THE BELEMNITE *ACROTEUTHIS* IN THE *HIBOLITES* BEDS (HAUTERIVIAN–BARREMIAN) OF NORTH-WEST EUROPE

by J. MUTTERLOSE, G. PINCKNEY, *and* P. F. RAWSON

ABSTRACT. *Hibolites*, a Tethyan-derived genus, was the dominant belemnite in north-west Europe for most of Hauterivian to earliest Barremian (Early Cretaceous) time, while the Boreal genus *Acroteuthis* continued to thrive in more northerly latitudes. Rare *Acroteuthis* occur in the *Hibolites* beds and are easily confused with the slightly younger *Aulacoteuthis*. Two new *Acroteuthis* species belonging to the subgenus *Boreioteuthis* are described here by Pinckney: *A.* (*B*). *rawsoni* and *A.* (*B.*) *stolleyi*.

THE latest Jurassic–early Cretaceous belemnite genus *Acroteuthis* is a member of the boreal subfamily Cylindroteuthinae, occurring mainly in Siberia, the Russian Platform, north-west Europe, East Greenland, and Arctic Canada. In north-west Europe it first appeared in mid-Volgian (late-Tithonian) times and died out early in the Barremian; over that interval, seven discrete assemblages are distinguished (Pinckney and Rawson 1974). However, while the genus was the dominant belemnite in late Volgian to earliest Hauterivian sediments, it was almost completely replaced early in the Hauterivian by the immigration of *Hibolites* from Tethys (Rawson 1973; Mutterlose *et al.* 1983). In England the faunal change was taken as one of the main boundaries in the Speeton Clay (D/C beds boundary: Lamplugh 1889), though here the abruptness of the change is exaggerated by condensed sedimentation. *Hibolites* was almost completely replaced by a new boreal immigrant, *Praeoxyteuthis*, early in the Barremian (C/B beds boundary at Speeton) though *H. minutus* continued through the Barremian.

While *Hibolites* was flourishing in north-west Europe during Hauterivian and earliest Barremian times, *Acroteuthis* continued to evolve in other boreal areas. A few examples have been found in the *Hibolites* beds of England and north Germany (text-fig. 1) and their occurrence is reviewed here. They include two new species (assigned to the subgenus *Boreioteuthis*) described here by G. Pinckney. The described specimens are from the following collections: BGS, British Geological Survey, Keyworth; BM, British Museum (Natural History), London; GM, Geological Museum, Copenhagen; GPIG, Geologisches-Paläontologisches Institut, Göttingen University; GPIH, Geologisches-Paläontologisches Institut, Hannover University; NLfB, Niedersächsisches Landesamt für Bodenforschung, Hannover; SC, Stühmer collection, Heligoland; WC, C. W. and E. V. Wright Collection, London; UC, University College London.

ACROTEUTHIS ASSEMBLAGES IN THE *HIBOLITES* BEDS

Acroteuthis assemblages 6 and 7 of Pinckney and Rawson (1974) are represented in the *Hibolites* beds. Assemblage 6 includes four species, *A.* (*A.*) *subquadratus* (Roemer), *A.* (*A.*) *explanatoides* (Pavlow), *A.* (*A.*) *acmonoides* Swinnerton, and *A.* (*A.*) *paracmonoides* (Swinnerton), all of which also occur in the underlying assemblage 5. It is characterized by greater numbers of the more slender species *A. acmonoides* and *A. explanatoides*. Assemblage 6 occurs in the highest part of the *Acroteuthis* beds and, at Speeton, as a relic fauna in the lower part of the *Hibolites* beds (text-fig. 2). The constituent species are well known from Swinnerton's (1937, 1948) monograph and are not redescribed here.

Assemblage 7 is completely distinct from the underlying ones. It is characterized by forms with an apical groove. Three species occur, *A.* (*A*?) *conoides* Swinnerton and two previously undescribed

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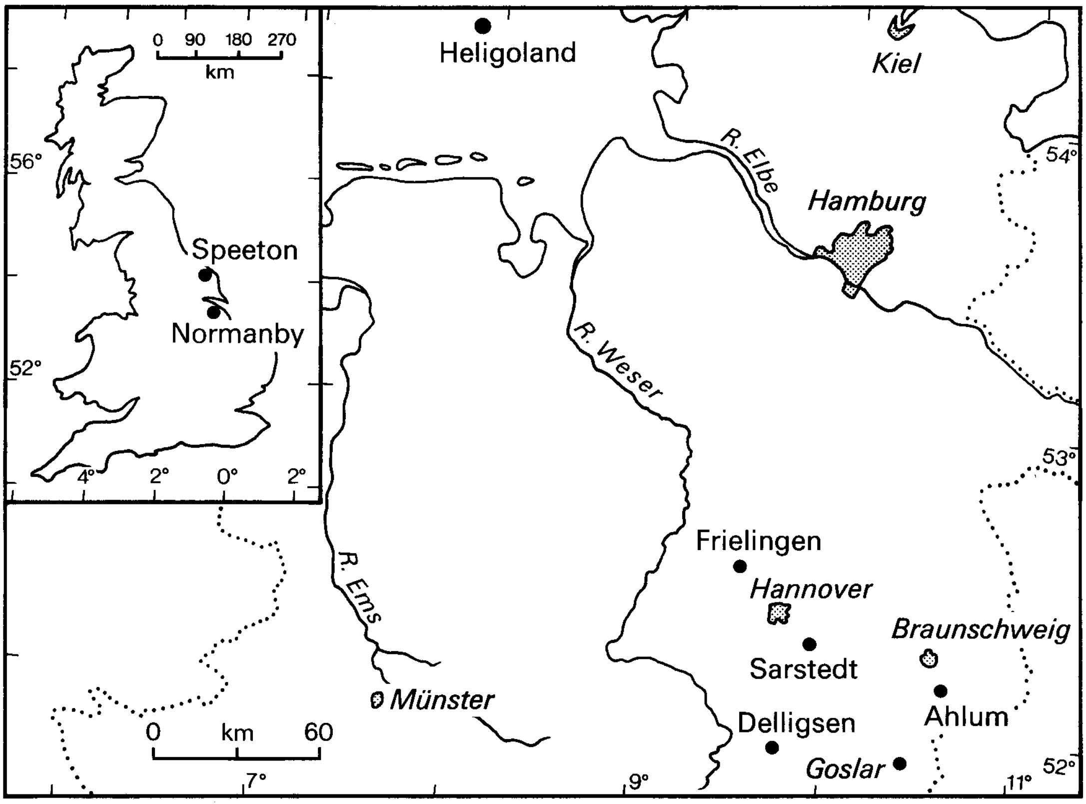


TEXT-FIG. 1. Map showing localities at which *Acroteuthis* occurs in the *Hibolites* beds.

ones, A. (*Boreioteuthis*) *rawsoni* Pinckney sp. nov. and A. (*B. stolleyi*) Pinckney sp. nov. All three species are described and their phylogenetic significance discussed below. The assemblage 7 fauna occurs in the middle to upper part of the *Hibolites* beds in both England and north Germany.

LOCALITIES

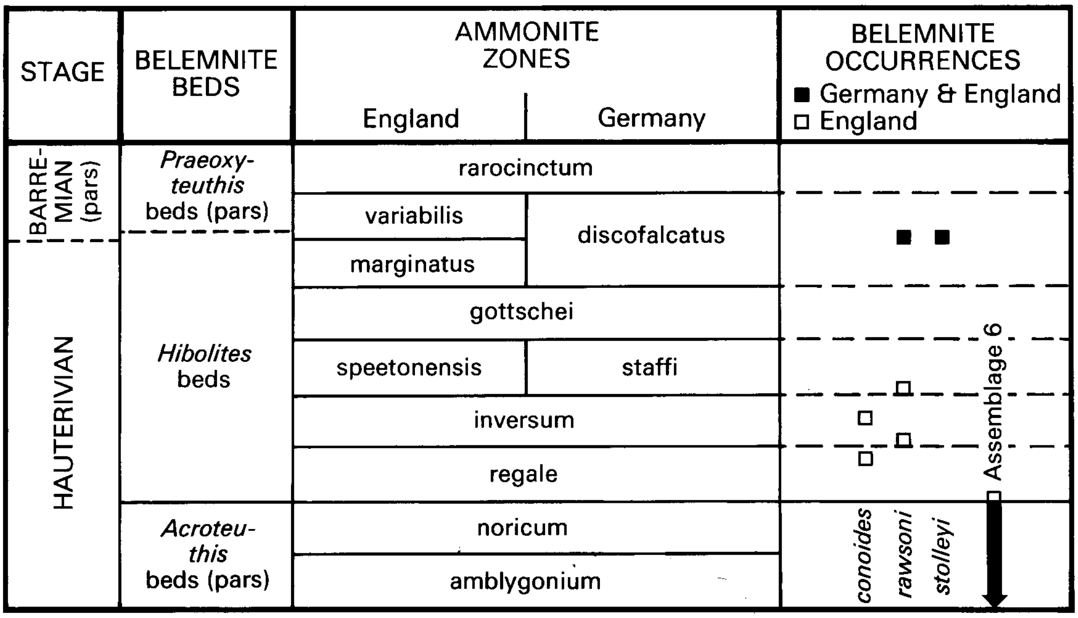
Seven localities in the *Hibolites* beds have yielded *Acroteuthis*: Speeton and Lincolnshire in eastern England, the North Sea island of Heligoland, and four sections in Lower Saxony (text-fig. 1).

Speeton. The lithostratigraphy of the C beds (*Hibolites* beds) has been described in detail by Fletcher (1969) and a lithic log published by Rawson (1971). *Acroteuthis* representing assemblages 6 and 7 have been found in the mid C beds (*regale* to *speetonensis* Zones) and bed C1 (*variabilis* Zone).

Lincolnshire. A single *A*. (*B*). *rawsoni* was collected from the Tealby Limestone of Normanby during the last century by the Revd J. Lee. The limestone is of earliest Barremian (*variabilis-rarocinctum* Zones) age.

Heligoland. Lower Cretaceous rocks are exposed on the sea-floor east of Heligoland in the 'Skit Gatt'. In recent years skin divers have collected rich cephalopod faunas from these outcrops. The ammonite faunas indicate that the lower part of the Hauterivian (*amblygonium*, *noricum*, and possibly *regale* Zones) is condensed or missing but the remainder of the Hauterivian and Barremian are well represented (Kemper *et al.* 1974; Rawson 1975). The belemnites include several hundred *H. jaculoides* and one specimen each of *A*. (*B*.) *rawsoni* and *A*. (*B*.) *stolleyi*.

Ahlum. This old section is no longer visible: it was situated south of Ahlum, about 4 km east of Wolfenbuttel (TK 25 Wolfenbüttel, Nr. 3829, re: 36 44 048, h: 57 82 550). Stolley (1906) described the sequence; from the lowest beds he recorded *Simbirskites* (*Craspedodiscus*) of the *phillipsi* group which indicates the *discofalcatus* Zone. Two large *Belemnites* aff. *subquadratus* were noted and later Stolley (1925) included them (with additional material) in *A. ahlumensis* Stolley *nom. nud.* He also recorded some much more slender forms. Stolley's records apparently represent *A.* (*B.*) *stolleyi* and *A.* (*B.*) *rawsoni*, several examples of which are still preserved in old collections from Ahlum.



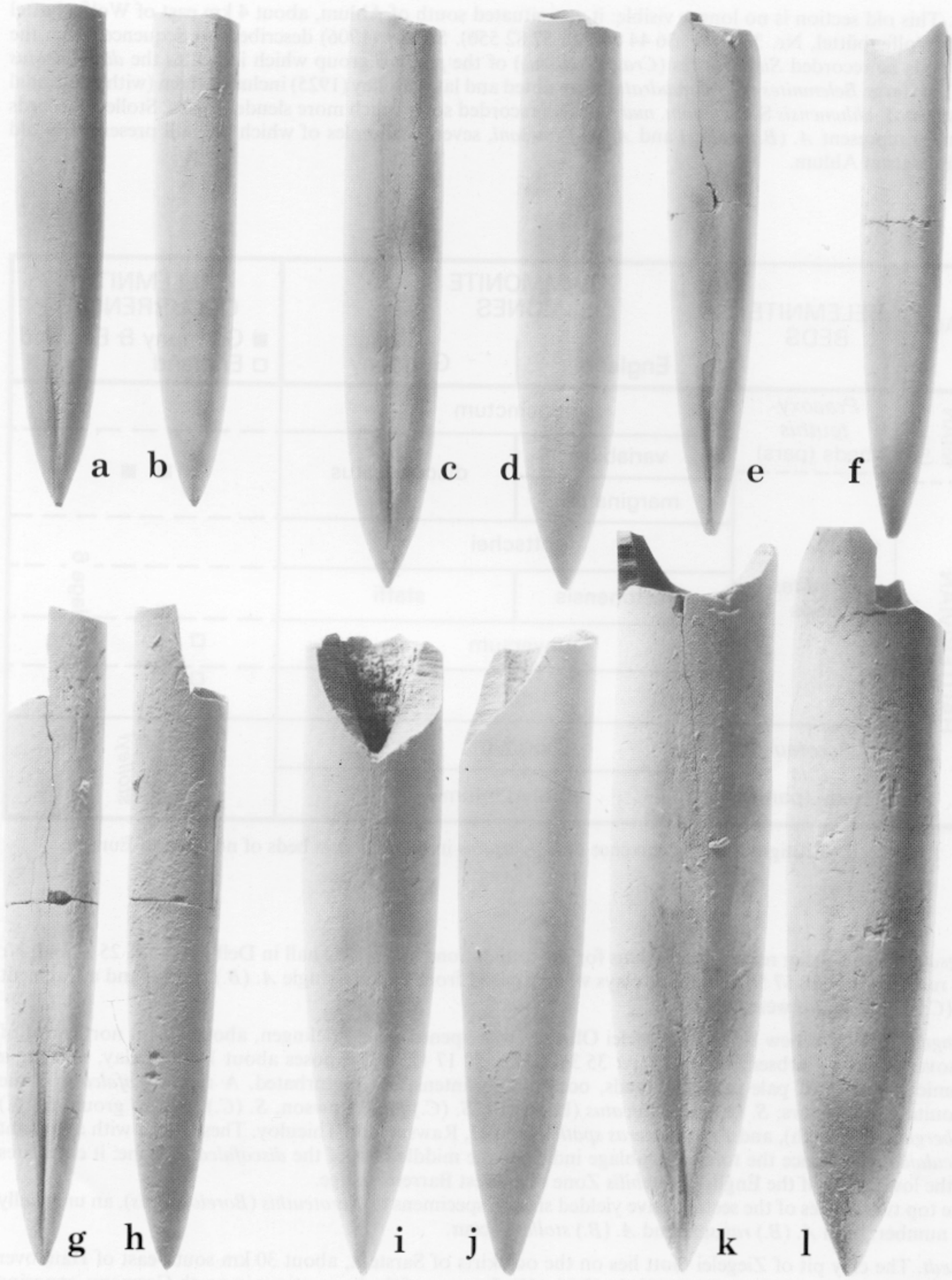
TEXT-FIG. 2. Stratigraphical occurrence of *Acroteuthis* in the *Hibolites* beds of north-west Europe.

Delligsen (*Hils*). During recent excavations for the foundations of a sports hall in Delligsen (TK 25 Alfeld, Nr 4024, re: 35 54 900, h: 57 56 460), dark clays were exposed from which a single *A.* (*B.*) *stolleyi* and a fragment of *S.* (*C.*) *discofalcatus* were collected.

Frielingen. In 1979 a new clay pit, Ziegelei Oltman, was opened near Frielingen, about 20 km north-west of Hannover (TK 25 Garbsen, Nr. 3523, re: 35 34 275, h: 58 17 125). It exposes about 14 m of clay, forming a rhythmic sequence of pale and dark beds, occasionally intensively bioturbated. A rich *discofalcatus* Zone ammonite fauna occurs: *S.* (*C.*) *discofalcatus* (Lahusen), *S.* (*C.*) *juddi* Rawson, *S.* (*C.*) *phillipsi* group, *S.* (*S.*) *toensbergensis* (Weerth), and *Paracrioceras spathi* Kemper, Rawson and Thieuloy. These occur with abundant *H. jaculoides* and hence the total assemblage indicates the middle part of the *discofalcatus* Zone: it correlates with the lower part of the English *variabilis* Zone of earliest Barremian age.

The top two metres of the section have yielded sixteen specimens of *Acroteuthis* (*Boreioteuthis*), an unusually large number: both *A.* (*B.*) *rawsoni* and *A.* (*B.*) *stolleyi* occur.

Sarstedt. The clay pit of Ziegelei Gott lies on the outskirts of Sarstedt, about 30 km south-east of Hannover (TK 25 Sarstedt, Nr. 3725, re: 35 60 400, h: 57 90 650). It is one of the key sections in north Germany, exposing about 70 m of shallow-water Upper Hauterivian, Barremian and Upper Aptian clays deposited on the flank of a salt stock. (For section details see Mutterlose 1983, fig. 4). The section has yielded two loose specimens of *A.* (*B.*) *stolleyi*, probably from the *discofalcatus* Zone.



TEXT-FIG. 3. *a–h*, *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney sp. nov. *a–d*, Paratypes, *discofalcatus* Zone, Frielingen (GPIH 1985-I-1, 1985-I-2); *e*, *f*, Paratype, bed C6 base (*speetonensis* Zone), Speeton (BM.C.59522); *g–h*, Holotype, mid C Beds, Speeton (BGS 24454). *i*, *j*, *A.* (*A.*?) *conoides* Swinnerton. Bed 'C7 or above', Speeton (WC 18350). *k*, *l*, *A.* (*B.*) *stolleyi* Pinckney sp. nov., Paratype, *discofalcatus* Zone, Frielingen (GPIH 1985-I-11). *a*, *c*, *e*, *g*, *i*, *k*, ventral views; *b*, *d*, *f*, *h*, *j*, *l*, lateral views; × 1.

SYSTEMATIC PALAEONTOLOGY

(by G. Pinckney)

Order BELEMNITIDA Zittel, 1895
Suborder BELEMNITINA Zittel, 1895
Family BELEMNITIDAE d'Orbigny, 1845
Subfamily CYLINDROTEUTHINAE Stolley, 1919

Genus ACROTEUTHIS Stolley, 1911

Diagnosis. Rostrum depressed, generally wedge-like in profile; apical line markedly displaced towards the venter; alveolus excentric and moderately deep.

Subgenus ACROTEUTHIS Stolley, 1911

Type species. Belemnites subquadratus Roemer, 1836.

Diagnosis. Acroteuthis with relatively large rostra that are wedge-like in profile, with only a weakly-developed ventral groove. Juvenile rostra moderately slender, spindle-shaped.

Acroteuthis (*Acroteuthis?*) *conoides* Swinnerton, 1937

Text-figs. 3*i*, *j*, 4*a*, *b*

v* 1937 *Acrouteuthis conoides* Swinnerton; p.17, pl. 6, fig. 2
?1964 *Acroteuthis* cf. *conoides* Swinnerton; Jeletzky, p. 56, pl. 14, fig. 3.
?1964 *Acroteuthis* aff. *conoides* Swinnerton; Jeletzky, p. 58, pl. 15, fig. 3.

Type. Holotype, BGS 17298 (Danford Collection), Beds C7–C8, Speeton Clay, Speeton, Yorkshire.

Material. 6 specimens from the C beds of the Speeton Clay: BM.C.59521 (Rawson Collection) from C7E; WC 21284 from C8 and 18350 from 'C7 or above'; BGS (Danford Collection) 17299, 17318, and 17319 from 'mid C'.

Diagnosis. Rostrum slender and conical; ventral apical groove well developed; apical angle acute in both outline and profile; transverse sections slightly depressed in alveolar and stem regions, becoming compressed posteriorly. Alveolus occupies about half length of guard and is weakly excentric.

Discussion. A. (*A.?*) *conoides* was described in detail by Swinnerton (1937). It is only tentatively referred to the subgenus *Acroteuthis* because it appears to be a transitional form towards *Boreioteuthis*. It resembles the latter in the weakly depressed condition of the rostrum and in the slight excentricity of the alveolus, but differs in the more feeble development of the ventral groove. Its stratigraphical horizon is also transitional between the ranges of the two subgenera in north-west Europe.

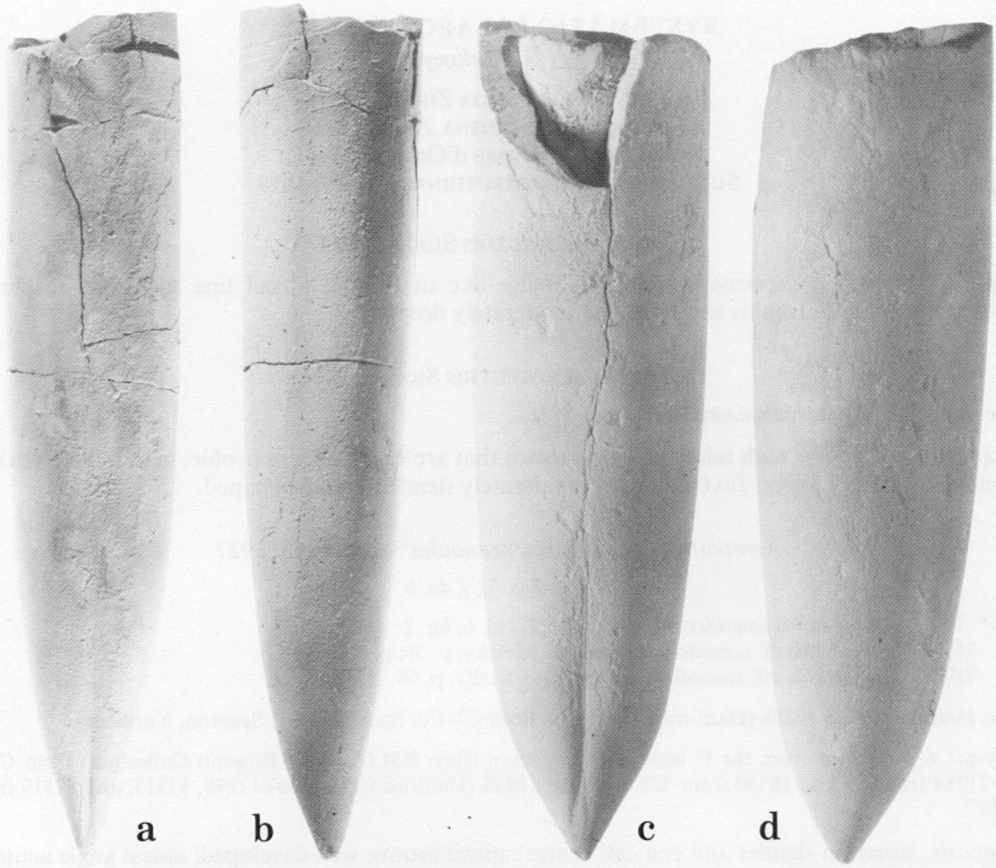
A. (*A.?*) *conoides* most closely approaches conical variants of *A.* (*A.*) *explanatoides* (Pavlow), but has a more compressed rostrum, better developed ventral groove and more acute apex in both outline and profile.

Geographic distribution: A. (*A.?*) *conoides* is known only from England, though very similar, possibly identical, forms have been figured from Northern Canada (Jeletzky 1964).

Subgenus BOREIOTEUTHIS Saks and Nalnyaeva, 1966

Type species. Acroteuthis (*Boreioteuthis*) *niiga* Saks and Nalnyaeva, 1966. Lower Volgian, northern Siberia.

Diagnosis. Acroteuthis with relatively large, moderately elongate, weakly depressed rostra; with a well-developed ventral groove extending into the stem region; and with markedly slender, clavate juvenile rostra.



TEXT-FIG. 4. *a*, *b*, *Acroteuthis* (*A.*?) *conoides* Swinnerton, bed C8 (*regale* Zone), Speeton (WC 21284); *c*, *d*, *A.* (*Boreioteuthis*) *stolleyi* Pinckney sp. nov., holotype, *discofalcatus* Zone, Ahlum (NLf B Kv56). *a*, *c*, ventral views; *b*, *d* lateral views; × 1.

Discussion. The subgenus *Boreioteuthis* is distinguished from *Acroteuthis s.s.* by its better-developed median ventral groove, which extends beyond the apical region, and by its more slender juvenile rostrum. It differs from the subgenus *Microbelus* in the possession of a larger 'adult' rostrum, and in the better development of the median ventral groove.

Our concept of *Boreioteuthis* is broader than that of Saks and Nalnyaeva (1966). Here, all *Acroteuthis* species with a median ventral groove that extends beyond the apical region are included, whereas Saks and Nalnyaeva (1966) only placed species possessing a ventral groove that extended into the alveolar region in this subgenus.

Stratigraphical distribution. According to Saks and Nalnyaeva (1966), *Boreioteuthis* ranges in age from Oxfordian to Barremian. However, in western Europe it is known only from strata of late Volgian and late Hauterivian to earliest Barremian age.

Acroteuthis (*Boreioteuthis*) *rawsoni* sp. nov.

Text-fig. 3*a*–*h*

?1901 *Belemnites speetonensis* Pavlow and Lamplugh; Pavlow, p. 82 pl. 8, fig. 7.
vp. 1937 *Acroteuthis festucalis* Swinnerton, pl. 9, fig. 2, *non* pl. 9, figs. 1 and 3.

v. *1974* *Acroteuthis* (*Boreioteuthis*) sp. nov. b, Pinckney and Rawson, p. 202.
v. 1982 *Acroteuthis* (*Boreioteuthis*) cf. *festucalis* Swinnerton; Stuhmer, Spaeth and Schmid, pl. 20, fig. 2.
v. *1983* *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney [MS]: Mutterlose, p. 15 (*nomen nudum*).
v. *1983* *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney [MS]: Mutterlose, Schmid and Spaeth, p. 299 (*nomen nudum*).

Type series. Holotype: BGS 24454 (Danford Collection), mid C beds, Speeton Clay, Speeton. Paratypes: 1 specimen from the Tealby Limestone of Lincolnshire (BM. C.59519); 2 from the Speeton Clay of Speeton (UC Pinckney Collection 366 from C7H, BM.C.59522 [Rawson collection] from the base of C6); 8 from the middle of the *discofalcatus* Zone at Frielingen (GPIH 1985-I-1-1985-I-8); 4 from Ahlum, probably *discofalcatus* Zone (GM 1923.599 [1 of 3 specimens], GPIG 3 uncatalogued specimens); 1 from Heligoland (SC 1503, figured Stuhmer *et al.* 1982).

Diagnosis. Rostrum slender and weakly depressed; apex very acute and only slightly depressed; median ventral groove quite well developed, extending into stem region; alveolus shallow.

Description. Rostra quite short, subconical to subcylindrical, very slender; actual length of rostrum up to 6·5 times the maximum width. In outline the sides of the alveolar and stem regions are usually quite straight and subparallel, but may converge slightly adapically. Rostral sides are weakly curved in the apical region and converge with moderate rapidity to form a long, acute to very acute apex, varying from about 32° to 40°. In profile the sides of the rostrum are almost straight in alveolar and stem regions. They are subparallel in front but converge gently adapically, so that the point of maximum thickness of the rostrum is near the alveolar rim. Convergence of rostral margins in apical region is quite gentle. Dorsal surface only slightly more curved than ventral, producing a feebly depressed, weakly asymmetrical apex, ranging from about 30° to 36°.

Transverse sections are weakly depressed and strongly quadrate through most of length of rostrum, except in apical region where they approach an oval form. Dorsal surface almost semicircular. Ventral surface, which is about same width as dorsal, is also semicircular in the alveolar region but flattens adapically. Flattening is accompanied by the development of a distinct, long, median ventral groove which is deep and narrow in the apical region but shallow and often excavate in the stem region, where it disappears. Rostral flanks markedly flattened.

Lateral lines are generally poorly visible. On well-preserved rostra, the upper main lateral line is represented by a relatively broad, flattened belt, and the lower by an indistinct, narrow, flattened belt. The minor lateral line has not been seen.

Alveolus shallow, occupying about one third of the actual length of the rostrum. It consists of a ventrally curved, conical depression, the apex of which is weakly excentric. The apical line is also excentric and curves gently towards the venter throughout its course.

No juvenile specimens are known. Evidence from dorsoventral longitudinal sections indicates that the juvenile rostrum is clavate and very slender, the maximum thickness being up to eight times the total rostral length.

Discussion. Swinnerton (1937) included specimens here regarded as *A.* (*B.*) *rawsoni* in his new species *A. festucalis*. However, the holotype of the latter differs from *A.* (*B.*) *rawsoni* in its greater size, more weakly developed median ventral groove, and in the possession of a feebly clavate rostrum. Moreover, the species are well separated stratigraphically, *A.* (*A.*) *festucalis* being of Volgian age and *A.* (*B.*) *rawsoni* of mid to late Hauterivian age.

A. (*B.*) *rawsoni* superficially resembles *Aulacoteuthis descendens* (Stolley) but differs principally in its slightly stouter form, less strongly developed ventral groove, and in the occurrence of cylindroteuthid lateral lines.

Acroteuthis (*Boreioteuthis*) *stolleyi* sp. nov.

Text-figs. 3*k*, *l*, 4*c*, *d*, 5*a*, *b*

v ?1906 *Belemnites* aff. *pseudopanderi* Sinzov; Danford, p.7, pl. 3, fig. 16; pl. 6, fig. 16.
? *1925* *Acroteuthis ahlumensis* Stolley, p. 117 (*Nomen nudum*).
v. *1974* *Acroteuthis* (*Boreioteuthis*) sp. nov. c, Pinckney and Rawson, p. 202
v. *1980* *Acroteuthis* (*Boreioteuthis*) *stolleyi* Pinckney [MS]; Mutterlose, pp. 239, 240 (*nomen nudum*).
v. *1983* *Acroteuthis* (*Boreioteuthis*) *stolleyi* Pinckney [MS]; Mutterlose, Schmid and Spaeth, p. 299 (*nomen nudum*).

TEXT-FIG. 5. *Acroteuthis* (*Borioteuthis*) *stolleyi* Pinckney sp. nov., paratype, *discofalcatus* Zone, Frielingen (GPIH 1985-I-10). *a*, ventral view; *b*, lateral view; × 1.

Type series. Holotype: NLfB Kv56, Simbirskiten Schichten, Ziegelei Ahlum, Wolfenbuttel, near Braunschweig. Paratypes: 8 specimens from Frielingen (GPIH 1985-I-9–1985-I-16); 6 from Ahlum (GM 1923·599 [2 of 3 specimens], 1923.600 [2 specimens], GPIG 2 uncatalogued specimens); 2 from Sarstedt (GPIH); 1 from Heligoland (SC), 1 from Delligsen (Strohmeyer private collection: cast in GPIH).

Diagnosis. Rostrum quite stout and weakly depressed; apex obtuse and inflated; median ventral groove quite well developed, extending into stem region; alveolus quite deep.

Description. Rostra large, subcylindrical to subconical and moderately stout, actual length of rostrum being about 3·5 times the maximum width. In outline the sides of alveolar and stem regions are almost straight and subparallel, but they converge slightly adapically. Rostral sides converge more rapidly and curve quite strongly in apical region to form a moderately obtuse apex, ranging from about 55° to 65°. In profile, sides of rostrum almost straight and subparallel in alveolar region, but they curve gently and converge in stem region. Convergence of rostral margins in apical region is strong. Ventral surface quite weakly curved, but dorsal surface markedly inflated, producing an obtuse, asymmetrical apex, varying from about 50° to 60°.

Transverse sections are weakly depressed and quadrate in alveolar region, but become more compressed and oval adapically. Dorsal surface is subsemicircular in front and closely approaches a semicircular condition in the apical region. The ventral surface, which is about the same width as the dorsal, is subsemicircular in the alveolar region but becomes flatter and weakly concave in apical and stem regions, where the median groove is developed. The groove is quite deep in the apical region but shallows adorally, eventually disappearing in the stem region. It does not extend quite to the apical tip, where the venter is feebly swollen. Rostral flanks quite strongly flattened.

Evidence of lateral lines is poor. The upper main lateral line is best developed and forms a broad, indistinct belt in the alveolar and stem regions that disappears adapically. The nature of the other lateral lines is unclear.

The alveolus is deep and occupies almost two thirds of the total length of the rostrum. It comprises a ventrally curved conical depression, the apex of which is moderately excentric. The apical line is also excentric and curves gently towards the venter throughout its course.

No juvenile specimens of *A.* (*B.*) *stolleyi* have been seen. However, smaller individuals are more slender with a more acute, less inflated apex and a shallower alveolus.

Discussion. A. (*B.*) *stolleyi* very closely resembles *A.* (*A.*) *pseudopanderi* (Sinzov emend. Pavlov) but has a better-developed median ventral groove and a shallower alveolus. It can be distinguished from *A.* (*A.*) *acrei* Swinnerton, *A.* (*A.*) *partneyi* Swinnerton, *A.* (*A.*) *bojarkae* Saks and Nalnjaeva, and *A.* (*A.*) *chetae* Saks and Nalnjaeva chiefly in the stronger development of the ventral groove, which extends into the stem region.

A. (*B.*) *stolleyi* apparently embraces *A. ahlumensis* Stolley. The latter was neither figured nor described and is therefore a *nomen nudum*. However, specimens of *A.* (*B.*) *stolleyi* from Ahlum were purchased from Stolley by the Mineralogisk Museum, Copenhagen (now Geologisk Museum), and bears his labels '*A. ahlumensis*'.

A. (*B.*) *stolleyi* probably occurs in bed C1 (*variabilis* Zone) at Speeton. Two specimens are known, though both are too corroded for firm identification. One, Danford's (1906) figured *Belemnites* aff. *pseudopanderi*, came from 'the lower of the two mottled beds at the upper limit of the C division' (= C1B), while a fragment with the apical region missing has been collected recently from bed C1A (BM.C.59523: Rawson Collection).

PHYLOGENETIC PROBLEMS

The Acroteuthis *subgenera*

The origin and phylogeny of the *Acroteuthis* subgenera is relevant to our interpretation of the late forms described here and is therefore discussed briefly.

Acroteuthis is divided into three subgenera: *Microbelus* (Callovian–Hauterivian in the USSR, Middle and Upper Volgian in north-west Europe), *Boreioteuthis* (Oxfordian–Barremian in the USSR, Upper Volgian–Early Barremian in north-west Europe), and *Acroteuthis s.s.* (Middle Volgian–Upper Hauterivian in USSR and north-west Europe, ?Aptian in USSR).

Microbelus is characterized by a relatively small, quite slender, depressed guard, with a median ventral groove confined to the apical region. According to Saks and Nalnyaeva (1966, p. 172) it evolved from *Pachyteuthis* (*P.*) *parens* Saks and Nalnjaeva in the Callovian. Saks and Nalnyaeva (1966, p. 174) also suggested that *Boreioteuthis* and *Acroteuthis s.s.* both evolved from *A.* (*Microbelus*) *pseudolateralis* Gustomesov, the former in the Oxfordian and the latter during the Volgian. Both *Boreioteuthis* and *Acroteuthis s.s.* are larger than *Microbelus*: *Boreioteuthis* has a well-developed ventral groove extending on to the stem region while *Acroteuthis s.s.* has a weakly developed one.

Saks and Nalnyaeva (1966, p. 173) suggested that from the Volgian onward each subgenus represented an independently evolving lineage.

While we agree that *Boreioteuthis* is probably derived from *M. pseudolateralis* by an increase in the length of the ventral groove, the evolution of *Acroteuthis s.s.* is more problematic for two reasons:

1. There is a long time gap between the extinction of *M. pseudolateralis* in the Late Oxfordian and the first appearance of true *Acroteuthis* in the Middle Volgian, and no transitional forms are known.

2. Many of the earliest *Acroteuthis s.s.* (e.g. *A.* (*A.*) *lindseyensis* Swinnerton) closely resemble *Pachyteuthis* species. These resemblances may be homeomorphic, but if not then *Acroteuthis s.s.*

may have evolved directly from *Pachyteuthis* (Callovian–Kimmeridgian) and the genus *Acroteuthis* as currently defined would be polyphyletic in origin.

Origin and evolution of the conoides–rawsoni–stolleyi *group*

A. (*A.*) *explanatoides* (Pavlow) is a long-ranging form (earliest Ryazanian to early Hauterivian) which apparently gave rise to several shorter-lived species. The last of these was *A.* (*A.*?) *conoides*, an interpretation on which we concur with Saks and Nalnyaeva (1966, p. 175). The species occur in stratigraphic succession at Speeton (text-fig. 2) with only a small gap between them which may well reflect simply their rarity in the *Hibolites* beds.

Stratigraphic occurrences (text-fig. 2) suggest that there may be an evolutionary lineage from *A.* (*A.*?) *conoides* through *A.* (*B.*) *rawsoni* to *A.* (*B.*) *stolleyi*. Early *A.* (*B.*) *rawsoni* slightly overlap with *A.* (*A.*?) *conoides* in the *inversum* Zone while younger examples occur with *A.* (*B.*) *stolleyi* in the *discofalcatus* Zone. Three main evolutionary trends are identified in this apparent lineage:

1. an increase in the length and depth of the ventral groove;
2. a decrease in the degree of depression of the rostrum in transverse section;
3. a progressive change from an essentially conical to a cylindrical rostrum.

If this lineage is confirmed by further finds, then the species *rawsoni* and *stolleyi* will need to be placed in a new subgenus which bears only a homeomorphic relationship to *Boreioteuthis*.

HOMEOMORPHY WITH *AULACOTEUTHIS*

The development of an apical groove characterizes not only *Boreioteuthis* and some *Acroteuthis* but also the oxyteuthinid genus *Aulacoteuthis*. The subfamily Oxyteuthinae characterizes strata immediately overlying the *Hibolites* beds in north-west Europe (Mutterlose 1983) and exhibits an evolutionary lineage: *Praeoxyteuthis*, a slender, ungrooved genus gave rise to *Aulacoteuthis*, characterized by an apical groove, which in turn evolved into the ungrooved *Oxyteuthis*.

Most *Aulacoteuthis* are readily distinguished from the north-west European *Boreioteuthis* by a longer groove and a slimmer guard. However, *A. descendens*, the youngest (mid-Barremian) form, has a short, stout guard with a groove that is sometimes short. Such forms closely resemble *A.* (*B.*) *rawsoni* and can only be differentiated by the lateral lines. While the latter possesses cylindroteuthid lateral lines, *A. descendens* has oxyteuthid ones (Mutterlose 1983, fig. 57). The close homeomorphy of the two species has caused confusion in the literature. From Simbirsk (now Ulyanovsk) on the Volga, Pavlow (1901, p. 82, pl. 8, fig. 7) described a short-grooved, stout belemnite from the mid-Hauterivian *versicolor* Zone and identified it as *Belemnites speetonensis* (i.e. *Aulacoteuthis*). It is here tentatively placed in *A.* (*B.*) *rawsoni*, though Swinnerton (1948, p. 48) identified the same specimen as *A. descendens*. This may be one of the reasons why Swinnerton regarded *Aulacoteuthis* and *Oxyteuthis* (including *Praeoxyteuthis*) as two forms derived from a common stock rather than agreeing with Stolley (1925, 1927) that the former was a grooved stage interposed in the evolution of the latter two genera. The proven stratigraphic separation of the late Hauterivian to earliest Barremian *Boreioteuthis* from the mid-Barremian *Aulacoteuthis* supports the morphological evidence that they are homeomorphs.

CONCLUSIONS

While the rare *Acroteuthis* in the lower part of the north-west European *Hibolites* beds are simply relics of an earlier fauna, later examples of the *Acroteuthis* (*A.*?) *conoides–Boreioteuthis* group are a new, more strongly grooved group that can be confused with slightly younger *Aulacoteuthis*. Material is insufficient to prove whether the *conoides–rawsoni–stolleyi* succession evolved in the area or whether the species migrated individually from other boreal areas, but *in situ* evolution is our preferred model. It is striking that while *Hibolites* is abundant in both shallow and deep water clays, *Boreioteuthis* is unusually common in the one section (Frielingen) where deeper water clays are exposed, so it may have adapted to an offshore environment.

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REFERENCES

DANFORD, C. G. 1906. Notes on the belemnites of the Speeton Clays. *Trans. Hull geol. Soc.* **5,** 1-14.

FLETCHER, B. N. 1969. A lithological subdivision of the Speeton Clay C Beds (Hauterivian), East Yorkshire. *Proc. Yorks. geol. Soc.* **37,** 323-327.

JELETZKY, J. A. 1964. Illustrations of Canadian fossils. Lower Cretaceous marine index fossils of the sedimentary basins of Western and Arctic Canada. *Geol. Surv. Pap. Can.* **64-11,** 1-101.

KEMPER, E., RAWSON, P. F., SCHMID, F. and SPAETH, C. 1974. Die Megafauna der Kreide von Helgoland und ihre biostratigraphische Deutung. *Newsl. Strat.* **3,** 121-137.

LAMPLUGH, G. W. 1889. On the subdivisions of the Speeton Clay. *Q. Jl geol. Soc. Lond.* **45,** 575-618.

MUTTERLOSE, J. 1980. Zur Gliederung des Unter-Barrême in NW-Europa mit Hilfe der Unter-Familie Oxytenthinae Stolley (Belemnitida). *Newsl. Strat.* **8,** 238-243.

—— 1983. Phylogenie und Biostratigraphie der Unterfamilie Oxyteuthinae (Belemnitida) aus dem Barrême (Unter-Kreide) NW-Europa. *Palaeontographica,* **A180,** 1-90.

—— SCHMID, F. and SPAETH, C. 1983. Zur Paläobiogeographie von Belemniten der Unter-Kreide in NW-Europa. *Zitteliana,* **10,** 293-307.

PAVLOW, A. P. 1901. Le Crétacé inférieur de la Russie et sa faune. *Nouv. Mem. Soc. (imp.) Nat. Mosc.* NS **16,** 1-87.

PINCKNEY, G. and RAWSON, P. F. 1974. *Acroteuthis* assemblages in the Upper Jurassic and Lower Cretaceous of northwest Europe. *Newsl. Strat.* **3,** 193-204.

RAWSON, P. F. 1971. The Hauterivian (Lower Cretaceous) biostratigraphy of the Speeton Clay of Yorkshire, England. Ibid. **1** (4), 61-75.

—— 1973. Lower Cretaceous (Ryazanian-Barremian) marine connections and cephalopod migrations between the Tethyan and Boreal Realms. *In* CASEY, R. *and* RAWSON, P. F. (eds). *The Boreal Lower Cretaceous,* 131-144. Seel House Press, Liverpool.

—— 1975. Hauterivian (Lower Cretaceous) ammonites from Helgoland. *Geol. Jb.* **A25,** 55-83.

SAKS, V. N. and NALNYAEVA, T. I. 1966. *Upper Jurassic and Lower Cretaceous belemnites of northern USSR. Genera* Pachyteuthis *and* Acroteuthis, 260 pp. Nauka, Moscow and Leningrad. [In Russian.]

STOLLEY, E. 1906. Uber alte und neue Aufschlusse und Profile in der unteren Kreide Braunschweigs und Hannovers. *Jber. Ver. Nat. Braunschweig,* **15,** 1-44.

—— 1925. Beiträge zur Kenntnis der Cephalopoden der norddeutschen unteren Kreide. 1. Die Belemniten der norddeutschen unteren Kreide. 2. Die Oxyteuthinae des norddeutschen Neokoms. *Geol. Paläont. Abh.* NF **14,** 177-212.

—— 1927. Zur Systematik und stratigraphie median gefurchter Belemniten. *Jber. Vols. Geol. Ver.* **20,** 111-136.

STÜHMER, H. H., SPAETH, C. and SCHMID, F. 1982. *Fossilien Helgolands, Teil 1.* Niederelbe-Verlag, 184 pp.

SWINNERTON, H. H. 1937. A monograph of British Lower Cretaceous belemnites. *Palaeontogr. Soc. [Monogr.],* Part 2, 17-30.

—— 1948. A monograph of British Lower Cretaceous belemnites. Ibid., Part 3, 31-52.

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