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SOFT-PART PRESERVATION IN HETEROMORPH AMMONITES FROM THE CENOMANIAN–TURONIAN BOUNDARY EVENT (OAE 2) IN NORTH-WEST GERMANY

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Abstract: From thinly laminated marlstones of the Hesseltal Formation, representing the Late Cenomanian Oceanic Anoxic Event (OAE) 2, at Lengerich in the Teutoburger Wald (Westfalen, north-west Germany), 17 sediment-compacted baculitid ammonites with carbonised and partially phosphatised soft parts are recorded. Some preserve remains of the buccal mass, including jaws (occasionally articulated) and radulae, as well as of the cephalic cartilage, such as eye capsules. Such have not yet been recorded previously for the order Ammonoidea. In addition, originally unmineralised parts found preserved in these specimens include extensive portions of the digestive tract, the siphonal tube, false colour patterns (megastriae), as well as traces of what would appear to be the oviduct. At the same levels, patches with numerous isolated horny upper and rarer lower jaws as well as radulae occur; these may represent regurgitates or faeces of larger predators. The cephalopod remains described were deposited in an epicontinental setting, possibly at palaeodepths between 200 and 600 m. In this particular Late Cretaceous fossil Lagerstätte, upper jaws and anaptychi of ammonites rank among the commonest fossils.

Key words: Ammonoidea, radula, buccal mass, Lagerstätte, Cretaceous, north-west Germany.

In the fossil record, molluscan soft parts occur much more rarely than shells. Contrary to those cephalopod groups that have modern-day representatives (Kröger *et al.* 2011), our knowledge of the unmineralised parts of extinct groups such as ammonites and belemnites is rather limited (Schweigert and Dietl 1999; Landman *et al.* 2010). In particular for ammonites, the discrepancy between the sheer number of specimens collected and available data on internal morphology is marked. Only few examples of soft-tissue preservation in ammonites have been published to date (Table 1).

On the other hand, there are repeated records of fossilisation of originally organic tissues for the less abundant coleoids (Rieber 1970; Pinna 1972; Fischer and Riou 1982*a*, *b*, 2002; Reitner and Engeser 1982*a*, *c*; Riegraf and Hauff 1983; Reitner and Urlichs 1983; Riegraf *et al.* 1984, 1998; Allison 1987, 1988; Kluessendorf and Doyle 2000; Doguzhaeva *et al.* 2003, 2004; Fuchs *et al.* 2003; Wilby *et al.* 2004; Klug *et al.* 2005, 2010*a*, *b*; Fuchs 2006; Fuchs and Weis 2009; Mapes *et al.* 2010; Fuchs and Larson 2011*a*, *b*; Keupp *et al.* 2011). Apparently, almost every coleoid organ has now been documented in fossils. For ammonites, however, there are records to date of some remains of the digestive tract, two specimens with gill remains, one unpublished specimen with musculature and perhaps arm parts, one specimen with questionable eggs, and a couple of individuals with beaks and radulae (Table 1).

In 1991, one of us (WR) collected the specimens described here from the Cenomanian–Turonian Boundary Event (CTBE; Kuhnt *et al.* 1986) in the central Teutoburger Wald. The grey, laminated clayey marlstones are made up of two-thirds of coccoliths and one-third of clay minerals with an average grain size of 1–3 μm. In this area, a series of reddish brown, greenish to olive green marlstones and limestones, and various types of laminated clayey marlstones, first attracted the attention of scientists who recorded articulated fish skeletons in the mid-nineteenth century (von der Marck 1860, 1862). Locally, these beds are referred to as ‘Rotpläner’ and ‘Schwarzbunte Wechselfolge’; elsewhere, the name ‘CTBE’, which comprises the ‘*Plenus* Marls’ or ‘*Plenus* Event’ in the lower

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TABLE 1. Occurrences of unmineralised body parts of ammonites; occurrences with beaks only are not listed.

Age, country	Genus	Organ preserved	References
Carboniferous Uruguay	*Eoasianites*	Buccal mass, radula, musculature, crop, stomach, digestive tract	Closs and Gordon (1966), Closs (1967), Bandel (1988) and Riegraf *et al.* (1984)
Carboniferous USA	*Girtyoceras*	Buccal mass, radula	Miller *et al.* (1957), Kullmann (1981) and Doguzhaeva *et al.* (1997)
Carboniferous USA	*Cravenoceras*	Buccal mass, radula	Mapes (1987) and Tanabe and Mapes (1998)
Carboniferous USA	?*Anthracoceras* ?*Rhadinites*	Buccal mass, digestive tract, eggs?	Landman *et al.* (2010)
Triassic Greenland	*Ophiceras*	Buccal mass, digestive tract, gills	Lehmann and Weitschat (1973)
Triassic Germany	*Ceratites*	Buccal mass, radula, oesophagus	Klug and Jerjen (2012)
Jurassic Germany	*Harpoceras*, *Hildoceras*, *Lytoceras*, *Phylloceras*	Buccal mass, digestive tract	Riegraf *et al.* (1984)
Jurassic Germany	*Arnioceras*, *Dactylioceras*, *Eleganticeras*, *Hildaites*	Buccal mass, radula, gills	Lehmann (1967, 1979)
Cretaceous Russia	*Aconeceras*	Buccal mass, radula	Doguzhaeva and Mutvei (1992)
Cretaceous Lebanon	*Allocrioceras*	Buccal mass, digestive tract	Wippich and Lehmann (2004)
Cretaceous Russia	*Australiceras*	Buccal mass, radula	Doguzhaeva and Mikhailova (2002)
Cretaceous USA	*Baculites*	Buccal mass, radula	Kruta *et al.* (2011)
Cretaceous Japan	*Gaudryceras*	Cell imprint, buccal mass	Tanabe and Fukuda (1983)
Cretaceous Slovenia	Placenticeratidae gen. et sp. indet.	Rollmarks interpreted as imprints of soft parts, possibly hyponome, cluster of minute brachiopods interpreted as crop content	Summesberger *et al.* (1999)

part (i.e. the Hesseltal Formation of Niebuhr *et al.* 2007, pp. 37–42), is used. Until 1990, this sequence was exposed at a number of quarries near Rheine, Borgholzhausen, Brochterbeck, Lengerich and Halle/Westfalen (Ernst *et al.* 1983, 1984; Hilbrecht 1986; Kaplan *et al.* 1998; Lehmann 1999; Diedrich 2001) and in temporary road cuts at Bielefeld (Breitkreutz *et al.* 1991). Subsequently, these outcrops were protected by law as nature reserves or turned into waste dumps, and no additional palaeontological material was forthcoming. Most accounts (Riegraf and Schmitt-Riegraf 1995; Diedrich 2001, 2010; Wippich 2005; Grzegorczyk *et al.* 2006; Müller 2008; Hauschke *et al.* 2011) were based chiefly on finds made prior to 1992.

The present material had been misinterpreted by us as a new coleoid taxon, rather than as an orthoconic ammonite, on account of the supposed presence of a pair of coleoid arm hooks near the head of one specimen, as discussed below. In addition, we here briefly describe a fossil Lagerstätte, in which the commonest macrofossils are tiny, very fragile cephalopod jaws, chiefly identified as upper (i.e. rhynchoteuthids) and lower ammonite jaws (anaptychi) and fish remains. The Lengerich accumulations of ammonite jaws are comparable with epicontinental Late Triassic (Anisian and Ladinian; upper Muschelkalk) settings in Germany (Rein 1993, 2000, 2003; Klug 2001; Klug and Jerjen 2012), with the condensed Oxfordian Tauglboden Member in the Salzburg Alps (Huckriede 1971), with the latest Jurassic – Early Cretaceous Aptychenschichten or Aptychenmergel Formation and their equivalents in the northern Calcareous Alps and the Polish Carpathians (Gasiorowski 1962, 1968, 1971, 1973), as well as with condensed layers of Oxfordian age in Cuba (Housa 1969) and with the Campanian Kiebitzbank Member (Ahlen Formation) in south-east Westfalen (Riegraf 1995; Riegraf and Schmitt-Riegraf 1995). The abundance of coleoid beaks on modern deep-sea bottoms is similar as well (Belyayev 1959, 1962, 1964).

In addition to a range of hook-less squids, which often retain soft tissues (Engeser 1988), hook-bearing coleoids such as Belemnitida, Phragmoteuthida and Belemnoteuthida are comparatively rare and occurred scattered in Mesozoic shelf sediments. For instance, there are records from the Triassic (von Mojsisovics 1882, 1902; Jeletzky 1966; Rieber 1970), the Lower Jurassic (Jeletzky 1966;

Pinna 1972; Reitner and Engeser 1982*a*; Riegraf and Hauff 1983; Reitner and Urlichs 1983; Riegraf *et al.* 1984, 1998; Fuchs 2006; Klug and Fuchs 2010), the Middle Jurassic (Etter and Tang 2002; Tang 2002; Wilby *et al.* 2004; Fuchs 2006), the Upper Jurassic (Crick 1896; Abel 1922; Bandel and Leich 1986; Fuchs *et al.* 2003; Fuchs 2006; Klug *et al.* 2005, 2010*a*, *b*; Fuchs and Weis 2009) and the Cretaceous (Engeser and Reitner 1981, 1986; Reitner and Engeser 1982*b*, *c*; Haas 2002; Tanabe *et al.* 2006, 2008). This admittedly incomplete list of references reflects an interest in exceptionally preserved material rather than a high number of localities, specimens or taxa. In contrast, the number of Mesozoic localities from which commoner specimens with soft tissues preserved is quite low. Examples are the Holzmaden area and Dotternhausen (southern Germany; Lower Jurassic), Christian Malford (Great Britain; Middle to Upper Jurassic), La Voulte-sur-Rhône (southern France; Middle to Upper Jurassic), Nusplingen, Solnhofen and Eichstätt (southern Germany; Upper Jurassic) and Sahel Alma, Hejoula and Haqel (Lebanon; lower Upper Cretaceous).

The fossil Lagerstätte in the Teutoburger Wald (Fig. 1) described here is one of the few places where also ectocochleate cephalopods with soft-tissue remains are moderately common. Taphonomically and palaeoecologically speaking, it is of note that all specimens originate from a bituminous clayey marlstone surface of merely a few square metres, within a 2- to 3-cm-thin matrix.

Here, we present a brief outline of the geological setting and palaeoceanographical conditions to characterise the environment and describe the baculitids and their soft tissues, as preserved; in addition, their taxonomic assignment is discussed.

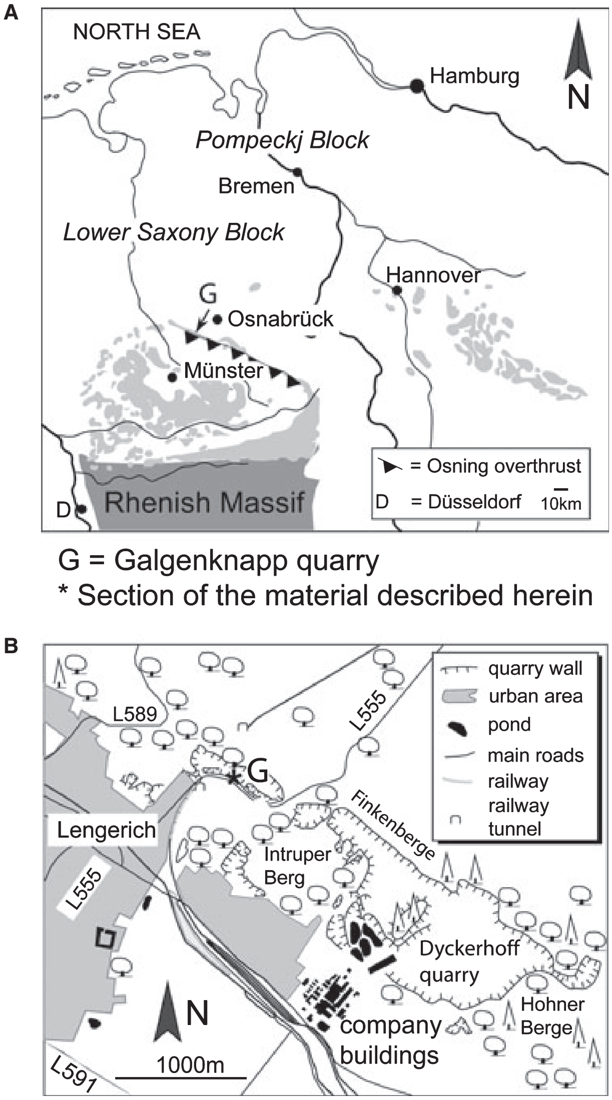
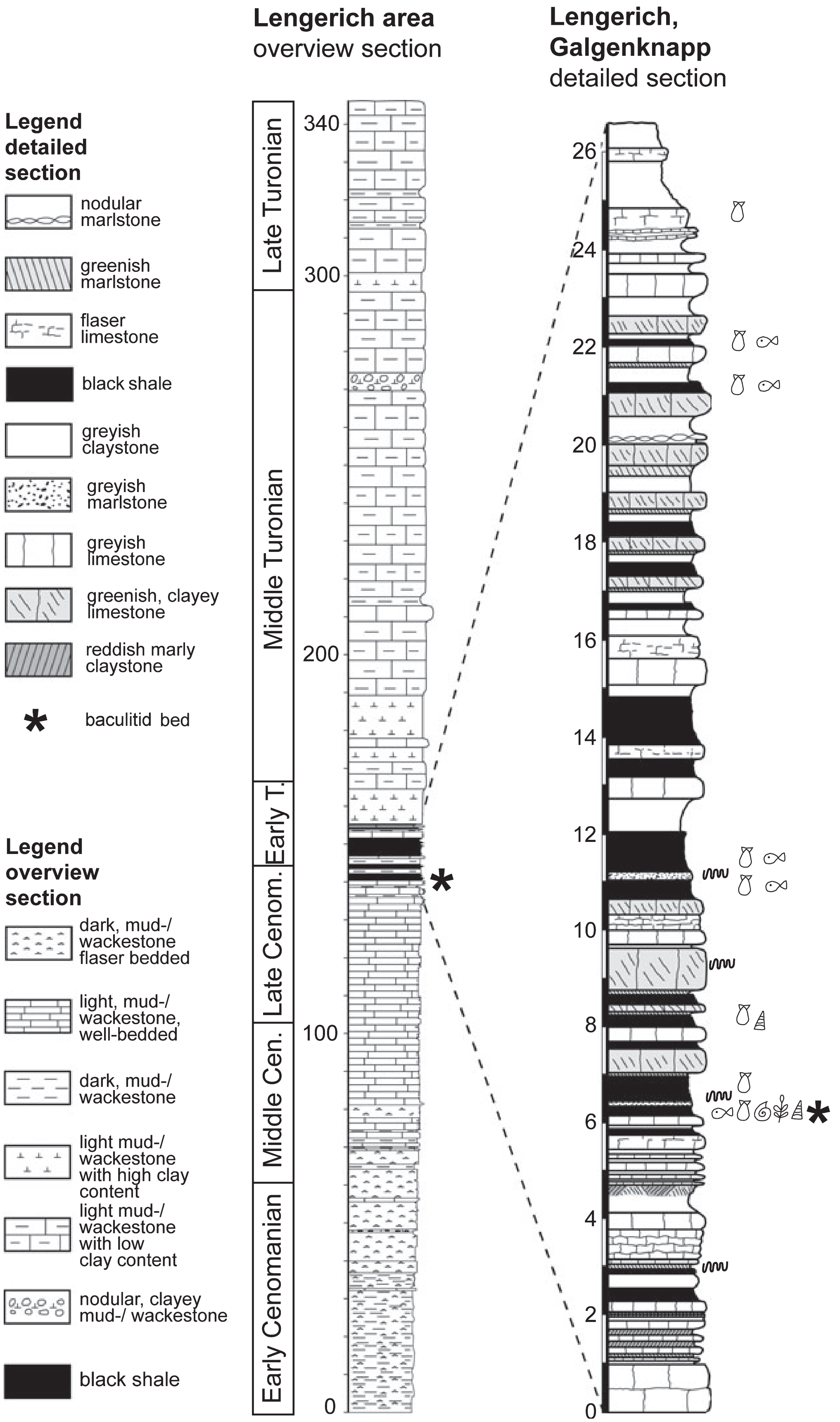


FIG. 1. Locality map. A, position of Lengerich within the framework of Upper Cretaceous sediments cropping out in northern Germany (light grey) and relevant tectonic elements in the area. B, the Galgenknapp quarry along the northern rim of Lengerich with the approximate position of the section (*) that yielded the material described here.

MATERIAL AND METHODS

Seventeen more or less complete baculitids were collected at the disused Galgenknapp quarry, east of Lengerich, in 1991 (Fig. 1). Isolated jaws were also recovered from a pale greenish to reddish brown clayey marlstone facies at Rheine-Waldhügel (now refilled part of the Middle quarry). The baculitid material originated from an Upper Cenomanian – Lower Turonian sequence within the CTBE (Fig. 2); this corresponds to a spot about 200 m north-west-north of section 3 (Middle Cenomanian) at locality 4 of Lehmann (1999). This tectonically limited occurrence has subsequently been completely excavated; currently, this horizon is no longer exposed at quarry.

All specimens illustrated as well as additional material are housed in the Geowissenschaftliche Sammlung (Geosciences Collection) of Bremen University, bearing registration numbers GSUB C5833–C5849. All are sediment-compacted, delicate remains on thinly laminated, light grey and slightly yellowish bituminous, indurated marlstones. The carbonaceous nature of the preservation is supported by the absence of fluorescence under ultraviolet and the fractured surface of the carbonised parts. It is difficult to split the unaltered, grey to dark grey sediment along bedding planes; it is easier with weathered, yellowish to brownish slabs such as the ones that occur at the Galgenknapp quarry where the formerly horny and coaly remains contrasted more clearly with the matrix. A small flat chisel was used to split the clayey marlstones, and all slabs were studied carefully under a binocular microscope and cut to size. In view of


Lengerich area
overview section
Lengerich, Galgenknapp
detailed section
Legend detailed section
nodular marlstone
greenish marlstone
flaser limestone
black shale
greyish claystone
greyish marlstone
greyish limestone
greenish, clayey limestone
reddish marly claystone
* baculitid bed
Legend overview section
dark, mud-/ wackestone flaser bedded
light, mud-/ wackestone, well-bedded
dark, mud-/ wackestone
light mud-/ wackestone with high clay content
light mud-/ wackestone with low clay content
nodular, clayey mud-/ wackestone
black shale
Late Turonian
Middle Turonian
Early T.
Late Cenom.
Middle Cen.
Early Cenomanian
340
300
200
100
0
*
26
24
22
20
18
16
14
12
10
8
6
4
2
0
*

their fragility, fossils were coated with superglue to prevent mechanical damage.

Material. Seventeen specimens (GSUB C5833–C5849), most of which consist of imprints of dissolved shell, but do preserve primarily organic, nonmineralised body parts.

GEOGRAPHICAL AND STRATIGRAPHICAL SETTING

These exceptionally preserved baculitids are restricted to the Galgenknapp quarry at Lengerich (county of Steinfurt, Nordrhein-Westfalen, sheet 3813 Lengerich, scale 1:25 000, Gauss Krueger grid reference R 25 23 500, H 57 85 100). The level that produced the material was not recorded (either not observed or absent altogether) from comparable sections nearby, that is, the Dyckerhoff cement quarry at Lengerich (Lehmann 1999) and at Halle, Westfalen (Diedrich 2001).

Bed 125 with the baculitids is part of a 20-cm-thick grey, clayey marlstone level, 5.2–5.25 m above the top of barren, massive pelagic coccolithic limestones (formerly referred to as '*Rhotomagense* Pläner' or 'Arme *Rhotomagensis* Schichten'; currently Brochterbeck Formation; see Hiss *et al.* 2007) and below the base of thin-bedded claystone, marlstone and clayey, greenish to reddish brown limestone, the 'Schwarzbunte Wechselfolge' or 'Rotpläner' of German authors (Keller 1982; Kaplan and Schmid 1983; Breitkreutz *et al.* 1991; Schönfeld *et al.* 1991; Hilbrecht and Dahmer 1994; Lehmann 1999; Wiese *et al.* 2004). This marked boundary level, between beds 99 and 100 (Appendix S1, see Supporting Information), characterises an abrupt change in depositional and palaeoceanographical conditions from shelf carbonates to more distal sedimentation during a time of increased waterdepth in this region. The grey, laminated clayey marlstone ('black shales') belong to the global OAE 2 (for an overview, see Jenkyns 1980). The reddish or greenish claystone (pelites) and marlstone were laid down in a well-oxygenated environment (Hilbrecht and Dahmer 1994).

From the thin clayey marlstone bands, an extremely impoverished fauna was collected, comprising baculitids, *Allocrioceras annulatum* (Shumard, 1860), ?*Watinoceras/Neocardioceras* sp. indet., indeterminate ammonite jaw/buccal elements (*Neoanaptychus* sp., *Rhynchoteuthis* sp., isolated radulae), a few belemnitellid coleoid arm hooks (*Praeactinocamax*?) and small (3–4 cm long) bony fishes reminiscent of the genus *Sardinoides* von der Marck, 1858. Müller (2008) described a partially articulated skeleton of the durophagous shark *Ptychodus decurrens* Agassiz, 1843, while Diedrich (2001) recorded the pachycormid *Protosphyraena* sp. From a temporary exposure in the Bielefeld city area, Breitkreutz *et al.* (1991) illustrated aff. *Sardinoides*, *Ptychodus* cf. *elevatus* (Leriche, 1927), '*Inoceramus pictus*' (uncertain due to poor preservation), a land-derived fragmentary cycadean ('fern') and several ammonites referred to as '*Neocardioceras juddii*'. Alternatively, the last-named might represent *Watinoceras* sp. (compare Kennedy *et al.* 2003), possibly *W.* cf. *devonense* Wright and Kennedy, 1981; the same holds true for '*Neocardioceras juddi*' of Kaplan *et al.* (1998). In view of the fact that *Watinoceras devonense* marks the base of the Turonian in the United States Western Interior (Kennedy *et al.* 2005), this species is of great biostratigraphical interest. However, the Lengerich specimens are sediment compacted, and ornament is not preserved.

Microfossils from the grey calcareous shale bands include abundant flattened and pyritised radiolarians of the genera *Spumellaria* Ehrenberg, 1875 and *Nassellaria* Ehrenberg, 1875 as well as diagenetically compressed planktonic foraminiferal shells of the genus *Rotalipora* Brotzen, 1942; these were identified by one of us (WR) on bedding planes of slabs and in sieve residues. Deep-water agglutinated foraminifera (DWAF; a *Placentammina placenta* fauna of lesser diversity, yet rich in individuals) were recovered from greenish, brownish and reddish thin shale bands both above and below the calcareous shales (see Appendix S1; samples Lng. 290–312). Comparable, albeit more diverse, foraminiferal faunas were recorded by Holbourn and Kuhnt (2000) from a pelagic, deep-marine environment below the CCD.

As far as biozonation is concerned, this particular horizon is assigned to the *Inoceramus pictus* inoceramid Zone of the Upper Cenomanian (Kaplan 1992; Lehmann 1999). In ammonite terms, this level corresponds either to the *Metoicoceras geslinianum* Zone or the *Neocardioceras juddii* Zone. However, *M. geslinianum* has been collected exclusively from the *Plenus* Bank at Lengerich; the overlying beds have yielded very rare and poorly preserved ammonites that cannot be unequivocally assigned and are thus unsuited for biostratigraphical resolution (compare Kaplan 1992; Lehmann 1999).

The horizon that yielded the baculitids formed during a high sea level stand in the study area, as a part of the

FIG. 2. A, Generalised section of the Cenomanian–Turonian in the Lengerich area, with position of the detailed section shown in B. B, Section of the Galgenknapp quarry at Lengerich, with the stratigraphic origin of the type material that is dated as Late Cenomanian *Inoceramus pictus* inoceramid Zone. The Cenomanian–Turonian boundary was drawn following Lehmann (1999), who documented index inoceramids for both sections and carbon isotope data for the Dyckerhoff quarry section. Correlation of both sections is unequivocal because the lithological succession is highly distinct and almost identical in both outcrops.

Oceanic Anoxic Event OAE 2 (Owen 1996; Lehmann 1999). In sequence-stratigraphic terms, the Late Cenomanian facies change can be interpreted as a sequence boundary, the bed below the *Plenus* Bank as a transgressive surface, the maximum flooding surface being situated above the level with baculitids, at the base of the main clayey marlstone bundle (Fig. 2B; Appendix S1; Owen 1996; Lehmann 1999). Thus, this bed corresponds to an interval of marked sea level rise in the area. A strong rise and high sea level, respectively, are confirmed by finds by one of us (WR) of size-sorted radiolarians in the same bed and in overlying levels.

ORIGIN OF THE LAGERSTÄTTE AND FOSSIL PRESERVATION

The exceptional preservation in the Lengerich deep-water fossil Lagerstätte can be explained by an admixture of concentration, rapid burial and conservation processes. Over a distance of 80 km, trending north-west to south-east between Rheine and Bielefeld, the levels considered here crop out in an area of a few kilometres in width which follows the topography of the Teutoburger Wald mountain range. A series of 8–10 dark grey calcareous shale bands (Beds 125, 129, 134a, 155, 158, 162, 173, 177; see Appendix S1) have produced numerous ammonite upper jaws (Fig. 3). Such instances have so far been thought to be restricted to other Mesozoic occurrences outside the Alpine-Carpathian-Caucasus fold belt. The concentration of disarticulated cephalopod jaws, similar to modern oceanic examples (Belyayev 1959, 1962, 1964), may be linked to an extremely low depositional rate (condensation), a process potentially different from that which resulted in the Lengerich example. Riegraf and Schmitt-Riegraf (1995, p. 208, pl. 38, fig. 2h–o) offered another explanation on the basis of the Late Campanian upper jaw element *Rhynchoteuthis minima* from south-east Westfalen, assumed to have belonged to a gaudryceratid ammonite: those jaws might have come from concentrations of such elements in the stomach contents of vertebrate predators, in coprolites or as regurgitates of larger species of fish, pliosaurids or mosasaurids. Such a hypothesis is supported by etching traces (digestive acids) on and in the calcitic parts of the jaws not covered by horny tissue.

FIG. 3. Slab GSUB C5838 with numerous mandibles, one of which preserves the radula *in situ* (red circle), possibly of baculitids; Cenomanian–Turonian boundary interval at Lengerich, north-west Germany.

At Lengerich, turbiditic currents, perhaps originating from the Nordwestfälisch-Lippische Schwelle (swell) in the north-east (Diedrich 2001, p. 158), might have swept remains of both the baculitids and isolated ammonite jaws (Fig. 3) down into the deepest basinal parts around Lengerich. There, they were gravitationally enriched, deposited and preserved by fairly rapid burial in clayey marlstones (i.e. obrutionary stagnant lagerstätte *sensu* Seilacher *et al.* 1985, p. 11).

According to Riegraf and Schmitt-Riegraf (1995), there are no other comparable Late Cretaceous cephalopod jaw occurrences known so far, except for the example described here and those from the Late Campanian Beckum Subformation in Westfalen. Other well-known deep-water ammonite jaw Lagerstätten are confined to the Bajocian–Barremian in the western Tethys (Cuba, Blake-Bahama Basin, Betic Cordillera, Vocontian Trough and French Alps, Northern Calcareous Alps, Carpathians, Caucasus, Atlas syncline of North Africa).

Contrary to the Late Campanian *Rhynchoteuthis minima*, the Lengerich upper jaws (chiefly or exclusively of baculitid ammonites) apparently were not mineralised by a thicker calcite coating. Ammonites with more heavily mineralised paired aptychi usually did not possess *Rhynchoteuthis*-type upper jaws, as proved by a few *in situ* finds of *Striaptychus cretaceus* (Breitkreutz *et al.* 1991, pp. 45–46, figs 6–7) and other Baculitidae (Schlüter 1876, pl. 39, fig. 16). One of us (WR) dissolved a dozen well-preserved specimens of *Rh. minima* in acetic acid and obtained tiny, horny inner lamellae; these cannot be differentiated from those collected at Lengerich. However, it should be noted that this, in part, is due to the poor two-dimensional preservation.

Anyway, preservation of the baculitids as imprints indicates that their aragonitic shells were diagenetically dissolved and only organic portions of the shell and soft tissues remained. It is more difficult to explain the absence of calcite in the ribbed baculitid aptychi ('*Striaptychus cretaceus*'; compare Klinger and Kennedy 2001; Landman *et al.* 2007 and references therein), which are best seen in Figure 4A–B. In view of the fact that the matrix of the soft-part ammonites consists of two-thirds of coccoliths, the calcite could not have been dissolved by diagenesis. As no calcite is preserved in these ammonites from Lengerich, the carbonaceous parts were most likely

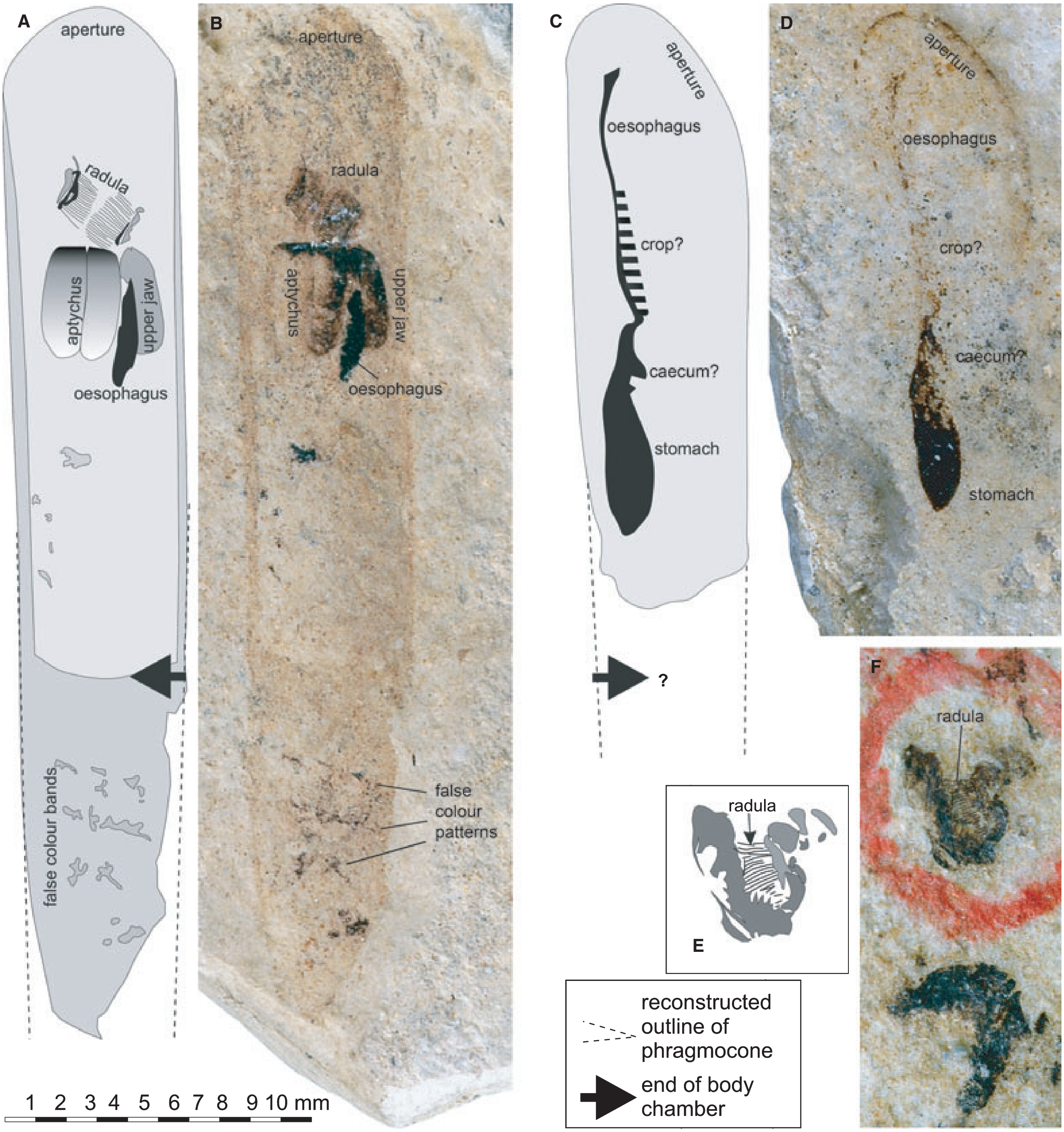


FIG. 4. Baculitid ammonites; Cenomanian–Turonian boundary interval at Lengerich, north-west Germany. All figures ×5. A, C and E are interpretative sketches of specimens photographed. A–B, GSUB C5833, showing false colour bands and complete body chamber with aperture; inside body chamber, remains of both beaks and radula are seen. C–D, GSUB C5834, obliquely deposited shell fragment with aperture (marked by a dark band); note apertural asymmetry, indicative of a ventral projection; the digestive tract is fairly well preserved. E–F, GSUB C5838, a mandible (or both jaws?) with radula *in situ*. Detail of slab is illustrated in Figure 3.

dissolved. One of us (WR) has previously suggested that the absence of calcitic and aragonitic skeletal elements in these ammonites could be explained along the lines explained above. Having been eaten by a predator, their shells and aptychi were dissolved in its stomach and the remainder was regurgitated. However, such a scenario requires an explanation for the excellent preservation of unmineralised parts: in a predator's stomach, enzymes would probably have altered or destroyed the soft parts, while acid led to dissolution of all aragonite and calcite.

In addition, for all sections between Lengerich and Bielefeld, deposition below the CCD can be excluded, based on the geological setting of the area. In summary, we cannot offer any satisfactory explanation for the peculiar preservation of baculitids described here.

SUPRAGENERIC AFFILIATION

The most prominent features of the material described and illustrated here are a more or less orthoconic shell (Fig. 4), with an apical angle smaller than 4 degrees (measured in flattened specimens), an oblique aperture, probably with lateral sinuses and dorsal and ventral projections, a thin ventral siphuncle and a buccal mass with well-developed radula (Fig. 5). Hence, we assign the specimens to the family Baculitidae Gill, 1871.

Our interpretation of these specimens as baculitids is corroborated by the near-perfect match between the radula of *Baculites* as described by Kruta *et al.* (2011) and the material described here (Fig. 4). Teeth proportions in the various rows, as well as the dimensions of some cusps, are closely comparable. However, in view of the poor shell preservation, generic and specific assignment is impossible. The baculitid nature also fits to the observation that baculitid ammonites occasionally occur in these strata (Hauschke *et al.* 2011).

Traditionally, such flattened baculitids have been assigned to the genus *Sciponoceras* Hyatt, 1894; whether separation from *Baculites* Lamarck, 1799 is justified or not cannot be decided on the basis of the present material, but needs three dimensionally preserved shells of both genera. Assignment to *Sciponoceras gracile* (Shumard, 1860), in accordance with previous central European records, cannot be substantiated either. For that reason, we merely refer to these specimens in terms of the family Baculitidae.

DESCRIPTION OF SELECTED SPECIMENS AND DISCUSSION

GSUB C5833 (Figs 4A–B, 5 and 8D–E), 34 mm long and 7.5 mm wide, is one of the most informative specimens. The apical end is slightly darker and contains four dark transverse structures that we interpret to be false colour bands. The lighter part in front probably represents the body chamber, a conclusion corroborated by the presence of carbonised organs. The slightly darker field of the phragmocone continues on either side of the body chamber in a narrow line. The anterior end of the body chamber is rounded; this most likely represents the typically baculitid ventral projection of the aperture (Davis *et al.* 1996; Klinger and Kennedy 2001; Larson 2012). Based on the preserved shell outline, we have extrapolated shell shape and size. The complete shell must have been *c.* 125 mm in length; the apical angle in the diagenetically flattened shell is *c.* 3 degrees. It appears wider than before compaction and deformation.

Within the body chamber, dark patches of various shapes and colour shades are preserved, which most likely represent carbonised remains of several organs. Some small (<1 mm) patches in the posterior half of the body

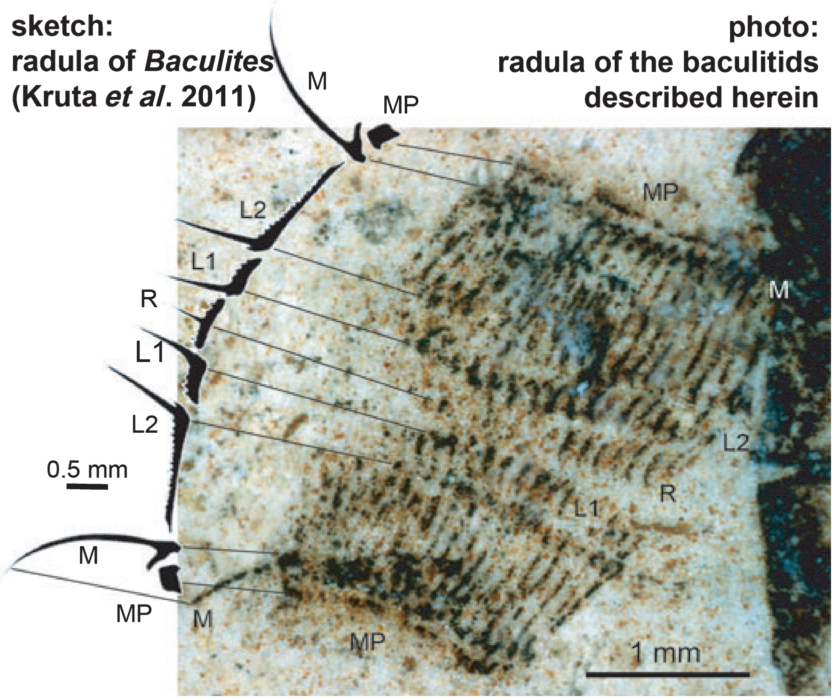


FIG. 5. Comparison of radulae of *Baculites* as published by Kruta *et al.* (2011) and of a baculitid from the Cenomanian–Turonian boundary interval of the Teutoburger Wald.

chamber lack detail and cannot be interpreted further. In contrast, the anterior portion of the body chamber reveals a few recognisable organs, of which some details can be observed. On the basis of colour, shape and internal structure, they are here interpreted as part of the beak/radula and buccal mass complex. The darkest structure measures *c.* 5.0 by 0.6 mm; its long axis is parallel to that of the shell. In view of its dark colour, it is here interpreted as remains of the oesophagus; this is occasionally preserved because it has chitinous coatings (Klug and Jerjen 2012). To the left of this dark patch are two identical, gently vaulted, rounded rectangular to oval patches. These are fused mesially and probably represent the unmineralised portions of remains of the flattened outer lamella of the lower beaks, that is the aptychi. A third structure, *c.* 3.4 mm in length and up to 0.6 mm in width, is stituated to the right of the oesophagus. It is almost as dark as the oesophagus and probably represents the inner lamella of the upper beak and its rostrum (compare Landman *et al.* 2007; Kruta *et al.* 2011). Although poorly visible, it would seem that this structure becomes darker anteriorly, where the outer lamella with the rostrum used to be.

Anterior to what we interpret to be the lower beak, a nearly bilaterally symmetrical structure of *c.* 3 by 2 mm, and composed of two sets of 16–20 fine and irregular, subparallel lines, which are separated in the centre (Figs 4A–B and 7), is seen. A comparison with radular tooth proportions documented by Kruta *et al.* (2011) demonstrates that this structure indeed represents the radula, thus facilitating interpretation of its morphological details, as follows:

1. the same number of teeth per row is present in *Baculites* (Kruta *et al.* 2011);
2. width proportions of types of teeth are identical; and
3. the main cusps are of equal proportions and positions, where preserved.

GSUB C5834 (Fig. 4C–D) is smaller than the previous specimen, measuring *c.* 20 by 5.8 mm. It appears to represent mainly the body chamber. The extrapolated shell length attains *c.* 100 mm, with an apical angle of 3.5 degrees in the flattened state; originally, the angle might have been even smaller. The anterior edge of the body chamber, that is the ventral apertural projection, is obliquely rounded, being accentuated by a fine brown line along its edge. With some reservation, we interpret this structure as the black band (*sensu* Klug 2004; Klug *et al.* 2007*a*, *b*); alternatively, it could represent a false colour band. The asymmetrical apertural outline probably indicates the oblique position the specimen was in prior to compaction.

Within the body chamber, a single carbonised structure is preserved. Its posterior part is a black blob, measuring 6 by 1.5 mm, with the dark matter fading out anteriorly and the outline becoming slightly irregular. Adaperturally, a fine, 9-mm-long and gently curved black line follows. These structures might be the remains of the digestive tract, with the anterior spot as part of the oesophagus, the rugged, lighter part in the centre the crop and the posterior dark spot the stomach. The small protrusion at the anterior end might represent the caecum.

Of GSUB C5835 (Figs 6A–D, 8B and 9), both part and counterpart are available, of a maximum shell width of 6.2 mm and a reconstructed total length of approximately 160 mm. The better-preserved part is only 55 mm long, while the counterpart measures 71 mm. In the deformed state, the apical angle is as low as *c.* 2.5 degrees. In the better-preserved part, traces of six straight false colour bands and the siphuncle are seen. The latter is subcentral in position, which probably is caused by the oblique orientation of the specimen prior to compaction. Unlike GSUB C5833, the present specimen has a much darker body chamber, while the phragmocone is of a slightly lighter hue. Near the presumed position of the (unpreserved) aperture, a dark spot is seen. A black structure, showing fine details and measuring 4 by 2 mm, is situated in this dark spot. Both short ends of the dark area display angular indentations. On the right side, a comb-like structure is visible; this consists of approximately 24 rows of teeth. As in GSUB C5833, we interpret this structure as the remains of the radula. The indentation probably is ‘homologous’ to the gap noted in the radula of GSUB C5833. Interpretation of this structure as the gills, another filamentous organ, appears unreasonable, because this structure is associated with beak remains in GSUB C5833, C5836 and C5838 and is positioned anterior of rather than behind the beaks.

Directly posterior to this radula and the surrounding dark spot, additional structures are preserved. Two elongate, light grey and more or less symmetrically arranged spots are seen, particularly when contrast is increased by means of image-processing software (PhotoShop). These light patches are slightly elevated and oval to subcircular in outline; they measure approximately 4 by 2 mm and are separated by a darker area that is 1 mm in width in the front part and 2 mm posteriorly (Fig. 9A, C). In view of the fact that no further details are preserved, our interpretation is tentative. With regard to dimension, shape and localisation just behind the buccal mass, the bright spots might represent traces of eye capsules, slightly retracted into the body chamber. In modern coleoids, the cephalic cartilage and eye capsules have similar positions and proportions. Their position within the body chamber of GSUB C5835 may be the result of some stressful predeath condition, which led to retraction of the soft parts.

Posterior to the two larger light spots, there are a series of six lighter, oval to subcircular spots, roughly 0.8–1.4 mm diameter, at a distance of about 0.8 mm in an


A
radula
outline of counterpart
eye capsule
eye capsule
eggs in oviduct?
?
false colour bands
siphuncle
B
radula
cephalic cartilage
eggs in oviduct?
1 2 3 4 5 6 7 8 9 10 mm
C
disarticulated fish remains
siphuncle
false colour pattern
1 cm
E
arm hooks
buccal mass?
arm bases?
cephalic cartilage
jaw?
crop + stomach
F
1 cm
false colour pattern
siphuncle
curved apical part of phragmocone
D
1 cm
G
arm hooks
arm bases?
oesophagus
eye capsule
eye capsule
jaw?
crop
stomach
?
false colour bands
siphuncle

irregular dark field (Fig. 9B). These spots cannot be interpreted unequivocally, because morphological details are not preserved. They do not resemble gills; in addition, they are too regular and too large to be ganglia. The nidamental gland would also have displayed a finer striation or no structure at all at this magnification; hence, this interpretation is unsupported. We may speculate that the sole structure in the soft tissues of cephalopods that could produce such subcircular traces of similar size in such a serial arrangement could be the egg mass (compare Landman *et al.* 2010). In many cephalopods, the ovaries lie posteriorly, often behind the mantle cavity and more or less directly anterior to the last septum. Near-mature eggs may be preserved in the oviduct and thus would have occupied a more anterior position. Presuming that these ammonites had typical ammonite eggs and embryos (the ammonitella being probably less than 1 mm at hatching), their shape and size would more or less coincide with these fossil structures.

The body chamber of this specimen is covered by tiny black and brown spots (Figs 5B and 9E–F) that represent a simple diagenetic feature. They are dendrite-like, dot-shaped iron and manganese oxide deposits of altered pyrite/marcasite. These spots follow, or form, broad seams at the boundary between the altered (yellowish) and unaltered (grey) calcareous shale, best observed in larger-sized slabs.

GSUB C5836 (Fig. 6E–G), 59 mm in length and 5.2 mm in width, also preserves remains of several unmineralised organs. Based on the arrangement of soft-tissue remains, the body chamber is estimated to have been *c.* 27 mm in length. The reconstructed shell length would have been in excess of 70 mm. Thus, this specimen is much shorter than the others that are *c.* 125 and 160 mm in length, perhaps indicating a younger growth stage. Of this specimen, shell length is more difficult to estimate because the preserved part of the phragmocone is slightly curved.

Immediately behind the aperture, several dark areas are seen. The anteriormost brownish spots are nearly symmetrical and show a faint striation. These striae run at an oblique angle to the shell outline (venter or dorsum, respectively) and bend anteriorly below the middle of the whorl height. A set of three to five striae on either side can barely be made out. Otherwise, these two spots do not reveal any distinct structure. In view of position, proportions and striated appearance, we suggest that this structure represents the remains of the base of the arm crown, of the nuchal muscles or of the buccal mass.

Directly posterior of this questionable structure, an irregular dark spot roughly of 4 by 4 mm is seen; this consists of two parts of slightly different size and shape. In view of shell diameter, the overall proportions and dimensions of these interconnected spots resemble those of what we assume to be the eye capsules in GSUB C5835. Additionally, an elongate, 5-mm-long and almost 1-mm-wide structure is seen in the centre. This might be the oesophagus, which traverses the cephalic cartilage in recent cephalopods. Thus, the two dark spots might well represent the eye capsules. These are followed by a largely symmetrical, triangular and V-shaped spot that resembles a beak both in shape and dark colour characteristic of fossil cephalopod beaks. As far as shape goes, it could be the lower beak. However, its position behind the cephalic cartilage is odd, and casts doubt over an interpretation as a beak.

About 6 mm behind the above-mentioned structures, there is a dark structure with a fairly distinct outline, consisting of two drop-shaped spots, about 1 by 3 mm in size, interconnected by two very fine, subparallel black lines. The entire structure is here interpreted as remains of the digestive tract. If this interpretation is correct, the anterior spot could be the crop or the digestive gland and the posterior one the stomach.

Seventeen millimetres behind this dumbbell-shaped structure, remains of the apparently slightly curved phragmocone are preserved. Traces of twelve false colour bands and the ventral siphuncle are present. The siphuncle remains are interrupted where they cross the false colour bands.

GSUB C5837 (Figs 7E and 8F) is *c.* 7.4 mm wide and *c* 60 mm long, at least 21 mm of this length corresponding to the body chamber. The reconstructed shell length would be about 170 mm, with an apical angle of 2.5 degrees in the flattened shell. Thus, this specimen would have been the longest with the smallest apical angle.

Near the presumed aperture, a brownish spot of *c.* 4 by 3.3 mm, with a U-shaped anterior outline, occurs. In view of shape, position, association with an ink sac and duct,

FIG. 6. Baculitid ammonites; Cenomanian–Turonian boundary interval at Lengerich, north-west Germany. All figures ×5, except C–D that are natural size and F that is ×2. A and G are interpretative sketches of specimens photographed. A–D, GSUB C5835. A, sketch with outlined structures visible in the specimen; B, detail of C, showing the alleged body chamber with eyes; buccal mass remains include radula and ?oviduct; C, complete slab, showing disarticulated remains of an actinopterygian fish; D, counterpart. E–G, GSUB C5836, near-complete specimen, showing false colour bands and ventrally positioned siphuncle in apical part of phragmocone; in body chamber, remains of digestive tract, beaks and other parts of the animal are seen, probably parts of buccal mass with radula and/or arm crown; E, detail of D, showing animal remains and digestive tract, as well as associated pair of coleoid arm hooks; F, complete specimen, showing phragmocone with false colour bands; G, sketch with outlined structures visible in this particular specimen.

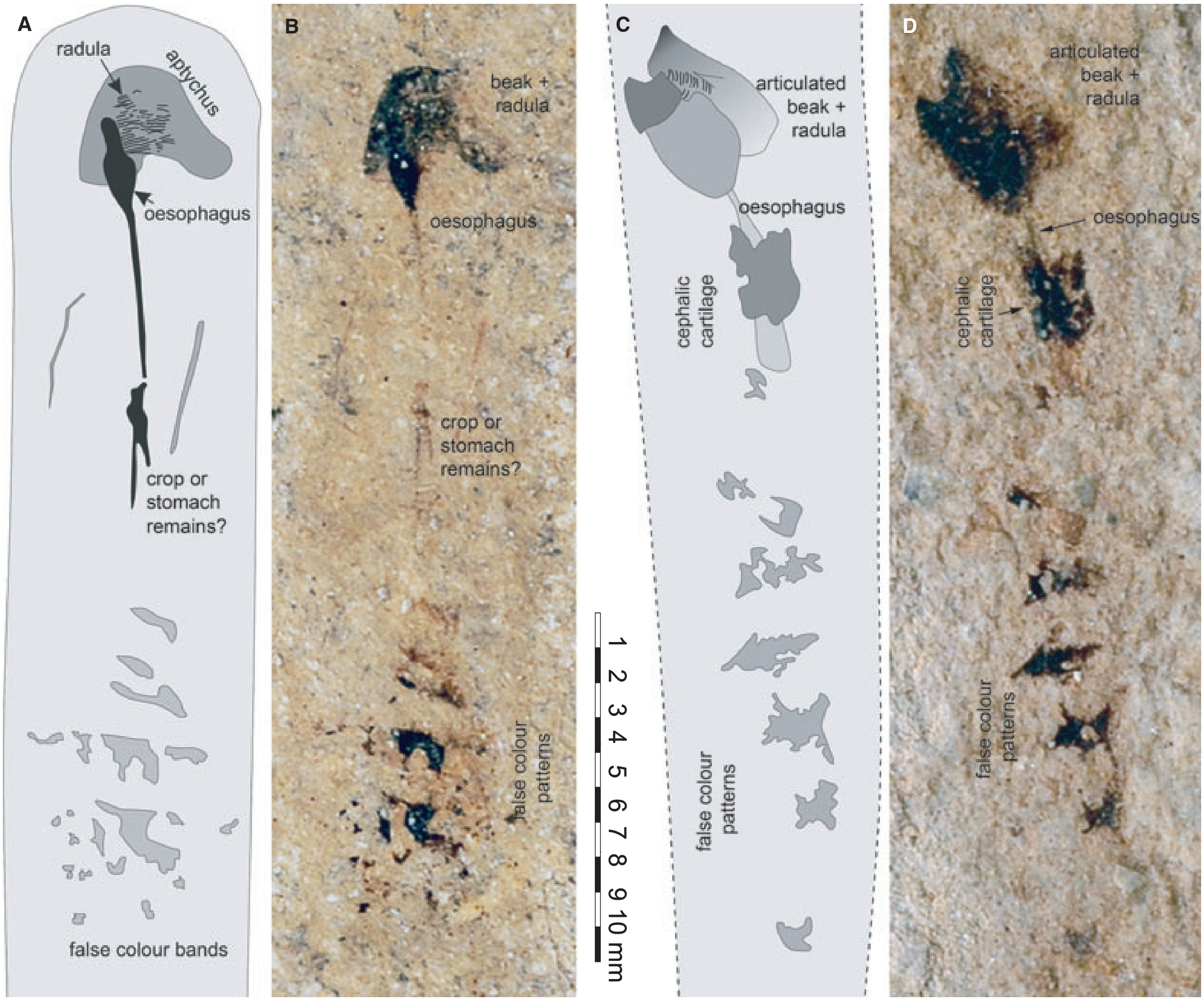


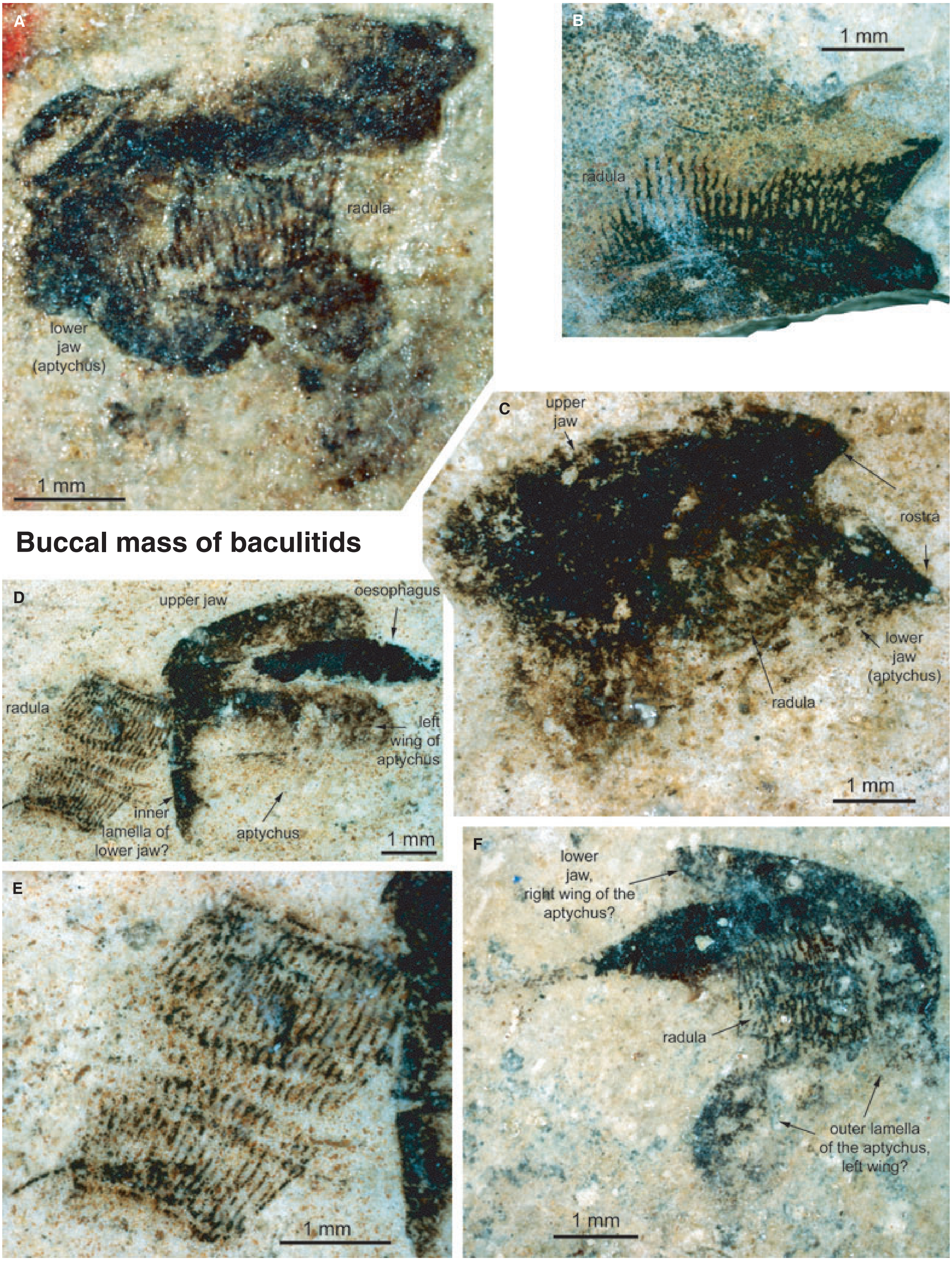
FIG. 7. Baculitid ammonites, Cenomanian–Turonian boundary interval, Lengerich, north-west Germany. All figures ×5. A and C are interpretative sketches of specimens photographed. A–B, GSUB C5837, poorly preserved shell remains with false colour bands, digestive tract and lower mandible with radula *in situ* and with ?oesophagus (black elongate structure). C–D, GSUB C5839, showing articulated mouth parts, including *in situ* radula, with attached ?oesophagus and around it, remains of cephalic cartilage(?). Numerous false colour bands preserved.

and its dark colour, we suggest that this represents the remains of the lower beak. This interpretation is corroborated by remains of the radula which are seen in the centre of this structure (Fig. 8F).

On top of and behind it, remains of two elongated structures are seen. These consist of a 3 by 1-mm-sized spot, attached to a 5-mm-long, fine dark line. At the posterior end of the line, a narrow and irregular spot (4 mm in length and 0.5 mm in width) is visible. These structures might represent remains of the oesophagus and crop (or stomach?).

Nearly 3 mm behind the dark remains of the digestive tract, transverse structures are preserved, some of which probably represent remains of false colour bands.

FIG. 8. Baculitid ammonites, Cenomanian–Turonian boundary interval, Lengerich, north-west Germany. A, GSUB C5838, remains of lower mandible with *in situ* radula. B, GSUB C5835, radula on radula support or, alternatively, both sides of radula overlapping. C, GSUB C5839, articulated mandibles with *in situ* radula. D, GSUB C5833, lower mandible with radula and oesophagus (black). E, detail of D, showing anterior part of radula, characteristically spread out. Rows of radular denticles are discernible, although only few details of denticles themselves are visible; note long cusp of marginal tooth to lower left. F, GSUB C5837, lower mandible with *in situ* radula and with ?oesophagus (black elongate structure).


A
radula
lower jaw (aptychus)
1 mm
B
1 mm
radula
Buccal mass of baculitids
C
upper jaw
rostra
lower jaw (aptychus)
radula
1 mm
D
upper jaw
oesophagus
radula
left wing of aptychus
inner lamella of lower jaw?
aptychus
1 mm
E
1 mm
F
lower jaw, right wing of the aptychus?
radula
outer lamella of the aptychus, left wing?
1 mm

GSUB C5838 (Figs 4E–F and 7A), which lacks shell remains, is preserved on a 143 by 84-mm-sized slab and is associated with other dark remains; being 0.6 to 5.5 mm in size, portions of beak are rather small. This slab contains remains of probably over 80 beaks, all potentially belonging to the same species. Many are more or less U-shaped, which is why they could be outer lamellae of lower beaks. In contrast, some are preserved only in the form of minute dark triangles with a much brighter patch attached; such specimens might represent remains of upper beaks.

Of this slab, two specimens are here singled out for detailed description. These are illustrated in Figures 4E–F and 8A. In the latter figure, the dark structure in the upper half of the image most likely represents the deformed outer lamella of a lower beak, of which the tip ripped during compaction, which would explain the small indentations at the alleged rostrum. It measures about 5 by 4 mm and preserves two wings of 2–3 mm in length. Three millimetres away, there is a second structure of 5 by mm, which reveals a striated structure at its centre. This structure displays about 20 fine lines, up to 1 mm long, and closely resembles the radula of GSUB C5833. It is surrounded by an irregular U- to V-shaped dark brownish structure. This complex represents parts of the buccal mass, inclusive of the radula and possibly of the oesophagus.

GSUB C5839 (Figs 6C–D and 8C) is fairly complete as well, comprising phragmocone remains, beaks and some additional organs. Overall length is about 46 mm, but there is no distinct shell outline preserved. Remains of 11 or 12 false colour bands are visible. In this particular specimen, both mandibles are still articulated, with the radula preserved in between. Overall, the upper mandible is darker than the lower, clearly revealing the dorsal part of the inner and outer lamellae. The rostral tip can also be seen; it is pointed, with the lateral cutting edges slightly vaulted dorsally. The lower mandible reveals less detail, but its tip has a triangular outline with a darkened anterior edge. Both mandibles are about 5 mm in length. In between both mandibles, two sets of irregular subparallel rows of teeth are exposed. About 12 rows of teeth are seen on one side, the other showing merely two to three rows of the radula. This specimen constitutes another piece of evidence in support of the interpretation of these striated structures as the radula. We know of no other striated organ between cephalopod mandibles with a certain preservation potential.

Behind these buccal mass remains, two additional soft-tissue structures can be made out. A light beige, elongate structure, 6 mm length and 0.5–0.9 mm in width, is here interpreted as the oesophagus because it originates directly at the buccal mass. On top of it, there is a 3.2-mm-long and 2-mm-wide subrectangular structure of darker colour. This shows indentations at both ends and is here tentatively interpreted as the remains of the cephalic cartilage (potentially with the bases of the eye capsules).

ANATOMY

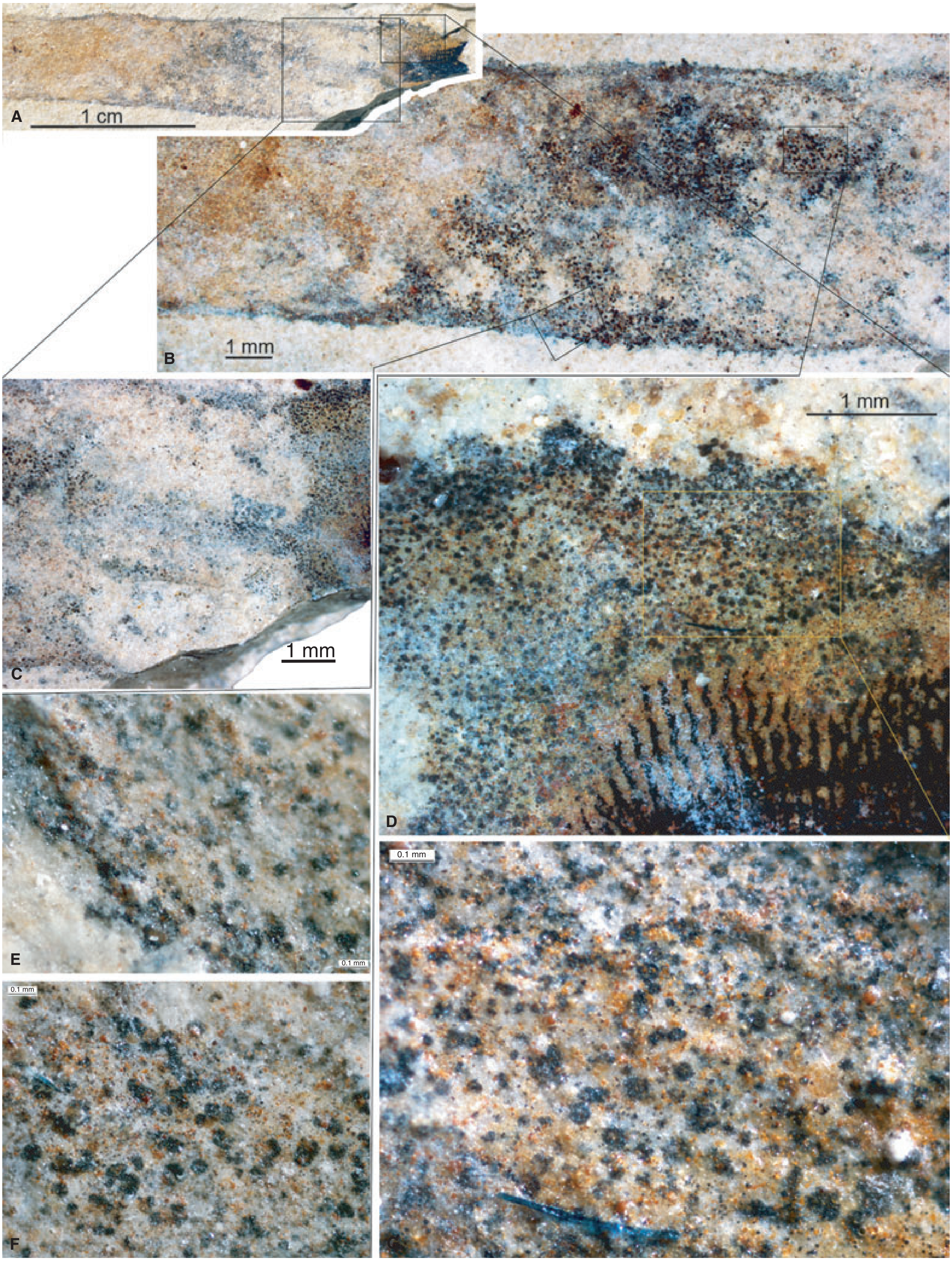
Shell. In spite of the flattened nature and the absence of shell material, we have been able to extract certain data on shell morphology (Figs 3–4 and 6). The orthoconic phragmocone has a small apical angle of 3–4 degrees. The body chamber, as inferred from the extent of the siphuncle, makes up about one-third of the entire shell length.

The aperture had a pronounced ventral projection and probably also lateral sinuses. However, these sinuses cannot be made out in the present specimens, but they are clearly seen in shells of *Baculites* from North America (Larson 2012). During life, the large eyes were located in these lateral (ocular) sinuses.

Based on the present material, maximum shell length is estimated to have been approximately 170 mm, but as clear indications of adulthood are missing, they might well have attained significantly larger sizes. Other baculitids grew much larger, which is why the present specimens represent either a small-sized species or juveniles of a larger one at the time of death.

The shell imprint shows severely weathered, dark transverse bands. Interpretation of these bands as septa is erroneous, because ammonite septa did not contain melanin that would have been conducive to such preservation. In contrast, at growth halts (megastriae), some ammonites did deposit melanin in their shell, which occasionally is preserved (Klug *et al.* 2007*a*, *b*; references therein). Mapes and Davis (1996) referred to these dark stripes, which are occasionally well visible, as 'false colour patterns'. They represent remains of growth halts, also called 'megastriae', 'alte Mundränder' (former apertures), 'demarcation lines' or 'transitional mouth borders' (Diener 1895; Matsumoto *et al.* 1972; Bucher and Guex 1990; Matsumoto 1991; Tozer 1991; Bucher *et al.* 1996; Bucher 1997). Commonly, the shell forms some kind of constriction, either distinct or shallow, around such a growth halt, thus forming ribs. In the flattened state of the specimens described herein, such morphological detail is not preserved, but the false

FIG. 9. Baculitid ammonites, Cenomanian–Turonian boundary interval, Lengerich, north-west Germany. A, GSUB C5835, overview of body chamber. B, magnification of detail in A, showing putative eggs in oviduct. C, detail of eye capsules. D, detail showing parts of radula and putative remains of integument. E–F, subcircular dendritic remains in body chamber, probably both limonite (brownish, smaller aggregates) and manganese oxide (black, larger aggregates).


A
1 cm
B
1 mm
C
1 mm
D
1 mm
E
0.1 mm
F
0.1 mm
G
0.1 mm

colour bands may be interpreted as indication of the presence of faint ribs.

Mandibles. This baculitid had a massive buccal mass with a wide lower beak (aptychus; Figs 6 and 7) with two wings of elongate subrectangular outline and a short anteroventral tip and rounded posterior ends. The mandibles of *Baculites* appear to be quite commonly preserved, which is not surprising, considering the great abundance of representatives of this genus locally. Therefore, baculitid mandibles have been described on numerous occasions (for a comprehensive list of references see Landman *et al.* 2007). Based on the specimen shown here in Fig. 7F, the upper mandible had a pointed triangular rostrum with a broad outer lamella and a long inner one, which extended far beyond the outer lamella, as in other previously described *Baculites* (aptychus type; compare Klinger and Kennedy 2001; Engeser and Keupp 2002; Landman *et al.* 2007; Kruta *et al.* 2011). In particular, the upper mandibles are carbonised, similar to most of the preserved parts of these ammonites (compare also Trauth 1927, 1935; Matern 1931; Lehmann 1967, 1970, 1972, 1978, 1981; Seilacher *et al.* 1976; Lehmann *et al.* 1980; Tanabe *et al.* 1980; Tanabe 1983; Mapes 1987; Tanabe and Fukuda 1987; Lehmann and Kulicki 1990; Seilacher 1993; Doguzhaeva *et al.* 1997; Tanabe and Mapes 1998). In the mandibles, the darkness of the preserved material probably also reflects the original dark colour of the mandibles. We suggest that these are remains of mainly melanin, which accounts for colour preservation (compare Mathur 1977; Doguzhaeva *et al.* 2004; Klug *et al.* 2004, 2007*a*, *b*, 2010*a*, *b*; Miserez *et al.* 2008; Vinther *et al.* 2008).

For reasons unknown, the lower beaks do not show their calcitic portion, presuming they had one. We have measured wing length of 54 mandibles on the slab with GSUB C5838, revealing an obliquely normal size distribution with an abundance maximum near 1.5 mm (Fig. 11). It is likely that there are preservational biases underlying this size distribution, namely weak currents and a lower preservation and recognition potential of even smaller mandibles. This association of cephalopod beaks might also contain mandibular elements of various taxa. However, this appears unlikely in view of the rather uniform shape, size and state of preservation. Assuming that this association does contain beaks of but a single species and that sorting or other biases played only a subordinate role, with the exception that the smallest beaks are probably underrepresented, the size distribution might reflect a type III survivorship curve or an r-selected species, respectively. This corresponds well to recently published interpretations of the reproductive strategy of ammonites (De Baets *et al.* 2012). The beaks of GSUB C5833, C5837 and C5838 are comparatively large, which may be explained by preservational bias; such unmineralised structures have a higher preservation potential with increased size.

Radula. The radula was very wide and bore delicate teeth; these are poorly preserved in the present specimens. Comparison with the radula of *Baculites* described recently by Kruta *et al.* (2011) shows that the rachidian tooth was narrow with cusps of moderate length, the adjacent lateral teeth 1 were of comparable width and cusp length, while the lateral teeth 2 had very long bases with many short cusps and a long mesial one. The base of the marginal tooth was small and carried a single, very long cusp, its length roughly corresponding to the width of the L2 tooth (Fig. 7D–E). The marginal plates are similarly very small to the bases of the M teeth in size. Tooth proportions of the present specimens and of *Baculites* described by Kruta *et al.* (2011) are very closely similar and substantiate both our assignment to the Baculitidae and our interpretation as the radula. Between 12 and 22 denticles, rows are preserved in these specimens. In any case, this constitutes an additional example of rare occurrences of ammonoid radulae (Closs and Gordon 1966; Closs 1967; Lehmann 1967, 1979, 1990; Nixon 1988, 1996; Doguzhaeva and Mutvei 1990, 1992; Kennedy *et al.* 2002; Kruta *et al.* 2011; Klug and Jerjen 2012).

Oesophagus. Obviously, the digestive tract of fossil cephalopods does have a certain preservation potential (Figs 3–4 and 6). There are records of ammonite oesophagi (Lehmann and Weitschat 1973; Riegraf *et al.* 1984; Lehmann 1985, 1988, 1990; Jäger and Fraaye 1997; Keupp 2000; Klug and Jerjen 2012) and those of several coleoids (Larson *et al.* 2010; Fuchs and Larson 2011*a*, *b*; references therein). GSUB C5836 and C5839 both display elongate structures in association with remains of what we interpret as cephalic cartilage. As the only comparatively broad organ passing the cephalic cartilage in the plane of symmetry is the oesophagus, such an interpretation appears reasonable. In GSUB C5833 (Figs 4A–B and 8D), C5835 and C5837 (Figs 7A–B and 8F), an elongate black spot is situated within the buccal apparatus, also suggesting this to be the oesophagus. A similar association of mandibles and radula, with a possible oesophagus, has been suggested by Klug and Jerjen (2012) for a ceratitid from the Middle Triassic (Muschelkalk) of Germany.

Crop, digestive gland, caecum and stomach. GSUB C5834, C5836 and C5837 preserve additional dark spots, connected by a fine black line. These are here considered to be additional remains of the digestive tract, the anterior spot representing either the crop (which is of greatly variable size in Recent *Nautilus*; see Westermann *et al.* 2002) or the digestive gland (which may be larger than the crop in Recent squid; compare Nixon and Young 2003) and the posterior spot possibly being the stomach. In GSUB C5836, this is situated far behind the buccal apparatus, while in GSUB C5834, interpretation of this posterior

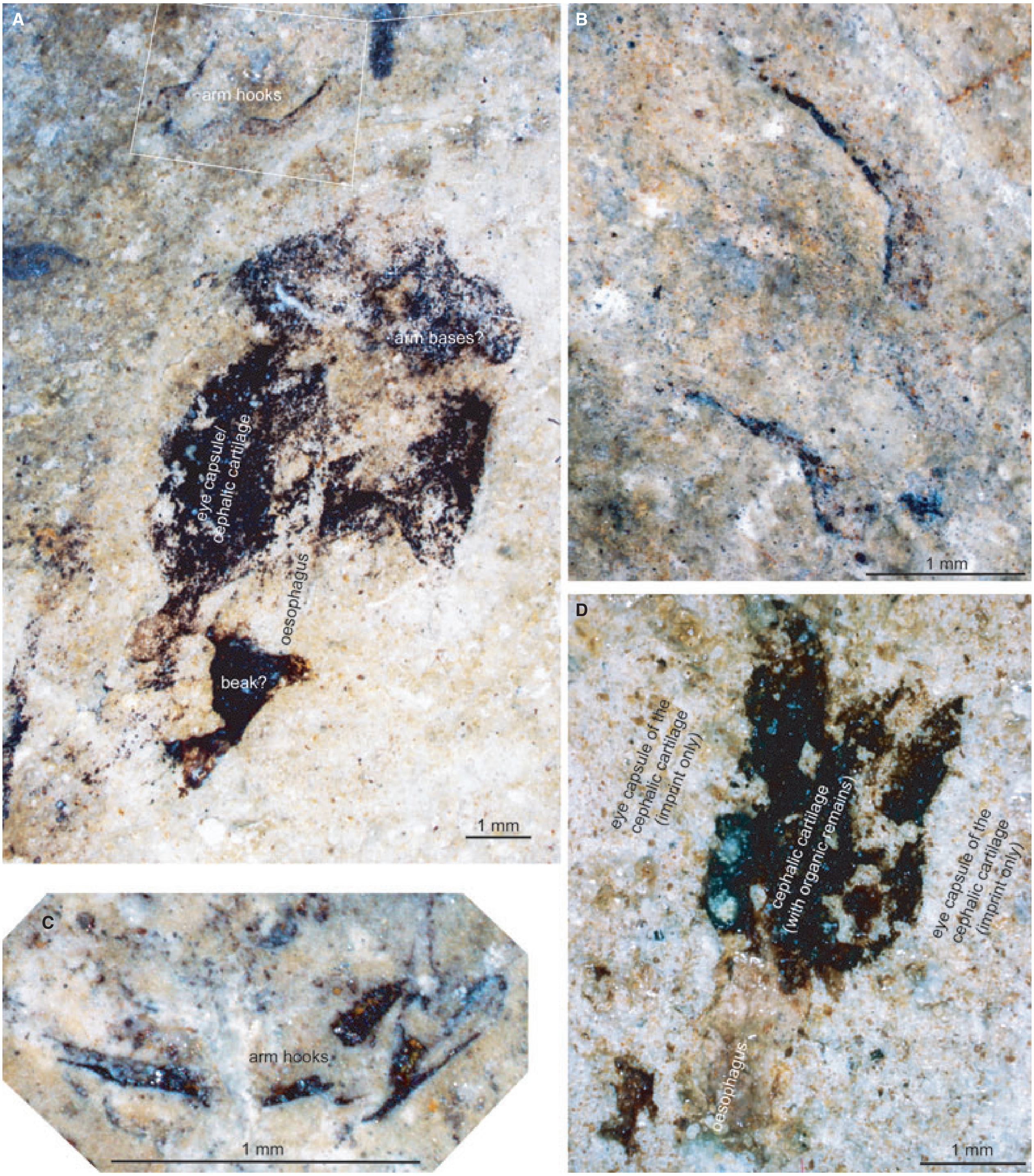


FIG. 10. Baculitid ammonites, Cenomanian–Turonian boundary interval, Lengerich, north-west Germany. A, GSUB C5836, showing associated pair of (?belemnoteuthid) arm hooks, eye capsules of cephalic cartilage, oesophagus and possibly arm bases (above cephalic cartilage). B, detail of A, to show arm hooks at larger magnification. C, isolated arm hooks, GSUB C5836. D, GSUB C5839, remains of cephalic cartilage and oesophagus.

spot as the stomach finds some support in the presence of a small anterior bulge which is reminiscent of the caecum in *Nautilus* (Westermann *et al.* 2002). However, in view of the fact that fine morphological details are lacking, support of the above interpretations is admittedly weak. Within these parts of the digestive tract, no details of the ingested food are discernible (compare Lehmann 1975).

Cephalic cartilage and eye capsules. The cephalic cartilage and eye capsules of fossil cephalopods are occasionally well preserved, for example, in Cretaceous coleoids from Lebanon (Larson *et al.* 2010; Fuchs and Larson 2011*a*, *b*). In support of our interpretation as remains of the cephalic cartilage in GSUB C5835–C5836 and C5839, we may refer to proportions, close proximity to and position immediately behind the buccal apparatus, in addition to its symmetrical appearance and the presence of two suboval structures. Only in the former, two are the eye capsules preserved (Figs 6–8). In GSUB C5835, the interpretation of the two oval light-coloured spots as eye capsules is supported by their symmetry, their dimensions and position relative to other organs (buccal mass). In particular, the argument of symmetry finds some support in the fact that the animal is positioned with its plane of symmetry more or less perpendicular to the sediment surface, as evidenced by the submedial position of the siphuncle. However, anatomical details are lacking, precluding definitive proof. The alleged eye in *Belemnoteuthis* as illustrated by Engeser and Reitner (1981, figs 2–3) might also represent a remnant of the cephalic cartilage.

Oviduct(?). The row of ovoid, light-coloured spots in GSUB C5835 defies unequivocal interpretation (Fig. 8B). The linear association of subcircular to oval structures of an approximately 1-mm diameter matches egg-containing ovaries. However, morphological details are missing. As far as we know, gonads and oviducts of extinct cephalopods have never been described so far, which can probably be explained by the interior position of these organs. In other words, in cases where all soft tissues are preserved, gonads and oviducts would be covered. Additionally, there is their low preservation potential, compare Redelstorff and Orr (2010), who described the sequence of organ decomposition observed in Recent tadpoles. In contrast, alleged fossil mollusc eggs have been reported occasionally, mainly from internal moulds (Kaiser and Voigt 1977; Riegraf and Schubert 1991; Etches *et al.* 2009; Zatoń *et al.* in press).

Arm hooks. Close to the aperture in GSUB C5836, there are a pair of arm hooks. However, the close proximity to the shell is here interpreted as mere coincidence (Fig. 9). For now, we are unable to determine whether these hooks are of the belemnitellid coleoid *Praeactinocamax plenus* (de Blainville, 1927), from a squid such as '*Belemnoteuthis*' *syriaca* Roger, 1944 or from the baculitids themselves. Although not enough details are preserved to decide which of these interpretations is the correct one, the last-named view appears unlikely because other baculitids should have been found with such hooks because representatives of this family are very common in many places. Whether both the ammonite remains and the arm hooks were originally part of the stomach content or of a coprolite cannot be decided for now.

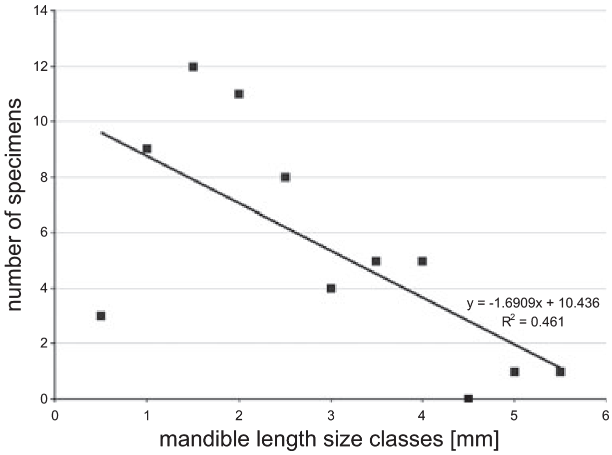


FIG. 11. Size distribution of cephalopod mandibles on slab GSUB C5838, illustrated in Figure 3.

ONTOGENY OF BACULITID MOUTH PARTS AND IMPLICATIONS FOR MODE OF LIFE

The baculitid mouth parts described herein, reconstructed in Figure 12B–C, are rather small. With overall lengths between 3 and 6 mm, at whorl heights of *c.* 5 mm, these jaws were about 25 per cent the size of jaws in *Baculites*, at whorl heights of *c.* 33 mm, as described by Kruta *et al.* (2011). In the present baculitids, upper and lower jaws both appear to be more or less of the same length, whereas in *Baculites*, the upper jaw is much shorter. This might, however, be linked to the difficulty of detecting the very thin posterior parts of the upper jaw in the synchrotron image stack (Kruta *et al.* 2011). Concerning the size of the radula in relation to jaw size, the laterally stretched-out radula appears to be about 25 per cent narrower than the length of the lower jaw in both. Remarkably, the proportions of the radular elements are almost identical in both, which would support comparability of diet, at least between these two growth stages. Naturally, numerous representatives of the genus *Baculites* grew much larger than the specimens described herein, or those recorded by Kruta *et al.* (2011). Large-sized shells of *Baculites* may reach overall lengths of >1 m, with whorl heights at the aperture exceeding 100 mm (Larson *et al.* 1997). In view of the fact that there was no significant change in proportions of the mouth parts between apertural heights of *c.* 4 and 33 mm, we assume that there were no significant changes in these proportions until adulthood was reached. In accordance with the study by Kruta *et al.* (2011), this would suggest a more or less continuously planktotrophic diet of baculitids throughout most of their lives after hatching. A nektonic habitat and mode of life (Fig. 10A)

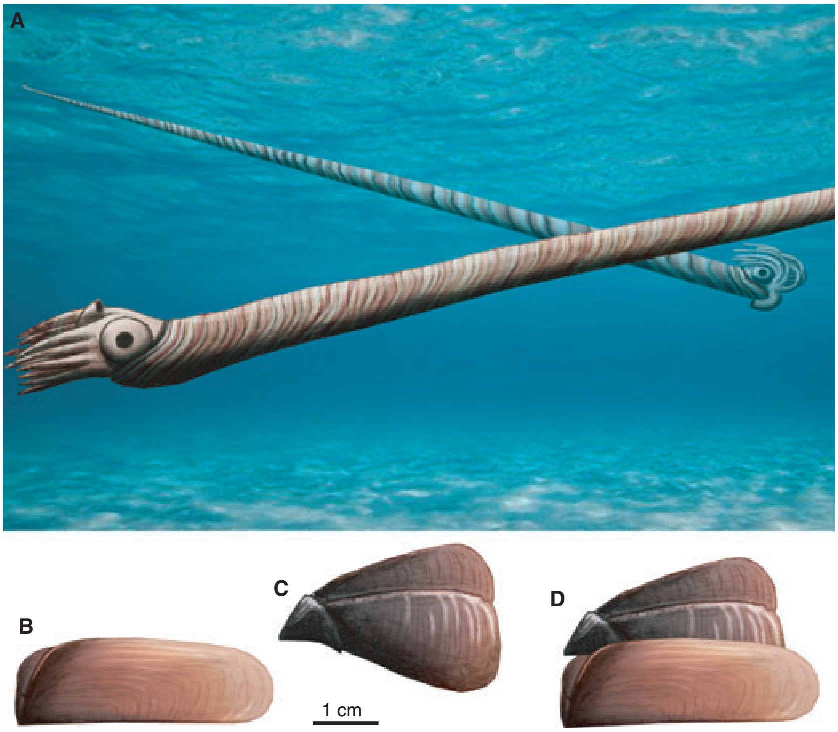


FIG. 12. Reconstruction of a baculitid ammonite. A, reconstruction of live animal. Arm length and shape are speculative, note large eyes. Horizontal swimming position is in accordance with recent data supplied by Hauschke *et al.* (2011). Stripes on shell are assumed to be 'false colour bands' (*sensu* Davis *et al.* 1996), that is, representing darkened shell parts at growth halts. B–D, reconstruction of beak; due to poor preservation of beaks, some parts of mandibles as shown here are reconstructed following data supplied by Tanabe and Landman (2002) and Kruta *et al.* (2011). B, lower beak, aptychus-type. C, upper beak. D, both mandibles in articulation.

was already postulated for heteromorphs by, for example, Westermann (1996), Cecca (1997), Fatherree *et al.* (1998) and Lukeneder *et al.* (2010). Additionally, a moderately deep habitat for baculitids is corroborated by both the presence of large eyes (the present material; also supported by the presence of wide ocular sinuses in the aperture of other baculitids; Larson 2012) and the oxygen isotope values of aragonitic shells (Fatherree *et al.* 1998; Lukeneder *et al.* 2010).

CONCLUSIONS

The remarkably preserved early Late Cretaceous cephalopods from the Teutoburger Wald can be assigned to the heteromorph ammonite family Baculitidae, on account of shell shape and ornament of faint ribs, preserved in the form of false colour bands. More significantly, their radular morphology is typical of baculitids.

In addition to shell imprints, the present material preserves several unmineralised body parts that we interpret, with varying degrees of certainty, as upper and lower mandibles, radula, cephalic cartilage with eye capsules(?), and digestive tract including oesophagus, crop as well as stomach. Some organ remains cannot be interpreted unequivocally to date, yet there is weak support for the presence of remains of eggs in the oviduct.

These new anatomical details, in combination with published data on baculitids (Fatherree *et al.* 1998; Lukeneder *et al.* 2010; Kruta *et al.* 2011), suggest that these heteromorphs were planktotrophic and lived at depths where some light penetrated, probably <100 m, throughout most of their postembryonic life.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Base data on the locality and stratigraphy.

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