, B2 WMNM P81316, B3 WMNM P81313, B4 WMNM P81308, B5-B9 dentary tooth crowns, B5 WMNM P81059, B6 WMNM P48332, B7 WMNM P81058, B8 WMNM P81073, B9 WMNM P81289, **C** pedal ungual phalanx, WMNM uncat. **D** Chelonia: *Helochelydra* sp., WMNM uncat., carapax fragment, **E** Dinosauria: Theropoda indet., manual ungual phalanx, WMNM P82323, **F** Crococdyliformes: Goniopholididae indet., WMNM P47516, para-vertebral osteoderm, **G** Dinosauria: Theropoda, WMNM uncat., dorsal vertebral centrum, lateral view. Scale bare: A, C-G 10 cm, B 1 cm.

Fig. 4: Palaeogeographic reconstruction of Central Europe during the Late Barremian (125 ma). The sea-level corresponds to the early phase of the Late Barremian - Early Aptian regression. Three important Barremian-Aptian upland vertebrate localities are indicated: Balve, Brilon-Nehden, and Bernissart. Base map by Ron Blakey, Colorado Plateau Geosystems, Phoenix, Arizona.

Institutional abbreviations

NHMUK – Natural History Museum, London, United Kingdom; WMNM – Westfälisches Museum für Naturkunde, Münster in Westfalen, Germany.

Systematic palaeontology

Dinosauria Owen, 1842
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995

Gen. et sp. indet.
(Fig. 5)

Material

WMNM P82311, a right(?) manual ungual phalanx (I-2), from the Balve II locality.

Description

The manual ungual phalanx (Fig. 5) is generally well preserved but misses part of the proximolateral half of the cotyle and has a slight abrasion at the apex. The element is anteroposteriorly elongate and distally it shows a gentle ventral curvature. An elongate, depressed-elliptical outline is evident in lateral and medial views. The cross-section is nearly isolaterally trihedral with a pronounced apicodorsal edge that broadens and becomes flatter proximally. In lateral view, the dorsal edge forms a smoothly rounded transition into the ventrodistal edge. The ventral surface of the element widens proximally but is otherwiese nearly flat or very gently convex. The lateral surface is slightly concave and the lateral and ventral surfaces bear several slightly irregular longitudinal grooves. Some of these grooves merge proximally with vascular foramina. Somewhat medially and parallel to the apicodorsal edge a sharp deep groove for attachment of the keratineous sheath extends along most of the elements mediodorsal surface. The medial side follows a gently convex curvature that is formed along the dorsal and ventral margins and lead to an overall slight lateral curvature of the element. However, the central region of the medial surface bears a deep depression. From here the posteroproximal part of the ventral margin curves medially to project as a small flange. The cotylus misses

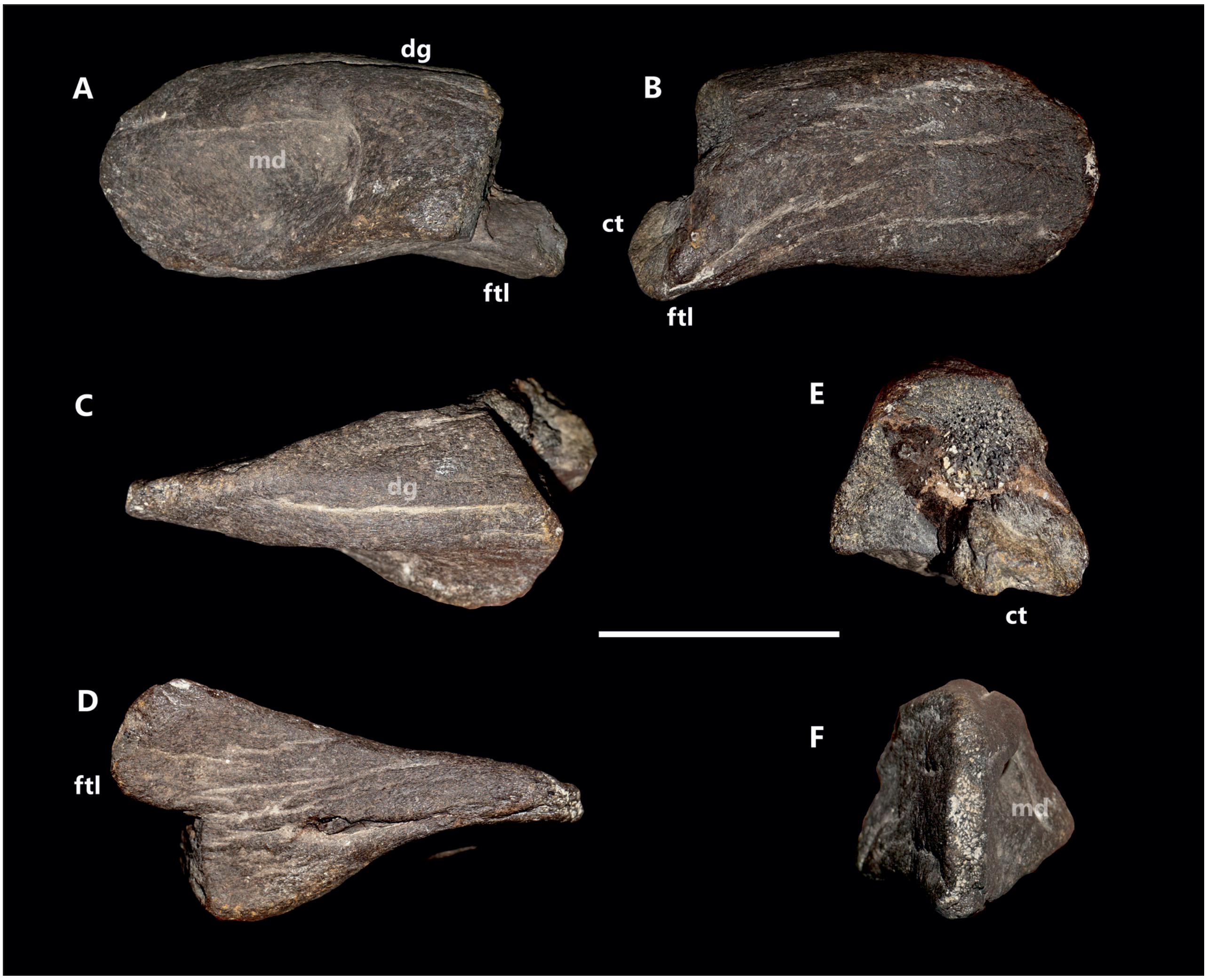


Fig. 5: Eusauropoda indet., WMNM P82311, right(?) manual ungual phalanx I-2, Balve cave deposits, Upper Barremian – Lower Aptian, Balve, in **A** medial, **B** lateral, **C** dorsal, **D** ventral, **E** posterior, **F** anterior aspects. Abbreviations: ct – cotylus, dg – deep dorsal groove, ftl – flexor tendon lip, md – medial depression. Lighting in C from lower left, in E-F from upper right. Scale bar: 5 cm.

most of its dorsal and medial portions. From what is observable the cotylus forms a deep cup that was bounded ventrally by a thick, rugose and proximally projecting lip for attachment of the flexor tendon. The breakage reveals that the element is composed by a massive bony tissue with a dense substantia spongiosa and only a limited zone of larger cancellae in the centre.

Measurements

Overall length: 77.0 mm; Cotylus width (max.): >35.0 mm; Cotylus height (max.): 29.5 mm; max. height of distal part: 35.3 mm.

Taxonomic affinities

The identification of WMNM P82311 as a sauropod manual ungual phalanx I-2 is supported by the elements massive and basically trihedral morphology, its lateral curvature, the laterally and ventrally compressed aspect, and the blunt apex. In addition, the slight lateral curvature indicates that the element originates from the right side.

Manual unguals in basal sauropodomorphs, including basal sauropods, resemble the plesiomorphic saurischian condition, which is characterised by a strong overall curvature and pointed apices. Straighter and blunter morphotypes, on the other hand, are widespread at more derived eusauropods in contrast to the condition seen in basal taxa (e.g. Allain & Aquesbi 2008). A manual ungual of an undetermined eusauropod from the Upper Jurassic of Tanzania (previously referred to *Janenschia robusta* (Fraas, 1908)), resembling the morphology of WMNM P82311, was described by Mannion et al. (2019). In contrast, derived titanosauriforms generally lack manual unguals (Upchurch et al. 2004). Despite their peculiar morphology, isolated manual unguals of sauropods are currently not considered to be diagnostic at lower systematic levels. Therefore, the specimen from Balve is herein referred to as Eusauropoda indet.

?Titanosauriformes Salgado, Coria & Calvo, 1997

Ornithopsis Seeley, 1870
Ornithopsis? sp.
(Fig. 6)

Material
WMNM P82326, a damaged centrum of a dorsal vertebra, from the Balve II locality.

Description
WMNM P82326 (Fig. 6) is a strongly worn centrum of a dorsal vertebra which as indicated by the presence of dorsolateral paraxial camerae (e.g. Wedel 2003). The portion dorsal to a line limiting the anterior articular condyle is lost to damage. The substantia compacta is missing on most of the surface, hence the camellate internal structure is largely exposed. The camellae are small (average diameter 1-5 mm) but tend to become larger and irregular in outline towards the interior of the centrum. Two steeply-walled, ovate grooves on the dorsal surface, being placed slightly posterior to the centrums mid-length, mark the location of camerae that relate to the lateral pneumatic foramina. These characters are typical for the semicamellate type of pneumatization in derived sauropods (Wedel 2003). The centrum's articulation surfaces are partly present and indicate a strong opisthocoely. As preserved, the anterior condyle has a semielliptical shape in transverse cross-section. Its ventral portion is damaged but it is still evident that the anterior cotyle was dorsoventrally higher than transversely wide. The posterior cotyle is flat-dish shaped in its central region, has an overall ovate outline, and is dorsoventrally higher than transversely wide. The cotyle and condyle are connected along the ventral margin of the centrum by a ventral bulge (Fig. 6: vb) that is formed by the centrum's converging lateral margins. The latter condition is evidenced by preserved patches of substantia compacta on the ventrolateral flanks of the centrum which demonstrate that the ventral bulge is not an artefact of erosion. The centrum was thus higher dorsoventrally than transversely wide, an uncommon morphology in sauropod dorsal vertebrae (see discussion below). The centrum also was axially slightly longer than transversely wide. As preserved the axial length is only very slightly longer than the centrum's dorsoventral height. However, when adding the substantial missing portion in the dorsal region, the complete centrum was probably higher than long.

Most of the circumferential regions of the centrum show surface-parallel cracks that intensify towards the periphery and caused the loss of most of the substantia compacta by exfoliation (Fig. 6: pcr). Towards the centre of the element, these cracks become conspicuously less intense and camellate tissue is contrastingly in a good state of preservation.

Measurements
Centrum length: >164.0 mm; Centrum width: >134.5 mm; Centrum height (max.)*: >145.5 mm.

Taxonomic affinities
The semicamellate tissue indicates that WMNM P82326 belongs to an eusauropod. The opithocoelous vertebral type in conjunction with the presence of camerae further indicate that the centrum derives from the dorsal series. Even though the state of preservation hampers an easy assessment of the taxonomic relationships of WMNM P82326, an unusual and most indicative feature is the laterally compressed aspect of the centrum in axial view and its ventrally converging ventrolateral sides. Dorsal vertebrae in most eusauropods are ventrally broad and rounded and transversely expanded in axial view (e.g. Upchurch et al. 2004). The only known exception is *Ornithopsis hulkei* Seeley, 1870, from the lower Barremian Wessex Formation of the Isle of Wight (southern England), that is likewise known only from a poorly preserved dorsal vertebra (NHMUK R28632, see Blows 1995; Naish & Martill 2001a, 2007; Naish 2010; Upchurch et al. 2011; Fig 7). Upchurch et al. (2011) considered this character as diagnostic for this very imperfectly known taxon and regarded it as a titanosauriform of uncertain position. They rejected the previous assumption of a closer relationship to brachiosaurids by Blows (1995). Assuming titanosauriform affinities would point to a mid- to posterior position of WMNM P82326 in the dorsal series, and owing to the relatively slightly shorter axial length, probably to a somewhat more posterior position than NHMUK R28632. The dorsoventral expansion, ventrolateral convergence and relatively small size of the centrum are conspicuous similarities between WMNM P82326 and NHMUK R28632. The size of both, WMNM P82326, as well as NHMUK R28632 (Naish 2010), indicate that they belonged to comparatively small individuals given the average sauropod dimensions. Extrapolated to the proportions of the basal titanosauriform *Giraffatitan brancai* (Janensch, 1914), the holotype of *O. hulkei* would have belonged to an animal of about 16 to 18 meters in length (comparative data from Janensch 1950a, b). The length of the centrum from Balve can be estimated to be about 75% of that from NHMUK R28632 (~17 cm versus ~23 cm), indicating that the former belonged to a slightly smaller individual. This assessment acknowledges the incomplete preservation of

both specimens, hence other morphometric indices can only be compared with less confidence.

The most striking difference between WMNM P82326 and NHMUK R28632 can be found in the structure of the camellae which is coarser and cancellate in NHMUK R28632. According to Wedel (2003) the pneumatic structures in sauropod bones underwent ontogenetic changes: The size of peripheral camerae shows a negative allometric relationship with increasing individual age in taxa with camerate and polycamerate structure. Given the fact that WMNM P82326 is overall smaller than NHMUK R28632 an ontogenetical scenario would involve a positive allometric relationship between individual age and size of the camellae. This would imply a remodeling of preformed bone tissue with individual growth by invasion and expansion of the air sacs rather than a synchronous diverticulation of the air sacs with progressing bone formation as suggested by Wedel (2003) for camerate tissues. According to the presence of larger camellae in the centre of WMNM P82326 such a remodelling would have occurred in a centrifugal direction. However, as Wedel (2003) pointed out, the data on ontogenetic patterns in semicamellate and camellate sauropod vertebrae is too much scarce for the development of a robust hypothesis. Therefore, the taxonomic significance of these differences is unknown. They may be related to the individual's ontogenetic stage, the position within the vertebral column, or to intraspecific or interspecific variation.

The poor preservation of WMNM P82326 and the incompleteness of the type material of *O. hulkei* (NHMUK R28632) precludes the comparison of further characters. Therefore, we can only tentatively refer WMNM P82326 to the genus *Ornithopsis*. Nevertheless, a close taxonomic relationship appears to be supported by similar characters found in both specimens.

Discussion

Taphonomy

The vertebral centrum (WMNM P82326) underwent strong taphonomic wear before finally being embedded within the karst cavity. It not only lacks the complete neural arch but also most of the substantia compacta, being factually reduced to a "core" of the substantia spongiosa. The mechanical damage to the periphery of the centrum was controlled by a system of cracks that were formed subparallel to the bone surface in the peripheral few centimetres of the centrum (Fig. 6: pcr). They result in an exfoliation pattern of damage that indicate subaerial weathering of the bone before embedding. In places – especially on the ventral surfaces of the bone – the exfoliation was incomplete and some patches of substantia compacta are preserved. According to the weathering stages as defined by Behrensmeyer (1978), this exfoliation (or flaking) corresponds to stage 2 and 3. This suggests a subaerial exposure of 2 to 8 years, assuming semi-arid tropical climatic conditions for the Balve area in Cretaceous times, similarly to that in present-day Kenya (compare also Behrensmeyer & Miller 2012). The estimate for subaerial exposure time of WMNM P82326 may be closer to the lower part of the range, as mechanical transport into the karstic fissure probably strongly increased the damage exerted to the bone's periphery. The internal structure of the bone, including the thin walls of the camellae which are in good condition, indicating that degradation by weathering did not affect the entire element before burial (therefore not reaching stages 4 and 5 of Behrensmeyer 1978). There is also hardly an indication of post-burial or excavational damage and in at least one place fine-grained sediment of the karstic fill still covers an exfoliated bone surface. The sediment also impregnated the camellae.

It is of interest to note, that the vertebrate material from Balve shows a broad range of pre-burial damage. This damage comprises strongly abraded and broken and (even though rarer), nearly pristinely preserved specimens, which indicates a variety of taphonomic histories for these elements. Such varying preservation qualities indicate that different degrees of fluvial transport wear were exerted on the skeletal remains prior to their final deposition within the cave system. Additionally, the exfoliation cracks on WMNM P82326 reveal that desiccation during prolonged subaerial exposure contributed to the taphonomic history. However, the broad variety in preservational states may not only be related to the transport distance. It could also be influenced by the number of transport phases which the material underwent before reaching the final burial place and by the capacity of the flows transporting them. Low capacity flows resulted in salient bedload transport with intermittent deposition during waning flow phases, while high capacity flows allowed floating of the components and higher transport distances during a single flow event.

Another karstic fill deposit in northwestern Germany revealing Lower Cretaceous vertebrate faunas was found at Brilon-Nehden (see discussion below). The preservation of associated skeletal elements referrable to a single juvenile individual of *Iguanodon bernissartensis* (see Norman 1987), and the often fragmentary but largely unworn state of the bones indicates, that the taphonomic history in this locality did not involve extended transport phases. Instead, some bodies may have reached the cavern interior prior to full disintegration. Final trapping within the cave system terminated the transport history of the elements in all cases.

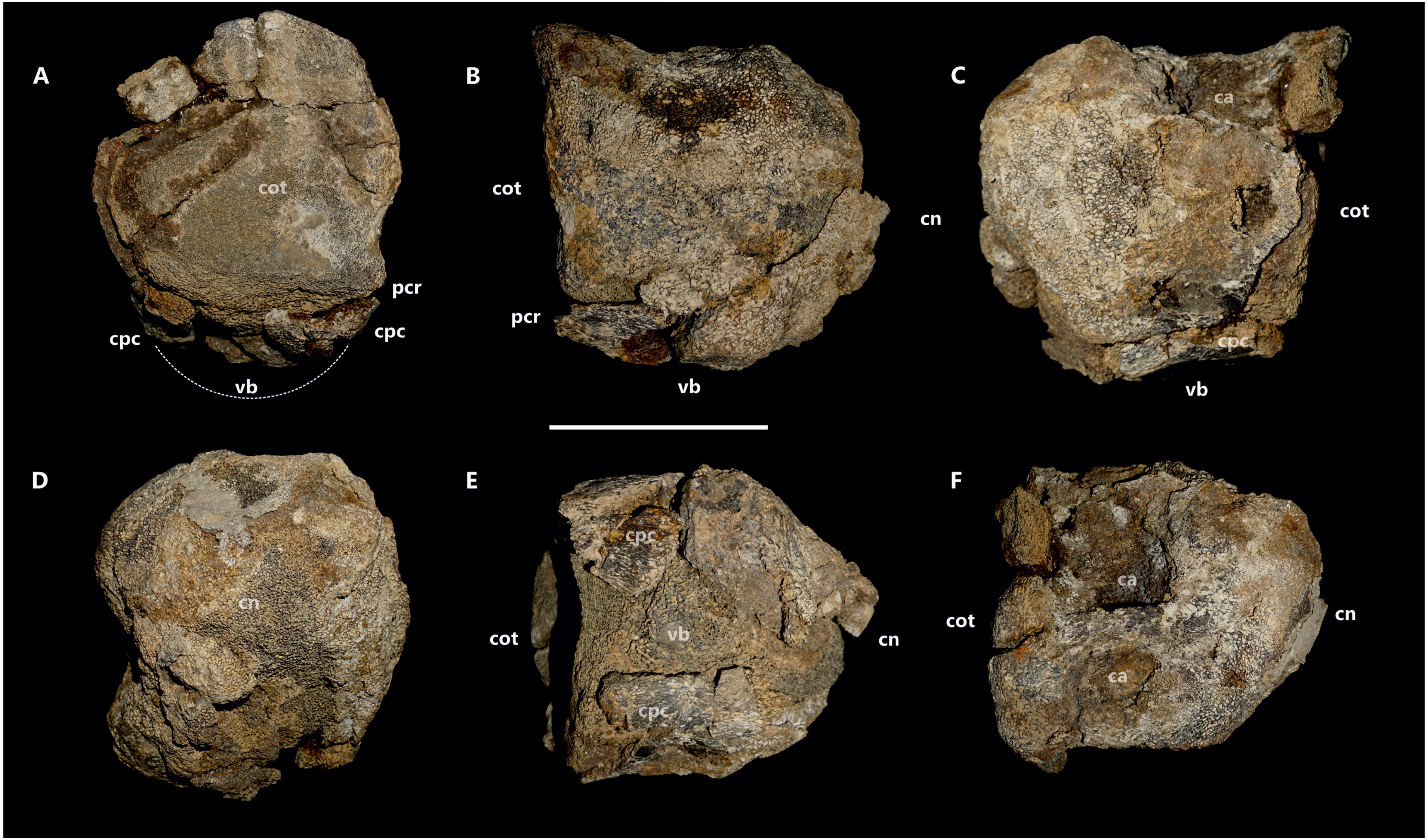


Fig. 6: *Ornithopsis*? sp., WMNM P82326, fragmentary dorsal vertebral centrum, Balve cave deposits, Upper Barremian – Lower Aptian, Balve, in **A** posterior, **B** right lateral, **C** left lateral, **D** anterior, **E** ventral, **F** dorsal aspects. Abbreviations: ca – camara pneumatica, cn – condylus vertebralis cranialis, cot – cotylus vertebralis caudalis, cpc – remains of substantia compacta, pcr – circumperipheral cracks, vb – ventral "bulge". The dotted line in A delimits the approximate outline of the reconstructed ventral "bulge". Lighting in B, E, F from lower right. Scale bar: 10 cm.

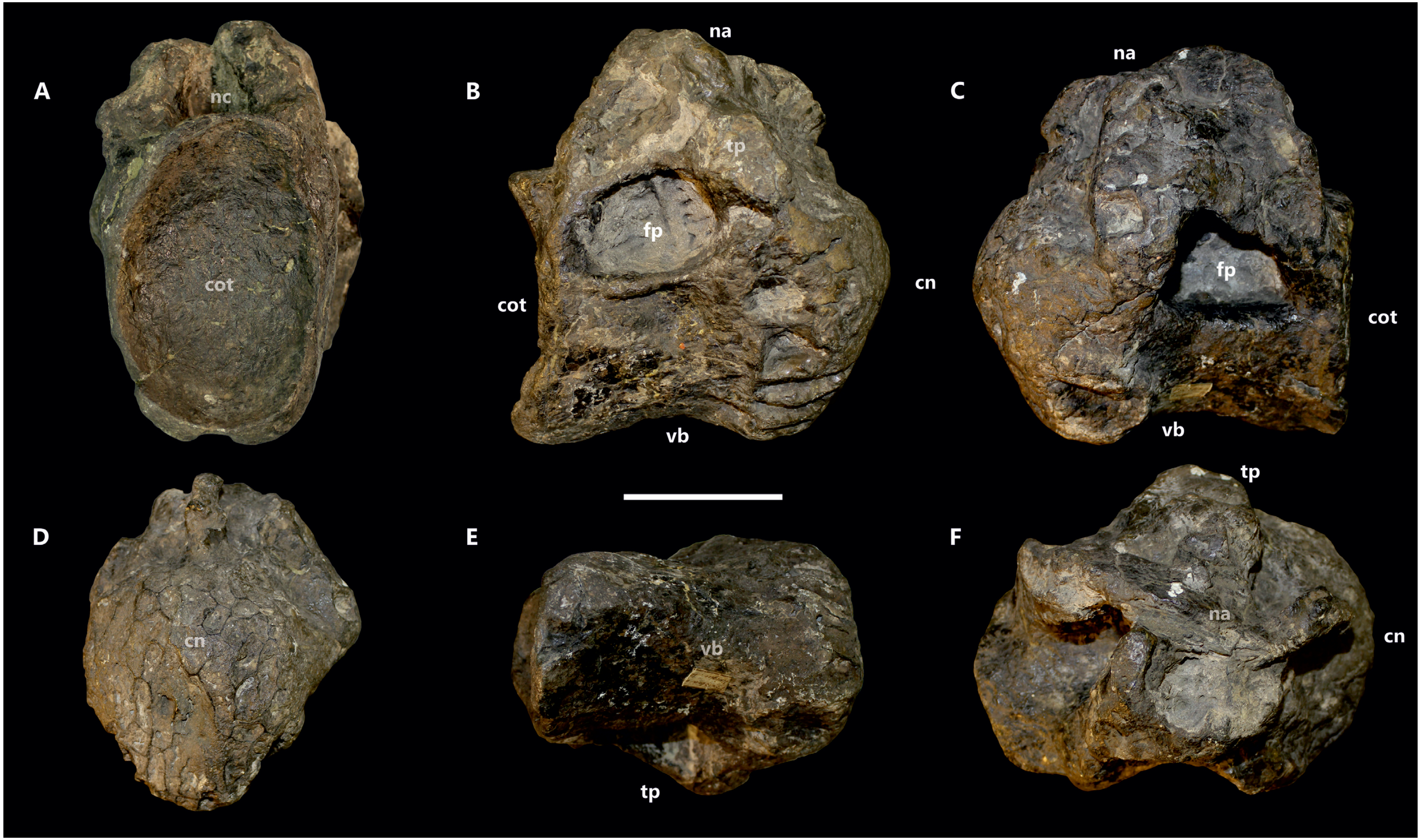


Fig. 7: *Ornithopsis hulkei* Seeley, 1870, NHMUK R28632 (holotype), dorsal vertebral centrum Wessex Formation, Lower Barremian, Isle of Wight, England, in **A** posterior, **B** right lateral, **C** left lateral, **D** anterior, **E** ventral, and **F** dorsal aspects. Abbreviations as in Fig. 6 and additionally: fp – foramen pneumaticum, na – neurapophysis, nc – canalis neuralis, pt – processus transversus. Scale bar: 10 cm.

Palaeoelevation and palaeoenvironment of the northern Rhenish Massif in the Early Cretaceous

The Balve locality shares with the roughly contemporaneous dinosaur occurrences of Bernissart and Brilon-Nehden (Fig. 4) its formation as a sediment trap in an uplifted, exposed, karstified Palaeozoic carbonate platform. The Bernissart accumulation resulted from preservation in an open sink-hole lake (e.g. Martin et al. 2012; Quinif & Licour 2012), while the Brilon-Nehden (e.g. Huckriede 1982; Kampmann 1983; Oekentorp 1984; Schudack 1987) and Balve deposits (Lanser 2015) were formed in subterranean cave-fissure systems by fluvial processes.

However, while all current models support a terrestrial setting as source for the Lower Cretaceous biota from the Sauerland palaeokarst fillings, they considerably vary with regard to local palaeogeography and -topography.

There is consensus that the cavities were corroded within a specific lithofacies of Middle Devonian marine limestones (Massenkalk facies) that was – together with other mid-Palaeozoic strata – uplifted, folded and partially thrusted into a belt of WSW-ENE trending anticlines and synclines during the Late Carboniferous Variscan Orogeny (Drozdzewski et al. 2017). The central region of this fold belt, the Rhenish Massif, underwent considerable erosion during the Permian through Early

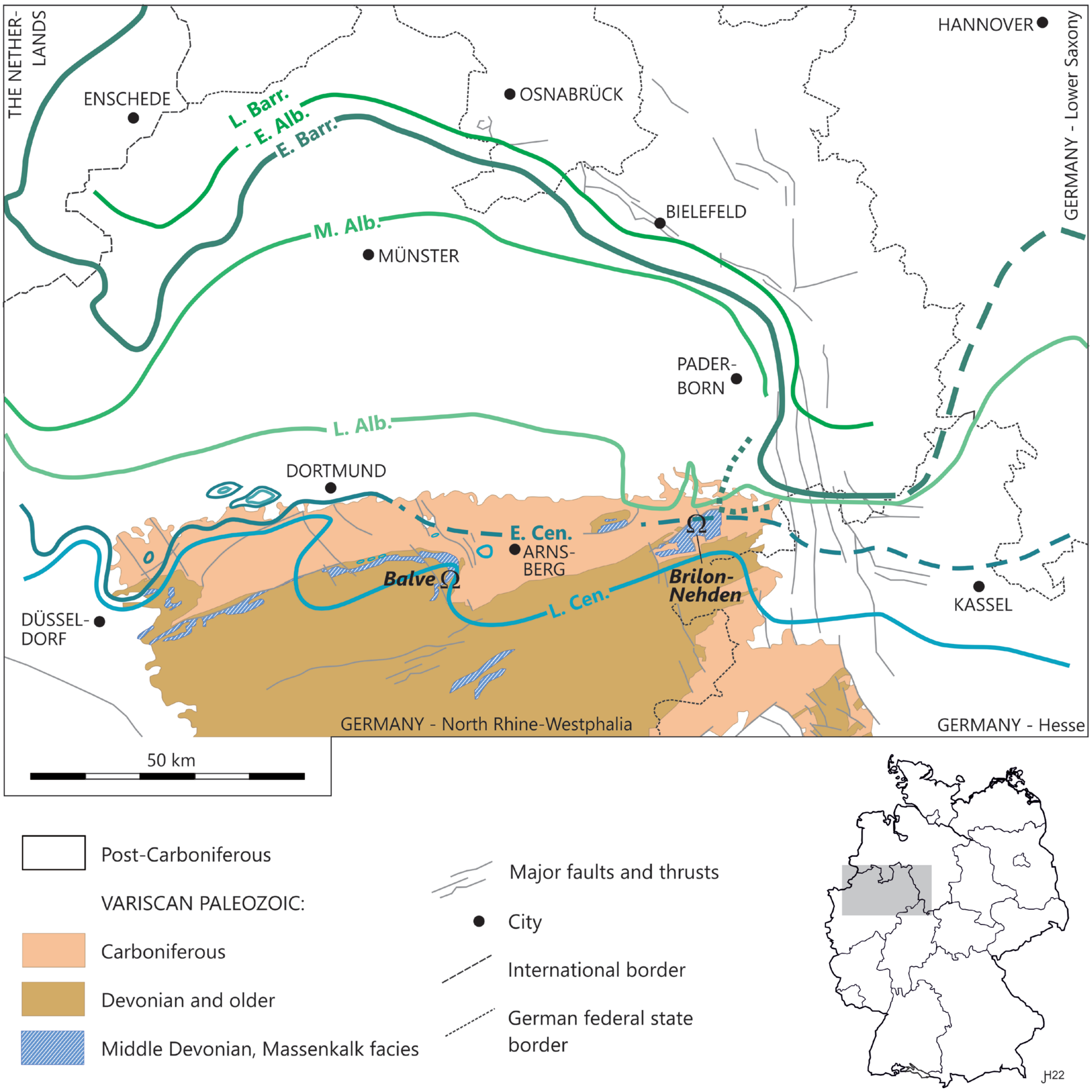


Fig. 8: Early Cretaceous regional palaeogeography of the northern Rhenish Massif and western Lower Saxony Basin. The dotted line of the Early Barremian coastline represents a possible short-term extension of marine influence to the northern reaches of the Brilon Anticline according to data from Ribbert & Skupin (2009). Transgression occurred in southward direction. Geological information by GEOportal.NRW (2022), palaeo-coastline data from Schott et al. (1967/69), Meiburg (1979), Schudack (1987), Mutterlose & Harding (1987), Frieg et al. (1990), Mutterlose et al. (1995), Wilmsen et al. (2005), Kaplan (2008), Hoffmann & Mutterlose (2011), Püttmann et al. (2018).

Cretaceous interval, during which it was subjected to several episodes of subsidence and uplift. After moderate rates during the Early and Middle Jurassic, uplift slowed down during the Late Jurassic but continued throughout the Cretaceous (Büker 1997). Concurrently, linked to incipient opening of the North Atlantic and intense rifting in the North Sea Basin, the Lower Saxony Basin – forming the northern foreland of the Rhenish Massif – underwent strong subsidence and marine flooding (e.g. Betz et al. 1987, Mutterlose et al. 1995). Uplift in the south and subsidence in the north confined marine submergence between the Valanginian and Late Albian to a line about 60-100 kms north of the Sauerland localities. Only in the west (Alstätte Embayment) and the east (Egge Embayment, Hessian Depression) local subsidence centres allowed marine ingressions as early as the Hauterivian-Barremian (Jaritz 1969; Mutterlose et al. 1995; Hoffmann & Mutterlose 2011; Fig. 8).

The palaeoelevation and -topography of the Sauerland area during the Lower Cretaceous, and especially during the Late Barremian / Early Aptian interval when the dinosaur-bearing deposits were formed, have been reconstructed to various models. Clausen et al. (1978) and Clausen & Leuteritz (1989) assumed an upland situation with the karstified, faster eroding limestones forming „highland valleys" surrounded by slower eroding not karstified siliciclastics. Similar karst windows were envisaged by Hölder & Norman (1986). These authors emphasized the „close proximity" of the Brilon-Nehden locality to the Barremian shoreline (Egge Embayment) and speculated about a „slowly flowing river" as source of the karst fill sediments. They implied a relatively low palaeotopographic situation. None of the afore-named authors suggested detailed palaeohydrological or speleogenetic models for the formation of the karst structures. However, Hölder & Norman (1986) and Lanser (2015) discussed a rapid base level rise connected to marine eustasy and crustal subsidence to explain the infill and preservation of allochthonous deposits within the caves.

Niggemann (2003) on the other hand pointed out that the observable facts can well be explained by generalized meteoric epigenic karst processes in an eroding upland setting, involving cave formation even below the base level by invoking bathyphreatic flow patterns (sensu Ford & Ewers 1978). According to this model, the necessary flow gradient was provided by an incising network of streams in the eroding Palaeozoic bedrock, resulting in a high local palaeotopographical relief.

Additionally, hypogenic karst formation was initiated by raising hydrothermal fluids during various episodes (Drozdzewski et al. 1998, 2017; Götte & Richter 2003; Richter et al. 2014). Drozdzewski et al. (2017) show that there is clear evidence for intense hydrothermal karstification in the Mesozoic in the northern Rhenish Slate Mountains and also in parts of the Eifel Mountains. The deep formation of fissure- and hall-like cavities in the Devonian mass limestone also reached the palaeosurface in several places and led to the formation of sediment traps (sinkholes and sinking streams). Theoretically, the karst cavities may have formed by coastal hypogene speleogenesis at the contact of a freshwater aquifer with saltwater intrusion in a littoral setting as well (e.g. Mylroie & Carew 1995; Klimchouk 2017). However, there is no direct evidence for the latter scenario, while the deposition of terrestrial fossils clearly indicates an epigenic component in the formation of the cavities here of interest. Drozdzewski et al. (2017) showed that the filling of karst cavities was not contemporaneous with the end of karstification. Rather, they document subsidence of the sediments in individual cases. Similar observations result from the excavation in Balve (pers. obs. AHS) and Brilon-Nehden (Schudack 1987), where the sediments after their deposition in the karst cavities partly slumped considerably. A progressive dissolution of the limestone in the underground at the time of deposition or afterwards therefore seems plausible.

The relationships of the Palaeozoic basement to transgressive Albian-Cenomanian deposits are better preserved in the Brilon-Nehden area than at Balve. The following considerations are thus mostly based upon data from the Brilon Anticline, hosting the Brilon-Nehden locality that is located about 50 km to the east of the Balve locality. The latter is assumed herein to have undergone a very similar geological history during the Cretaceous.

In contrast to earlier suggestions of a late Lower Cretaceous subsidence from circumstantial evidence, models of crustal uplift generally assume a slow but persistent uplift of the area throughout the Cretaceous (about 3.5 m*myr^{-1}, Büker 1997; see also Jaritz 1969; Karg 1998, Fig. 9). In order to assess the effective uplift rate (crustal uplift minus erosion rate), we superimpose here the crustal uplift gradient (expressed as uplift*time^{-1}) of Büker (1997) to the eustatic sea-level curve of Haq (2014). The intersection datum of the crustal uplift gradient as well as the effective net uplift gradient (expressed as [uplift-erosion]*time^{-1}) with the sea-level curve is provided by the onlap of coarse-grained near-shore deposits of Mid- to Upper Albian age onto the Palaeozoic basement of the Brilon Anticline (Wünnenberg and Keddinghausen beds, Hiss & Speetzen 1986, Ribbert & Skupin 2009). The second calibration point for the (maximum) effective net uplift gradient is given by the Early Barremian highstand that did not inundate the Brilon Anticline (e.g. Meiburg 1979; Hiss & Speetzen

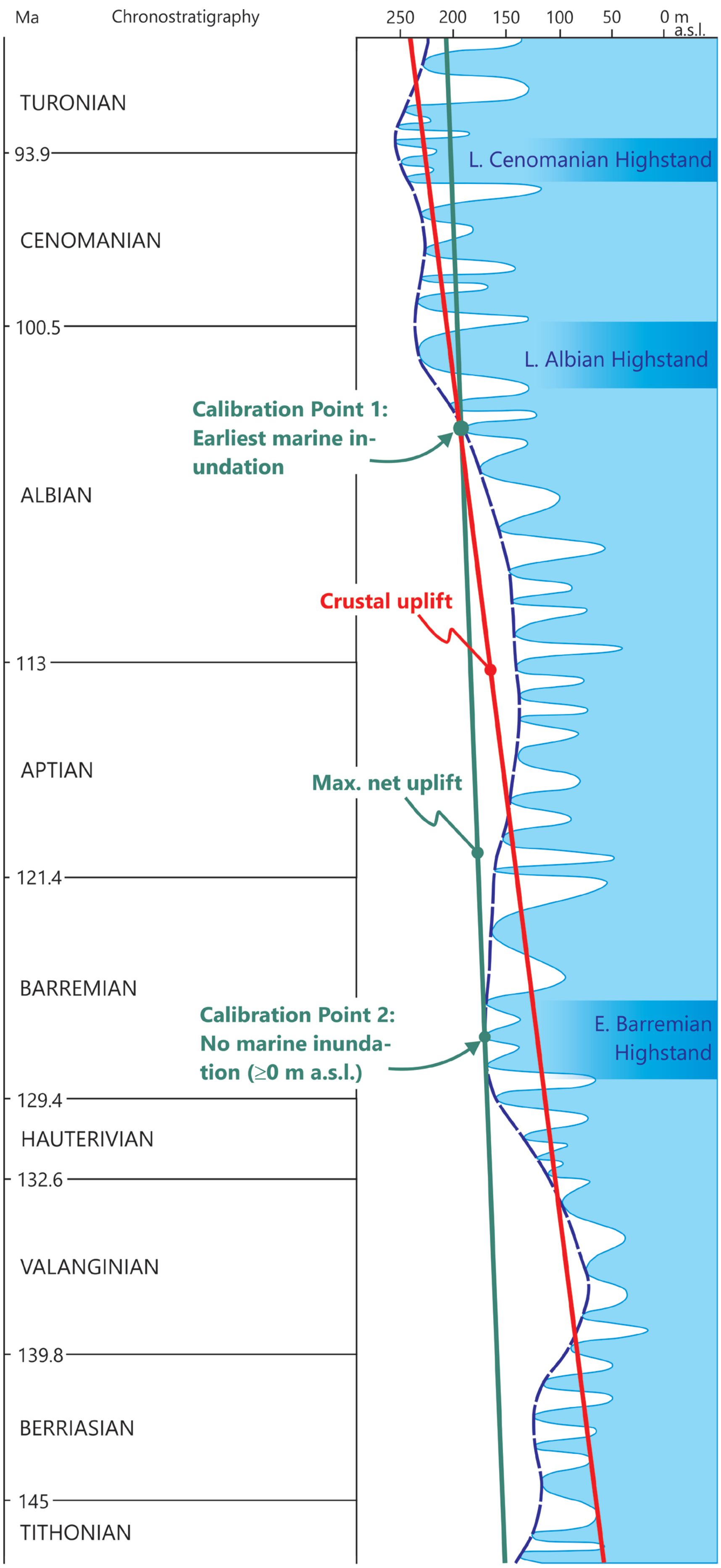
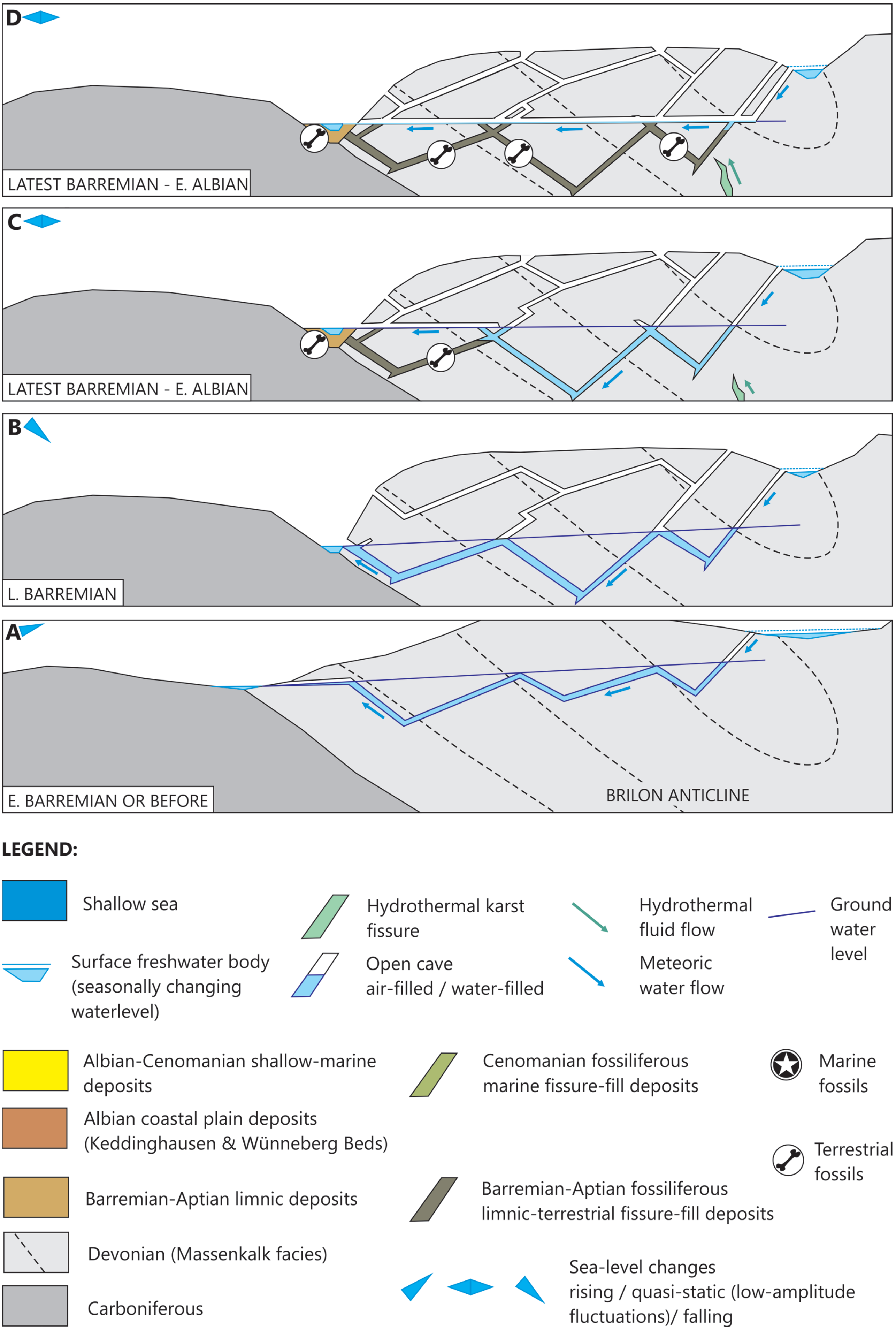


Fig. 9: Reconstruction of effective net uplift gradient and palaeotopographic history for the northern Brilon Anticline during the Early Cretaceous. Geological evidence indicates inundation (mean sea-level datum) of the Brilon Anticline twice, at the Barremian and Late Albian highstands, respectively (Ribbert & Skupin 2009). Net uplift and eustasy account for local baselevel fluctuations of 50 to 150 m during this interval. These are minima, assuming a position of the immediate northern foreland of the Brilon Anticline at sealevel during the Early Barremian. Palaeoelevation in the hinterland may have been substantially higher, especially at Balve that was only peripherally reached even by the Late Cenomanian transgression (see Fig. 8). Crustal uplift gradient after Büker (1997), eustatic sealevel curve from Haq (2014),adapted to absolute ages according to the International Chronostratigraphic Chart (version 2022/10). The altitude scale refers to meters above present day sea level (a.s.l.).

1986; Schudack 1987). Coarse-grained, plant-bearing, clastic deposits of Barremian-Aptian age, previously interpreted to represent a Barremian transgression in the area, have recently been interpreted to be fluvial in origin (Ribbert & Skupin 2009). They may have intercalated towards the north with similar beds that contain indicators of marine influence (glauconite grains and marine invertebrates, Ribbert & Skupin 2009), representing a distal coastal setting during the Barremian highstand. These considerations result in the estimation of the maximum effective net uplift rate to have been about 0.95 m*myr^{-1} during the late Early Cretaceous. This rate may have been in fact much lower or even negative, as the palaeotopographical altitude of the land surface of the Brilon-Nehden locality above the Barremian sea-level is unknown (for the model it is assumed to be zero as a minimum, almost certainly a too low value). Therefore, it gives only a minimum of thickness that has been eroded between the Barremian and Albian highstands. The same applies for the palaeoelevation estimates that can be read from the relationship of the effective net uplift gradient to the sea-level for the Late Barremian to Late Albian interval that provides only rough – and again certainly too low – minima for the palaeoelevation. The presence of a differentiated local topographic profile well into the Cenomanian is also evidenced by Lower Cenomanian marine karst fill deposits in the Brilon Anticline. These deposits demonstrate that parts of the anticline were not inundated before the maximum highstand of the Late Albian/Early Cenomanian transgression (Ribbert & Skupin 2009). A more structured relief of the Albian/Cenomanian transgressive surface on the southern onlap zone to the Rhenish Massif has also been demonstrated by Wilmsen et al. (2005). Earlier authors on the other hand suggested a 'featureless', very low-gradient erosive peneplain.

In accordance to the considerations by Drodzewski et al. (2017), we assume here a formation of the dinosaur-bearing deposits of Brilon-Nehden and Balve within a cave/fissure system that was composed by a combination of hypogenetic and meteoric processes and from an upland source through the Devonian carbonates to a lower fluvial base-level (Fig. 10). The karstification processes started possibly already during the Permian by hydrothermal fluids (Fig. 10A). An intensive phase of meteoric karst formation probably occurred when the sea-level began to drop rapidly after the Barremian highstand (cycles KBa4 to KAp2 according to the nomenclature by Haq 2014), which caused increased incision of the drainage system (Fig. 10B). At the lowest stage of sea-level the horizon of the preserved cave deposits at Brilon-Nehden may have been located at a minimum of about 100-120 m above sea-level, compared to 40-60 m at the Barremian highstand (KBa1 to KBa3). According to the 'four-state model of speleogenesis' (Ford & Ewers 1978; Audra & Palmer 2015), cave systems were probably formed during this phase as bathyphreatic loops, that resulted in permanently water-filled conduits, reaching well below the base-level. Water flow in these conduits is maintained by hydrostatic pressure and may be episodic according to seasonal water supply. Drodzewski et al. (2017) reconstructed a similar hydraulic regime for the deposition of unfossiliferous sands, clays and fusite seams, presumably of Lower Cretaceous age, within the Rohdenhaus palaeo-cave (Wülfrath Anticline, western Rhenish Massif). Thick-bedded carbonates, such as in the Massenkalk facies (e.g. May 1987), foster the generation of bathyphreatic conduits (Ford & Ewers 1978). The subcircular cross-section of the subhorizontal fossil conduit in Brilon-Nehden (as far as known, Huckriede 1982, Norman & Hilpert 1987; Schudack 1987) supports such an interpretation as an originally fully water-filled cavity, as vadose (not completely water-filled) conduits commonly produce key-hole shaped cross-sections and canyons (e.g. Palmer 2003). At present the nearly vertical conduits exposed in Balve do not allow such an assessment. With the Early Aptian KAp2 cycle, the sea-level rose again by ca. 50 m (averaged over high-frequency cycles) and then quasi-stabilized at this level well into the Early Albian. As a reaction, the drainage system backfilled with fluvial terraces (Figs. 10C-D). The remnant, plant-bearing, coarse-grained Barremian-Aptian fluvial deposits identified by Ribbert & Skupin (2009) on the Brilon Anticline can be interpreted in this context. The relatively long-term stability of the base-level presumably transformed the cave-system into a water-table (vadose) cave at a higher level than the previous system. This led to horizontal intersection of the older bathyphreatic loops, which acted as sediment traps, accumulating clastic deposits and biogenic remains. These processes may have repeated within the baselevel amplitude during the prolonged timespan (c. 20 myr) of the Aptian through middle Albian, creating a multitude of cave system tiers. Vadose processes in conjunction with concordant hypogenic hydrothermal karstification (Drodzdzewski et al. 2017) may have led to reworking, redeposition, and mixing of older cave-fillings through this period. Gravitational deformation of cave sediments may result from floor collapse by later karstification of a lower level (Schudack 1987, Drodzdzewski et al. 2017). Ongoing erosion in the source area probably reduced the transport distance from the surface to these sediment traps and fostered the accumulation of more complete vertebrate remains, as in the case of the iguanodontians from Brilon-Nehden (Norman 1987; Norman & Huckriede 1987). Variable grain-sizes and


D
LATEST BARREMIAN - E. ALBIAN
C
LATEST BARREMIAN - E. ALBIAN
B
L. BARREMIAN
A
E. BARREMIAN OR BEFORE
BRILON ANTICLINE
LEGEND:
Shallow sea
Surface freshwater body (seasonally changing waterlevel)
Hydrothermal karst fissure
Open cave air-filled / water-filled
Hydrothermal fluid flow
Meteoric water flow
Ground water level
Albian-Cenomanian shallow-marine deposits
Albian coastal plain deposits (Keddinghausen & Wünneberg Beds)
Barremian-Aptian limnic deposits
Devonian (Massenkalk facies)
Carboniferous
Cenomanian fossiliferous marine fissure-fill deposits
Barremian-Aptian fossiliferous limnic-terrestrial fissure-fill deposits
Marine fossils
Terrestrial fossils
Sea-level changes rising / quasi-static (low-amplitude fluctuations)/ falling

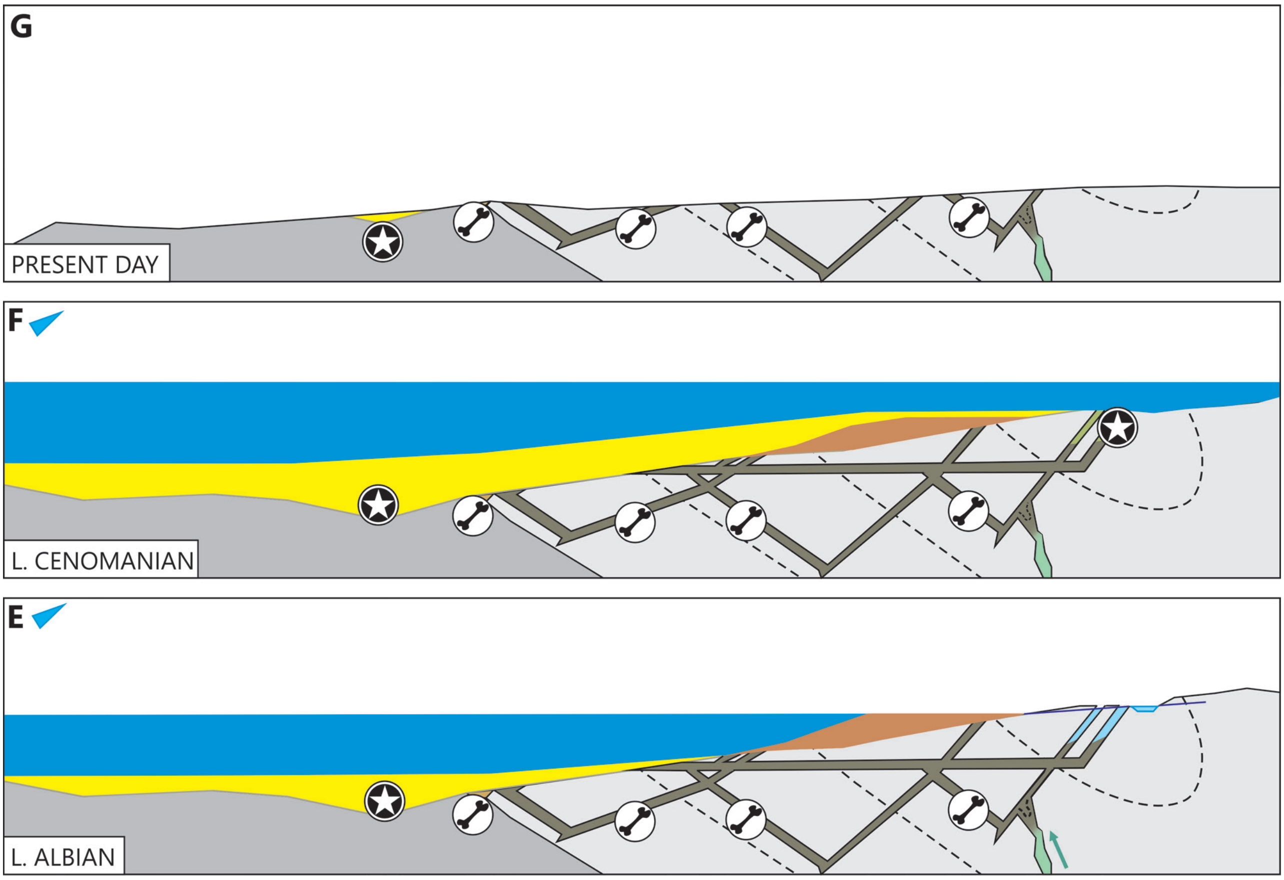


Fig. 10: Speleogenetic model for the Lower Cretaceous vertebrate lagerstätten in the Brilon Anticline. This is considered an analogue model for the Balve locality as in the latter bounding conditions are less well known, but the sedimentological and palaeontological evidences point to a similar mechanism. The model focus on meteoric processes as they played the main role in transport and deposition of the vertebrate remains. However, hypogenic hydrothermal karstification most probably also contributed to an unknown extent in speleogenesis (Drozdzewski et al. 2017). Geological cross-section through the northwestern part of the Brilon Anticline in NW-SE direction (NW is to the left). **A** Cave systems existed already before the Barremian to an unknown extent and configuration. The Early Barremian highstand may have reached the foot of the Brilon Anticline (Ribbert & Skupin 2009, not shown). The cave systems may have already connected episodically an upper catchment area (right) through the karstified Massenkalk succession to the foreland (upper reaches of a foreland stream: left). **B** A significant drop in sealevel during the latest Barremian resulted in increased erosion of surface drainage systems and the creation of lower tiers of cave systems. Rapid baselevel drop and the Massenkalk lithology favours the formation of bathyphreatic loops. **C-D** A moderate rise at the beginning and quasi-stabilisation of the sealevel further during the Aptian resulted in the sedimentation of fluvial deposits in the lower surface drainage systems (plant-bearing coarse sandstones, Ribbert & Skupin 2009, left) and the formation of open groundwater-table caves. The latter progressively cut off the bathyphreatic loops that acted as sediment traps in which vertebrate and other fossil remains accumulated. Note that B to D may have repeated several times at a lower amplitude due to Aptian through Albian minor sealevel fluctuations. **E** The Late Albian transgression resulted in deposition of marine sediments in the foreland and of coastal sands in a littoral fringe. The southern part of the Brilon Anticline is still emerged. In the lower right, hypogenic karstification interferes with an older, filled cave system, resulting in local collapse and slumping of the cave deposits (note: this process could have happen at any time during phases of hydrothermal activity). **F** The Late Cenomanian transgression fully inundated the Brilon Anticline. Superficial karst fissures became filled with marine deposits (Ribbert & Skupin 2009). **G** Present-day situation after Cretaceous-Cenozoic uplift of the Paleozoic basement and erosion. Schematic and not to scale. Paleozoic basement geology after May (1987).

sediment composition (e.g. the presence of fusinites, Kampmann 1983; Lanser 2015; Uhl et al. 2019; personal observation AHS) reflect seasonal changes of discharge in accordance with a warm, wet/dry seasonal climate (e.g. Pelzer & Wilde 1987).

The formation of the hosting cave system and the sedimentary infill are therefore well explainable in the context of Barremian-Aptian sea-level changes, and does not require a specific phase of Lower Cretaceous subsidence of the area. The accumulation of the preserved cave sediments probably occurred mainly during the earliest Aptian, well within their biostratigraphically constrained age (Barremian-Aptian, e.g. Schudack 1987, Lanser & Heimhofer 2013). All data, including palaeophytogeographic aspects (see below), are in accordance with a setting within an eroding upland at a palaeoelevation of up to several hundred meters.

Ongoing erosion levelled most of the Brilon-Nehden deposit, removing the upper tiers of the cave system until submergence by the Late Albian transgression. Some areas were emergent until the earliest Cenomanian (Figs. 10E-F). It is most likely that the Balve area underwent a very similar history but as it was probably not reached by the Late Albian transgression and only inundated by the Late Cenomanian highstand (e.g. Frieg et al. 1990; Kaplan 2008). Its Barremian/Aptian

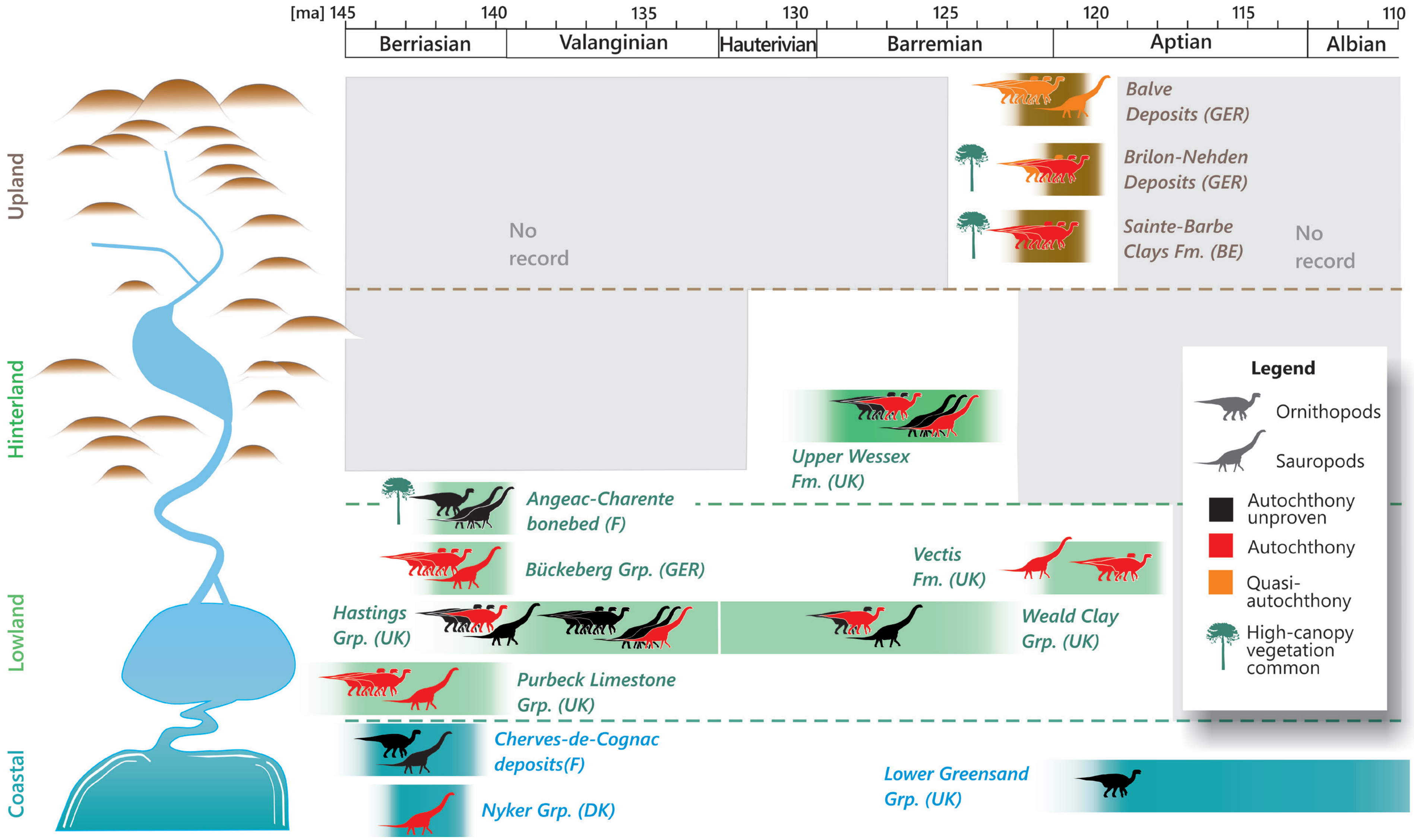


Fig. 11: Graphical overview of megaherbivorous dinosaur assemblages (ornithopods and sauropods) in the Early Cretaceous of Central and Western Europe according to their respective palaeoenvironments. Number of icons in each occurrence illustrate the relative abundance (semi-quantitatively). Definition of palaeotopographical settings according to Table 1, details and data sources in Table 2; country abbreviations: BE – Belgium, DK – Denmark, F France, GER – Germany, UK – United Kingdom.

palaeoelevation can be assumed even higher than that of the Brilon Anticline, albeit calibration points for a quantification are wanting.

Cretaceous marine sediments were later removed from most of the area by the last, intensive, Neogene uplift (Büker 1997; Fig. 10G). The exposed Devonian limestones underwent additional phases of karstification following their ongoing exhumation – the latest during the Quaternary (e.g. Niggemann 2003; Richter et al. 2014).

The flora and fauna deposited in the Brilon-Nehden locality have been studied in much detail (e.g. Huckriede 1982; Kampmann 1983; Norman & Hilpert 1987; Norman 1987; Schudack 1987; Schultz & Noll 1987; Kunzmann 2007). The Balve biota are still under investigation but various faunal components have already been identified, including mammals, ornithopod, theropod, ankylosaur dinosaurs, pterosaurs, crocodyliforms, chelonians, salamandroid amphibians, and selachians (e.g. Lanser & Heimhofer 2013; Lanser 2015; Schwermann et al. 2018; Skutschas et al. 2020; Martin et al., 2020; 2021; Sachs et al. 2022, Schwermann pers. obs.). At present plant remains are restricted to fusite, palynomorphs (Lanser & Heimhofer 2013), wood fragments, and very rare seeds (pers. obs. AHS). The more abundant terrestrial flora in Brilon-Nehden is dominated by conifers and ferns, with a high admixture of aquatic to riparian plant taxa (especially water-ferns, lycopodiales, and characeans; Kampmann 1983; Kunzmann 2007; Schudack 1987; Schultz & Noll 1987).

Early Cretaceous megaherbivorous dinosaur palaeozoogeography in northwestern Europe

The Lower Cretaceous saw a major though gradual change in megaherbivore faunal composition from Late Jurassic sauropod communities being replaced by ornithopod-dominated communities (e.g. Bakker 1978; Benson et al. 2013). The global sauropod fossil record suffered a severe, 'mid-Cretaceous diversity bottleneck', potentially arising from various biological, geological, as well as statistical factors (Mannion & Upchurch 2011; Mannion et al. 2011; Benson & Mannion 2012). With a view on the subsequently reinvigorated titanosaur radiation during the latter part of the Cretaceous, a recent study by Cashmore et al. (2020) suggested three possible reasons to explain this bottleneck: (1) a reduction of terrestrial fossil preservation space due to sea level rise in the Lower Cretaceous, (2) ecological specificities and relatively high diagnosability of Upper Cretaceous taxa and/or (3) increased sampling of newly explored Upper Cretaceous sites with many previously unknown taxa.

The Upper Barremian in northwestern Europe is a favourable temporal interval and geographic realm for the reconstruction of a palaeotopographical faunal palaeoelevation transect from the upland to near-coastal lowlands as it embraces three of the rare upland occurrences (Fig. 11). Upland deposits like those from Balve, Brilon-Nehden, and Bernissart are very rare in the fossil record and exceptional in the Lower Cretaceous. They give a glimpse into an important habitat from which otherwise only very sparse information is available. Palaeogeographically, the region comprises the landmasses of Anglia, Armorica, the Central European Rise with the London-Brabant, Rhenish and Bohemian Massifs, the Pompeckj Block, and southwestern Fennoscandia, as well as the epicontinental basins with partial limnic-terrestrial infill surrounded by them: e.g. the Wessex, Weald, and Paris basins, the Lower Saxony Basin, and the Danish-Polish Trough (e.g. Mutterlose 1997). The Berriasian through Barremian interval is mostly represented by lowland to coastal palaeoenvironments while post-Barremian strata are commonly shallow-marine in origin and terrestrial tetrapods occur therein only allochthonously.

To facilitate the assignment of the dinosaur communities here under consideration, palaeotopographical settings are subdivided into four broad categories from coastal to upland (Tables 1-2, Fig. 11). As limnic environments (sensu lato) provide the most common depositional systems containing the dinosaur fossils and water is the most ubiquitous transport agent, the palaeotopographical transect is defined along an idealized hydrological network from the source / upper catchment area to the discharge into the sea. While several environments may typically be associated with these settings (Table 1), such an association is in most cases not exclusive – and the judgement to which setting a specific occurrence can be assigned needs to result from a holistic analysis of the palaeogeographical and palaeoenvironmental situation. This is exemplified e.g. by the Brilon-Nehden locality, as the cave-deposits *per se* could have been formed in any palaeotopographical situation. Accordingly it was originally believed that the deposition took place in an upland environment (e.g. Clausen et al. 1978). A lowland setting was advocated later e.g. by Hölder & Norman (1986). As discussed above, the original interpretation of an upland setting is supported herein.

With regards to the palaeotopographical origin of the vertebrate fossils, it is of importance that fluvial transport results in a mixing of autochthonous, parautochthonous, and allochthonous skeletal elements. While the influx of parautochthonous and allochthonous elements accumulate along the course of a river (e.g. Behrensmeyer 1982; Wood et al. 1988), the admixture of allochthonous components from distant

Tab. 1: Definition of the palaeotopographical settings used in this work. Note that the associated environments are exemplary and often non-exclusive to a specific setting. A comprehensive assessment is necessary to refer a fossil occurrence to a palaeotopographical setting with confidence. See text for more details.

Palaeotopographical setting	Typical altitude above m.s.l.	Typical fossiliferous environments/deposits	Comments
Coastal	< 10 m	Foreshore and deltaic environments, shallow lagoons, coastal barriers, back barrier swamps, estuaries, strandplains, tidal flats, coastal sabkhas…	Evidence for marine influence present.
Lowland	0 to 10s of m	Lacustrine deltaic plains, lacustrine shallow lagoons, lower reaches of rivers (typically anastomosing or meandering) and associated alluvial plains, inland sabkhas…	No or only very sporadic evidence for marine influence present.
Hinterland	10s to 100s of m	Upper reaches of rivers (typically braided or meandering) and associated alluvial plains and inland lake deposits, distal zones of alluvial fans, inland lake marginal deposits…	Fluvial clastic deposits generally more immature than in the lowland, components may show signs of short transport distance. Upland environments were more closer than in the lowland, even if palaeoelevation was low (e.g. along graben margins). Taphocoenoses may contain higher shares of parautochthonous and allochthonous elements than in the lowland and upland. No evidence of marine influence present
Upland	100s of m and higher	Predominantly areas of non-deposition; preservation of sediments can occur within intramontaneous basins and high plateaus (high altitude rivers and lakes), proximal zones of alluvial fans, and karstic features as sinkholes, caves, and fissures…	Upper catchment of drainage systems – remains of terrestrial (non-flying) and aquatic organisms encountered in this setting can be considered quasi-autochthonous if other than gravitational transport mechanisms can be ruled out.

proximal environments may decrease to some degree in distal reaches of the fluvial system due to bedload transport fragmentation and degradation. Only floating transport might exempt the fresh carcasses from downstream destruction and bring a considerable amount of bodies even into marine offshore deposits. In a simplified concept, the highest relative amount of non-autochthonous remains accumulates in the hinterland reaches of streams where they mix with autochthonous remains in the catchment area prior to downstream reworking. Concurrently, due to the absence of a significant transport distance, skeletal remains in upland settings can be considered 'quasi-autochthonous', even if they show signs of intense local reworking, as in the Balve specimens. The simple model of downstream degradation of transported skeletal elements may be complicated by the presence of sediment traps – such as lake basins or karst fissure systems – along the course of the stream, that hamper the further downstream transport, and affected by pre- and intertransport taphonomical processes. These circumstances have to be considered with a view to the fossil record along a palaeotopographical gradient. Therefore, the best evidence for autochthonous presence of a certain taxon in the environment under study is the unequivocal identification of tracks. Second to this evidence are articulated and complete specimens or extraordinary preservation (e.g. soft tissue), but the role of pre-depositional carcass floating may be uncertain in these cases. Finally, the preburial and prediagenetic degradation of bones give an indicator of their exposure and transport history (e.g. Behrensmeyer 1978; Eberth 2015), but its significance at population level is commonly not quantifiable on isolated or rare specimens.

With regard to the Lower Cretaceous of Europe, the autochthonous presence of sauropods in lowland to coastal habitats as non-dominant faunal constituents is documented for the Berriasian by track occurrences in Denmark (Bonde 2012), southern England (Ensom 2002a), and Germany (Hendricks 1981; Fischer 1998). With the exception of the Danish records, the abundant evidence of autochthonous iguanodontian ornithopod tracks demonstrates that they were already a quantitatively dominant group in the Berriasian-Valanginian (e.g. Woodhams & Hines 1989; Parkes 1993; Ensom 2002a; Pollard & Radley 2011; Hornung et al. 2012; Shillito & Davis 2019). Isolated skeletal remains of ornithopods, stegosaurs, and sauropods have been recorded also from Berriasian coastal deposits of southwestern France (Cherves-de-Cognac; Pouech et al. 2006; Barrett et al. 2016). Lowland deltaic deposits of the Hastings Group in southern England yielded a relatively diverse record of sauropod skeletal remains in the Valanginian part of the section (Upchurch et al. 2011). Partially articulated skeletons and soft tissue preservation (Mantell 1852; Upchurch et al. 2015) support an autochthonous origin. The Berriasian-Valanginian Ashdown Formation at the base of the Hastings Group represents a lowland-hinterland transitional fluvial environment and produced trackways which may have been left by sauropods. However further investigations are needed to confirm their origin (Jarzembowski et al. 2015; Shillito & Davis 2019). The late Berriasian/early Valanginian Angeac-Charente bonebed of southwestern France produced – among a diverse vertebrate fauna – many remains of sauropods, as well as stegosaurs and very

Tab. 2: Lower Cretaceous dinosaur localities of northwestern Europe with their stratigraphical age, palaeotopographical settings, occurrence of megaherbivorous dinosaurs, and high-canopy conifer trees. Symbols: '+' – presence (autochthony cannot be proven or improbable), 'A' – presence (autochthony can be demonstrated or is highly likely). See also Figure 11.

[1] Sauropod footprints occur only at the basal contact to the Wessex Fm. (White Rock Sandstone, Sweetman 2011).

[2] Material is considered quasi-autochthonous due to the proximity to the local hydrographic upper catchment area.

[3] Fragmentary sauropod material (tooth) considered to be reworked from older deposits (Barrett 2021).

Locality / Occurrence	Age	Palaeotopographical setting	Dominant megaherbivorous dinosaurs		High-canopy conifers abundant	Primary sources herbivorous dinosaur diversity	Primary sources palaeoenvironment
			Ornithopoda	Sauropoda			
Purbeck Limestone Grp. (UK)	Uppermost Tithonian –Berriasian	Coastal/Lowland	A	A		Sarjeant et al. (1998), Wright (1998, 1999, 2005), Ensom (2002a, b), Ensom & Delair (2007)	Riboulleau et al. (2007)
Cherves-de-Cognac deposits (F)	Berriasian	Coastal/lowland	+	+		Pouech et al. (2006), Barrett et al. (2016)	Mazin et al. (2006), Pouech et al. (2015)
Nyker Grp. (DK)	Berriasian	Coastal		+		Bonde (2012)	Bonde (2012)
Bückeberg Grp. (GER)	Berriasian	Lowland	A	A		Lehmann (1978), Hendricks (1981), Fischer (1998), Lockley et al. (2004), Hornung et al. (2012)	Pelzer & Wilde (1987), Pelzer (1998)
Angeac-Charente bonebed (F)	Upper Berriasian	Lowland or hinterland	+	A	+	Allain et al. (2022)	Rozada et al. (2021)
Hastings Grp. (UK)	Upper Berriasian – Valanginian	Predominantly lowland to lowland/hinterland transition	A	A		Woodhams & Hines (1989), Parkes (1993), Upchurch et al. (2011), Norman (2011), Pollard & Radley (2011), Jarzembowski et al. (2015), Shillito & Davis (2019)	Radley (2006), Batten & Austen (2011), Shillito & Davis (2019)
Weald Clay Grp. (UK)	Hauterivian – Barremian	Lowland	A	+		Upchurch et al. (2011), Norman (2011), Pollard & Radley (2011)	Radley (2006), Batten & Austen (2011)
Upper Wessex Fm. (UK)	Upper Hauterivian – Barremian	Hinterland in the West, passing eastwards into lowland	A	A		Naish & Martill (2001b), Norman (2011), Lockley et al. (2014), Lockwood et al. (2014, 2021), Pond et al. (2014)	Sweetman & Insole (2010), Sweetman (2011), Radley & Allen (2012), Penn et al. (2020)
Vectis Fm. (UK)	Uppermost Barremian – Aptian	Lowland transiting upwards into coastal	A	(A)[1]		Radley et al. (1998), Norman (2011)	Radley et al. (1998), Sweetman (2011), Radley & Allen (2012)
Saint Barbe Clays Fm. (BE)	Upper Barremian – Lower Aptian	Upland	A		+	Norman (1980, 2012)	Dejax et al. (2007), Martin et al. (2012), Spagna et al. (2012), Quinif & Licour (2012)
Brilon-Nehden cave deposits (GER)	Upper Barremian – Lower Aptian	Upland	A		+	Norman (1987), Norman & Hilpert (1987)	Schudack (1987), this work
Balve cave deposits (GER)	Upper Barremian – Lower Aptian	Upland	A[2]	A[2]		Lanser (2015), Sachs et al. (2022), this work	This work
Lower Greensand Grp. (UK)	Aptian – Albian	Coastal/marine	+	?[3]		Norman (1993), Barrett (2021)	Ruffell & Batten (1994)

rare iguanodontian ornithischians (Allain et al. 2022). The autochthonous presence of sauropods and stegosaurs is documented by tracks (Rozada et al. 2021). The palaeotopographical setting of Angeac-Charente is not fully assessed: While an earlier study suggested a coastal deltaic or estuarine environment (Benoit et al. 2017), the results of Rozada et al. (2021) do not support a marine influence. According to the latter, the local environment was a swamp or bog associated with a fluvial system, but the wider regional palaeotopographic context is missing. It may have belonged either to the lowland or hinterland palaeotopographic setting. Other than this, the hinterland and upland faunas remain unknown for the Berriasian-Valanginian interval due to a lack of geological record.

While the Hauterivian dinosaur record of this region is generally poor, the Barremian shows a slightly different picture when compared to the occurrences of the Berriasian-Valanginian interval. The peak of sauropod abundance and diversity is reached in the fluvial hinterland environment of the Wessex Formation (Isle of Wight, England, Upchurch et al. 2011), and their at least partial autochthony is likewise evidenced by footprints (Pond et al. 2014). Sauropod fossils are accompanied by more abundant ornithopod skeletal remains and footprints (Naish & Martill 2001b; Norman 2011; 2014;

Lockley et al. 2014; Lockwood et al. 2014; Pond et al. 2014). Notably, sauropod footprints occur for the last time immediately at the boundary of the Wessex to the overlying Vectis Formation (Sweetman 2011), that marks the transition from a distal fluvial to a lowland lacustrine, and further on coastal-lagoonal environment (late Barremian transgression, e.g. Ruffell & Allen 2012). Ornithopod tracks remain abundant in the lowland-coastal strata of the lower Vectis Formation (Radley et al. 1998). Concurrently, sauropod bones, in contrast to those of iguanodontian ornithopods, are very rare in the lacustrine lowland environments of the contemporaneous Upper Weald Clay Formation (Sussex, England, Upchurch et al. 2011), and sauropod tracks are completely unknown from this unit. Finally, in the overlying shallow-marine Lower Greensand Group (Aptian-Albian) of southwestern England, sauropods are only represented by very fragmentary, most probably reworked, remains (Barrett 2021), while iguanodontian ornithopods are documented by a semi-articulated skeleton (Mantell 1834; Norman 1993), supporting short transport distance from the shore.

In this context, the material from Balve is especially remarkable as it represents the first direct proof of an upland habitat for sauropods. In all known Belgian and German upland deposits ornithopods dominate the dinosaur taphocoenoses, but theropods (Norman & Hilpert 1987; Lanser & Heimhofer 2013), as well as other tetrapods also form minor constituents. The semiaquatic and aquatic vertebrates (crocodyliforms, turtles, fishes) at Bernissart were at least partially autochthonous to the sink-hole lake, while the assemblages from the German localities are parautochthonous to allochthonous. If the dominance of ornithopod skeletal elements reflects a dominance of their biomass within the source ecosystem(s) remains uncertain as pre-burial taphonomical processes and autecological aspects are largely unknown.

In conclusion, sauropod distribution in the Lower Cretaceous of northwestern Europe, with regard to the autochthonous or parautochthonous records, show a shift during the Valanginian – Hauterivian interval from rare but widespread occurrences in lowland settings towards more abundant and diverse occurrences in hinterland to upland environments. While the clade probably retreated from coastal areas and lowlands, its distribution in hinterland/upland environments of the Upper Jurassic and lowermost Cretaceous cannot be evaluated due to a bias in the geological record. It therefore remains open if sauropods already occupied higher regions during this time and if their retreat from the coastal lowlands marks a shift or a reduction of habitat area. Remarkably, sauropods also form a rare constituent of the latest Barremian/earliest Aptian Jehol biota from China (Wang et al. 2007). Most recently, it has been suggested that the Jehol assemblage thrived in a high-altitude mountainous setting (2800 – 4100 m palaeoelevation), with low annual mean temperatures (5.9 +/-1.7 °C) and freezing in winter (Zhang et al. 2021).

Upper catchment regions are massively underrepresented in the sedimentary record compared to lowland and coastal topographies, and non-marine environments shrank during the Early Cretaceous due to eustatic coastal onlap (e.g. Haq 2014). While the quantitative effect of the sea-level rise on the sauropod record is difficult to assess, the absence (Vectis Formation) or rarity (Weald Clay Group) of sauropods in well-sampled, non-marine lowland deposits suggest that ecological preferences indeed played a role. Insufficient preservation potentials of hinterland deposits may mask a higher abundancy and diversity of sauropods than preserved in the known fossil record, exacerbating the perception of a Lower Cretaceous diversity bottleneck (Mannion & Upchurch 2011). The current dataset, however, is probably a result of multiple biological, geological as well as statistical factors (Mannion et al. 2011, Benson & Mannion 2012).

Trophically driven habitat segregation in Lower Cretaceous megaherbivorous dinosaurs?

The presence of sauropods in Berriasian-Valanginian lowland habitats of England and Germany, together with abundant ornithopod occurrences, support the hypothesis by Tennant et al. (2017) that major faunal transitions near the Jurassic/Cretaceous boundary were fundamental but gradual and occurred regionally at a variable pace. In contrast to sauropods, the abundance of iguanodontian ornithopods in the Belgian and German upland as well as in the lowland deposits of the English Wealden Supergroup indicates that ornithopods were obviously more widespread.

A potential explanation of this pattern may be found in the strong reduction of ground- to medium-canopy browsing sauropod clades (especially non-rebbachisaurid diplodocoids) at or shortly after the Jurassic/Cretaceous boundary in northwestern Europe – either caused by competition with ground to medium-canopy browsing ornithopods, or by other reasons. Aside from the possible exception of *Haestasaurus becklesii* (Mantell, 1852), the exact phylogenetic position of which is not yet resolved (it was recovered as a basal eusauropod by Mannion et al. 2019, a potential diplodocoidean or alternatively a turiasaur by Gomez et al. 2021), the still undescribed turiasaurs from Angeac-Charente (Allain et al. 2022), and the potential rebbachisaurid *Xenoposeidon prononeukos* Taylor & Naish, 2007 (see Taylor

2018), sufficiently preserved sauropod remains from the Berriasian-Late Hauterivian interval of northwestern Europe are exclusively referable to the Titanosauriformes. In contrast to the low-browsing groups that vanished from the European record near the Jurassic/Cretaceous boundary, basal titanosauriforms were typically medium- to high-canopy browsing (e.g. Stevens & Parrish 2005, Whitlock 2011, Tütken 2011). Therefore, they stood not in a direct trophic competition to iguanodontian ornithopods, although an overlap may have existed in subadult individuals.

An exception with a rare fossil record are low-browsing rebbachisaurid sauropods, that coexisted with ornithischians and titanosauriform sauropods probably in the Berriasian-Valanginian of England, and in the Barremian-Aptian of Croatia, Spain and England (Dalla Vecchia 1998, Torcida Fernández-Baldor et al. 2011, Upchurch et al. 2011, Taylor 2018). The identification of *Xenoposeidon prononeukos* as a potential basal rebbachisaurid questioned the widely-held assumption that this group is of Gondwanan origin (Taylor 2018). It may have radiated in Laurasia and only later in the Early Cretaceous migrated into Gondwana. In England and Spain, they occurred in lowland environments (Ashdown Formation, Berriasian-Valanginian) and fluvial hinterland deposits (Castrillo de la Reina Formation [Clemente 2010] and Wessex Formation, Barremian-Aptian). How long this co-existence with low- to mid-canopy browsing non-sauropod megaherbivores prevailed is unknown due to the overall rarity of sauropod remains in younger strata.

Other late Lower Cretaceous and Upper Cretaceous sauropods from Europe, however, belong exclusively to high-browsing clades (see also Poropat et al. 2022). As indicated by their presence in the Barremian-Aptian upland locality of Balve, the decreasing abundance of sauropods in lowland settings during the Early Cretaceous may reflect a habitat change during this interval. While increased trophic competition from ornithischians may have affected most ground- to medium-browsing sauropod clades, the distribution of high-browsing sauropods was potentially influenced by shifts in the distribution of high-canopy vegetation at this interval. Again, the data are sketchy, but lowland floras from the early Lower Cretaceous of Germany and England (e.g. Schenk 1871; Seward 1894, 1895; Watson 1969; Oldham 1976; Riegel et al. 1986; Watson & Batten 1990; Saward 1992; Watson & Harrison 1998, 2001; Watson & Alvin 1996, 1999; Pelzer 1998; Coiffard et al. 2007; Austen & Batten 2011; Pott et al. 2014; Pott 2019; Uhl et al. 2019) show a marked rarity of auraucariacean conifers, trees that typically provide high-raising canopies. Plant communities of these floras comprise – aside from herbaceous pteridophytes and equisetales – low- to mid-canopy taxa like „tree-ferns", cycadeales, bennettitales, and ginkgophytes. A number of conifer taxa are likewise abundant, especially in England. However, their habitus is largely unknown, and it remains uncertain if they belonged to the mid-canopy or high-canopy level. In contrast, various remains of araucariaceans (*Araucaria carolae* Kunzmann, 2007) are known from the upland locality of Brilon-Nehden. They appear together with *Pinus* sp. and *Taxus* cf. *jurassica* Florin, 1958, as well as various cupressaceans, *Brachyphyllum* sp. – a conifer of unknown habit that occurs also in lowland floras – and various pteridophytes, cycadeales, lycopodiales, characeans, and possibly ginkgophytes, angiosperms and ascomycetes (Huckriede 1982; Grebe 1982; Kampmann 1983; Wilde & Goth 1986, 1987; Schultz & Noll 1987; Goth & Wilde 1990; Kunzmann 2007). The presence of araucariaceans at Brilon-Nehden is also in accordance with their present-day preference of higher altitudes (Hill & Brodribb 1999; Kershaw & Wagstaff 2001; Ledru & Stevenson 2012) and other reconstructions of their palaeophytogeography (e.g. Volkheimer et al. 2011). Similarly to Brilon-Nehden, araucariacean and pinacean conifers have been identified in the surroundings of the upland Bernissart locality (Dejax et al. 2007). There are currently no diagnostic macrofloral remains known from the coeval Balve locality (Schwermann et al. 2018).

It is therefore plausible to assume that at least species of *Araucaria*, and possibly also *Pinus*, provided emergent canopies in the uplands of northwestern Europe, suitable for high-browsing sauropods but out of reach – to our current knowledge – for ornithopods (see also Gee 2011). The latter, as well as juvenile sauropods, foraged on the low- and mid-canopy levels that grew as underbrush beneath the emergent conifers. The ubiquity of the latter levels from coastal to upland habitats allowed such low- to mid-level browsers a wider habitat range that was obviously of advantage to the iguanodontian radiation. The high-browsing sauropods in turn occupied an exclusive trophic niche. This niche – in a poorly sampled habitat – gave Cretaceous titanosauriforms an ample ecospace to diversify into the highly successful titanosaurian clade that existed probably globally alongside other megaherbivorous dinosaurs well up to the K/Pg-boundary (e.g. Vila et al. 2012; Poropat et al. 2022).

In many basal Cretaceous lowlands high-canopy vegetation may have been rare or absent (e.g. reconstruction of the German Berriasian flora in

Fig. 12: Reconstruction of the taphonomical processes involved in the vertebrate accumulation in upland cave deposits of Balve and Brilon-Nehden. A titanosauriform sauropod (*Ornithopsis*? sp.) observes a small stream that drains an outcrop of karstified Paleozoic carbonates following a rainstorm at the end of the wet season. The stream plunges into a karst crevice, carrying with it the disarticulated remains of a sauropod skeleton, scattered at the surface. The bones were transported within the fissure according to their mass and shape properties and deposited at various sediment traps. The water table in the fissure is still high from the previous wet season, but might drop in the subsequent dry season. Renewed flow intensity in the subsequent rainy season will partially remobilize the bones and add to their taphonomic wear, until they will be finally buried in sediment traps deeper in the fissure system. Illustration by Joschua Knüppe, 2022.

Pelzer 1998). This might have restricted the presence of large sauropods to migratory phases and could explain their rare autochthonous record. Notably in this context, the rich, mainly turiasaur, sauropod remains of Angeac-Charente are associated with an abundance of the araucariacean *Agathoxylon* sp. (Rozada et al. 2021). Similarly, the high-browsing titanosauriform *Sauroposeidon proteles* Wedel, Cifelli & Sanders, 2000 is closely associated with the high-canopy cheirolepidiacean conifer *Frenelopsis ramosissima* Fontaine, 1889 in the Aptian of Texas, USA (see Axsmith & Jacobs 2005, Winkler et al. 2013). Furthermore, the diversity and abundance of sauropods in the hinterland Hauterivian-Barremian Wessex Formation indicates that these relationships may have been more complicated in reality, including the (at least temporary) establishment of mid-level browsing rebbachisaurid sauropods alongside iguanodontians. However, it needs to be taken into consideration that the fluvial facies of the Wessex Formation probably contains a mixture of autochthonous and allochthonous remains which partly derived from higher catchment areas.

Mannion & Upchurch (2010) found statistical support for the hypothesis that titanosaur sauropods which gradually replaced non-titanosaurian sauropods in the fossil record from the Lower Cretaceous onwards, had a strong preference for inland habitats. This contrasts to the preference for coastal habitats found in non-titanosaurian sauropods by these authors. Most interestingly, the statistical signal blurred in the phylogenetical transition from macronarians through titanosauriforms to titanosaurs, indicate a gradual shift of habitat preference along this phylogenetic trend. This shift took place from the latest Jurassic to the end of the Lower Cretaceous. The finds from Balve seem to indicate that part of this transitional process may be masked by a sampling bias in palaeotopographic upland regions. Titanosaurs were high-canopy browsers whose anatomy might have enabled them to adopt a tripodial stance to increase their vertical browsing-range (Carrano & Wilson 2001, Mannion & Upchurch 2010). In doing so they could establish an exclusive trophic niche that allowed them to flourish well until the end of the Cretaceous alongside ornithischian megaherbivorous dinosaurs. If the strong preference for inland habitats was exclusively linked to the distribution of high-canopy vegetation during the Late Cretaceous, or other factors were involved in their habitat preferences, needs to be assessed by more detailed future studies.

Palaeoclimatic aspects

Based on data from the marine realm, Kemper (1987) discussed distinct cold phases during the Early Cretaceous, linked to the influx of cold currents of Arctic origin into the southern North Sea and Lower Saxony Basins. While origin, severity, extent, and consequences of these marine cool phases are a matter of ongoing discussions, more recent research has supported their existence (see reviews e.g. by Ladant & Donnadieu 2016; O'Brien et al. 2017; Huck & Heimhofer 2021). These climatic fluctuations are traceable by a multitude of proxies from the marine realm. However, their effects on and correlation with climate changes in the terrestrial realm are challenging. Most palaeoclimatic reconstructions for the terrestrial Early Cretaceous of western Europe indicate a long-term “stable” warm, wet/dry seasonal climate of varying humidity from the late Berriasian onwards (e.g. Pelzer & Wilde 1987; Allen 1998; Wright et al. 2000; Haywood et al. 2004; Sweetman & Insole 2010; Batten 2011). However, phases of reduced humidity have been recorded, corresponding to cold sea-water episodes, e.g. in the late Early Valanginian (Sladen & Batten 1984), and in the Late Barremian/Early Aptian (Ruffell & Batten 1990). The latter was probably interrupted in the earliest Aptian by an episode of short-term sea surface warming (e.g. Wilkinson 2011; Huck & Heimhofer 2021), linked to increased humidity in terrestrial realms of northwestern Germany (Batten & Li 1987).

A vertical zonation of plant communities in the Barremian (that may be considered an example of “typical” Early Cretaceous NW European regional climate) is also supported by the results of palaeoclimatic modelling (Haywood et al. 2004). The model predicted a higher amplitude of annual surface temperature variation for the uplands of the Central European Rise (18°C to 34°C) than for the lowlands of the Wealden and Wessex Basins (22°C to 30°C). Concordantly, average precipitation was lower in the winter months in the uplands than in the basins, but slightly higher in the summer months.

Precipitation-evaporation ratios were positive in mountainous regions while negative in basins. Run-off rates are higher and perennial in elevated areas (0.5-1 mm/day), while lower elevations may have had no run-off due to the high evaporation rates. The model supports an interpretation as a "flashy" precipitation regime (Haywood et al. 2004), with seasonal alternations of dry phases – coupled to frequent thunderstorms and wildfire incidence – with intense high-precipitation events. This is in accordance with the sedimentary and taphonomical record. Seasonal droughts are also indicated for the uplands by abundant charcoal in cave-fill sediments (e.g. Drozdzewski et al. 2017, Uhl et al. 2019). Increased aridity at the Barremian-Aptian boundary (Ruffell & Batten 1990, Allen 1998) may have shifted the climatic conditions further in favour of araucariacean forests on the Rhenish Massif upland (compare Abbink et al. 2004).

The co-occurrence of the ornithischians *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* in lowland (S-England) as well as in upland (Bernissart, Brilon-Nehden) localities indicates a degree of euryecology in these taxa. This may have been achieved either by broader habitat tolerance of the ornithopods or by seasonal migrations. Due to a lack of data and stratigraphic resolution, the potential effects of short-term climatic perturbation on ornithopod and sauropod communities near the Barremian/Aptian boundary and their habitats in northwestern Europe cannot be resolved at the moment. According to Chiarenza et al. (2022) an increased aridity may have been beneficial for sauropod diversity. However, as the purported high-altitude, low temperature environment of the Jehol assemblage (Zhang et al. 2021) may indicate, both clades could have diversified into a very broad range of palaeoecological and palaeoclimatic boundary conditions.

Conclusions

The currently known sauropod material from Balve incorporates a dorsal vertebral centrum and a manual ungual phalanx (Figs. 5-6). The dorsal centrum exhibits potential synapomorphies with the enigmatic genus *Ornithopsis*, which allow a probable assignment to a titanosauriform. These specimens represent the stratigraphically youngest sauropod record from Germany.

The Balve material bears further significance as it represents the only known direct record of this clade from an upland environment in Europe. A review of geological and speleogenetic models for the region during the Lower Cretaceous supports the hypothesis that the palaeoelevation in this upland reached several hundred meters above sea level (Figs. 9-10). Taphonomic signatures indicate prolonged surface exposure and various stages of wear by water transport for at least some of the dinosaur bones (including the herein described sauropod vertebra). The remains were finally deposited in sediment traps in a karst cave or fissure system (Fig. 12). Sedimentary features and stratinomical data indicate episodically changing flow intensities that may be coupled to intermittent transport of skeletal elements and flooding of the caves during wet seasons.

The available data suggest a retreat or shift of sauropod habitat range from coastal plains and lowlands to hinter- and uplands in northwestern Europe during the Early Cretaceous (Fig. 11). It is hypothesized that this was linked to replacement of low- and mid-level browsing sauropods (e.g. many diplodocoideans) by iguanodontian ornithopods towards the Jurassic-Cretaceous boundary, although rebbachisaurid sauropods may have been successful as low-browsers into the Early Cretaceous. In contrast, high-browsing titanosauriform sauropods had less to no overlap in the trophic niche with the ornithopods. This facilitated a sympatric coexistence. However, their range was dependent on high-canopy forming vegetation that was probably more abundant in uplands. The previously observed 'mid-Cretaceous bottleneck' in sauropod diversity may therefore be a result of partial extinction combined with a sampling bias, as the preservation of quasi-in-situ upland faunas is very exceptional.

It may be cautioned to expand these regional observations to global sauropod diversity patterns, even if they appear to fit global models (e.g. Mannion & Upchurch 2010). Two examples may illustrate potential contradictions:

(1) the radiation of rebbachisaurids indicates that some low-browsing sauropods occurred in Europe concordant to the ornithischian radiation, and successfully expanded into other continents at least into the Turonian (Taylor 2018, Poropat et al. 2022).

(2) trackway data from Portugal (Santos et al. 2015) indicate the presence of non-titanosauriforms in Albian coastal plain settings in Iberia. Possible explanations may include – among others – a regional rather than of global nature of faunal changes, underestimated palecological diversity across the clades investigated, or a lack of recognition of migratory behaviours.

Finally, from a statistical point of view, the historical research intensity provided a substantial share of data input from northwestern Europe to global datasets of Lower Cretaceous diversity models that may result in a skew towards an over-representation of data points from this area and period.

The excavations at Balve are still ongoing and additional sauropod remains can hopefully be found in the next years which may support and/or supplement the results of this study.

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