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RESEARCH PAPER

Belemnoid arm hooks from the Middle–Upper Albian boundary interval: taxonomy and palaeoecological significance

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Abstract For the first time, a large number of belemnite arm hooks is described from the Lower Cretaceous (Middle–Upper Albian boundary interval) of the classic locality of Folkestone in southern England. The arm hooks originate from six individual claystone layers; some could have been attributed to the parataxon *Arites* sp. Comparison is made with material from a drill core from Hannover, northern Germany that shows similarities and also allows the description of a new parataxon: *Hughowenites incurvatus* n. gen. n. sp. The belemnite hooks might belong to either the diplobelids *Conoteuthis* and *Pavloviteuthis*, both characterised by a reduced guard and thus very rare finds at Folkestone, or the abundant guard-bearing belemnitinid *Neohibolites*. Within the studied succession, belemnite hooks are more abundant in sediments deposited during an earliest Late Albian warming event that is accompanied by an increased abundance of guards of the belemnite *Neohibolites*. Concurrently with this warming event primary productivity was enhanced, as indicated by fluctuations in the composition of the calcareous nannoplankton assemblage. The shift in belemnite abundance might be interpreted as triggered by a combination of warming and increased productivity and/or condensation.

Keywords Belemnites · Arm hooks · Palaeotemperature · Palaeoproductivity · Cretaceous Albian · England

Kurzfassung Erstmals wird eine größere Anzahl von Belemniten-Armhaken aus der Unterkreide (Grenzbereich mittleres/oberes Alb) der klassischen Lokalität Folkestone in Südengland beschrieben. Die Armhaken stammen aus sechs verschiedenen Tonsteinhorizonten, einige können dem Parataxon *Arites* sp. zugeordnet werden. Ein Vergleich mit Material aus einer Bohrung in Hannover, Norddeutschland, zeigt Übereinstimmungen und führt zudem zu der Beschreibung eines neuen Parataxons: *Hughowenites incurvatus* n. gen. n. sp. Die Belemnitenhaken dürften entweder von den Diplobeliden *Conoteuthis* und *Pavloviteuthis* stammen, die durch ein reduziertes Rostrum charakterisiert sind und deren Rostren deshalb in Folkestone sehr selten sind, oder dem sehr häufig auftretenden Rostrum-tragenden Belemnitiden *Neohibolites*. Innerhalb des untersuchten Profils sind Belemnitenhaken in Sedimenten, die während eines Erwärmungsereignisses im frühen Oberalb abgelagert wurden am häufigsten, ein Zeitabschnitt der zudem durch das häufigere Auftreten von Belemnitenrostren von *Neohibolites* charakterisiert wird. Parallel zur Erwärmung war die Primärproduktion erhöht, wie durch Häufigkeitsfluktuationen in den Vergesellschaftungen indikativer kalkiger Nannoplanktonarten belegt ist. Das vermehrte Auftreten von Belemniten könnte durch eine Kombination von Erwärmung und erhöhter Produktivität und/oder Kondensation erklärt werden.

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Schlüsselwörter Belemniten · Armhaken · Paläotemperatur · Paläoproduktivität · Kreide · Alb · England

Introduction

After the pioneering work of Neumayr (1883), who established faunal provinces and was among the first to link macrofossil distribution to climatic differences, it soon became clear that many groups of Jurassic and Cretaceous belemnites show differing palaeogeographic distribution patterns. In fact, belemnite faunas typifying the Boreal-Arctic region can be distinguished from those characterising the Tethyan region (e.g. Stevens 1963; Combemorel et al. 1981; Mutterlose 1986; Doyle 1992; Gale and Christensen 1996; Alsen and Mutterlose 2009; Wilmsen et al. 2010). Several decades ago it became clear that generalisations about the palaeotemperature preferences of belemnite higher taxa are not possible (e.g. Stevens 1965). Different belemnite families and genera show different temperature tolerances, while the temperature preference of some belemnite groups changed during their evolution. The Tethyan belemnopseid *Hibolites*, for example, is regarded as ancestral to the important Boreal family Belemnitellidae as well as the southern endemic stock of the Dimitobelidae (Doyle 1987a; Doyle 1987b; Christensen 1988), therefore indicating a significant evolutionary change in temperature sensitivity. Changing palaeotemperature tolerance can also be traced at lower taxonomic levels, as in the case of the widespread Aptian-Albian emigration from the Tethys by the belemnopseid *Neohibolites* (Doyle 1987b). Based on palaeobiogeographical patterns, Mutterlose et al. (1983) were able to distinguish between eurythermal and stenothermal belemnite genera in the Early Cretaceous. *Hibolites* and *Neohibolites* are eurythermal warm-water genera with high potential for thermal adaption that occurred in the Boreal as well as in the Tethys, whereas *Duvalia*, *Berriasibelus* and *Parahibolites*, among others, are stenothermal warm-water genera that are limited to the Tethyan realm (Mutterlose et al. 1983).

Use of carbonate oxygen isotope ratios in belemnite guards for estimating palaeotemperatures sheds new light on belemnite palaeoecology and allows their application as palaeoclimatological and palaeoceanographical proxies (e.g. Bodylevskii 1957; Tejs and Naidin 1969; Wefer and Berger 1991; Price 1998). In the early years of isotope analysis, belemnite rostra were regarded as imperfect sources for deriving palaeotemperature estimates, since it was thought that there might be a high ratio of secondary cement, leading to alteration of the primary signal (e.g. Wefer 1982). These doubts largely have proved unfounded (Sellwood et al. 1994; Ditchfield et al. 1994; Pierri et al. 1995; Price 1998), because belemnites are composed of low-Mg calcite and thus the chance of preserving the original carbonate is high (e.g. Marshall 1992). Belemnite values are nevertheless different from values obtained from other groups of organisms, and reasons for this remain unclear (Price 1998; Voigt et al. 2003). As an example, measurements obtained from the Late Cenomanian *Actinocamax plenus* indicate a cooler temperature compared with those from brachiopod shells from the same region or results obtained from modelling (Voigt et al. 2003). Hence, palaeoceanographic interpretation is not unequivocal, and in this instance Voigt et al. (2003) propose either migration from a cooler/deeper water mass or an unknown vital effect. Nevertheless, geochemical data derived from belemnite rostra constitute important data for the palaeoclimatologic interpretation of belemnites.

These different approaches show that belemnite data are useful for reconstructing palaeoclimates with respect to palaeoceanography. However, the classical approach in directly relating the distribution of belemnite guards to climatic factors is naturally limited in its argumentation, and a number of contradictions still cannot be explained (e.g. Doyle and Pirrie 1999). Therefore, further environmental factors have been considered to avoid the over-simplification that water temperature had the major biogeographical control on distribution patterns. These factors include changing oceanography and physical barriers, water depth and salinity (Doyle 1988). Here, we test these different hypotheses by investigating the immediate response of belemnites to a discrete, short-term climatic warming event that is known from a number of further proxies besides the belemnite data themselves. We use belemnite hooks obtained from washed claystone samples for this innovative approach.

Locality details and methods

The present paper deals mainly with a series of samples from the classical section near Folkestone, southeastern England, that is located in the Anglo-Paris Basin (Fig. 1). Additionally, test samples and single specimens originating from the Hannover area in northwestern Germany (Lower Saxony Basin) have been considered, a region that showed an open shelf connection to the Anglo-Paris Basin (Fig. 1).

Folkestone section

Important accounts of the research history of the classical Gault Clay section (Middle–Upper Albian) at Copt Point, East Cliff, Folkestone have been provided by early authors such as Parkinson (1819), Fitton (1836), De Rance (1868) and Price (1874) and, more recently, by Casey (1966) and

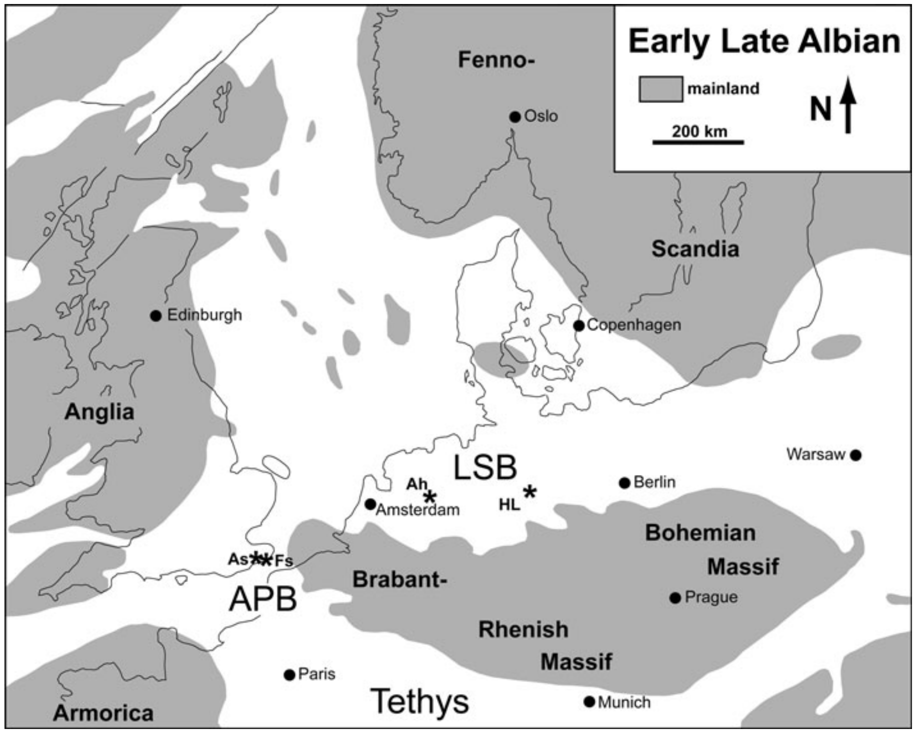


Fig. 1 Palaeogeography of the early Late Albian in northern Europe with localities and areas mentioned in the text. Localities: *Fs* Folkestone, Kent; *As* Ashford, Kent; *HL* drilling core in Hannover-Lahe, Lower Saxony; *Ah* Ölbach stream cut S of Ahaus, Northrhine-Westphalia. *APB* Anglo-Paris Basin, *LSB* Lower Saxony Basin. Map modified after Ziegler (1982, 1990)

Owen (1971a, b). In particular the outstanding preservation of ammonites, including their iridescent shells, is famous and constitutes a major reason why this site has been—and still is—intensively collected (Clouter 2007). The ammonite fauna was monographed by Spath (1923–1943), and the biostratigraphy has been revised, for example, by Owen (1971b, 1976). Results of more recent investigations on calcareous nannoplankton (Kanungo et al. 2004; Kanungo 2005) and dinoflagellate assemblages (Dunn et al. 2006) have not yet been fully published. The belemnite *Neohibolites minimus* (Miller ex Lister, 1826) occurs frequently in the Middle–Upper Albian at Folkestone (see Swinnerton 1955 and Clouter 2007). Recently, Knight (2010) figured a well-preserved specimen with phragmocone and aragonitic pro-ostracum preserved in association with the rostrum. Oxygen isotopes from belemnite guards from Folkestone were used by Bowen (1961) for palaeotemperature estimates, and Spaeth (1971b) demonstrated that they are very well preserved. Additionally, a couple of phragmocones referred to diplobelid belemnoids have been recorded from the Albian of Folkestone: *Conoteuthis woodwardi* Spath 1939 and *Pavloviteuthis cantiana* (Spath 1939) (Woodward 1856; Spath 1939; Jeletzky 1981; not *V. vectensis* Spath 1939 as stated by Fuchs et al. 2004, which originates from the Aptian). Sampling took place in July 2008 (J.L., O.F.).

Our study was systematically performed on six samples from six individual beds of the Folkestone section obtained during fieldwork in July 2008 (J.L., O.F.). Our sampling point in the cliff at 51° 5′2.62″N, 01°11′57.95″E was recorded using GPS and is documented in Fig. 2. Each sample was obtained over a sediment thickness of ~0.5 m (Fig. 3). First, dried and weighed samples of between 2,066 and 3,909 g were carefully mechanically disaggregated and then washed and sieved over a 63 µm mesh (Table 1). For a detailed description of this method see Wissing and Herrig (1999). Samples were dry-sieved into >63 µm, >125 µm and >250 µm fractions. All fractions were picked completely, and a total of 161 belemnite hooks were obtained from the 63–125 µm fraction, 19 hooks from the 125–250 µm fraction and no hooks from the >250 µm fraction. Since the dry weight of samples differed, we normalised values to equal weight of 500 g to compare the results. We used the formula $(n/w) \times 500$ (here called the hook abundance index), with n being the total number of hooks per sample, w the total dry weight, and 500 the factor to calculate the hook number per 500 g (Fig. 3, Table 1). The hook abundance index shows values around 3.5 for samples 1–2 and 5–6 but increases significantly (up to 5.7) in samples 3 and 4.

Scanning electron microscope images (Plate 1) were taken using a Zeiss Supra 40 SEM at the Faculty of Geosciences, Bremen. The terminology of hook features as defined in Fig. 4 follows Kulicki and Szaniawski (1972), Fuchs (2006) and others.

Ölbach section

The Middle–Upper Albian Ölbach stream-cut near Ahaus, northwestern Germany was mentioned by Bentz (1930) and

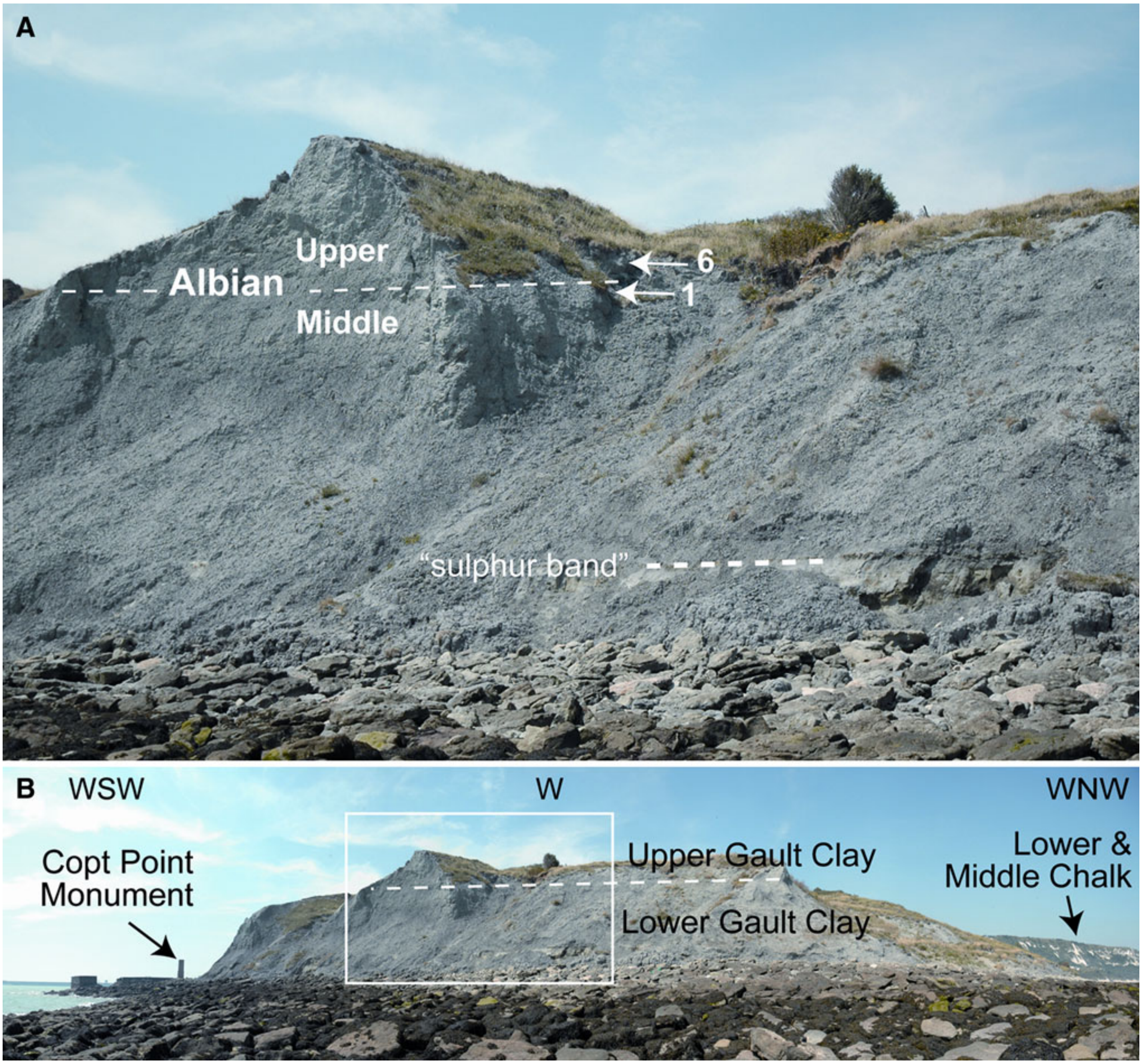


Fig. 2 The Gault Clay (Lower Cretaceous, Albian) section at Copt Point, Folkestone. a Sampling points at 51°5′2.62″N, 01°11′57.95″E in the *upper center* of the picture: *1* indicates the lowermost sample and *6* the uppermost (compare Fig. 3). The *sulphur band* is an index bed of the Middle Albian [boundary between beds III and IV sensu Price (1874)]. b Panoramic view, the *rectangle* shows the position of the close-up of the sampling points in a

briefly described by Kemper (1976), who also figured some fossils. Owen (1979) referred to the ammonite fauna. This locality exposes the Minimus Greensand that is named after the abundant occurrence of guards of the belemnite *Neohibolites minimus*. The belemnite fauna from the Ölbach section has been studied by Spaeth (1971a, b). For this project a large quantity of claystone with abundant belemnite rostra was washed from a sampling point close to the bridge leading to the Schulte-Frankenfelde farm at GPS coordinates 52°23′27.1″N, 006°57′16.9″E (collected by J.L. in February 2008). This site produced fresh claystone material with total weight of 5,000 g that was carefully mechanically disaggregated, dried, then washed and sieved following the same procedure as described for the Folkestone samples. The residues contained no hooks.

Hannover-Lahe core

Three hooks from a drill core at Hannover-Lahe, northwest Germany are considered for comparison. These are of the same geological age as the Folkestone specimens. Locality details and a drawing of the section were given by

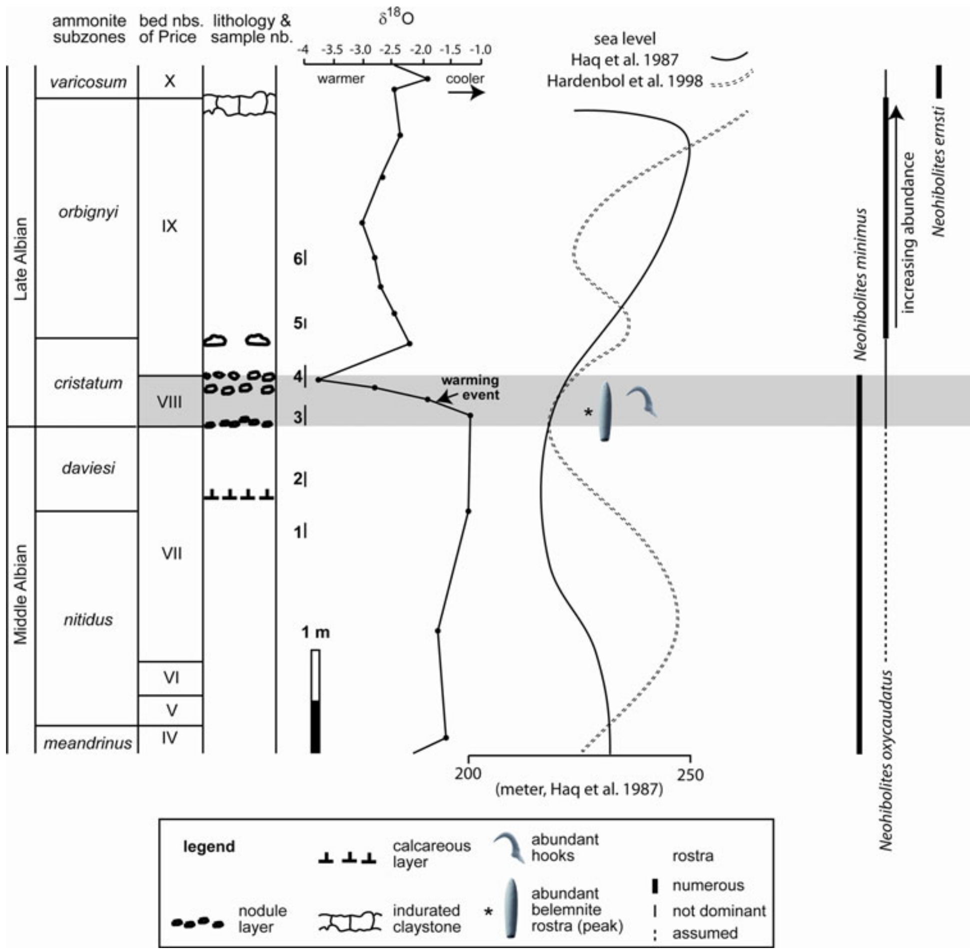


Fig. 3 Position of samples in the Copt Point section, Folkestone, Kent (southern England) with stable oxygen isotope data following Kanungo (2005). The warming event in bed VIII coincides with a higher abundance of belemnite rostra and hooks obtained from microsamples 3 and 4. ProÞle sketch modiÞed after Þeld notes by H.G. Owen and added with own data. Bed numbers after Price (1874). Belemnite rostrum and hook indicate abundant occurrence at Folkestone, whereas *range bars* of belemnite species are an estimate following Spaeth (1973) given for the Ashford section, Kent (a Middle Albian occurrence of *N. oxycaudatus* at Folkestone is assumed following Keller et al. 1989, p. 279). *N. oxycaudatus* and *N. ernsti* are probably endemic to northwest Europe, whereas *N. minimus* is known from many areas in the Tethys (Mutterlose et al. 1983)

Table 1 Dry weight of samples and number of belemnite hooks obtained

	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Dry weight (g)	2,201.9	2,066.0	3,778.4	3,909.9	3,643.0	3,836.8
Hooks in >63 μm fraction	13	12	40	37	22	25
Hooks in >125 μm fraction	4	1	3	4	4	3
Hooks in >250 μm fraction	Ð	Ð	Ð	Ð	Ð	Ð
Total number of hooks	17	13	43	41	26	28
Normalised to 500 g of sample	3.9	3.1	5.7	5.2	3.6	3.6

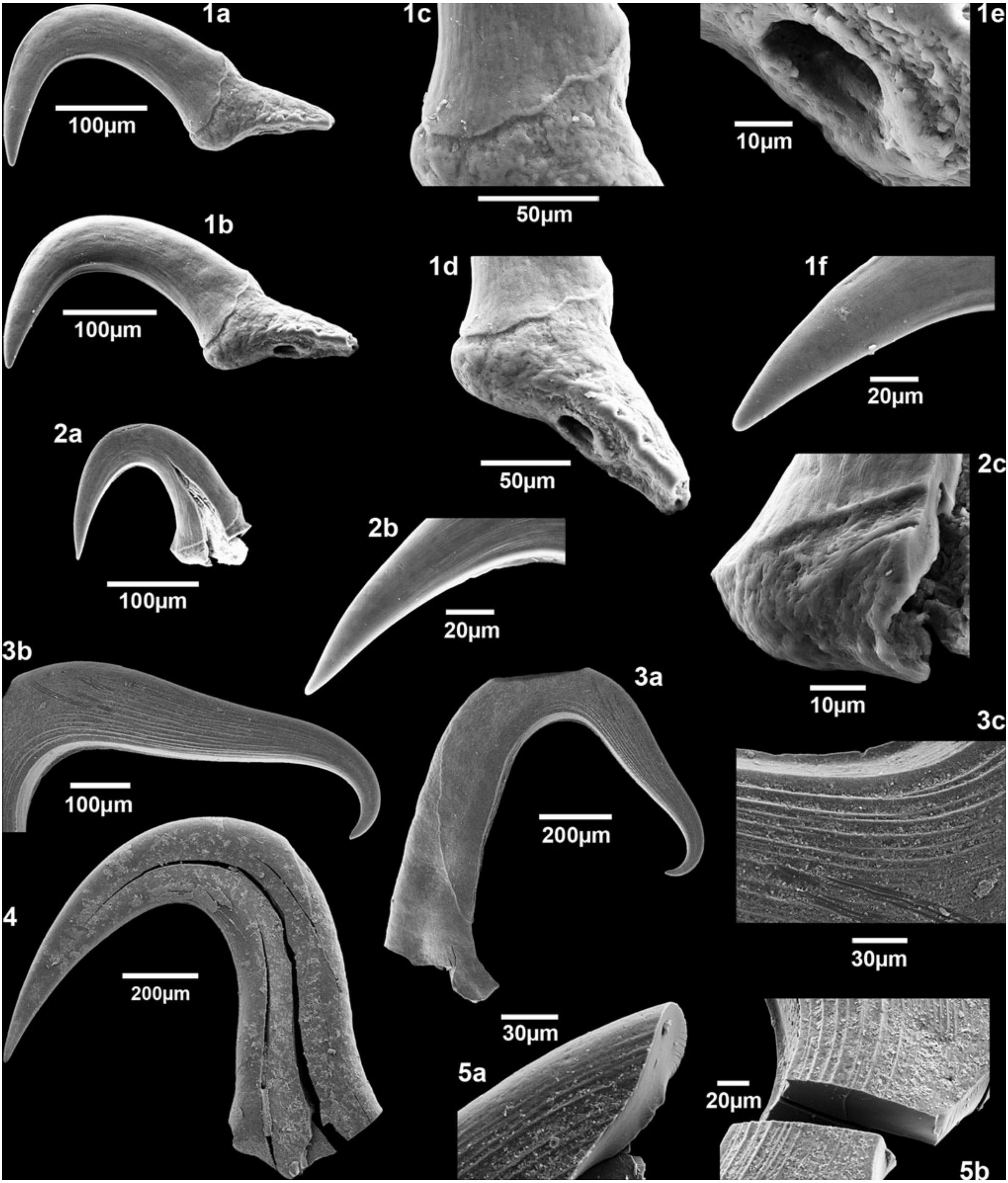
Lehmann et al. (2007). Recent revision of the biostratigraphy of this site suggests that the critical core interval in between 67.45 and 86.90 m depth is not Middle Albian, as interpreted by Lehmann et al. (2007), but corresponds in fact to the earliest Late Albian (early part of the *Dipoloceras cristatum* ammonite Subzone; see also Erbacher et al. in press).

Repository

The abbreviation ÔGSUBÕ indicates the repository in the Geosciences Collection of the University of Bremen, Germany. This applies to the material from the Copt Point section, East Cliff, at Folkestone. The material from the Hannover-Lahe borehole (abbreviation ÔBGRÕ) is stored in the Bundesanstalt für Geowissenschaften und Rohstoffe (Federal Institute for Geosciences and Natural Resources), Hannover, Germany.

Systematic palaeontology

The Þrst belemnoid arm hooks encountered in the 19th century were meso- and macrofossils. Quenstedt (1858)



encountered isolated larger hooks in the Jurassic of Swabia and termed these ‘‘*Onychiten*’’. He thereby introduced the parataxon *Onychites* that became extensively used later (e.g. Riedel 1938; Kulicki and Szaniawski 1972; Schweigert 1999). These larger hooks are arranged in pairs, one per individual, and they are much larger than the other arm hooks of the individual belemnite (Klug et al. 2009). Kulicki and Szaniawski (1972) used the term ‘‘onychites’’ as synonymous with only the smaller belemnite hooks, thus some subsequent authors have differentiated between

◀ Plate 1 SEM images of belemnite hooks. 1 *Arites* sp.: 1a lateral view, 1b oblique lateral view, 1c detail of the transition between base and shaft, 1d base and lowermost part of the shaft in oblique lateral view, 1e part of the supraopening area with basal opening, 1f detail of uncinus with striae; GSUB C5639 (from sample 3 in Fig. 3). 2 *Arites* sp.: 2a lateral view, 2b detail of uncinus with striae, 2c detail of the inner part of the base and lowermost tip of the shaft; GSUB C5640 (from sample 4 in Fig. 3). 3 *Hughowenites incurvatus* n. gen. n. sp. (holotype): 3a lateral view, 3b close-up of the uncinus, 3c surface detail of the inner margin at the bend between the shaft and the uncinus; BGR 13804 (from 86.85–86.90 m depth). 4 *Arites* sp.: lateral view; BGR 104796 (from 67.45–67.65 m depth). 5 *Hughowenites incurvatus* n. gen. n. sp. (paratype): 5a detail of outer margin in lateral view, 5b detail of the inner margin, showing the inner main ridges, oblique lateral view; BGR 13867 (from 70.32–70.37 m). 1, 2 Earliest Late Albian, *Dipoloceras cristatum* ammonite Subzone, Folkestone; from the 63 µm size fraction. 3–5 Same stratigraphic interval, Hannover-Lahe borehole, northern Germany, for comparison with the hooks from Folkestone; see Lehmann et al. (2007) for details

mega-onychites and micro-onychites (Engeser 1987; Engeser 1988; Fuchs 2006). Among the smaller hooks, a number of parataxonomic genera have been established, as summarised by Schlegelmilch (1998); among these, *Paraglycerites* is the most characteristic type because of its lateral appendage (e.g. Riegraf 1996; Schweigert 1999). For a recent and full discussion of belemnoid hook types and their distinction from allied forms see Fuchs (2006). We agree with Engeser (1987) that it makes sense to use a parataxonomy for isolated hooks, and we apply a parataxonomy wherever possible for our material. However, to avoid the confusion that exists through different definitions of the term ‘‘onychite’’, we use the neutral term ‘‘hooks’’ for the material discussed in this paper, contrary to the usage of Engeser (1987) and others.

Description of hooks

The majority of hooks originate from the 63–125 µm size fraction. Complete, undamaged hooks are confined to this fraction (Plate 1, Figs. 1, 2, 5a–c). Hooks are generally morphologically very variable, but two general types can be distinguished: Most hooks show a bow-like outline and are typically hook-shaped (e.g. Fig. 5a, b). A second type is more elongated and saber-like (Fig. 5e–g, m). After Klug et al. (2009) the former type is referred to the distal (tip) or middle part of the belemnoid arm and the latter to the proximal part.

The specific hook-like morphology of the first type can be referred to the paragenus *Arites* Kozur, 1967 as defined below. The elongated type of hooks shows a variety of simple, non-characteristic shapes. Since we do not possess specimens preserved perfectly including the bases, they are not assigned to a parataxon.

Belemnoidea Steinmann, 1890
Uncinifera Engeser, 1990
Belemnite hooks (micro-onychites sensu Engeser and Suthhof 1992)
Paragenus *Arites* Kozur 1967

Type species *Arites vulgaris* Kozur 1967

Diagnosis Hooks with a moderate to strong bend and a large uncinus. The base is usually slightly shorter than the maximum length. The angle between the shaft inclination and the baseline lies between 30° and 70°. The surface is smooth; very faint lateral striae occur in some specimens. The inner margin occasionally bears distinct main ridges

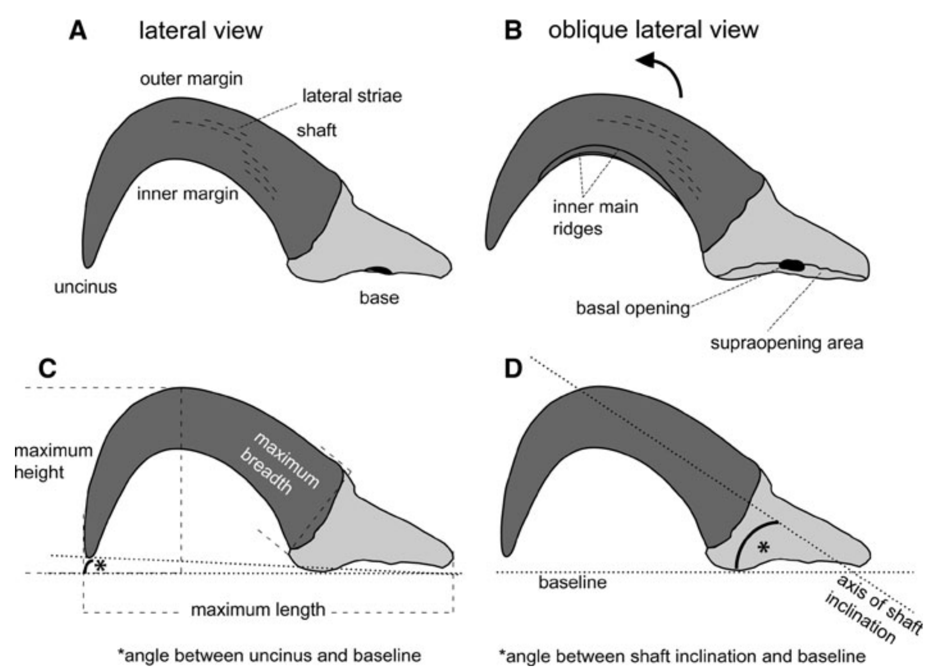


Fig. 4 Terminology of features and measures of belemnite hooks used in the text. Note that *inner main ridges* visible in the oblique lateral view (b) are not visible in the *lateral view* (a). *Stippled lines* in (c) and (d) indicate angle measurements, *dashed lines* are length and height dimensions

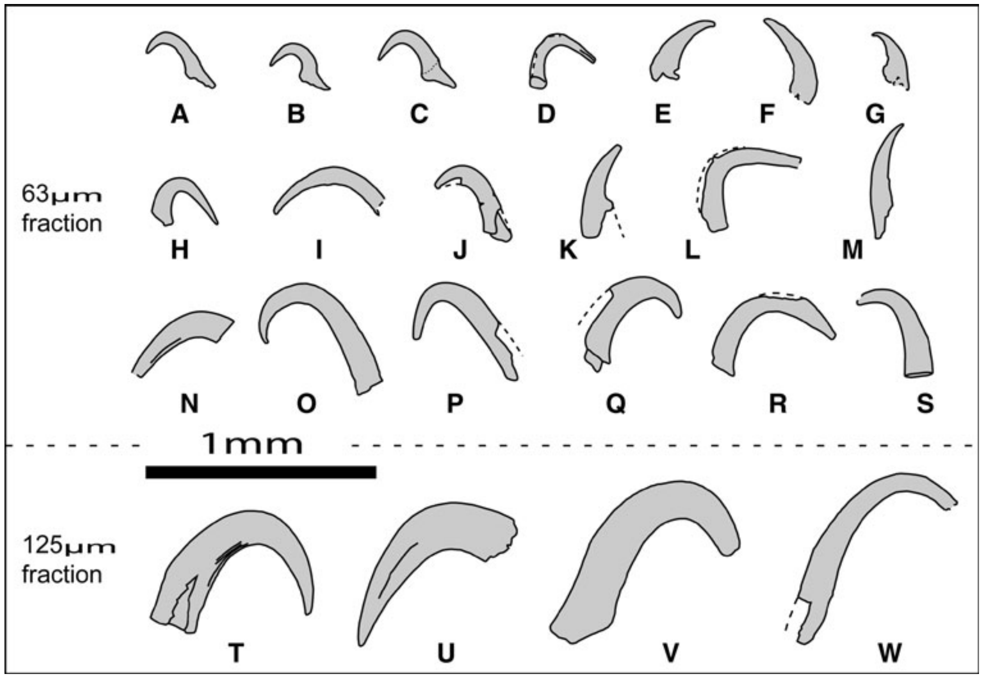


Fig. 5 Outlines of belemnite hooks from the Albian of Folkestone. Hooks figured in a–c are perfectly preserved and referable to the parataxon *Arites* sp., all others show damage and fractures and are not determined. d, e, g, k, l, n, t, u (GSUB C5641-C5648): sample 1; m, w (GSUB C5649-C5651): sample 2; a, b, f, i, o, r, v (GSUB C5652-C5658): sample 3; c, h, j, q, s (GSUB C5639, C5659-C5662): sample 4; p (GSUB C5663): sample 5. Position of samples see Fig. 3

(‘‘*Längsrücken*’’ of Engeser and Suthhof 1992). The elements lack a spur at the base of the inner margin. The base is almost flat in lateral view.

Remarks See Engeser and Suthhof 1992 for a distinction of *Arites* from similar parataxa and a discussion of their affiliation.

Arites sp. (Fig. 5a–d; Plate 1, Figs. 1, 2, 4)

Description Complete hooks of this type have maximum length of about 400 µm, maximum breadth of 100 µm and maximum height of 190 µm (Fig. 4c for definition). The curvature of this hook type is very variable, from wide (Fig. 5a and Plate 1, Fig. 2) to strongly incurved, tending to develop a U-shaped outline (Fig. 5b; Plate 1, Fig. 2). The angle between shaft inclination and the baseline varies largely in between 40° and 80°, whereas the angle between uncinus and the baseline varies only little between 0° and 6°. The central part of the inner margin bears a main ridge on each side of the specimen, thus the hook shows two edges in cross-section rather than being well rounded. Shaft and uncinus can be covered by faint lateral striae (Plate 1, Figs. 1a, 2b). The base of the hook is covered by wrinkles (Plate 1, Fig. 1c, d; light grey area in Fig. 5). The supra-opening area is widely concave, with a basal opening that is located in the middle of the base and is surrounded by a shallow crest.

Remarks Most of the fragmentary material at hand probably belongs to this paragenus, but it is too poorly preserved for any measurements. Estimating the position of the uncini in relation to the baseline in the fragmentary specimen indicates that the angles must have been much larger than in the few specimens where measurements are possible. This is particularly true in some of the specimens representing larger hooks (e.g. Fig. 5p–s). Therefore, *Arites* is probably highly variable.

Morphologies comprise that of the type species *Arites vulgaris* Kozur 1967 as well as that of *Arites keuperianus* Kozur 1967 (both from the Triassic) and include features seen in *Arites riedeli* Engeser & Suthhof 1992 from the Early Cretaceous. Since the two Triassic species are documented only by light-microscopic photographs, it was not possible to properly compare the described taxa. Therefore, it makes no sense to assign the present material to a species or to establish a new species on the basis of morphology. Furthermore, the full range of variability cannot be established from the present material, and it would be poor taxonomic practice to establish a new parataxon solely on the basis of different stratigraphic occurrence.

A large part of the material is indeterminable at parageneric level since it is too fragmentary. A part of it probably represents *Arites* (e.g. Fig. 5j, t). Specimens in Fig. 5v, w are examples of very widely curved hooks that might be referrable to *Falcunus* Kulicki and Szaniawski 1972, a genus similar to *Arites* but that is described as possessing a spur (Kulicki and Szaniawski 1972). Figure 5f, m shows sabre-blade-shaped hooks that are missing their bases. They resemble species of *Uncinakuncus* Kulicki & Szaniawski 1972 but do not possess the characteristic short spur high above the base (Kulicki and Szaniawski 1972). Some authors interpret the occurrence of spurs in belemnite hooks as indicative for guard-bearing belemnites (e.g. Riegraf and Hauff 1983; Engeser 1987; Riegraf 1996). This hypothesis is based only on specimens of *Passaloteuthis* with in situ hooks, and contradictory ideas about the presence of spurs in this genus might indicate preparatorial or preservational artefacts. Thus spurs might also occur in belemnoteuthids and diplobelids and are possibly a feature typical at only the species level (Fuchs 2006).

Comparison with new material

Lehmann et al. (2007) mentioned the occurrence of a couple of belemnite hooks from a drill core from Northern Germany. This material was discovered because the comparatively large specimens attracted attention during standard micropalaeontological screening. Since these belemnite hooks are the only other specimens known from Albian sediments they are compared with the Folkestone material.

The specimens from northern Germany (Plate 1, Figs. 3, 4, 5) agree in their bow-like outline with the majority of hooks from Folkestone, but are fairly large compared with the British specimens, of which only two fragments (Fig. 5u, v) may have reached a similar size. Their large size might indicate that they belong to a larger animal or that they originate from the middle part of a belemnite arm. The hook illustrated on Plate 1, Fig. 4 is attributed to *Arites* sp., but that on Plate 1, Fig. 3 differs from all other material of *Arites* and therefore is described as a new parataxon below.

Paragenus *Hughowenites* n. gen.

Type species *Hughowenites incurvatus* n. gen. n. sp.

Derivatio nominis After Hugh G. Owen, London, outstanding geoscientist, who has worked on the Albian of Europe for many decades.

Diagnosis Large uncinus strongly recurved inwards; with ultimate tip of the uncinus showing an extreme flexion, pointing towards the middle of the shaft (Plate 1, Fig. 3a). Strongly pronounced ridges on the uncinus, except for the smooth recurved tip. Very thin and distinct main ridges on the inner margin.

Comparison *Hughowenites* differs from all other belemnite hooks in the extreme flexion of the ultimate tip of the uncinus which points towards the middle of the shaft, as represented in the holotype. Furthermore, pronounced ridges on the uncinus are characteristic (Plate 1, Figs. 3, 5). These strong ridges clearly differ from the weak striae of all British specimens of the same geological age that are referred herein to *Arites* sp. (compare Plate 1, Figs. 1, 2).

Occurrence See locus typicus and stratum typicum, species description below.

Hughowenites incurvatus n. gen. n. sp. (Plate 1, Figs. 3, 5)

Derivatio nominis After Latin *incurvatus*, curved inward.

Holotype BGR 13804; Plate 1, Fig. 3

Paratype BGR 13867; Plate 1, Fig. 5

Locus typicus Hannover-Lahe drilling core (holotype: 86.85–86,90 m depth, paratype: 70.32–70.37 m depth; Lehmann et al. 2007)

Stratum typicum Earliest Late Albian, *Dipoloceras cristatum* ammonite Subzone

Description Large hook with maximum length of the shaft of >800 μm and a large uncinus with total length of about 600 μm. The shaft is of constant breadth of about 200 μm for most of its length, except for the basalmost part of the inner margin that is curved about 45° inwards. The shaft shows a slight depression in the centre of the basal part that is regarded as a primary feature. The largest part of the uncinus is strongly tapering; it is ornamented by pronounced ridges, about 20 on each side. The tip of the uncinus is smooth, strongly bent and inwardly recurved, thus it points towards the middle part of the shaft (Plate 1, Fig. 3a). On the inner margin, there are very thin and distinct main ridges.

Comparison As for genus.

Discussion

Preservation potential

Due to their massive nature, belemnite rostra are among the most abundant invertebrate fossils found in Jurassic and Cretaceous marine sediments (e.g. Boardman et al. 1987). Despite the large quantities, however, they are not abundant enough to yield significant numbers throughout a sedimentary succession—except through accumulation due to condensation, storms or currents (e.g. Mitchell 1992; Doyle and MacDonald 1993). Furthermore, there are several groups within the Belemnoidea that either lack a guard, like the Phragmoteuthida, or have strongly reduced guards like the Diplobelida (Fuchs 2006).

This limits the application of belemnite guards as palaeoceanographic proxies and suggests value in studying their hooks, which potentially should be abundant and occur across the whole belemnite fauna. Occasionally, larger belemnite hooks have been found in microsamples from claystones or by collecting macrofossils (Rieber 1936, 1938; Lehmann et al. 2007). Very few studies have successfully focussed on onychites (e.g. Engeser 1987; Engeser and Clarke 1988; Engeser and Suthhof 1992). Belemnites preserved with hooklets and soft parts in situ are known from not more than a couple of famous sites, such as the Early Toarcian Posidonia Shale in southwest Germany (Reitner and Urlichs 1983; Riegraf and Hauff 1983) and the Late Kimmeridgian Nusplingen Plattenkalk (Schweigert 1999; Klug et al. 2009). This shows that preservation of more than the rostra needs exceptional taphonomic conditions and is almost exclusively restricted to conservation Fossillagerstätten (sensu Seilacher et al. 1985).

Despite the abundance of *Neohibolites* rostra at both sampling sites, only Folkestone yielded hooks. This surprising observation may be explained either by *Neohibolites* being the only belemnoid occurring at the Ellbach stream cut and that it did not possess hooks, or by preservational differences. The pure claystone facies of the Gault Formation at Folkestone has allowed the preservation of organic hard parts, such as belemnite hooks, with high preservation potential indicated by the abundance of iridescent, aragonitic shells (e.g. Cloud 2007). In contrast, the marly greensand of the Ellbach locality probably provides poorer preservation potential with hooks having been lost through taphonomy or diagenesis.

Distinction of belemnite hooks from scolecodonts

Scolecodonts are fossil jaws of annelid worms (e.g. Kozur 1970), often possessing a row of denticles, and they are clearly different from belemnite hooks including those bearing a single spur on the basal inner margin. Nevertheless, both are superficially similar, and scolecodonts have occasionally been mistaken as belemnite hooks (Engeser and Clarke 1988; Engeser and Suthhof 1992; Riegraf 1995). In the case of fragmentary material, a large number of specimens usually permits unequivocal identification.

Among the present material, each microsample contains one to six scolecodont specimens. These resemble belemnite hooks in their dark colour and preservation. Among these, slender scolecodonts of curved conical shape are recorded and referred to as cf. *Glycera* sp., an extant genus that has been recorded from the Cretaceous by Charletta and Boyer (1974) and Reich and Frenzel (1997). These can be easily distinguished from belemnite hooks since they show two canals, the pulp and poison cavity, in cross-section. Another scolecodont type is very massive, with a very strongly curved hook and a series of lateral teeth. Scolecodonts can be additionally separated by their brownish colour from belemnite hooks that are blackish.

Arites sp. described above is among the parataxa referred to scolecodonts in the past (Kozur 1967; Kozur 1970; Kozur 1971), but good arguments for an assignment to belemnoid coleoids have been given by Engeser and Suthhof (1992).

Assignment of belemnite hooks

Although first reports of the common belemnites from Folkestone were published long ago, including the monograph of Swinnerton (1955), neither detailed range charts nor an estimate of their quantitative distribution have been given. This is probably due to mostly loose specimens having been collected. Most rostra belong to the Middle-Late Albian *Neohibolites minimus* (Miller ex Lister, 1826), a species comprising several subspecies. In addition, *Neohibolites oxycaudatus* Spaeth 1971a, b and *Neohibolites ernsti* Spaeth 1971a, b are early to middle Late Albian offshoots of *N. minimus*; all three are recorded from Ashford, Kent, close to Folkestone (Spaeth 1973; Fig. 1). According to our field observations, well-preserved guards of *Neohibolites* spp. occur most frequently in the lower part of bed VIII, corresponding to microsample 3 and therefore also to the sample with the highest hook abundance index (Fig. 3). This might indicate that the belemnite hooks belong to this genus. However, comparison of the present hooks with those that are preserved in situ on the closest relative of *Neohibolites* shows distinct differences. Klug et al. (2009) recently described a fossil that they attribute to *Hibolites*, a member of the same belemnite family—the Belemnopseidae. Hooks of this fossil show some variation, but all hooks differ from *Arites* by showing a much smaller uncinus compared with the shaft. Furthermore, the morphology of *Arites*, with a large uncinus compared with the shaft, is different from that of the hooks known from the few in situ finds of the massive guard-bearing belemnite order Belemnitida Zittel, 1895 (e.g. Riegraf and Hauff 1983; Schlegelmilch 1998; Klug et al. 2009). These specimens all bear hooks with a long shaft compared with the uncinus and with the uncinus not being strongly bent as in *Arites*. This argues against an assignment of our hooks to *Neohibolites*.

Arites has been attributed by Engeser and Suthhof (1992) to belemnoid cephalopods, "possibly squids similar to *Phragmoteuthis*" (translated from German). This is based on the observation that similar hooks as in *Arites* occur in *Phragmoteuthis*? *ticinensis* described by Rieber (1970), a coleoid that is questionably referred to the phragmoteuthids, and in the alleged diplobelid *Chondroteuthis*. Diplobelina are always a subordinate part of the fossil fauna, known from only a few genera from Europe, the Lebanon and Mozambique (Mutterlose 1984). At Folkestone: two genera of the belemnite suborder Diplobelina have been described: *Conoteuthis woodwardi* Spath 1939 and *Pavloviteuthis cantiana* (Spath 1939) (Spath 1939; compare 'Locality details and methods', above). These single records do not allow estimation of peak abundances within the Gault succession but clearly show the presence of Diplobelina.

Engeser (1987) recorded arm hooks of *Chondroteuthis wunnenbergi* from the Early Toarcian of Gomaringen near Tübingen in southern Germany, which show wide variation and lack a spur, but that also include very similar morphologies to the material from Folkestone. Isolated hooks of *Arites*-like morphology have been recorded from the Early Triassic (Kozur 1967, 1970, 1971; Saslavskaja 1989), the Late Jurassic (Kulicki and Szaniawski 1972) and the Early (Engeser and Suthhof 1992) to Late Cretaceous (Reich and Frenzel 2002). This supports Fuchs et al.'s (2004) inference that co-occurrence of typically curved hooks and diplobelid belemnoids in many intervals of the Mesozoic might indicate an origin of diplobelids as early as the Triassic. Thus *Arites* in the Albian of Folkestone might represent the hooks of the two diplobelids *Conoteuthis woodwardi* and *Pavloviteuthis cantiana* rather than belonging to the predominant guard-bearing *Neohibolites*. Nevertheless, it is possible that the paragenus *Arites* is paraphyletic and this hook morphology might have developed separately in several belemnite lineages since the Triassic.

Climate preference indicated by belemnite shells

Among the Albian belemnite fauna of Folkestone, the diplobelid records are much too rare to permit any discussion in terms of possible climatic preferences, but there are enough data for *Neohibolites* (Belemnitina). The belemnite genus *Neohibolites* is believed to be of Tethyan origin (Stevens 1965; Doyle 1988). Aptian representatives are described as having had wide temperature tolerance and being able to migrate from the Tethys into the Boreal realm during times of warm-water conditions (Mutterlose 1987, 1988). In the Boreal realm the palaeogeographic and general stratigraphic distribution of *Neohibolites* reveals a correspondence of increased abundance with warmer intervals. An interpretation of *Neohibolites* as eurythermal (Mutterlose et al. 1983) is in accordance with its distribution pattern ranging across climatic zones in the Aptian and Albian (Doyle 1987b), which indicates fairly high temperature tolerance. On the other hand, Mitchell (2005) provides little evidence for temperature control on the distribution of Cenomanian belemnites based on $\delta^{18}O$ data obtained from *Neohibolites* among others. Recently, Gale and Owen (2010) assumed a temperature control on the occurrence of *Neohibolites minimus* in the Middle Albian *Hoplites spathi* Subzone because the species is relatively uncommon south of Bedfordshire and East Anglia, but more abundant to the north. This observation appears contradictory to all previous results mentioned above, however this has not been discussed by these authors.

There are palaeotemperature estimates for the Albian based on a few *Neohibolites* rostra. Price (1998) calculated mean water palaeotemperatures of 15.9–16.8°C from the oxygen isotope composition of *Neohibolites* rostra from the Albian claystones at Speeton and Ferriby in northeast England. These values are in accordance with those derived from circulation models (Barron et al. 1995) but are lower than sea-surface temperature estimates based on well-preserved Late Albian foraminifera (24–30°C for the northern mid latitudes, Wilson and Norris 2001; Erbacher et al. in press) or the TEX_{86} proxy (33°C for the tropical Atlantic, Forster et al. 2007). Unfortunately oxygen isotope data derived from coccolith matrix as well as from benthic and planktic foraminifera from the very same samples as those yielding *Neohibolites* at Speeton and Ferriby exhibit a diagenetic overprint (Price 1998). Therefore, the temperatures estimated from *Neohibolites* cannot be compared with those from other groups of fossils. These generalised data indicate a gap in our knowledge because there is a lack of geochemical data documenting temperature fluctuations throughout a section from which quantitative belemnite occurrences can be obtained.

Hooks as proxies for belemnite productivity?

Since belemnite hooks are generally rare, the possibility of testing the usage of belemnite hooks as a proxy is limited currently to just a few sites. Nevertheless, under advantageous taphonomic conditions their preservation is not a lucky strike but may be routine. Hooks occur much more frequently than rostra in a lithofacies that preserves both organic and calcareous hard parts, and they are present also in guard-lacking belemnoids. Therefore, hooks are a potential proxy for higher belemnite productivity. Their poorly known morphological range is more problematic, as too is the relationship between different hook types and species. This can only be improved by classifying a larger number of hook associations. Less significant is the fact that hooks might get concentrated, like belemnite guards, in the stomach of larger vertebrates (Böttcher 1989). Preservation of such accumulations seems inherently less likely than accumulation of rostra. Any preferential sorting of different hook types also seems unlikely for most occurrences. Under favourable conditions for preservation of hooks, one needs distinctly less rock material to obtain quantitative data. Nevertheless, our sampling is too limited and the total number of specimens per sample obtained is too sparse to permit statistical study. Thus, before suggesting a new proxy for belemnite productivity (i.e. belemnite abundance or standing stock), more studies from different stratigraphic levels and places are needed. Here, we propose to test if belemnite hooks might be established as a beneficial tool to better understand conservation Fossillagerstätten.

The earliest Late Albian warming event

During most of the Middle Albian, Tethyan macrofauna only sporadically invaded the Boreal shelf seas. This pattern changed considerably in the Late Albian (Owen 1996; Lehmann et al. 2007). A number of ammonites of Tethyan origin appear for the first time in the Folkestone section in bed VIII, namely *Hypophylloceras subalpinum*, *Beudanticeras beudanti*, *B. subparandieri*, *Neophlycticeras (Eotropidoites) jayeti*, *Protissotia itierianum*, *Oxytropidoceras cantianum*, *Dipoloceras* spp., *Mortoniceras rigidum*, *Hysteroceras orbignyi*, *H. capricornu*, *H. pseudocornutum*, *H. symmetricum*, *H. simplicicosta* and *H. serpentinum* (Casey 1966). Bed VIII represents the lower part of the *Dipoloceras cristatum* ammonite Subzone, thus the base of bed VIII corresponds with the base of the Late Albian (Fig. 3). Besides the Tethyan ammonites, including the most important group of mortoniceratids, a few Arctic elements also occur for the first time (Owen 1973), and thus, Owen (1996) assumed tectonic rather than primarily climatic factors as underlying this invasion. Although the *Dipoloceras cristatum* Subzone was clearly a time of considerable and widespread tectonic activity in Europe (Owen 1971a; Owen 1973), new geochemical data support the idea that this faunal change was above all climatically steered. The oxygen isotope data obtained from bulk rock samples at Folkestone (from the same spot as our samples; see Fig. 2) presented by Kanungo et al. (2004) and Kanungo (2005) indicate an increase of palaeotemperature during bed VIII (Fig. 3). The palaeotemperature rise from the Middle to Late Albian was estimated to have been on the order of about 5–6°C (Kanungo 2005, p. 80), but diagenetic overprinting in Albian claystones cannot be ruled out. Nevertheless, alteration of the absolute oxygen isotope values is not important for the present study, as the trend of the isotope curve very likely represents a primary signal for a number of reasons: (1) the excellent preservation and high diversity of calcareous nannoplankton in the samples, with even the more delicate coccolith rims being well preserved (Kanungo 2005); (2) the warming indicated by stable oxygen isotope data occurs synchronously with the shift to warm-water ammonite faunas; (3) a decline in the occurrence of the cold-water calcareous nannoplankton indicator *Repagulum parvidentatum* (Kanungo 2005); (4) lithology remains similar throughout the section, enhancing the likelihood that diagenetic conditions were similar for the different levels of the succession; and (5) the occurrence of a significant warming event across the Middle/Late Albian boundary in northern Germany based on study of glassy-preserved foraminifera (Erbacher et al. in press). Thus bed VIII at Folkestone can be assumed to have been deposited during a warming interval. This inferred warming corresponds to the observed increase in the hook abundance index as well as a higher abundance of rostra of *Neohibolites* (Fig. 3) and therefore might suggest a temperature control on belemnite productivity.

The earliest Late Albian warming event in bed VIII is also accompanied by an increase in palaeoproductivity as indicated by changing calcareous nannoplankton assemblages. Kanungo (2005) records increased abundances of *Zeugrhabdotus noeliae* of up to 40%. This is interpreted as reflecting surface waters rich in nutrients (following e.g. Erba 1992), because the warming event may have forced higher precipitation rates leading to higher nutrient input through run-off into the basin. *Biscutum constans* is a second high-nutrient-index taxon that shows its peak occurrence in the lower part of bed VIII (22%). A third high nutrient index is that of *Discorhabdus ignotus*, showing a minor peak in bed VIII only (2%). Based on these indicators for eutrophic conditions, Kanungo (2005) calculated an index to estimate the palaeoproductivity for the Gault Clay. There is a trend to higher primary productivity in bed VIII, with a peak in the upper part of bed VIII. Thus, there are good arguments for higher nutrient levels coinciding with the warming event.

Higher primary productivity is likely to have had a positive impact on organisms at higher trophic levels within the food web. Thus, we argue that the increased occurrence of belemnite hooks in bed VIII and possibly also the increased occurrence of rostra at the base of bed VIII might be due to both an increase in productivity as well as warmer temperatures (Fig. 3).

Sea level changes and their possible consequences

Following the classical papers on sea level change by Haq et al. (1987) and Hardenbol et al. (1998) as well as succeeding papers (e.g. Immenhauser and Scott 1999), the Middle–Upper Albian boundary interval comprises a sequence boundary (Fig. 3). The earliest Late Albian therefore not only correlates with a short-term warming event and increased palaeoproductivity, but also with a third-order sea level rise. The greatest rise in sea level probably took place during deposition of bed VIII, since this bed contains several nodule layers that might indicate condensation. Formation of these nodule layers might have been due to sediment starvation during rapid sea level rise at some distance from the shoreline (e.g. Sturrock 1996). Condensed deposits are often characterised by enhanced diversity and quantity of fossils (Loutit et al. 1988; Lehmann et al. 2007), thus the higher quantity of *Neohibolites* rostra in the lower part of bed VIII could be alternatively explained by sedimentological processes. Good preservation of the guards does not necessarily rule out accumulation through re-working, since the calcareous guards are very resistant and the Gault Clay is a fine-grained sediment. Despite their delicate nature and low preservation potential, accumulation of belemnite hooks due to condensation processes cannot be ruled out either.

Conclusions

Study of belemnite hooks from the Middle–Upper Albian boundary succession at Folkestone, southeast England, indicates dominance of the paragenus *Arites* sp., which might originate from either the diplobelids *Conoteuthis* and *Pavloviteuthis*, characterised by a reduced guard, or the prevalent guard-bearing belemnitinid *Neohibolites*. The morphology of hooks is very similar to that of the alleged diplobelid belemnite *Chondroteuthis* from the Lower Jurassic. This suggests an assignment of the Folkestone hook material to diplobelids and not to the belemnitinid *Neohibolites*, and would extend the stratigraphical range of this belemnite group significantly. The abundance peak of *Arites* sp. and other belemnite hooks at Folkestone, which possibly reflects higher belemnite productivity, coincides with an increase of primary productivity and temperature. The larger number of *Neohibolites minimus* guards might be connected to the same factors; however, accumulation due to condensation during the rapid early Late Albian sea level rise is also possible, since this interval represents a condensed deposit.

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References

Alsen, P., and J. Mutterlose. 2009. The early cretaceous of North-East Greenland: A crossroads of belemnite migration. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280: 168–182. doi: 10.1016/j.palaeo.2009.06.011

Barron, E.J., P.J. Fawcett, W.H. Peterson, D. Pollard, and S.L. Thompson. 1995. A ''simulation'' of Mid-Cretaceous climate. *Paleoceanography* 10: 953–962.

Bentz, A. 1930. *Blatt Ottenstein, Nr. 2139, ed*. Berlin: Preußisches Geologisches Landesamt.

Boardman, R.S., A.H. Cheetham, and A.J. Rowell. 1987. *Fossil invertebrates, 1–713*. Cambridge, Mass: Blackwell Science.

Bodylevskii, V.I. 1957. On the Boreal province of the Jurassic period (in Russian). *Vopr. Paleobiogr. biostratigr. Trudy— 1. Sess. Vsesoy. Paleont. Obshch.*: 91–96.

Böttcher, R. 1989. Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stuttgarter Beiträge zur Naturkunde* 155: 1–19.

Bowen, R. 1961. Oxygen isotope paleotemperature measurements on Cretaceous Belemnoidea from Europe, India and Japan. *Journal of Paleontology* 35: 1077–1084.

Casey, R. 1966. Lower Cretaceous. General account. Gault. Zoning of the Gault. In *British Geological Survey Memoirs*, eds. J. G. O. Smart, G. Bisson, and B. C. Worssam, 58: 102–113. Geology of the Country around Canterbury and Folkestone. London: The Stationery Office Books.

Charletta, A.C., and P.S. Boyer. 1974. Scolecodonts from Cretaceous Greensand of the New Jersey Coastal Plain. *Micropaleontology* 20: 354–366.

Christensen, W.K. 1988. Upper Cretaceous belemnites of Europe: State of the art. In *The Chalk district of the Euregio Meuse-Rhine*, ed. M. Streel, and M.J.M. Bless, 5–16. Maastricht & Liège: Natuurhistorische Museum Maastricht & Laboratories de Paléontologie de l'Université d'État à Liège.

Clouter, F. 2007. *Ammonites and other cephalopods of the Lower Cretaceous Albian (Gault Clay) and Folkestone beds of the South East of England, 1–71*. Minster: Medway Fossil and Mineral Society.

Combémorel, R., W.K. Christensen, D.P. Naidin, and C. Spaeth. 1981. Les Bélemnites. *Cretaceous Research* 2: 283–286.

De Rance, C.E. 1868. On the Albian or Gault of Folkestone. *Geological Magazine* 5: 163–171.

Ditchfield, P.W., J.D. Marshall, and D. Pirrie. 1994. High latitude palaeotemperature variation: New data from the Thithonian to Eocene of James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 79–101. doi: 10.1016/0031-0182(94)90166-X

Doyle, P. 1987a. The Cretaceous Dimitobelidae (Belemnitida) of the Antarctic Peninsula region. *Palaeontology* 30: 147–177.

Doyle, P. 1987b. Early Cretaceous belemnites from southern Mozambique. *Palaeontology* 30: 311–317.

Doyle, P. 1988. The belemnite family Dimitobelidae in the Cretaceous of Gondwana. In *Cephalopods—Present, Past, 539–552*, ed. J. Wiedmann, and J. Kullmann. Stuttgart: Schweizerbart.

Doyle, P. 1992. A review of the biogeography of Cretaceous belemnites *Palaeogeography, Palaeoclimatology, Palaeoecology* 92: 207–216.

Doyle, P., and D.I.M. MacDonald. 1993. Belemnite battlefields. *Lethaia* 26: 65–80.

Doyle, P., and D. Pirrie. 1999. Belemnite distribution patterns. Implications of new data from Argentina. In: Advancing Research on Living and Fossil Cephalopods: Development and evolution: Form, construction, and function: Taphonomy, palaeoecology, palaeobiogeography, biostratigraphy, and basin analysis, eds. Federico Olóriz, and F. J. Rodríguez-Tovar: 419Ð436. Proceedings of the IV International Symposium on Cephalopods: Present and past, held July 14Ð18, 1996, in Granada, Spain. New York: Kluwer Academic/Plenum.

Dunn, J., S. Feist-Burkhardt, and J.A. Young. 2006. Albian dinoßagellate cysts of the Gault Clay at Copt Point, Folkestone, South-East England. *Geophysical Research Abstracts* 8.

Engeser, T. 1987. Belemnoid arm hooks (ÔÔonychitesÕÕ) from the Swabian JurassicÑA review. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 176: 5Ð14.

Engeser, T. 1988. Ein neuer Mikro-Onychit aus dem Untertoarcium von Wolfsburg (Norddeutschland). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 67: 89Ð97.

Engeser, T., and M.R. Clarke. 1988. Cephalopod hook, both recent and fossil. In *The Mollusca, Paleontology and Neontology of Cephalopods, 133–151*, ed. E.R. Trueman, and M.R. Clarke. San Diego: Academic.

Engeser, T., and A. Suthhof. 1992. Onychiten (Belemniten-Armhaken) aus dem Barrême von Sarstedt (Niedersachsen). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 73: 99Ð117.

Erba, E. 1992. Middle Cretaceous calcareous nannofossils from the western PaciÞc (Leg 129): Evidence for paleoequatorial crossings. In *Proceedings of the Ocean Drilling Program, Scientific Results*, eds. Roger L. Larson, and Y. Lancelot, 189Ð201. Washington.

Erbacher, J., O. Friedrich, P.A. Wilson, J. Lehmann, and W. Wei§. In press. Short-term warming events during the boreal Albian (mid-Cretaceous). *Geology*.

Fitton, M.G. 1836. Observations on strata between the Chalk and the Oxford Oolite, in the South-east of England. *Transactions of the Geological Society* 4: 103Ð290.

Forster, A., S. Schouten, M. Baas, and J.S. Sinninghe Damste. 2007. Mid-Cretaceous (Albian-Santonian) sea surface temperature record of the tropical Atlantic Ocean. *Geology* 35: 919Ð922.

Fuchs, D. 2006. Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung. *Berliner paläobiologische Abhandlungen* 8: 1Ð130.

Fuchs, D., M. Reich, and F. Wiese. 2004. Onychites in diplobelid coleoids (Cephalopoda) ?ÑArguments and discussion. *Geobiologie, 74. Jahrestagung der Paläontologischen Gesellschaft, Göttingen, 02. bis 08. Oktober 2004, Kurzfassungen der Vorträge und Poster, 87–88*, ed. J. Reitner, M. Reich, and G. Schmidt. Göttingen: Universitätsdrucke Göttingen.

Gale, A.S., and W.K. Christensen. 1996. Occurrence of the belemnite *Actinocamax plenus* in the Cenomanian of SE France and its signiÞcance. *Bulletin of the Geological Society of Denmark* 43: 68Ð77.

Gale, A.S., and H.G. Owen. 2010. Introduction to the Gault. In *Field Guides to Fossils*, eds. J. A. Young, A. S. Gale, R. I. Knight, and A. B. Smith, 1Ð15. Fossils of the Gault Clay. London: University Printing House, Oxford.

Haq, B.U., J. Hardenbol, and P.R. Vail. 1987. Chronology of ßuctuating sea levels since the Triassic. *Science* 235: 1156Ð1167.

Hardenbol, J., J. Thierry, M.B. Farley, T. Jaquin, P. de Graciansky, and P.R. Vail. 1998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basinsÑChart 4: Cretaceous sequence chronostratigraphy. *SEPM Spec Publ., 60. Mesozoic, Cenozoic sequence stratigraphy of European basins*, ed. P. de Graciansky, J. Hardenbol, T. Jaquin, and P.R. Vail. Tulsa: SEPM.

Immenhauser, A., and R.W. Scott. 1999. Global correlation of middle Cretaceous sea-level events. *Geology* 27: 551Ð554.

Jeletzky, J.A. 1981. Lower Cretaceous diplobelinid belemnites from the Anglo-Paris Basin. *Palaeontology* 24: 115Ð145.

Kanungo, S. 2005. Biostratigraphy and palaeoceanography of Mid Cretaceous calcareous nannofossils: Studies from the Cauvery Basin, SE India; the Anglo Paris Basin, SE England; the Atlantic and the PaciÞc oceans. University College London, London. Unpublished PhD thesis, 1Ð260. London.

Kanungo, S., P.R. Bown, A.S. Gale, and J.A. Young. 2004. A signiÞcant paleoclimatic/palaeotemperature shift around the Middle/late Albian boundary in the Gault Clay Formation, Folkestone, SE England. *Journal of Nannoplankton Research* 26: 63.

Keller, S., E. Kemper, R. Koch, J. Mutterlose, T. Nöth, H.G. Owen, C. Spaeth, P. Stoffers, P. Walter, and W. Zimmerle. 1989. Das UnterÑund Mittel-Alb von Alfeld (Leine). In: Alb und Unter-Cenoman in MittelÑund Nordeuropa, ed. E. Kemper: 223Ð316. *Geologisches Jahrbuch*, A113. Hannover: E. SchweizerbartÕsche Verlagsbuchhandlung (Nägele & Obermiller).

Kemper, E. 1976. *Geologischer Führer durch die Grafschaft Bentheim und die angrenzenden Gebiete mit einem Abriß der emsländischen Unterkreide, 1–206*. Nordhorn & Bentheim: Heimatverein der Grafschaft Bentheim.

Klug, C., G. Schweigert, D. Fuchs, and G. Dietl. 2009. First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany). *Lethaia*. doi:10.1111/j.1502-3931.2009.00203.x

Knight, R.I. 2010. Belemnites. In: Fossils of the Gault Clay, eds. J. A. Young, A. S. Gale, R. I. Knight, and A. B. Smith: 215Ð217. *Field guides to fossils 12*. London: University Printing House, Oxford.

Kozur, H. 1967. Scolecodonten aus dem Muschelkalk des germanischen Binnenbeckens. *Monatsberichte der deutschen Akademie der Wissenschaften zu Berlin* 9: 842Ð864.

Kozur, H. 1970. Zur KlassiÞkation und phylogenetischen Entwicklung der fossilen Phyllodocida und Eunicida (Polychaeta). *Freiberger Forschungshefte* 260: 35Ð75.

Kozur, H. 1971. Die Eunicida und Phyllodocida des Mesozoikums. *Freiberger Forschungshefte* 267: 73Ð111.

Kulicki, C., and H. Szaniawski. 1972. Cephalopod arm hooks from the Jurassic of Poland. *Acta Palaeontologica Polonica* 17: 379Ð419.

Lehmann, J., O. Friedrich, F.W. Luppold, W. Weiss, and J. Erbacher. 2007. Ammonites and associated macrofauna from around the Middle/Upper Albian boundary of the Hannover-Lahe core, northern Germany. *Cretaceous Research* 28: 719Ð742.

Loutit, T.S., J. Hardenbol, P.R. Vail, and P. Baum. 1988. Condensed sections: The key to age dating and correlation of continental margin sequences. In *Sea-level changes: An integrated approach, 183–213*, ed. C.K. Wilgus, B.S. Hastings, C.A. Ross, H.W. Posamentier, J.C. Van Wagoner, G.St. Christopher, and C. Kendall. SEPM Special Publication, 42, Tulsa: SEPM.

Marshall, J.D. 1992. Climatic and oceanographic isotopic signals from the carbonate rock record and their preservation. *Geological Magazine* 129: 143Ð160. doi:10.1017/S0016756800008244

Mitchell, S.F. 1992. The belemnite faunal changes across the HauterivianÐBarremian boundary in north-east England. *Proceedings of the Yorkshire Geological and Polytechnic Society* 49: 129Ð134. doi:10.1144/pygs.49.2.129

Mitchell, S.F. 2005. Eight belemnite biohorizons in the Cenomanian of northwest Europe and their importance. *Geological Journal* 40: 363Ð382. doi:10.1002/gj.1016

Mutterlose, J. 1984. Belemnites of the suborder Diplobelina from the Hauterivian (Lower Cretaceous) of Speeton (Yorkshire, England). *Proceedings of the Geologists' Association* 95:181Ð184.

Mutterlose, J. 1986. Upper Jurassic belemnites from the Orville coast, Western Antarctica, and their palaeobiogeographical signiÞcance. *British Antarctic Survey Bulletin* 70: 1Ð22.

Mutterlose, J. 1987. Calcareous nannofossils and belemnites as warmwater indicators from the NW-German Middle Aptian. In *Das Klima der Kreidezeit, 293–313*, ed. E. Kemper. Geologisches Jahrbuch, A96, Hannover: Bundesanstalt für Geowissenschaften und Rohstoffe.

Mutterlose, J. 1988. Migration and evolution patterns in Upper Jurassic and Lower Cretaceous belemnites. In *Cephalopods—Present, Past, 525–537*, ed. J. Wiedmann, and J. Kullmann. Stuttgart: Schweizerbart.

Mutterlose, J., F. Schmid, and C. Spaeth. 1983. Zur Paläobiogeographie von Belemniten der Unter-Kreide in NW-Europa. In: *Symposium Kreide München 1982*, ed. D. Herm: 293–307. Zitteliana, 10. Munich.

Neumayr, M. 1883. Über klimatische Zonen während der Jura- und Kreidezeit. *Denkschriften der Akademie der Wissenschaften* 47: 277–310.

Owen, H.G. 1971a. Middle Albian stratigraphy in the Anglo-Paris Basin. *Bulletin of the British Museum of Natural History* 8: 3–164.

Owen, H.G. 1971b. The stratigraphy of the Gault in the Thames estuary and its bearing on the Mesozoic tectonic history of the area. *Proceedings of the Geologists' Association* 82: 187–207.

Owen, H.G. 1973. Ammonite faunal provinces in the Middle and Upper Albian and their palaeogeographical significance. In: *The Boreal Lower Cretaceous*, eds. R. Casey, and P. F. Rawson: 145–154. *Geological Journal Special Issue*, 5. Liverpool: Seel House Press.

Owen, H.G. 1976. The stratigraphy of the Gault and Upper Greensand of the Weald. *Proceedings of the Geologists' Association* 86: 475–498.

Owen, H.G. 1979. Ammonite zonal stratigraphy in the Albian of North Germany and its setting in the hoplitinid faunal province. In *Aspekte der Kreide Europas, 563–588*, ed. J. Wiedmann. Schweizerbart'sche Verlagsbuchhandlung (Nägele & Obermiller): IUGS (International Union of Geological Sciences) Series A, Stuttgart.

Owen, H.G. 1996. Boreal and Tethys late Aptian to late Albian ammonite zonation and palaeobiogeography. In: *New Developments in Cretaceous Research Topics, Proceedings of the 4th International Cretaceous Symposium, Hamburg 1992*, ed. C. Spaeth: 461–481. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg.

Parkinson, J. 1819. Remarks on the fossils collected by Mr. Phillips near Dover and Folkestone. *Transactions of the Geological Society of London* 5: 52–59.

Pierri, D., P. Doyle, J.D. Marshall, and G. Ellis. 1995. Cool Cretaceous climates: New data from the Albian of Western Australia. *Journal of the Geological Society* 152: 739–742.

Price, F.G.H. 1874. On the Gault of Folkestone. *Quarterly Journal of the Geological Society London* 30: 342–368.

Price, G.D. 1998. Isotopic variation in fossils and matrix of the Cretaceous Red Chalk at Speeton and South Ferriby, Yorkshire, England. *Proceedings of the Yorkshire Geological and Polytechnic Society* 52: 107–112. doi:10.1144/pygs.52.1.107

Quenstedt, F.-A. 1858. *Der Jura*, 1–842. Tübingen: Laupp & Siebeck.

Reich, M., and P. Frenzel. 1997. Onychiten (Cephalopoda, Coleoidea) aus der Schreibkreide (Unter-Maastrichtium) der Insel Rügen (Ostsee). *Greifswalder Geowissenschaftliche Beiträge* 4: 121–124.

Reich, M., and P. Frenzel. 2002. Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschiebekunde* 3: 73–284.

Reitner, J., and M. Urlichs. 1983. Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Südwestdeutschlands. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 165: 450–465.

Rieber, H. 1970. *Phragmoteuthis? ticinensis* n. sp., ein Coleoidea-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläontologische Zeitschrift* 44: 32–40.

Riedel, L. 1936. Ein Onychit aus dem nordwestdeutschen Ober-Hauterive. *Paläontologische Zeitschrift* 18: 307–310.

Riedel, L. 1938. Drei weitere Onychiten aus der nordwestdeutschen Unterkreide. *Paläontologische Zeitschrift* 20: 258–262.

Riegraf, W. 1995. Radiolarien, Diatomeen, Cephalopoden und Stratigraphie im pelagischen Campanium Westfalens (Oberkreide, NW-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 197: 129–200.

Riegraf, W. 1996. Belemniten-Fanghäkchen (Cephalopoda, Coleoidea) aus der Psilonotenbank (Unterer Jura, tiefstes Hettangium) von Südwestdeutschland. *Stuttgarter Beiträge zur Naturkunde* 239: 1–38.

Riegraf, W., and R. Hauff. 1983. Belemnitenfunde mit Weichkörper, Fangarmen und Gladius aus dem Untertoarcium (Posidonienschiefer) und Unteraalenium (Opalinuston) Südwestdeutschlands. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 165: 466–483.

Saslavskaja, N.M. 1989. O sistematiceskom polozenii rodov *Paraglycerites* Eisenack i *Arites* Kozur, 1967. *Trudy institua geologii i geofisiki Akademja nauk SSr, Sibirskoe Otdelenie* 732: 104–109.

Schlegelmilch, R. 1998. *Die Belemniten des süddeutschen Jura*, 1–151. Stuttgart: Gustav Fischer.

Schweigert, G. 1999. Erhaltung und Einbettung von Belemniten im Nusplinger Plattenkalk (Ober-Kimmeridgium, *Beckeri*-Zone, Schwäbische Alb). *Stuttgarter Beiträge zur Naturkunde* 273: 1–35.

Seilacher, A., W.-E. Reif, and F. Westphal. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London* 311: 5–23.

Sellwood, B.W., G.D. Price, and P.J. Valdes. 1994. Cooler estimates of Cretaceous temperatures. *Nature* 370: 453–455.

Spaeth, C. 1971a. Aragonitische und calcitische Primärstrukturen im Schalenbau eines Belemniten aus der englischen Unterkreide. *Paläontologische Zeitschrift* 45: 33–40.

Spaeth, C. 1971b. Untersuchungen an Belemniten des Formenkreises um *Neohibolites minimus* (Miller 1826) aus dem Mittel- und Ober-Alb Nordwestdeutschlands. *Beihefte zum Geologischen Jahrbuch* 100: 3–127.

Spaeth, C. 1973. *Neohibolites ernsti* and its occurrence in the Upper Albian of northwest Germany and England. In *The Boreal Lower Cretaceous*, eds. R. Casey, and P. F. Rawson: 361–368. *Geological Journal Special Issue*, 5. Liverpool: Seel House Press.

Spath, L.F. 1923–1943. *A monograph of the Ammonoidea of the Gault. Part I-XVI*, 1-X + 787. London: Palaeontographical Society.

Spath, L.F. 1939. On a new belemnoid (*Conoteuthis renniei*) from the Aptian of the Colony of Mocambique. *Boletim dos Servicos de Industria, Minas e Geologia* 2: 13–16.

Stevens, G.R. 1963. Faunal realms in Jurassic and Cretaceous belemnites. *Geological Magazine* 100: 481–497.

Stevens, G.R. 1965. *The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific region*, 1–283. Wellington: New Zealand Department of Scientific and Industrial Research.

Sturrock, S.J. 1996. Biostratigraphy. In *Sequence stratigraphy*, ed. D. Emery, and K. Myers, 89–107. Oxford: Blackwell Science.

Swinnerton, H.H. 1955. A monograph of British Cretaceous belemnites. Part V. *Palaeontographical Society Monographs* 1954: XXXIII-XL + 63–86.

Tejs, R.W., and D.P. Naidin. 1969. Bestimmung der Jahremitteltemperaturen und der jahreszeitlichen Temperaturen an Hand der

SauerstofÞsotopenverteilung im Kalzit von marinen Fossilien der Russischen Tafel. *Geologie* 18: 1062Ð1071.

Voigt, S., M. Wilmsen, R.N. Mortimore, and T. Voigt. 2003. Cenomanian palaeotemperatures derived from the oxygen isotopic composition of brachiopods and belemnites: Evaluation of Cretaceous palaeotemperature proxies. *International Journal of Earth Sciences* 92: 285Ð299. doi:10.1007/s00531-003-0315-1

Wefer, G. 1982. Paläotemperaturbestimmungen mit Hilfe von SauerstofÞsotopen an Ammoniten und Foraminiferen des Apt und Alb. In: Das späte Apt und frühe Alb Nordwestdeutschlands, Versuch der umfassenden Analyse einer Schichtenfolge, ed. E. Kemper: 273Ð281. *Geologisches Jahrbuch*, A65. Hannover: Schweizerbart.

Wefer, G., and W.H. Berger. 1991. Isotope paleontology, growth and composition of extant calcareous species. *Marine Geology* 100: 207Ð248.

Wilmsen, M., B. Niebuhr, and P. Chellouche. 2010. Occurrence and signiÞcance of Cenomanian belemnites in the lower Danubian Cretaceous Group (Bavaria, southern Germany). *Acta Geologica Polonica* 60: 231Ð241.

Wilson, P.A., and R.D. Norris. 2001. Warm tropical ocean surface and global anoxia during the mid-Cretaceous period. *Nature* 412 (26 July 2001): 425Ð429.

Wissing, F.-N., and E. Herrig. 1999. *Arbeitstechniken in der Mikropaläontologie. Eine Einführung*, 1Ð191. Stuttgart: Enke.

Woodward, S.P. 1856. On the occurrence of the fossil genus *Conoteuthis*, dÕOrb., in England. *Annals and Magazine of Natural History* 17: 402Ð403.

Ziegler, P.A. 1982. *Geological Atlas of Western and Central Europe*, 1Ð130. Amsterdam: Elsevier.

Ziegler, P.A. 1990. *Geological Atlas of Western and Central Europe*, 1Ð239. Amsterdam: Shell Internationale Petroleum Maatschappij B.V.