THE BRITISH TOARCIAN (LOWER JURASSIC) BELEMNITES

P. DOYLE

PART 1
Pages 1–49; Plates 1–17

MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

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ABSTRACT

Part 1 includes sections on the history of previous research, belemnite morphology and the stratigraphy of the British Toarcian outcrop. Five Toarcian belemnite biozones are proposed. 22 species belonging to 4 genera of the Belemnitidae d'Orbigny are described.

RÉSUMÉ

La première partie comprend l'histoire des recherches, la morphologie des belemnites, et la stratigraphie de l'affleurement Toarcien britannique. Cinq biozones à belemnites sont proposées. 22 espèces sont décrites; elles appartiennent à 4 genres de Belemnitidae d'Orbigny.

ZUSAMMENFASSUNG

Teil 1 enthält Abschnitte über die Geschichte der bisherigen Forschung, die Morphologie der Belemniten und die Stratigraphie des britischen Toarc-Ausstrichs. Fünf Belemniten-Biozonen werden im Toarc vorgeschlagen. 22 Arten aus 4 Gattungen der Belemnitidae d'Orbigny werden beschrieben.

Тоарские белемниты Великобритании.
Резюме Частв 1.

Первая часть включает главы по истории исследований, морфологии белемнитов и стратиграфии британских тоарских отложений. Для тоара предложено пять белемнитовых биозон. Описано 22 вида, принадлежащих к четырем родам сем. Belemnitidae.

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THE BRITISH TOARCIAN (LOWER JURASSIC) BELEMNITES

INTRODUCTION AND ACKNOWLEDGEMENTS

The British Toarcian belemnites have never been separately monographed, although the diversity of Toarcian species was recognized by many authors (e.g. Simpson 1855, 1884; Phillips 1865–1909; Tate & Blake 1879). The basis of this monograph is approximately 3500 belemnites collected mainly from Yorkshire (*in situ* from measured sections), with others from Dorset, the Midlands and Raasay. These specimens are housed in the Natural History Museum (**BMNH**), London.

The study is the result of a Ph.D project supervised by Dr P. F. Rawson at Queen Mary and University colleges of the University of London (1981–4). Financial assistance for the project was provided initially by a Draper's Company/Queen Mary College Studentship (1981–2), and then a Sir Edward Stern Scholarship of the University of London (1982–4). The Central Research Fund of the University of London provided valuable financial assistance for fieldwork. The Council of the Palaeontological Association is thanked for granting me the Sylvester-Bradley Award (1984), enabling me to study comparable material in mainland Europe. I am grateful to the following for access to collections in their care: M. K. Howarth, D. Phillips, Natural History Museum, London (**BMNH**); H. C. Ivimey-Cook, A. A. Morter, British Geological Survey, Keyworth (**BGS**); C. Daniels, Bundesanstalt für Bodenforschung, Hannover (**BfB**); W. N. Terry, Central Museum, Northampton (**CMN**); W. K. Christensen, Geologisk Museum, Copenhagen (**GMC**); R. Pickford, Geology Museum, Bath (**GMB**); A. Liebau, F. Westphal, Institüt und Museum für Geologie und Paläontologie, Universität Tübingen (**GPIT**); D. Thies, Niedersächisches Landesmuseum, Hannover (**LMH**); Y. Gayrard, Musée d' Histoire Naturelle, Paris (**MHNP**); M. G. Bassett, National Museum of Wales, Cardiff (**NMW**); H. P. Powell, Oxford University Museum (**OUM**); G. Dietl, Staatliches Museum für Naturkunde, Stuttgart (**SMNS**); D. Price, Sedgwick Museum, Cambridge (**SM**); P. Thornton, A. A. Berends, Whitby Museum (**WM**).

I am indebted to Drs A. S. Howard and M. J. Simms for their assistance and advice in the field, and to Dr P. F. Rawson for his guidance throughout the project. Professor D. T. Donovan and Drs T. Engeser, J. Mutterlose, M. K. Howarth, W. Riegraf and M. R. Sandy provided valuable assistance and advice, and I benefited greatly through correspondence and discussion with Drs W. K. Christensen, R. Combemorel, the late J. A. Jeletzky and G. R. Stevens. A. Maclachlin and P. Jones helped with preparation of material (at Queen Mary College), and M. Gray (University College) and the staff of the Natural History Museum photographic department supplied the photographs. My wife Julie assisted with all aspects of the project, both in and out of the field, and my parents provided invaluable support at all times.

PREVIOUS RESEARCH

The British Toarcian belemnites have received scant attention. For the most part descriptions are found in regional stratigraphical works such as Young & Bird (1822, 1828), Phillips (1829, 1835, 1875), Oppel (1856–58) and Tate & Blake (1876). Other early accounts include Miller (1826) and Brown (1837–49) who recorded "*Belemnites tripartitus*", representing indeterminate species of the Toarcian genus *Acrocoelites*, from Britain. The only monographic study remains Phillips' (1865–1909) monograph of the British Belemnitidae, which contains descriptions of 76 species, of which 30 are from the English Toarcian.

Belemnites from the Yorkshire Toarcian have received the most attention, the works mentioned above containing descriptions of mainly Yorkshire species. Simpson (1855, 1866, 1884) described 49 species from the Yorkshire Upper Lias, most of them new, but unfortunately without illustration. More recently, Doyle (1985) described *Youngibelus*. For the rest of the country, only scattered descriptions and illustrations of Toarcian belemnites exist, and in all, only seven of the

30 species described in Phillips' (1865–1909) monograph were from Dorset and the Midlands. Quenstedt (1846–49) and Oppel (1856–58) both illustrated and described *Belemnites dorsetensis* (so named by Oppel) from the Bridport Sands of Dorset, while Crick (1896) reported a complete belemnite pro-ostracum from the Fish Bed of Gloucestershire. Jeletzky (1966) illustrated an almost complete specimen of *Chondroteuthis wunnenbergi* Böde from the same horizon, and Lissajous (1927) described *Acrocoelites strictus* from the Toarcian of Northamptonshire. Toarcian belemnite species are also included in the faunal lists of the following: Woodward (1893), Fox-Strangways (1896), Thompson (1910), Buckman (1915), Bülow-Trummer (1920), Lissajous (1925), Jackson (1926) and Hallam (1967).

There have been several important foreign works describing Toarcian belemnites. The most important include: Voltz (1830), d'Orbigny (1842) and Dumortier (1874) in France; Zieten (1830–33), Quenstedt (1846–49), Kolb (1942), Schwegler (1961–71), Riegraf (1980) and Riegraf *et al.* (1984) in southern Germany; Stoyanova-Vergilova (1977) in Bulgaria; Činčurová (1967, 1971, 1975) in Czechoslovakia; Krimhol'z (1931) and Saks & Nal'nyaeva (1970, 1975) in USSR. However, few of these works make direct reference to British specimens or species.

STRATIGRAPHICAL SUMMARY

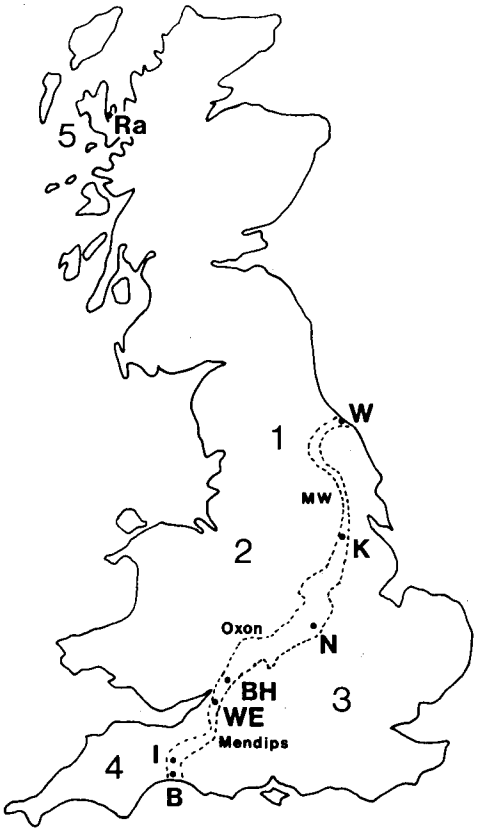
Toarcian belemnites are found throughout the Jurassic outcrop in Britain (Text-figs 1, 2). The correlation used here is that of Howarth (*in* Cope *et al.* 1980), based on the references given therein. The thickest exposed succession is that of the North Yorkshire coast, where approximately 120 m of Lower Toarcian shales and Upper Toarcian sands are developed (Text-fig. 2). Farther south in southern Yorkshire and Lincolnshire the Upper Toarcian is missing, Aalenian sands lying unconformably upon Lower Toarcian clays and shales similar to those of North Yorkshire (Text-fig. 2). In Northamptonshire, Oxfordshire and Leicestershire the basal zone of the Toarcian is represented by the upper part of the largely Domerian (Upper Pliensbachian) Marlstone Rock Bed (Howarth 1980), with overlying clays and intermittent limestones (e.g. the "Fish Bed") of early Toarcian age. This succession is present in the northern Cotswolds (Gloucestershire, Worcestershire) (Text-fig. 2), but here the Upper Toarcian is developed as a series of limestones, clays and sands. In the southern Cotswolds (Gloucestershire) (Text-fig. 2) the distinctive, friable, yellow, Cotteswold Sands of early to late Toarcian age are developed, overlying earlier Toarcian clays. They are succeeded by the condensed, limonitic Cephalopod Bed of late Toarcian age. Farther south in Avon, Somerset and Dorset (Text-fig. 2), the Lower Toarcian and part of the Upper Toarcian are developed in the condensed micritic limestone of the Junction Bed, with the Upper Toarcian Midford, Yeovil and Bridport sands above. These sands, like the Cotteswold Sands to the north, are lithologically equivalent, but are diachronous, becoming progressively younger to the south (Buckman 1889). Davies (1969) suggested that these sands represent the progressive southward movement of a shelf sand bar. In Scotland, Toarcian strata are present in the Inner Hebrides, where (in Raasay) the Lower Toarcian is represented by a series of sands and shales, with a chamositic ironstone above (the Raasay Ironstone). Part of the Upper Toarcian is represented by the Dun Caan Shales.

In this monograph the Toarcian outcrop is informally divided into five separate regions, discussed below. Individual localities within them are identified by name and through the use of a six figure National Grid reference.

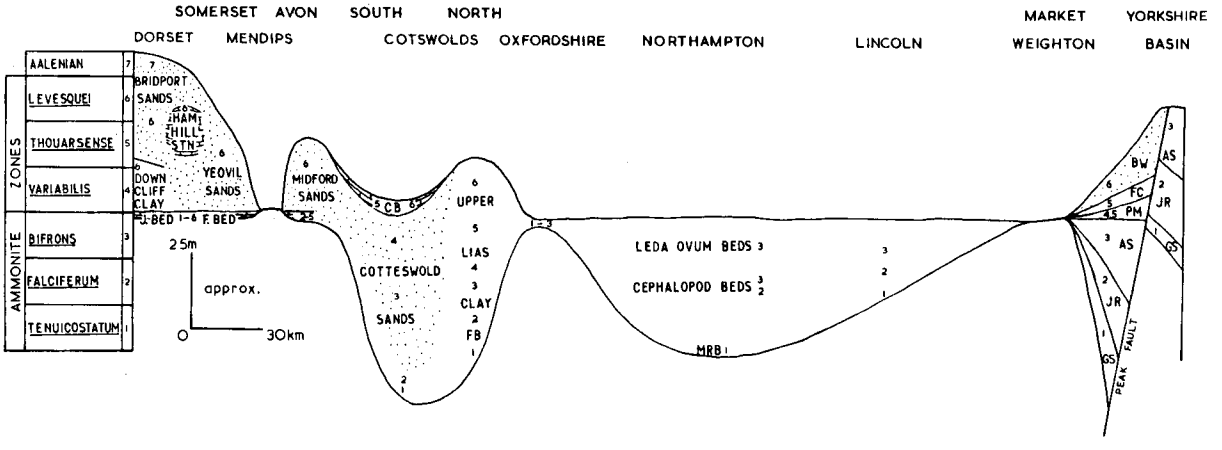
The Yorkshire Basin

The Toarcian lithostratigraphy of the Yorkshire Basin was revised by Knox (1984) and Powell (1984), who recognized two formations within the Toarcian of the Lias Group: The Whitby Mudstone Formation and the Blea Wyke Sandstone Formation. The former (Lower to Upper Toarcian) comprises five members: Grey Shale Member, Jet Rock Member, Alum Shale Member (Lower Toarcian); Peak Mudstone Member and Fox Cliff Siltstone Member (Upper Toarcian). The first three of these correspond to the "formations" and "series" of the same names

used by Howarth (1962, 1973), while the Peak Mudstone and Fox Cliff Siltstone members are roughly equivalent to the Peak Shales and Striatulus Shales of Dean (1954). The Blea Wyke Sandstone Formation (Upper Toarcian) comprises two members, the Grey Sandstone Member and the Yellow Sandstone Member, corresponding to the two units of similar name used by Dean (1954).



TEXT-FIG. 1. The British Toarcian outcrop. Numbers 1–5 refer to the informal regions of the stratigraphical discussion: 1, Yorkshire Basin, bounded to the south by the Market Weighton (MW) high; 2, North Midlands, bounded to the south by the Oxfordshire (Oxon) shallows; 3, Cotswolds, bounded to the south by the Mendips; 4, Somerset and Dorset; 5, Inner Hebrides. Important sections include: Raasay (Ra) Whitby (W), North Yorkshire; Kirton-in-Lindsey (K), Lincolnshire; Northampton (N); Bredon Hill (BH), Hereford and Worcester; Wotton-under-Edge (WE), Gloucestershire; Ilminster (I), Somerset; Bridport (B), Dorset.

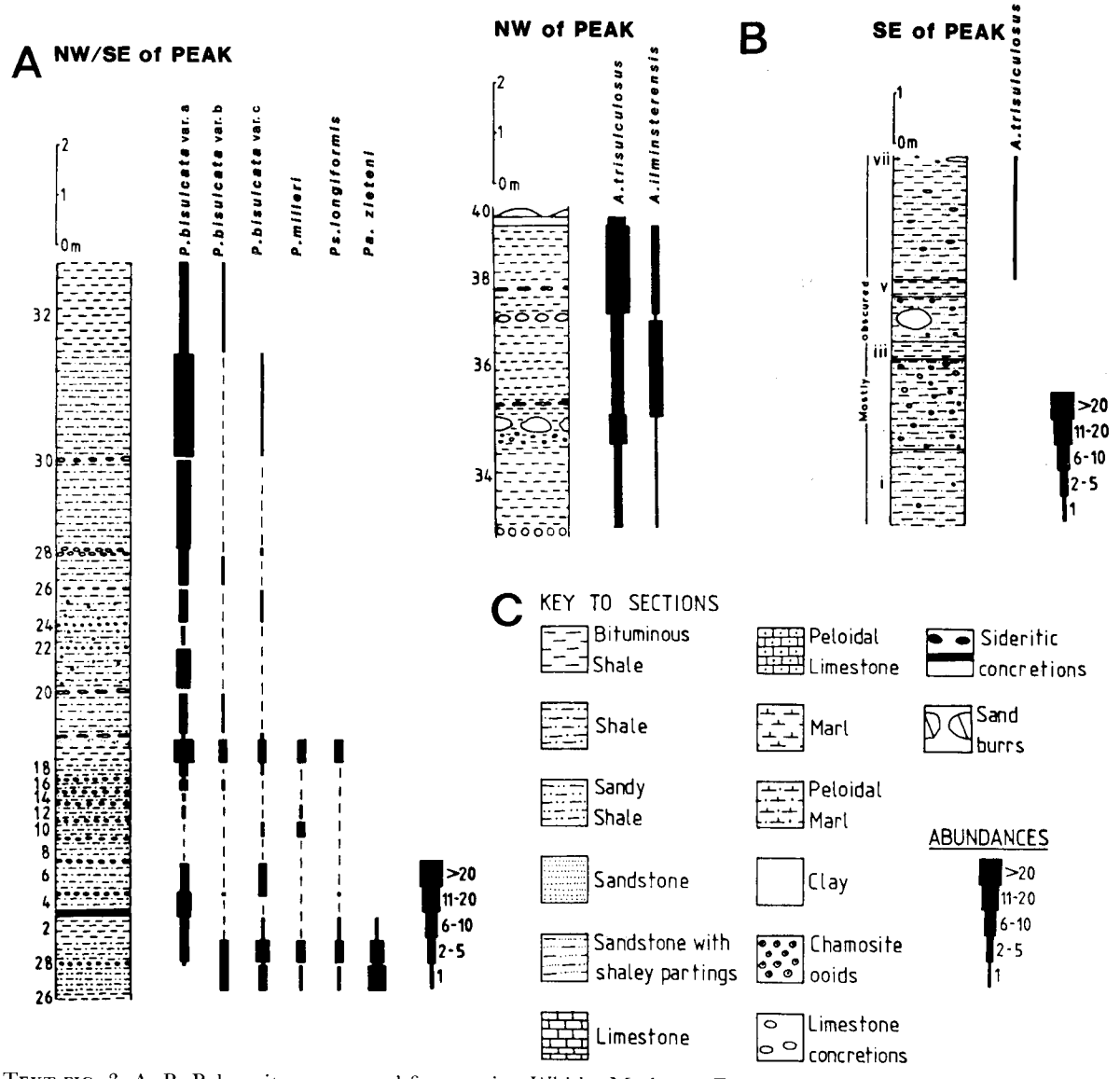


TEXT-FIG. 2. Outline of the stratigraphy of the main Toarcian outcrop from Dorset to Yorkshire. The Lower/Upper Toarcian boundary, at the base of the *Haugia variabilis* Zone, is reduced to a horizontal plane. Abbreviations: BW, Blea Wyke Sand Formation; FC, Fox Cliff Siltstone Member; PM, Peak Mudstone Member; AS, Alum Shale Member; JR, Jet Rock Member; GS, Grey Shale Member; MRB, Marlstone Rock Bed; FB, F. Bed, Fish Bed; J. Bed, Junction Bed. Modified and updated after Arkell (1933, fig. 30).

Whitby Mudstone Formation

1. Grey Shale Member (*Dactylioceras tenuicostatum Zone*). 13 m of silty grey shales with abundant calcareous and sideritic doggers and nodules (e.g. the "six red nodules" of Howarth 1973). The Grey Shales are exposed along the foreshore between Brackenberry Wyke (NZ 795182) and The Peak, Ravenscar (NZ 980027). Extensive collections were made at East Kettleness (NZ 835160), and Hawsker Bottoms (NZ 944084) (Text-fig. 3A).

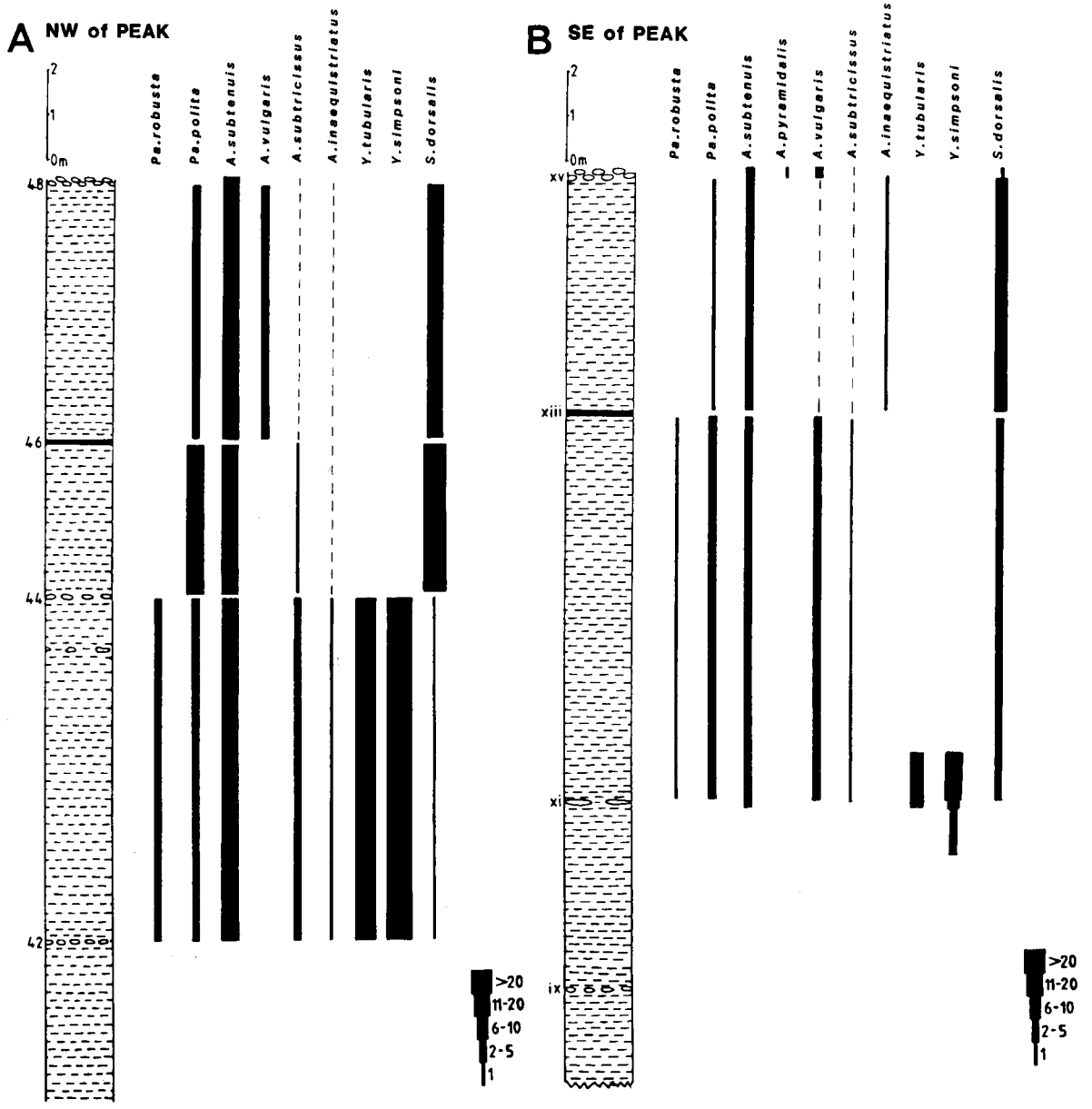
2. Jet Rock Member (*Harpoceras falciferum* Zone). Approximately 30 m of black bituminous shales alternating with frequent calcareous nodules and doggers that often bear a pyrite skin. The lower 6–7 m are known as the Jet Rock, characterized by the large number of pyrite-skinned doggers



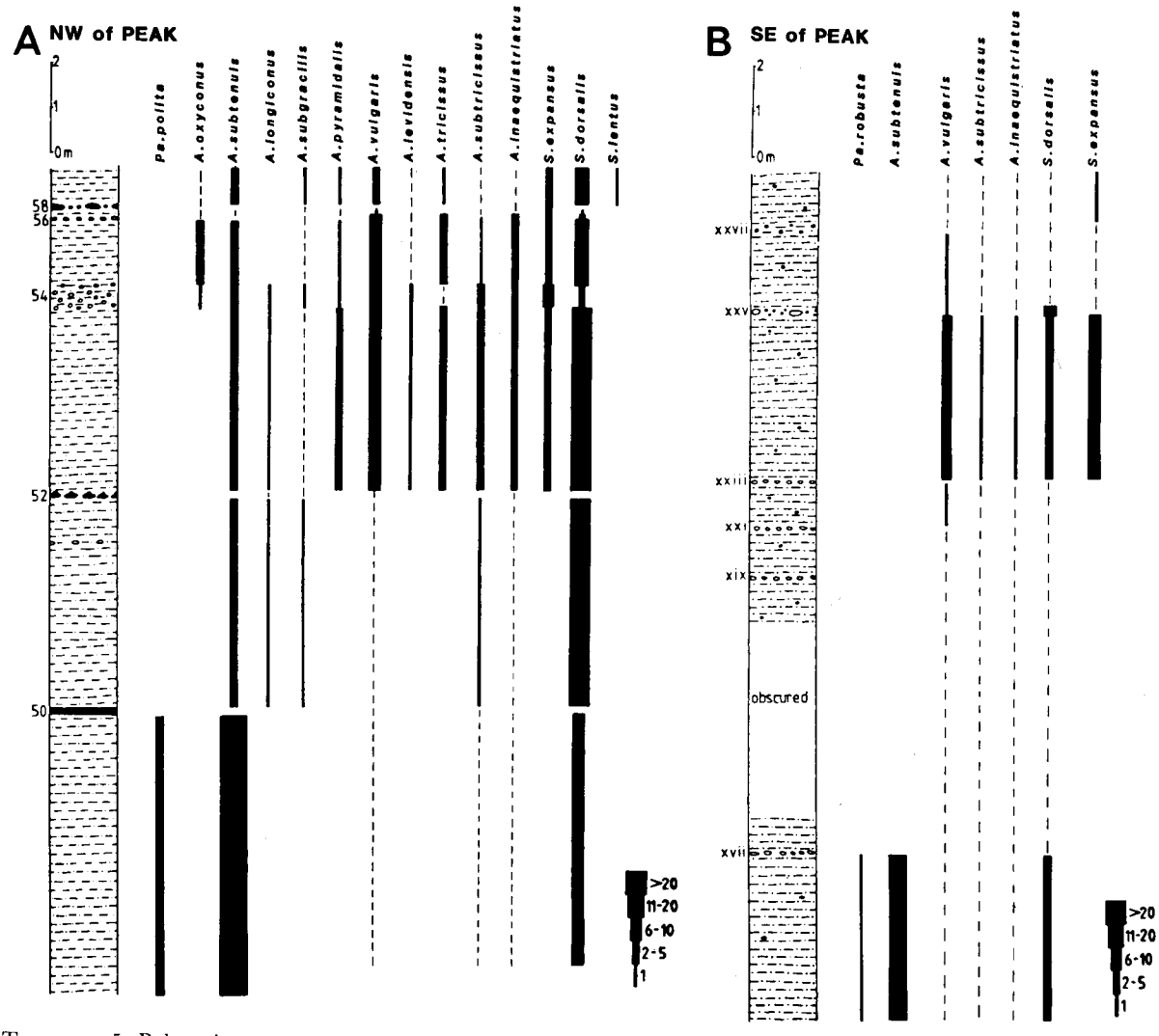
TEXT-FIG. 3. A, B. Belemnite ranges and frequencies, Whitby Mudstone Formation. A. Grey Shale Member (*Dactylioceras tenuicostatum* Zone). Exposures northwest and southeast of the Peak Fault. Bed numbers from Howarth (1973). B. The Jet Rock, Jet Rock Member (*Harpoceras falciferum* Zone, *Harpoceras exaratum* Subzone). Successions differ either side of the syndepositional Peak Fault. Bed numbers from Howarth (1962). C. Key to lithological sections in text-figs 3–10. Sand burrs are calcareous cemented horizons within the Bridport Sands and their lithological equivalents (see Bryant *et al.* 1988).

that it contains. The uppermost 23–24 m contain fewer nodules, and are known as the Bituminous Shales (Howarth 1962). The Jet Rock Member is exposed between Port Mulgrave (NZ 7980175–808173), Hawsker Bottoms (NZ 945082–948078) (both Jet Rock), Ravenscar (NZ 980025–983083) (Jet Rock and Bituminous Shales), Saltwick Bay (NZ 916114–925108) and Sandsend (NZ 860133–861139) (both Bituminous Shales). The configuration of nodules and actual thicknesses of the shales at Ravenscar differ from that developed north-west of the Peak Fault due to syndepositional movement of this fault (Howarth 1962) (Text-figs 2, 3B, 4A, B).

3. Alum Shale Member (*Hildoceras bifrons* Zone). Grey, non-bituminous shales with many calcareous or sideritic nodules or doggers. The effects of the syndepositional movements of the



TEXT-FIG. 4. Belemnite ranges and frequencies in the Bituminous Shales, Jet Rock Member, Whitby Mudstone Formation (*Harpoceras falciferum* Zone and Subzone). Bed numbers from Howarth (1962). A, exposures NW of Peak; B, exposures SE of Peak.

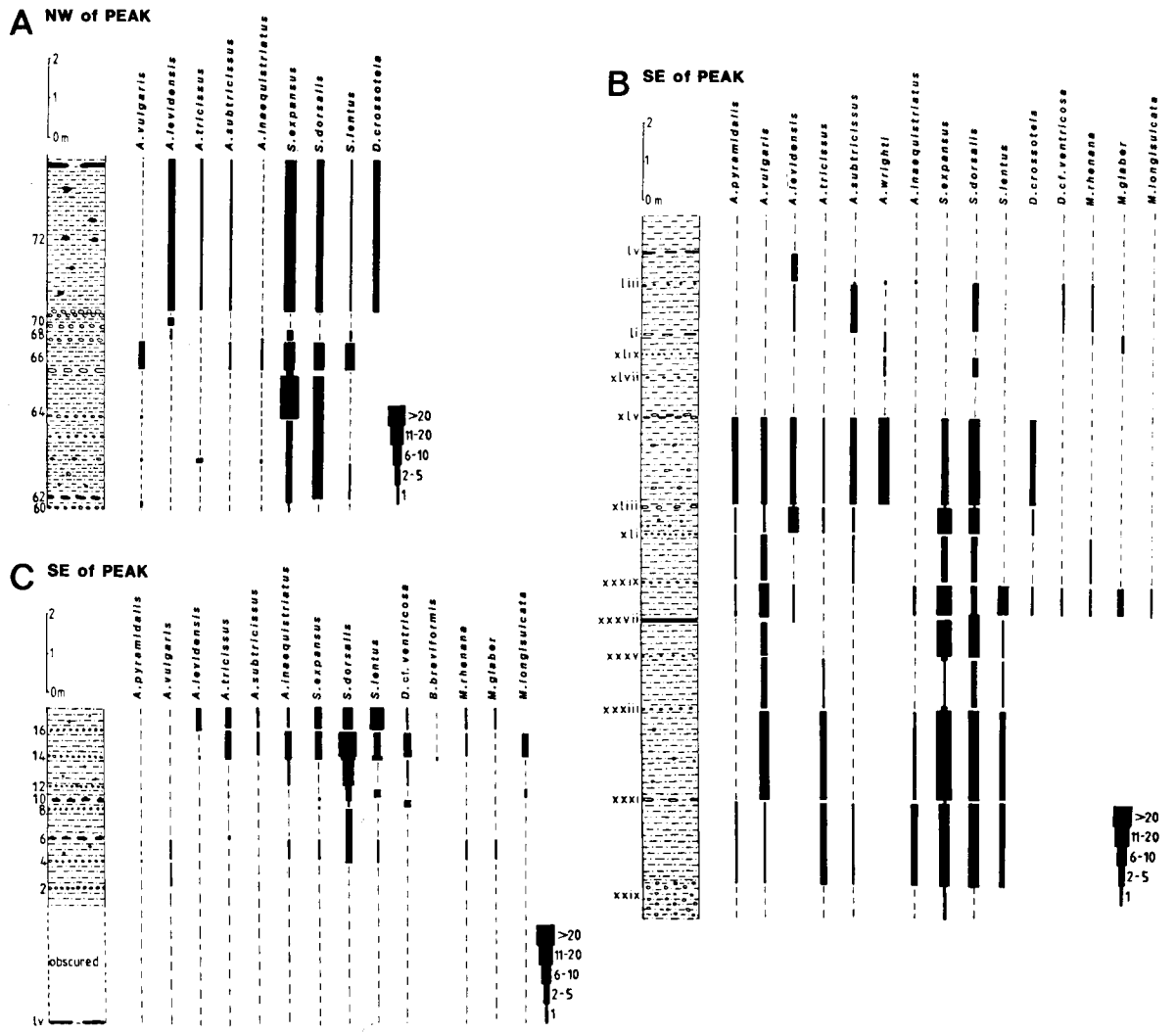


TEXT-FIG. 5. Belemnite ranges and frequencies in the Hard Shales and Main Alum Shales, Alum Shale Member, Whitby Mudstone Formation (*Hildoceras bifrons* Zone, *Dactylioceras commune* Subzone). Bed numbers from Howarth (1962). A, exposures NW of Peak; B, exposures SE of Peak.

Peak Fault at the Peak, Ravenscar, have resulted in differential thicknesses either side of the fault (27 m northwest of the fault, 37 m southeast of it), and in different configurations of their nodule bands (Howarth 1962, fig. 1) (Text-figs 5A, B, 6A, B). The Alum Shale Member is best exposed at Whitby (NZ 902115–913114) and at Ravenscar (NZ 984024–986018), and extensive collections were made from both localities (Text-figs 5A, B, 6A, B).

4. Peak Mudstone Member (*Haugia variabilis* Zone to *Grammoceras striatulum* Subzone, *Grammoceras thouarsense* Zone). 12–13 m of light grey, silty, non-bituminous shales corresponding to the Peak Shales and the basal part of the Striatulus Shales of Dean (1954) (Knox 1984). The Peak Mudstone Member is exposed only at Fox Cliff (NZ 988016), where extensive collections were made (Text-figs 6C, 7A).

5. Fox Cliff Siltstone Member (*Grammoceras thouarsense* Zone). 11 m of silty shales corresponding to the upper part of the Striatulus Shales of Dean (1954) (Knox 1984). It is exposed only at Fox Cliff (NZ 988016), where extensive collections were made (Text-fig. 7A).



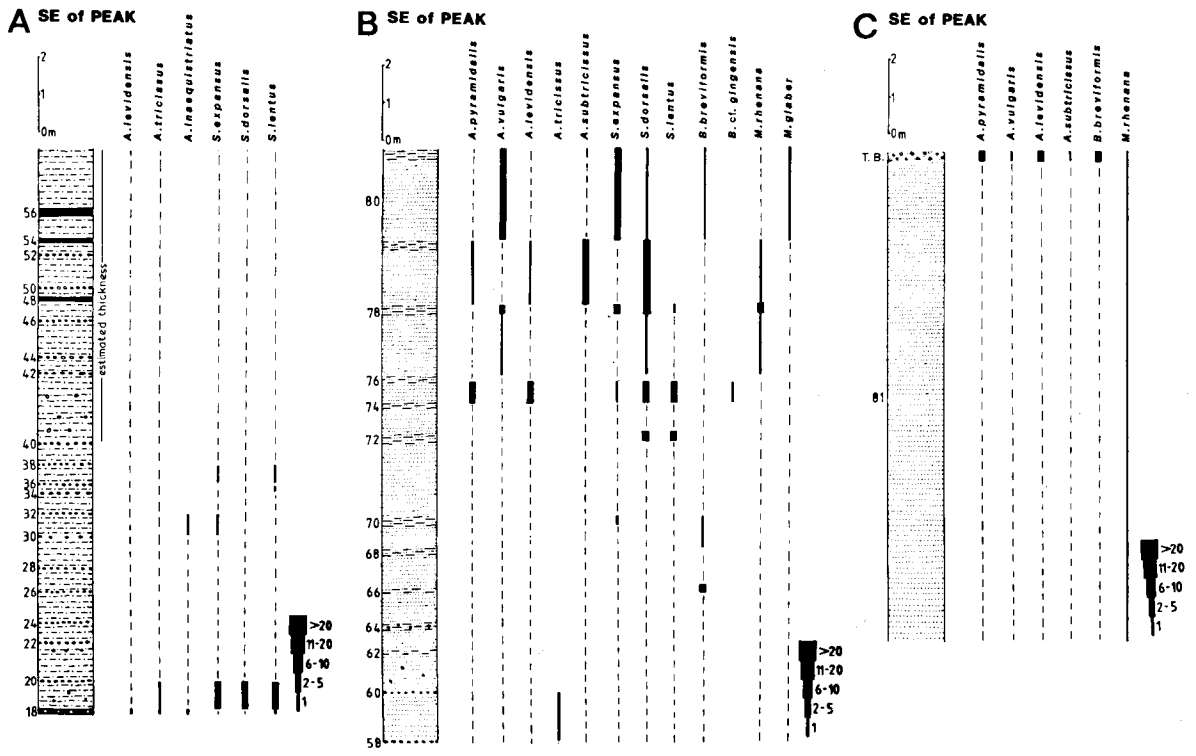
TEXT-FIG. 6. Belemnite ranges and frequencies in: A, B, the Main Alum Shales (top) and Cement Shales, Alum Shale Member, Whitby Mudstone Formation (*Hildoceras bifrons* Zone, *Peronoceras fibulatum – Catacoeloceras crassum* subzones). Bed numbers from Howarth (1962). A, exposures NW of Peak; B, exposures SE of Peak. C, the Peak Shales, Peak Mudstone Member, Whitby Mudstone Formation (*Haugia variablis* Zone), Fox Cliff, southeast of Peak. New bed numbers.

Blea Wyke Sandstone Formation

1. Grey Sandstone Member (*Dumortieria levesquei* Zone). 11 m of grey sandstones with sporadic indurated horizons, corresponding to the Grey Beds of Dean (1954) (Knox 1984). The Grey Sandstone Member is exposed at Blea Wyke Point (NZ 991016), where extensive collections were made (Text-fig. 7B).
2. Yellow Sandstone Member (*Dumortieria levesquei* Zone). 8 m of yellow friable sands corresponding to the Yellow Beds of Dean (1954) (Knox 1984). The Yellow Sandstone Member is exposed at Blea Wyke Point (NZ 991016), where extensive collections were made (Text-fig. 7C).

NORTH MIDLANDS

This region includes Lincolnshire and Northamptonshire. Neither was visited, because of relatively poor exposure, but extensive museum collections (BMNH, and Beeby Thompson Collection CMN) were consulted. The stratigraphy of the Lincolnshire Toarcian, which is



TEXT-FIG. 7. Belemnite ranges and frequencies in: A, the Striatulus Shales, top Peak Mudstone and Fox Cliff Siltstone members, Whitby Mudstone Formation (*Grammoceras thouarsense* Zone). Fox Cliff, southeast of Peak. New bed numbers; B, the Grey Sandstone Member, Blea Wyke Sandstone Formation (*Dumortieria levesquei* Zone). Blea Wyke Point, southeast of Peak. New bed numbers; C, the Yellow Sandstone Member, Blea Wyke Sandstone Formation (*Dumortieria levesquei* Zone), and overlying Aalenian Terebratula Bed (T.B.). Blea Wyke Point, southeast of Peak. New bed numbers.

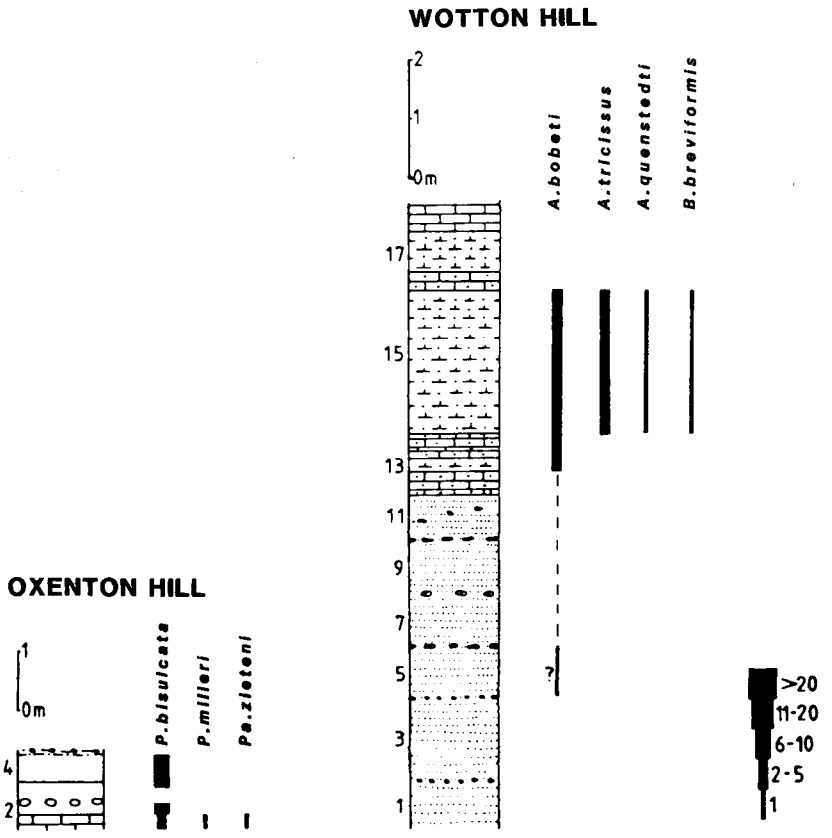
composed entirely of Lower Toarcian sediments, was discussed by Trueman (1918), Arkell (1933), Howarth & Rawson (1965, describing the succession at Kirton-in-Lindsey; the belemnites are housed in the Natural History Museum) and Howarth (1980). The Northamptonshire Toarcian was discussed in detail by Howarth (1978) (Text-fig. 2).

COTSWOLDS

This region comprises two areas with lithologically distinct successions: the northern Cotswolds, including all those localities north of Cheltenham, and the southern Cotswolds, in the vicinity of Stroud (Text-fig. 2).

Northern Cotswolds. Up to 100 m of argillaceous sediments comprise the Toarcian of this area (Richardson 1929; Green & Melville 1956; Whittaker & Ivimey-Cook 1972). Small exposures of Lower Toarcian were visited at Oxenton Hill (*tenuicostatum* Zone) (SO 997314) (Text-fig. 8) and Alderton Hill (*falciferum* Zone) (SP 009345), the latter exposing the famous Fish and Insect Bed (Brodie 1843; Crick 1896, 1921). Specimens were also collected from massive clay slumps at Bredon Hill (mainly Lower Toarcian, although capped by Upper Toarcian limestones) (SO 950400).

Southern Cotswolds. Approximately 100 m of argillaceous sediments, sands and limestones comprise the Toarcian sediments of this area. These sediments differ from those of the northern Costwolds due to the development of the Cotteswold Sands (Text-fig. 2). These consist of approximately 70 m of fine, friable, yellow sands of *bifrons* to *variabilis* zones age (Buckman 1889; Richardson 1910; Cave 1977). Both the Cotteswold Sands and the succeeding condensed, oolitic



TEXT-FIG. 8. Belemnite ranges and frequencies in sections exposed at Oxenton Hill (northern Cotswolds) and Wotton Hill (southern Cotswolds), Gloucestershire. New bed numbers. Oxenton Hill; Marlstone Rock Bed (bed 1, Pliensbachian, *Pleuroceras spinatum* Zone) and overlying Upper Lias Clay (beds 2–5) (*Dactylioceras tenuicostatum* Zone).

limestones of the Cephalopod Bed (*thouarsense* to *levesquei* zones) were examined at Wotton Hill, Wotton-under-Edge (ST 754939) (Text-fig. 8).

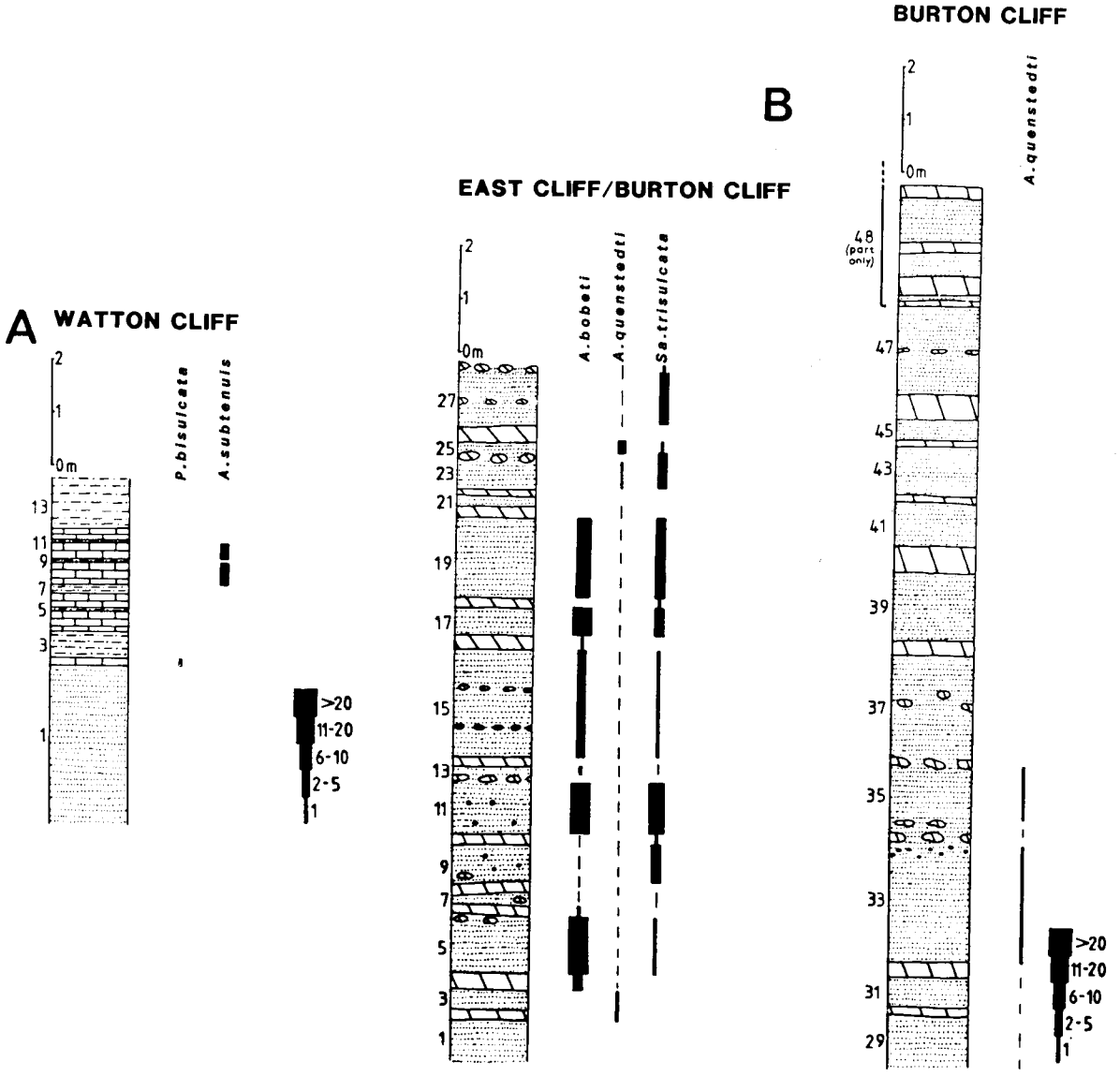
SOMERSET AND DORSET

Somerset. Toarcian exposures in this region are extremely limited, and no fresh material was collected. However, belemnites from the classic localities around Ilminster were examined in Bath (Charles Moore Collection, GMB). The Toarcian stratigraphy was discussed by Moore (1867), Buckman (1889), Hamlet (1922), Spath (1922), Arkell (1933) and Wilson *et al.* (1958).

Dorset. There is little recent work on the Dorset Toarcian; detailed studies were undertaken in the early part of this century by Buckman (1910, 1922) and Jackson (1922, 1926) and later by Parsons (1974), Jenkyns & Senior (1977) and Howarth (1980). The Toarcian succession is well exposed on the Dorset coast between Thorncombe Beacon (SY 437914) and Burton Bradstock (SY 490888). The Lower Toarcian and part of the Upper Toarcian are represented by the micritic limestones of the condensed Junction Bed (Jackson 1922, 1926; Howarth 1956, 1980). The Junction Bed at Watton Cliff (SY 452918) is rather thicker than elsewhere in Dorset (2.6 m as opposed to 1.4 m at Down Cliff), due to the movement of a syndespositional fault (Jenkyns & Senior 1977). The Junction Bed ranges in age from late Pliensbachian (*spinatum* Zone) to late Toarcian (*thouarsense* Zone) (Text-fig. 9A).

Most of the Upper Toarcian in Dorset is represented by the Down Cliff Clay (*levesquei* Zone) and the Bridport Sands (*levesquei* Zone to Aalenian). The Down Cliff Clay is a dark grey argillaceous deposit 21 m thick which is locally developed above the Junction Bed. It is seen high in the cliff near Down Cliff (SY 443913), above the Junction Bed at Watton Cliff (SY 452918) (Text-fig. 9A), and in fallen blocks on the foreshore, from which fossils were obtained. Overlying the Down Cliff Clay are the Bridport Sands, the lithological but diachronous equivalent of the

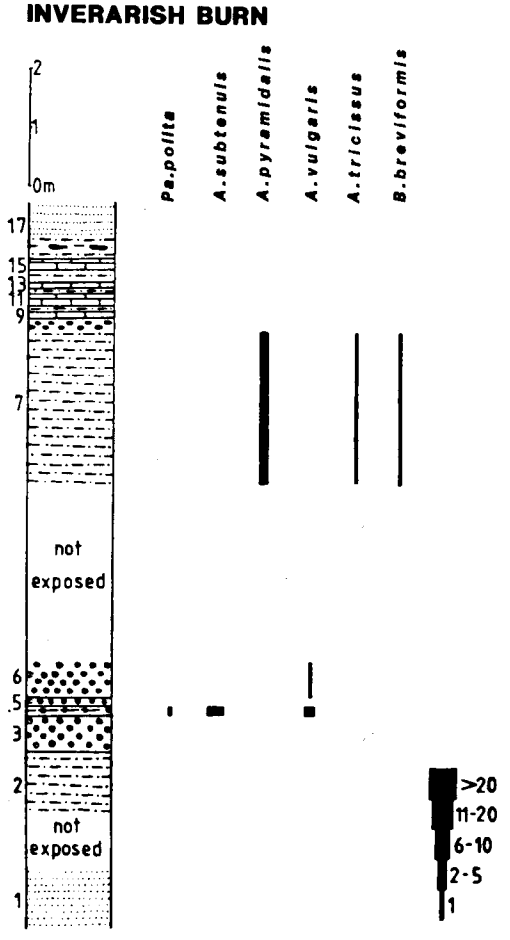
Yeovil (Somerset), Midford (Avon) and Cotteswold sands (Buckman 1889; Boswell 1924; Davies 1969; Text-fig. 2), but differing in the large numbers of cemented bands (locally known as 'sand burrs') that it contains (Bryant *et al.* 1988). The Bridport Sands were examined in detail at East Cliff, and West Bay, near Bridport (SY 465902–475897) and Burton Cliff, Burton Bradstock (SY 479895–490888), where extensive collections wre made (Text-fig. 9B).



TEXT-FIG. 9. Belemnite ranges and frequencies in: A, section at Watton Cliff ("Fault Corner"), Eypesmouth, Dorset. New bed numbers: Thorncombe Sands (bed 1, Pliensbachian, *Amaltheus margaritatus* Zone); Junction Bed (beds 3–12, Pliensbachian *Pleuroceras spinatum* Zone to *Dumortieria levesquei* Zone, ?*Phylseogrammoceras dispansum* Subzone); Down Cliff Clay (bed 13, *Dumortieria levesquei* Zone, ?*Dumortieria moorei* Subzone). B, sections through the Bridport Sands (*Dumortieria levesquei* Zone, to Lower Aalenian) at East Cliff, West Bay, Bridport, and Burton Cliff, Burton Bradstock. New bed numbers. These cliffs are interrupted by a fault at Freshwater Bay, but a continuous succession can be traced from East Cliff to Burton Cliff. The lower part of the succession (beds 1–15) was measured at East Cliff; the upper part in Burton Cliff. The lowest bed exposed at the western end of Burton Cliff (the beds dip slightly to the east) is bed 15.

HEBRIDEAN REGION (RAASAY)

There have been few studies of the Toarcian succession of this region, of which the most important are those of Lee (1920) and Howarth (1956). The Lower Toarcian on Raasay comprises the top of the mainly Upper Pliensbachian (Domerian) Scalpa Sandstone (*tenuicostatum* Zone), the Portree Shales (*tenuicostatum* Zone) and Raasay Ironstone (*bifrons* to *thouarsense* zones). The Upper Toarcian is mainly unrepresented, except for the base of the mostly Aalenian Dun Caan Shales (*aalensis* Subzone, *levesquei* Zone). All these units were examined on Raasay in the Inverarish Burn section near Inverarish (NG 576373) (Text-fig. 10).



TEXT-FIG. 10. Belemnite ranges and frequencies in section exposed in Inverarish Burn, near Inverarish, Raasay. New bed numbers: Top Scalpa Sandstone (bed 1, *Dactylioceras tenuiscostatum* Zone); Portree Shales (bed 2, *Harpoceras falciferum* Zone); Raasay Ironstone (beds 3–6, *Hildoceras bifrons* Zone, *Dactylioceras commune* Subzone to *Grammoceras thouarsense* Zone); Dun Caan Shales (beds 7–16, *Dumortieria levesquei* Zone, *Pleydellia aalensis* Subzone to Lower Aalenian); Calcareous Sandstone (bed 17, Aalenian).

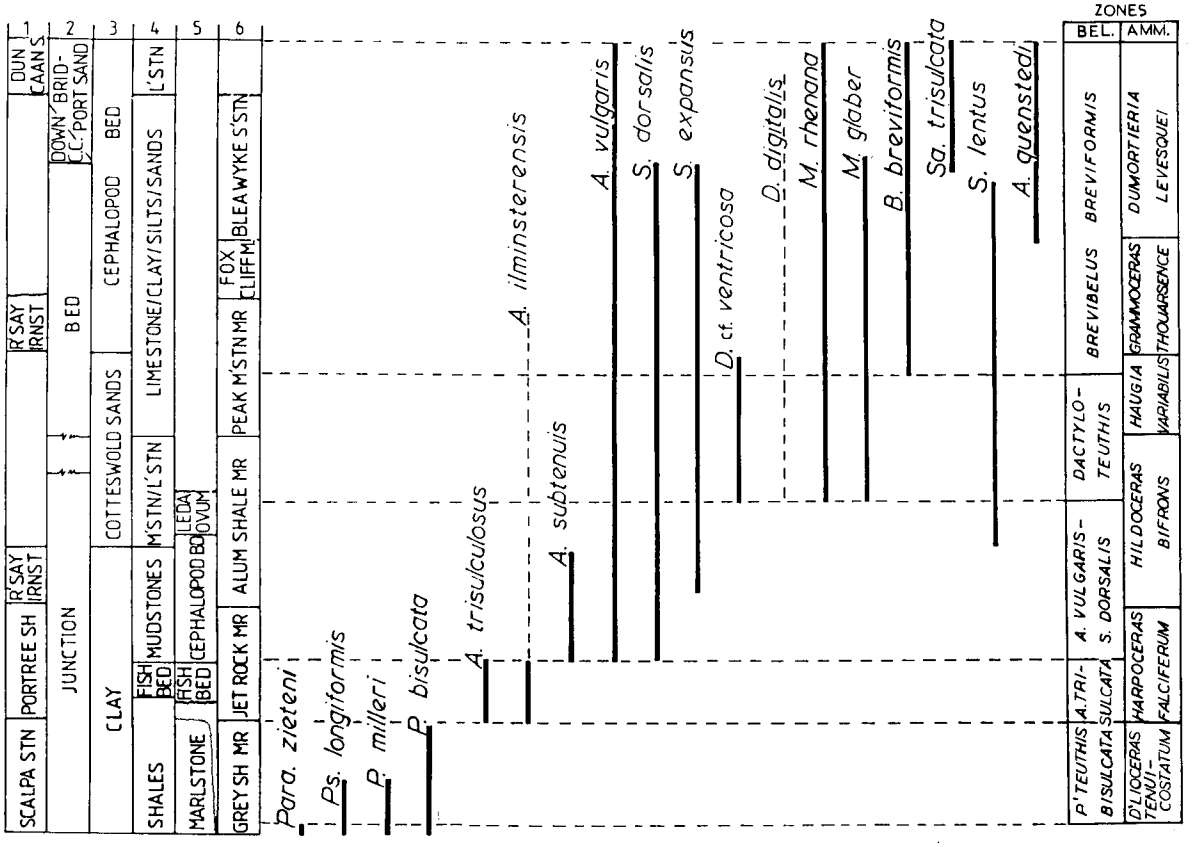
BELEMNITE BIOSTRATIGRAPHY

A biostratigraphical zonal scheme can be established using the ranges of the belemnites described in this monograph. Five belemnite biozones are recognised for northwest Europe, based in the main on detailed collecting from the expanded sequence in Yorkshire, and on comparable successions elsewhere in Britain and in Germany. Stoyanova-Vergilova's (1977) belemnite zonal scheme for Bulgaria is also closely comparable with that given below. The terminology used in this section follows the usage of Holland *et al.* (1978). The base of each biozone is defined at the first appearance of its index species; its top, at the first appearance of the index species of the succeeding biozone. Unless otherwise stated, the bed numbers refer to the published sections of Howarth (1962, 1973).

Passaloteuthis bisulcata partial-range Biozone. The base is at present undefined, as this species probably first appeared in the *margaritatus* Zone of the Pliensbachian (Riegraf 1980, table 1). The top is defined at the last appearance of the index species (in bed 32, Grey Shale Member). Also characteristic of this biozone, with limited ranges, are *Parapassaloteuthis zieteni* (up to bed 1), *Passaloteuthis milleri* and *Pseudohastites longiformis* (up to bed 20).

Acrocoelites trisulculosus total-range Biozone. The base is defined at the first appearance of the index species in bed 33 (Jet Rock Member), and the top as its last appearance in bed 41. The index species is not common in southwest England, although numerous in Germany. However, the zone may be defined in southwest England by the partial range of the closely related species *A. ilminsterensis*, from its first appearance in horizons equivalent in age to bed 33, to the first appearance of the indices of the succeeding zone. *Chondroteuthis wunnenbergi* is known only from within this zone in the Fish Bed in southern England and equivalent horizons in Germany.

Acrocoelites vulgaris—Simpsonibelus dorsalis partial-range Biozone. The base is defined by the first appearance of the index species in bed 43 of the Jet Rock Member. The top is defined at the first appearance of the indices of the succeeding zone in beds 72 (northwest of Peak) and xxxviii (southeast of Peak) of the Alum Shale Member. *Acrocoelites subtenuis* is common at the base of this zone, occurring from bed 43 (Jet Rock Member) to bed 53 (Alum Shale Member). Of the two indices of this zone, only *A. vulgaris* has so far been identified in southern England, but *A. subtenuis* is common and demonstrates the base of this zone. All the index fossils, including *A. subtenuis*,



TEXT-FIG. 11. Belemnite biozonation of the British Toarcian. Ranges of index species are given against six important successions in the Toarcian outcrop, summarized and revised from Howarth (*in* Cope *et al.* 1980). 1, Raasay, Inner Hebrides; 2, Dorset coast; 3, southern Cotswolds; 4, northern Cotswolds; 5, Northampton; 6, Yorkshire Basin. Proposed belemnite biozones are plotted against the ammonite biozones for comparison.

occur in the Raasay Ironstone, and are known from France, Germany and eastern Greenland (Rozenkrantz Collection, GMC).

Dactyloteuthis—Megateuthis partial-range Biozone. The base is defined at the appearance of both index genera in beds 72 (northwest of Peak) and xxxviii (southeast of Peak) of the Alum Shale Member. Its top is defined at the first appearance of *Brevibelus breviformis* in bed 14 (this monograph) of the Peak Mudstone Member. In Yorkshire, *D. crossotela* and *D.* cf. *ventricosa* are common in this zone, while *D. digitalis* and *D. ventricosa* are more common in southern England and mainland Europe, being possibly Tethyan in origin (Doyle 1987, p. 240). The three species of *Megateuthis* common in the Toarcian (*M. rhenana, M. glaber* and *M? longisulcata*) are known across England and the rest of northwest Europe.

Brevibelus breviformis partial-range Biozone. The base is defined at the first appearance of the index species in bed 14 (this monograph) of the Peak Mudstone Member. The top is not formally defined as it ranges into the Bajocian (Riegraf 1980, table 3). Other species common in this zone include *Salpingoteuthis trisulcata* (possibly of Tethyan origin, see Doyle 1987) in southern England and mainland Europe. The zonal index is common and occurs throughout the Toarcian outcrop in Britain and mainland Europe.

MORPHOLOGY AND TERMINOLOGY

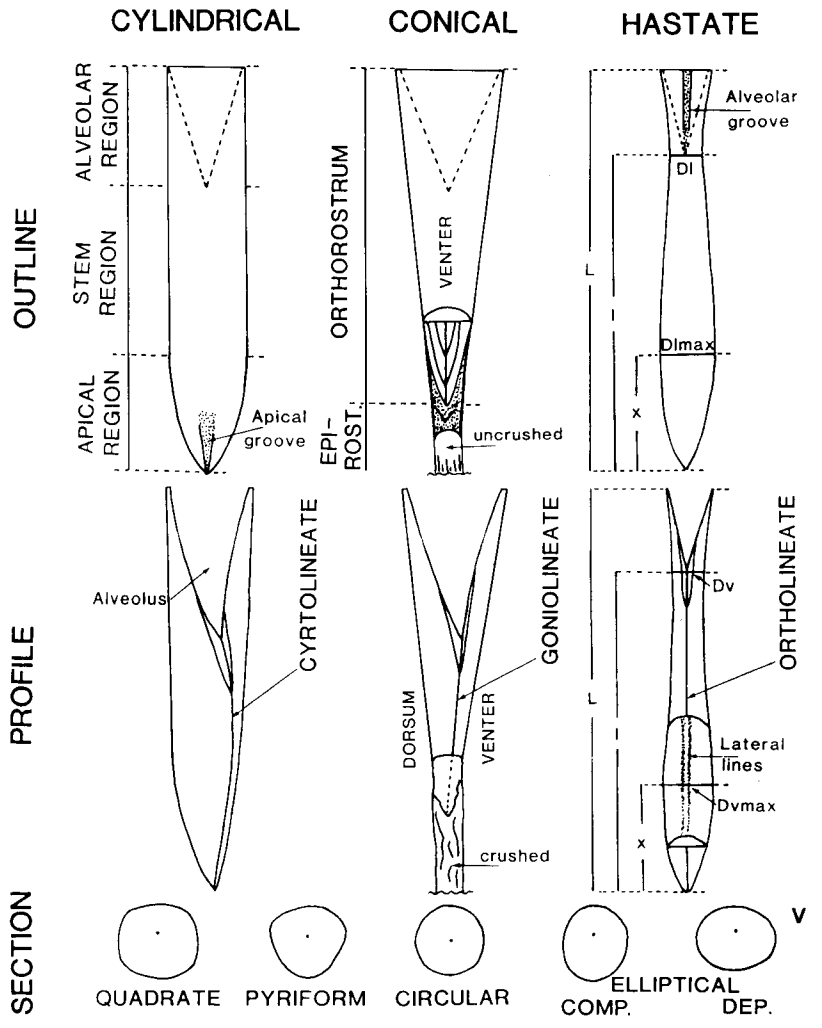
Belemnite morphology has been discussed by many authors, most notably Schwegler (1961), Pugaczewska (1961), Spaeth (1971), Riegraf (1980), Mutterlose (1983), Combémorel (1988) and Doyle & Kelly (1988). It is therefore only briefly discussed here. The rostrum is of most significance in belemnite systematics, the phragmocone being of use only at higher taxonomic levels (e.g. Jeletzky 1966). The following features are here considered to be of the greatest taxonomic importance in the study of belemnite rostra, and are given below in the order in which they appear in the diagnoses and descriptions that follow. The term "rostrum" is used in preference to "guard" throughout (cf. Stevens 1965), as the latter has an invalid functional connotation. As discussed by Stevens (1965), the effectiveness of this structure as a protection (i.e. a "guard") for the phragmocone would have been minimal. Terms not discussed below are given in Text-fig. 12).

Shape. This is an important specific character. There are three basic morphotypes (with intermediates), namely: *hastate* (spear-like; some authors employ the terms clavate (club-like) or lanceolate (lance-like), *conical* (cone-shaped) and *cylindrical* (parallel-sided) (see Schumann 1974). Shape is usually expressed by description of the outline (i.e. ventral or dorsal aspect), which is always symmetrical, and the profile (i.e. lateral aspect), which may be either asymmetrical or symmetrical.

Transverse section. This is an important specific character used in conjunction with shape. Sections may be described as (laterally) *compressed* or (dorso-ventrally) *depressed*, and are generally circular, elliptical, pyriform or subquadrate.

Grooves. Grooves are of great importance at generic and higher levels. There are two basic types: *apical* (confined to, or emanating from the apex) defining the Belemnitina, and *alveolar* (confined to, or emanating from the alveolar region) defining the Belemnopseina. Also present in all belemnites are fine lateral depressions and ridges known as "*lateral lines*", which provide useful criteria for differentiation at family and higher taxonomic levels. In the Belemnopseina, lateral lines are usually found as *Doppellinien*, closely-spaced narrow parallel lines, while in the Belemnitina (in most cases) they are less clearly defined, although commonly affecting the shape of the transverse section.

Other features. Those such as the form of the apical line (otholineate, goniolineate or cyrtolineate; see Schumann 1974) and the depth of penetration of the alveolus are useful at generic level. The alveolar angle, a feature employed by some authors, has been found to vary only slightly (in the range of approximately 25°–35°) within the Belemnitida (Schwegler 1961; Stevens 1965), and is of



TEXT-FIG. 12. Morphological terms and measurements employed in the systematic descriptions. Abbreviations: epirost., epirostrum; comp., compressed; dep., depressed. From Doyle & Kelly (1988), with permission of the Norsk Polarinstitutt.

little taxonomic value at generic or specific levels, although increasing in value at higher taxonomic levels.

Epirostrum. In some belemnites the rostrum comprises two separate parts, the orthrostrum and epirostrum. The *orthorostrum* is equivalent to the "normal" belemnite rostrum, and is cylindrical, conical or hastate with concentric growth lines and radial prismatic calcite crystals emanating from the apical line. The *epirostrum* consists of a posterior extention of this "normal" rostrum, with thin walls growing adapically from it, and an almost structureless, internal mass ("*corpus pulposum*" of Müller-Stoll 1936) with only crude growth lines. Spaeth *et al.* (1975), Bandel (1985) and Bandel & Spaeth (1988) have suggested that the epirostrum was largely aragonitic, compared with the calcitic orthorostrum.

It is clear that some genera (e.g. *Salpingoteuthis* and *Cuspiteuthis*) have been misused as "buckets" to unite those species with epirostra. In the present study, the genera *Acrocoelites*, *Megateuthis*, *Youngibelus* and *Dactyloteuthis* have been found with both epirostrate and non-epirostrate forms, indicating that the presence or absence of this feature can no longer be considered as a valuable taxonomic criterion for differentiation of genera. Indeed, d'Orbigny (1842–45),

Lissajous (1925) and Doyle (1985) have suggested that epirostra were sexual adaptions (see also Bandel & Spaeth 1988), and if this is the case, then their presence or absence is unreliable even as a specific character. However, at the present level of investigation, some morphospecies based partly on the presence of an epirostrum are used.

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SYSTEMATIC DESCRIPTIONS

In the main, the classification employed below follows that of Jeletzky (1966), with some modifications suggested by Saks & Nal'nyaeva (1967, 1970, 1975) and Doyle & Riegraf (1986, 1987).

In the descriptions, the terms small, medium and large refer to total preserved length and comprise the ranges of <60 mm, 60–95 mm and >95 mm respectively. Other measurements (in mm) are illustrated in Text-fig. 12. The annotation of synonymy lists follows the convention of Matthews (1973). In the synonymies, terms such as 'n. sp.' and 'sp. nov.' are omitted.

Phylum MOLLUSCA Linnaeus, 1758
Class CEPHALOPODA Cuvier, 1794
Subclass COLEOIDEA Bather, 1888
Order BELEMNITIDA Zittel, 1895
Suborder BELEMNITINA Zittel, 1895
Family BELEMNITIDAE d'Orbigny, 1845
[=Polyteuthidae Stolley, 1919]

Type genus. Doyle & Riegraf (1986, 1987) have requested that the ICZN use their plenary powers to suppress *Belemnites* Lamarck, 1799 and designate *Passaloteuthis* Lissajous, 1915 type genus of this family.

Subfamily BELEMNITINAE d'Orbigny, 1845
[=Passaloteuthinae Naef, 1922]

Genus **PASSALOTEUTHIS** Lissajous, 1915
[=*Holcoteuthis* Stolley, 1919]

Type species. Belemnites bruguierianus d'Orbigny, 1842 (junior subjective synonym of *Belemnites bisulcatus* Blainville, 1827); by original designation.

Diagnosis. Medium to large sized cylindrical to cylindriconical Belemnitinae. Profile similar to outline in most species, symmetrical, cylindrical to cylindriconical. Transverse sections subcircular to subquadrate. No ventral apical furrow, two dorso-lateral apical furrows, apex striated. Lateral lines indistinct, consisting of two weak, subparallel depressions and a weak ridge. Apical line goniolineate, phragmocone ventrally displaced, penetrating one third of the rostrum. Alveolar angle 25°–30°.

Range. Pliensbachian to Lower Toarcian (*tenuicostatum* Zone) of northwest Europe and USSR.

Remarks. Passaloteuthis is easily distinguished from the related genus *Pseudohastites* Naef which has a more compressed rostrum and an acute apex. Some species of *Passaloteuthis* may be confused in general form with some of *Acrocoelites* Lissajous, but they may be distinguished by their two (rather than three) apical grooves. The name *Passaloteuthis* is considered by some authors to be a junior objective synonym of *Belemnites* Lamarck, 1799 (e.g. Crickmay 1933; Jeletzky 1966; Schumann 1974), but due to the indeterminate nature of the designated lectotype (Klein 1731, pl.VIII, fig. 7; as selected by Crickmay 1933), and the fact that the other valid syntypes are all typical belemnitellids (see Jeletzky 1966, p. 140) this is undesirable. Doyle & Riegraf (1986) have formally applied to the ICZN for suppression of *Belemnites* Lamarck, 1799 (and its type species *Belemnites paxillosus* Lamarck, 1801).

Passaloteuthis bisulcata (Blainville, 1827) Pl. 1, figs 1–8; Pl. 2, figs 1–4; Pl. 3, figs 1–4

?1820 *Belemnites paxillosus* Lamarck; v. Schlotheim (*pars*), p. 46 [includes both Jurassic and Cretaceous belemnites].
* 1827 *Belemnites bisulcatus* Blainville, p. 79, pl. 2, fig. 7 *non* pl. 5, fig. 12 [=?*Acrocoelites wrighti* (Oppel)].
1827 *Belemnites paxillosus* v. Schlotheim; Blainville, p. 101.
v. 1829 *Belemnites elongatus* Miller, Sowerby, p. 178, pl. 590, fig. 1.
. 1830 *Belemnites paxillosus* v. Schlotheim; Voltz, p. 50, pl. VI, fig. 2.
. 1831 *Belemnites paxillosus* v. Schlotheim; Zieten, p. 29, pl. 23, fig. 1.

. 1831 *Belemnites papillatus* Plieninger [m.s.]; Zieten, p. 30, pl. 23, fig. 7 [abnormally elongated apex].
. 1831 *Belemnites subpapillatus* Zieten, p. 30, pl. 23, fig. 8 [abnormally elongated apex].
v. 1831 *Belemnites laevigatus* Zieten, p. 28, pl. 21, fig. 12.
v. 1842 *Belemnites bruguierianus* d'Orbigny, p. 84, pl. 7, figs 1–5.
. 1845 *Belemnites niger* Lister; d'Orbigny, p. 261, pl. 39, figs 1, 2, 4–7, 9; pl. 40, figs 1–5.
v. 1848 *Belemnites paxillosus amalthei* Quenstedt, p. 401, pl. 24, figs 5, 6.
. 1848 *Belemnites paxillosus* v. Schlotheim; Quenstedt, p. 403, pl. 24, fig. 8.
v. 1855 *Belemnites cylindricus* Simpson, p. 29 [Lectotype, here designated, WM 1981, Spinatus Beds, Kettleness, North Yorkshire].
. 1856 *Belemnites paxillosus* v. Schlotheim; Oppel, p. 272.
1863 *Belemnites paxillosus* v. Schlotheim; Mayer, p. 3.
v *non* 1864 *Belemnites elongatus* Sowerby; Huxley, pl. 1, fig. 1 [=?*Pseudohastites* sp, and indet. phragmoteuthid remains].
v *non* 1864 *Belemnites bruguierianus* d'Orbigny; Huxley, pl. 1, fig. 3 [=?*Passaloteuthis* sp, and indet. phragmoteuthid remains].
v. 1866 *Belemnites paxillosus* v. Schlotheim; Phillips, p. 47, pl. 6, fig. 15; pl. 20, fig. 52.
v. 1866 *Belemnites elongatus* Sowerby; Phillips, p. 50, pl. 7, fig. 17.
. 1867 *Belemnites cylindricus* Simpson; Phillips, p. 66, pl. 20, fig. 50.
. 1869 *Belemnites paxillosus* v. Schlotheim; Dumortier, p. 33.
v. 1876 *Belemnites cylindricus* Simpson; Blake (*in* Tate & Blake), p. 319.
. 1876 *Belemnites paxillosus* v. Schlotheim; Blake (*in* Tate & Blake), p. 321.
. 1878 *Megateuthis bruguieriana* (d'Orbigny); Bayle & Zeiller, pl. XXIII, figs 1, 34.
1883 *Belemnites paxillosus* v. Schlotheim; Mayer-Eymar, p. 641.
1883 *Belemnites cylindricus* Simpson; Mayer-Eymar, p. 641.
v. 1884 *Belemnites modestus*, Simpson, p. 31 [lectotype, here designated, WM 2712, U. Lias, Sandsend, North Yorkshire].
v. 1884 *Belemnites cylindricus* Simpson; Simpson, p. 37.
v. 1912 *Belemnites paxillosus* v. Schlotheim; Werner, p. 122.
1915 *Passaloteuthis bruguieriana* (d'Orbigny); Lissajous, p. 65.
1919 *Holcoteuthis paxillosa* (v. Schlotheim); Stolley, p. 39.
1920 *Holcoteuthis paxillosa* (v. Schlotheim); Bülow-Trummer, p. 85 [full synonymy].
1922 *Passaloteuthis paxillosa* (v. Schlotheim); Naef, p. 232.
1925 *Passaloteuthis bruguierianus* (d'Orbigny); Lissajous, p. 77 [full synonymy].
1933 *Belemnites paxillosus* Lamarck; Crickmay, pp. 12–15.
v. 1962b *Belemnites paxillosus* (v. Schlotheim) var. A Werner; Schwegler p. 135, fig. 26.
v. 1962b *Belemnites paxillosus* (v. Schlotheim) var. B Werner; Schwegler p. 137, fig. 27.
. 1962b *Belemnites paxillosus* (v. Schlotheim) var. C Werner; Schwegler p. 138, fig. 29.
1970 *Passaloteuthis bruguierianus* (d'Orbigny); Saks & Nal'nyaeva, p. 64.
1971 *Passaloteuthis cylindricus* (Simpson); Činčurová, p. 38, pl. 11, fig. 1.
non 1971 *Passaloteuthis paxillosus* (v. Schlotheim); Činčurová, p. 46, pl. 111, fig. 1 [=*Parapassaloteuthis* sp.].
v. 1974 *Belemnites paxillosus paxillosus* Lamarck; Schumann [*pars*], p. 21, pl. 2, fig. 1 [*non* figs 2–8=*Passaloteuthis* cf. *bisulcata*].
v. *1980* *Passaloteuthis* (*Passaloteuthis*) *paxillosa* (v. Schlotheim); Riegraf, p. 144.
? 1977 *Passaloteuthis bruguieriana* (d'Orbigny); Stoyanova-Vergilova, p. 182, pl. II, fig. 4 [resembles *Passaloteuthis tolli* (Pavlow)].
v. 1983 *Passaloteuthis paxillosa* (v. Schlotheim) var. A Werner; Reitner & Urlichs, p. 456, fig. 4.
v. 1983 *Passaloteuthis paxillosa* (v. Schlotheim); Riegraf & Hauff, p. 469, fig. 1.
v. 1984 *Passaloteuthis* (*Passaloteuthis*) *paxillosa* (v. Schlotheim) *sensu* Voltz; Riegraf *et al.*, p. 147, pl. 9, fig. 3.

Type specimen. Holotype, the original of Blainville (1827, pl. 2, fig. 7) from the "Middle Lias" (see Lissajous 1925, p. 59) (=Domerian) of Caen (Calvados), France. As this specimen is probably lost, a neotype from this locality should be designated.

Material. BMNH, 414 specimens, *tenuicostatum* Zone, Grey Shale Member, North Yorkshire; OUM, 1 specimen, Marlstone Rock, Horton, near Banbury, Oxfordshire; CMN; 54 specimens, Marlstone Rock (and Transition Bed), Northampton; NMW, 12 specimens, Junction Bed, Dorset; GMB, numerous unregistered specimens, Marlstone Rock, Ilminster, Somerset.

Diagnosis. Large, cylindrical to cylindriconical *Passaloteuthis*. Outline symmetrical and cylindrical, cylindriconical or weakly subhastate. Profile asymmetrical, but otherwise similar to outline. Transverse sections subcircular to subquadrate. Apex acute to slightly obtuse. Well-developed dorso-lateral apical grooves.

Description. Large rostra that are commonly cylindrical to cylindriconical, with a total length of approximately seven times Dv. The outline is symmetrical and cylindrical, slightly subhastate or cylindriconical, and the apex is generally acute (30°–45°), the flanks diverging only in the apical region in cylindrical forms. The profile is generally similar to the outline, being cylindrical, or in some cases slightly subhastate to cylindriconical. The transverse sections are generally subcircular, becoming subquadrate and weakly depressed in some individuals. It is usual for this species to have a subcircular stem section and a subquadrate apical section.

The apex is characterized by two well-defined dorso-lateral grooves. These are incised and extend generally 10–15 mm from the apex. There is no ventral apical groove, although the ventral and dorsal surfaces of the apex are generally striated. These striae may be more incised, and others may be pathologically deformed into a pseudo-ventral groove (see Riegraf *et. al.* 1984, pl. 9, fig. 10). Lateral lines are in the form of two shallow depressions in a dorso-lateral position, with no pronounced ridge between them. The phragmocone penetrates one third to one quarter of the rostrum, and the apical line is goniolineate.

Passaloteuthis bisulcata is a very variable species, and this has led to end members of variation being distinguished (e.g. Quenstedt 1848; Werner 1912; Schwegler 1962b). Werner's (1912) "Var. A" is commonly cylindrical to slightly subhastate with an acute apex ("*Belemnites cylindricus*"); "Var. B" is larger and more robust than "Var A", with an obtuse, blunt apex; and "Var. C" is smaller than the others, and generally more conical ("*Belemnites laevigatus*"). These informal "varieties" are useful as a guide to the range of morphology to be found within this species.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59392	125·3	64·6	18·1	17·7
C59393	143·1	78·2	19·1	18·7
C59400	120·5	78·5	18·3	18·4
C59404	141·4	85·0	17·4	16·7
C59405	126·8	87·6	19·7	19·5
C59408	142·1	88·4	18·7	17·8
C59409	133·7	88·8	18·0	17·4

Table 1. Measurements of *Passaloteuthis bisulcata* (Blainville, 1827).

Ontogeny. Passaloteuthis bisulcata occurs in great numbers in the lowermost Toarcian (*tenuicostatum* Zone) of Britain, where it is possible to collect individuals ranging from the smallest juvenile to the largest adult. These specimens are easily comparable with prepared sections of adult rostra enabling a true picture of the ontogeny of this species to be assembled. Three arbitrary stages are recognised (see Pugaczewska 1961):

1. *Nepionic.* This stage is characterized by a small (<10 mm L), thorn-like conical rostrum, developing into a more cylindriconical rostrum at approximately 15 mm L. Transverse sections are mainly subcircular. The phragmocone penetrates one third of the rostrum (81 specimens).

2. *Neanic.* There is a progressive elongation of the rostrum during this stage, producing a much more cylindriconical rostrum (at approximately 50 mm L). Transverse sections remain subcircular, and the penetration of the phragmocone also remains unchanged (107 specimens).

3. *Ephebic-Gerontic.* There is a further increase in the rostral length to produce the characteristic form of the species (at >100 mm L). Some individuals are larger than average, with obtuse apices and growth lamellae "overhanging" incised grooves (70 specimens, neanic-gerontic. See above for adult specimens).

Remarks. Passaloteuthis bisulcata may be confused with *Acrocoelites trisulculosus* (Simpson) which replaces it at the base of the *falciferum* Zone in Europe. However, the latter is more elongate, with a

marked subquadrate section and a ventral apical groove. *P. bisulcata* differs from *P. milleri* (Phillips) by its greater size, its more conical form and its acute apex.

Schumann (1974) interpreted *P. bisulcata* (as *Belemnites paxillosus* Lamarck) in a very broad sense, considering typical *Pseudohastites* species (e.g. *P. apicicurvata* (Blainville)) as subspecies. This interpretation is not followed here. The specimens figured by Huxley (1864) as *Belemnites bruguierianus* preserved with their soft parts are now considered to be reconstructions (Donovan 1977; Phillips 1980), using belemnite rostra and phragmoteuthid remains. However, Reitner & Urlichs (1983) and Riegraf & Hauff (1983) have recently described *P. bisulcata* (as *P. paxillosa* (Schlotheim)) with "true" soft parts from the *Posidonienschiefer* of southwest Germany.

Occurrence. Upper Domerian to lowermost Toarcian (*tenuicostatum* Zone) of Britain and mainland Europe. This species has been reported (as *P. paxillosa* (Schlotheim)) from Australia and South America (Tate 1880; Möricke 1895), but these are indeterminate specimens.

Passaloteuthis milleri (Phillips, 1867) Pl. 2, figs 5–9

v*. 1867 *Belemnites milleri* Phillips, p. 54, pl. VIII, fig. 19.
.1869 *Belemnites milleri* Phillips; Dumortier, p. 30, pl. I, figs 1–16.
.1876 *Belemnites milleri* Phillips; Blake (*in* Tate & Blake), p. 319.
?*1883* *Belemnites peregrinus*; Mayer-Eymar, p. 641 [*nomen nudum*].
v. 1912 *Belemnites ventroplanus* Voltz; Werner, p. 116 [*pars*], pl. X, fig. 10, *non* fig. 9 [=*Gastrobelus ventroplanus* (Voltz)].
.1912 *Belemnites milleri* Phillips; Werner, p. 120, pl. XI, fig. 5.
1920 *Holcoteuthis milleri* (Phillips); Bülow-Trummer, p. 84.
1925 *Passaloteuthis milleri* (Phillips); Lissajous, p. 110.
v. 1962b *Belemnites milleri* Phillips; Schwegler, p. 130, fig. 22.
? 1967 *Passaloteuthis milleri* (Phillips); Činčurová, p. 6, pl. 1, fig. 4.
1970 *Passaloteuthis milleri* (Phillips); Saks & Nal'nyaeva, p. 64.
?1971 *Passaloteuthis milleri* (Phillips); Činčurová, p. 44, pl. II, fig. 5.
v. *1980* *Passaloteuthis* (*Passaloteuthis*) *milleri* (Phillips); Riegraf, p. 144.

Type specimens. One of the specimens figured by Phillips (1867, pl. VII, fig. 19s) is preserved in OUM (J1870). This is a long section, and not easily comparable with more complete specimens. Although the other figured specimens were not identified, there is a range of unfigured specimens from Phillips' type series (OUM J15860–65). J15861 is well-preserved and typical of the species, and is designated lectotype. All are from the "Middle Lias of Golden Cap", Dorset.

Material. BMNH, 17 specimens, *tenuicostatum* Zone, Grey Shale Member, North Yorkshire; CMN, 4 specimens, *tenuicostatum* Zone (Transition Bed), Northampton.

Diagnosis. Medium sized, slender, cylindrical *Passaloteuthis*. Outline symmetrical, cylindrical. Profile symmetrical to slightly asymmetrical, cylindrical to slightly subhastate. Transverse sections subcircular to subquadrate. Rostrum smooth, dorso-lateral apical grooves feeble or undeveloped, apex unstriated.

Description. Medium sized, cylindrical *Passaloteuthis* with a total length of approximately eight times Dv. The outline is symmetrical and cylindrical, with a moderately obtuse to acute apex. The flanks diverge adorally only in the apical region. The profile is symmetrical to slightly asymmetrical and cylindrical to subhastate. In general the profile is similar to the outline, although the venter is slightly more inflated than the dorsum in the apical region. The transverse sections are subcircular, although they are subquadrate in some individuals.

The apex is very smooth, striation is uncommon, and the dorso-lateral grooves are usually developed only as shallow depressions. In general the apex is featureless, smooth and rounded. Lateral lines are similarly ill-formed, occurring as two shallow subparallel depressions similar to those of *P. bisulcata* (Blainville), and even this detail may be lost in more robust specimens. The phragmocone penetrates approximately one third to one quarter of the rostrum. The apical line is goniolineate, although slightly ventrally curved.

Remarks. Passaloteuthis milleri is readily distinguished due to its smooth, regular form. It is smaller than *P. bisulcata* (Blainville) which is also more conical, with well-developed apical

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59382	76·5	51·7	8·5	9·9
C59396	73·3	52·0	8·9	–
C59401	79·5	53·9	9·3	9·6
C59402	75·9	51·8	9·9	9·8

Table 2. Measurements of *Passaloteuthis milleri* (Phillips, 1867).

grooves. *P. milleri* can be distinguished from similarly sized juveniles of *P. bisulcata* which are more conical with an acute apex. *Pseudohastites longiformis* (Blake) approaches *P. milleri* in size, but can be readily distinguished by its compressed section, and subhastate profile.

Genus **PSEUDOHASTITES** Naef, 1922
[=*Catateuthis* Nal'nyaeva, 1967;
Passaloteuthis (*Propassaloteuthis*) Riegraf, 1980]

Type species. *Belemnites scabrosus* Simpson, 1866; by original designation.

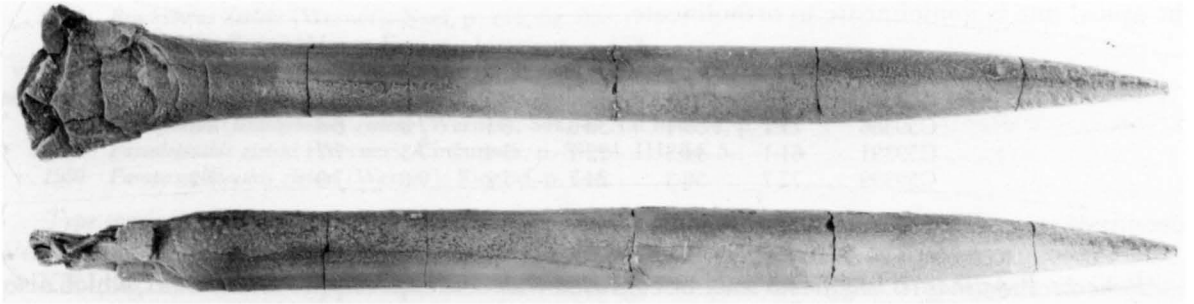
Other species. Include: *P. longiformis* (Blake); *P. virgata* (Mayer); *P. apicicurvata* (Blainville); *P. elongata* (Miller); *P. atrica* (Nal'nyaeva).

Diagnosis. Medium sized, elongate subcylindrical, cylindriconical or subhastate Belemnitinae. Profile asymmetrical, subhastate. Outline symmetrical, cylindriconical. Apex attenuated. Transverse sections elongate subquadrate to rounded subquadrate. No ventral furrow, two short dorso-lateral apical furrows, apex may be striated. Lateral lines distinct, consisting of two elongate subparallel depressions separated by a ridge. Phragmocone penetrates one third to a quarter of the rostrum. Apical line ortholineate to goniolineate. Aveolar angle approximately 22°.

Range. Pliensbachian to lowermost Toarcian of northwest Europe and the USSR.

Remarks. Species of *Pseudohastites* may be readily distinguished from those of *Passaloteuthis* as they are slender, with a compressed section and an attenuated apex. Species of *Pseudohastites* have generally been included previously in *Passaloteuthis* (e.g. Lang 1928; Schumann 1974; Riegraf 1980).

There has been some confusion surrounding the usage of the name *Pseudohastites*. Naef (1922), in his original diagnosis, stated that the belemnites included within his new genus were *Passaloteuthis*-like, with two dorso-lateral apical grooves, such as are found in the type species (Text-fig. 13). However, Lang (1928) applied the name to a series of belemnites from the Pliensbachian Belemnite Marls of Dorset (exemplified by *Belemnites junceus* Phillips), which although having some similarity to *Belemnites scabrosus*, lack clear apical grooves, possessing instead many short, but reasonably well-defined apical striae. The lateral lines of these forms are also somewhat different than those seen in the type species. Lang's belemnites can be recognised as belonging to a new genus, which was being described by the late J. A. Jeletzky in 1987. This manuscript is currently being prepared for posthumous publication by the present author.



TEXT-FIG. 13. Holotype of *Belemnites scabrosus* Simpson, 1855 (WM 976), type species of *Pseudohastites* Naef, 1922. Ventral outline (below) and left profile (above) xl. Lower Pliensbachian (*Uptonia jamesoni* Zone), North Cheek, Robin Hood's Bay, North Yorkshire.

Riegraf (1980, p. 145) continued to apply the name *Pseudohastites* in the sense of Lang, despite considering the type species to be an *Acrocoelites*, having been misled by Phillips' (1867, pl. X, fig. 27) illustration of Simpson's (1866) species. The type specimen (WM 976, text-fig. 13) of *Belemnites scabrosus* clearly displays typical *Passaloteuthis*-like dorso-lateral apical grooves without a ventral groove, and belongs to the group of belemnites exemplified by *Belemnites apicicurvatus* Blainville (as indicated by Jeletzky 1966). Therefore, the generic name *Catateuthis* Nal'nyaeva, 1967 (type species *C. atrica* Nal'nyaeva, 1967) and the subgeneric name *Propassaloteuthis* Riegraf, 1980 (type species *Belemnites apicicurvatus* Blainville, 1827) are both considered to be junior subjective synonyms of *Pseudohastites* Naef, 1922 (*non* Lang, 1928).

Pseudohastites longiformis (Blake, 1876) Pl. 3, figs 5–9

non 1824 *Belemnites tenuis* Stahl, p. 35, fig. 5 [=?*Hastites* sp].
v. 1855 *Belemnites tenuis* Simpson, p. 31 [Junior homonym of *B. tenuis* Stahl; lectotype, here designated, WM 2004, "*annulatus*" Zone, Hawsker Bottoms, North Yorkshire].
. 1869 *Belemnites virgatus* Mayer; Dumortier (*pars*), p. 41, pl. IV, figs 4–6.
v*. 1876 *Belemnites longiformis* Blake (*in* Tate & Blake), p. 320, pl. IV, fig. 8.
v. 1876 *Belemnites tenuis* Simpson; Blake (*in* Tate & Blake), p. 327.
v. 1884 *Belemnites tenuis* Simpson; Simpson, p. 34.
v. 1884 *Belemnites longiformis* Blake; Simpson, p. 46.
1920 *Holcoteuthis longiformis* (Tate & Blake); Bülow-Trummer, p. 84.
1925 *Passaloteuthis longiconis* (*sic*) (Tate & Blake); Lissajous, p. 106 [typographical error].
v? 1962 *Belemnites* cf. *charmouthensis* Mayer; Schwegler, p. 149, fig. 37.
v. *1982* *Catateuthis virgata* (Mayer); Phillips (*pars*), p. 63 [only the type specimens of *Belemnites longiformis* Blake].

Holotype. BMNH C11877, "*spinatus*" Beds (=*spinatum* Zone), Domerian, Eston, Cleveland.

Material. BMNH, 4 specimens, Domerian, Eston, Cleveland; 22 specimens, *tenuicostatum* Zone, Grey Shale Member, North Yorkshire.

Diagnosis. Small to medium sized, weakly subhastate *Pseudohastites*. Outline symmetrical, subhastate to cylindriconical. Profile asymmetrical, subhastate. Transverse sections compressed subquadrate.

Description. Small to medium sized, slender rostrum which is subhastate to cylindriconical in form with a total length of about nine times Dv. Some individuals are shorter, and slightly more robust than the norm. The outline is symmetrical and weakly subhastate, becoming cylindriconal in some individuals, and the apex is acute or even attenuated. The profile is asymmetrical and subhastate, generally more so than the outline, and the venter is slightly inflated. The transverse sections are compressed subquadrate, becoming rounded in the stem region of less compressed individuals.

The dorso-lateral apical grooves are only weakly developed, being shallow and short, and there is no ventral groove. The apex is generally not striated. The lateral lines are quite well developed, forming two weak depressions separated by a ridge, although they may be lost on the more robust specimens. The phragmocone penetrates one third to one quarter of the rostrum, and the apical line is goniolineate to ortholineate.

Specimen	*L*	*l*	*x*	*Dv*	*Dl*	*Dv max*	*Dl max*
BMNH C59372	52·8	39·1	19·4	6·7	6·5	7·4	6·9
C59386	71·1	53·4	30·6	8·1	7·8	8·5	8·8
C59391	61·1	44·3	22·1	7·4	7·3	7·7	–
C59399	77·7	58·3	24·7	7·1	7·0	7·9	7·2

Table 3. Measurements of *Pseudohastites longiformis* (Blake, 1876).

Remarks. Pseudohasties longiformis may be confused with some species of *Passaloteuthis*, which also possess paired dorso-lateral apical grooves. However, it can be distinguished by its slender, compressed elongate form and its attenuated apex. *Passaloteuthis bisulcata* (Blainville) is much more robust and cylindrical, and while *P. milleri* (Phillips) is of similar size, it has a smooth,

uncompressed cylindrical form. *P. longiformis* also resembles some species of the "*Pseudohastites*" *sensu* Lang, 1928 (*non* Naef 1922). It is closest to *P. charmouthensis* Mayer, a hastate form, but this species is distinguished by its grooveless apex.

Occurrence. Domerian to lowermost Toarcian (*tenuicostatum* Zone) of Britain and mainland Europe.

Genus **PARAPASSALOTEUTHIS** Riegraf, 1980

Type species. *Belemnites zieteni* Mayer-Eymar, 1884; by original designation.

Other species. *P. robusta* (Simpson); *P. polita* (Simpson).

Diagnosis. Small to large sized, robust cylindriconical to weakly subhastate Belemnitinae. Outline symmetrical, cylindriconical to weakly subhastate. Profile similar, although generally asymmetrical, apex obtuse to mucronate, recurved. Transverse sections subquadrate to quadrate, uncompressed. Dorso-lateral grooves weak to moderately developed, no ventral groove. Lateral lines from two parallel depressions, one broad and deep in a dorsal position that extends from the apical grooves; the second, a weaker depression below. The phragmocone penetrates one third to one half of the rostrum. Apical line cyrtolineate. Alveolar angle 23–28°.

Range. Upper Domerian to Lower Toarcian of Britain, mainland Europe, USSR and East Greenland.

Remarks. *Parapassaloteuthis* most closely resembles *Brevibelus* gen. nov. (see below) from the Upper Toarcian-Bajocian, but it differs in its more cylindriconical form and its dorso-lateral apical grooves. *Parapassaloteuthis* was based by Riegraf (1980, p. 146) solely on its type species *Belemnites zieteni* Mayer-Eymar. This restricted diagnosis is here emended to include species similar to the type that have previously been included in *Acrocoelites* (e.g. *Belemnites robustus* Simpson and *Belemnites politus* Simpson). Such forms were included in the subgenus *Brachybelus* (*Arcobelus*) Saks by Saks & Nal'nyaeva (1970), but this subgenus is characterized by small, blunt, '*Clasoteuthis*'-like species (type species *Dactyloteuthis dolosa* Nal'nyaeva) which are not directly related to *Parapassaloteuthis*.

Parapassaloteuthis zieteni (Mayer-Eymar, 1884) Pl. 4, figs 2, 3, 5, 7–9.

. 1831 *Belemnites breviformis* Voltz; Zieten, p. 27, pl. XXI, fig. 7.
v. 1848 *Belemnites breviformis amalthei*; Quenstedt, p. 404, pl. XXIV, figs 21–3.
. 1856 *Belemnites breviformis* Zieten (*non* Voltz); Oppel, p. 154.
v. 1866 *Belemnites breviformis* Voltz; Phillips, p. 41, pl. IV, figs 9, 10.
. 1869 *Belemnites breviformis* Voltz; Dumortier, p. 32, pl. 1, figs 9, 12.
v. 1876 *Belemnites breviformis* Voltz; Blake (*in* Tate & Blake), p. 320.
1883 *Belemnites breviformis* Mayer-Eymar, p. 640 [*nomen nudum*].
*. 1884 *Belemnites Zieteni* Mayer-Eymar; Mayer-Eymar, p. 47.
. 1911 *Belemnites* (*Pachyteuthis*) *Zieteni* (Mayer-Eymar); Lissajous, p. 13, pl. 1, fig. 21.
v. 1912 *Belemnites Zieteni* Werner, p. 110, pl. 10, fig. 5.
. 1916 *Belemnites Zieteni* Werner; Abel, p. 128, fig. 53.
1920 *Holcoteuthis Zieteni* (Mayer-Eymar) Werner; Bülow-Trummer, p. 88.
. 1922 *Brachybelus Zieteni* (Werner); Naef, p. 241, fig. 85e.
1925 *Pachyteuthis Zieteni* (Mayer-Eymar); Lissajous, p. 153.
v. 1965 *Belemnites zieteni* Werner; Schwegler, p. 82, fig. 51.
non 1965 *Brachybelus zieteni* (Werner); Stevens, p. 63, pl. 1, figs 1–3 [=?*Dactyloteuthis* sp.].
1970 *Brachybelus* (*Brachybelus*) *zieteni* (Werner); Saks & Nal'nyaeva, p. 27.
?1971 *Passaloteuthis zieteni* (Werner); Činčurová, p. 51, pl. III, fig. 5.
v. *1980* *Parapassaloteuthis zieteni* (Werner); Riegraf, p. 146.

Type specimen. This species was based on Zieten's (1830) interpretation of *Belemnites breviformis* Voltz by Mayer-Eymar (1884). The holotype is therefore the original specimen of Zieten (1830, pl. XXI, fig. 7) from the Upper Lias of Württemberg, southern Germany. It is not known whether this specimen survives.

Material. BMNH, 72 specimens, *spinatum* Zone, Cleveland Ironstone Formation; *tenuicostatum* Zone, Grey Shale Member, Whitby Mudstone Formation, North Yorkshire. OUM, 3 specimens,

spinatum Zone, Cleveland Ironstone Formation, Eston Nab, Cleveland; Marlstone Rock Bed, Glastonbury, Somerset and Alderton Hill, Gloucestershire. GMB, 1 specimen, *spinatum* Zone, Marlstone Rock Bed, Ilminster, Somerset.

Diagnosis. Small, conical to cylindriconical *Parapassaloteuthis*. Outline symmetrical, cylindriconical. Profile slightly asymmetrical, cylindriconical to conical. Transverse sections depressed quadrate. Apex recurved, apical grooves weakly developed.

Description. Small, conical to cylindriconical rostra with a total length of approximately four times Dv. The outline is symmetrical and cylindriconical, with strongly diverging flanks from an obtuse apex, which become parallel and cylindrical adorally. Some individuals may be more acutely conical in form. The profile is slightly asymmetrical, the venter being more inflated than the dorsum, although similar in form to the outline. The apex is recurved in profile. The transverse sections are subquadrate and moderately depressed.

There are two weak dorso-lateral apical grooves which are developed adorally into broad, shallow lateral lines. A second, weaker depression is found below this. There is no ventral apical groove. The phragmocone penetrates one half to a third of the rostrum, and the apical line is cyrtolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59383	55·2	21·4	10·6	11·4
C59384	43·4	22·3	11·1	11·4
C59385	43·0	21·9	9·8	10·6
C59390	47·5	23·7	11·0	11·5

Table 4. Measurements of *Parapassaloteuthis zieteni* (Mayer-Eymar, 1884).

Remarks. Parapassaloteuthis zieteni bears a great resemblance to *Brevibelus breviformis* (Voltz) (see Schwegler 1965, p. 83). However, this resemblance is purely homeomorphic, and *P. zieteni* can be distinguished by its distinctive apical grooves and lateral lines. *P. zieteni* can be distinguished from other species of *Parapassaloteuthis* by its small, conical form; *P. polita* is subhastate, and *P. robusta* is robust and cylindriconical.

Occurrence. Domerian to lowermost Toarcian (*tenuicostatum* Zone) of Britain and mainland Europe.

Parapassaloteuthis robusta (Simpson, 1855) Pl. 4, figs 1, 4, 6; Pl. 5, figs 1,2

non 1842 *Belemnites latesulcatus* d'Orbigny, p. 517 [=*Belemnopsis latesulcatus*].
v*. 1855 *Belemnites robustus* Simpson, p. 28.
v. 1855 *Belemnites obtusus* Simpson, p. 27 [Lectotype, here designated, WM 119, "*communis*" Zone, Whitby, North Yorkshire].
v. 1866 *Belemnites latisulcatus* Phillips, p. 46, pl. V, fig. 14.
. 1876 *Belemnites latesulcatus* Phillips; Blake (*in* Tate & Blake), p. 323.
v. 1884 *Belemnites robustus* Simpson; Simpson, p. 40.
v. 1884 *Belemnites obtusus* Simpson; Simpson, p. 40.
1920 *Homaloteuthis latisulcata* (Phillips); Bülow-Trummer, p. 123.
1925 *Pachyteuthis latisulcatus* (Phillips); Lissajous, p. 105.
1970 *Brachybelus* (*Arcobelus*) *latisulcatus* (Phillips); Saks & Nal'nyaeva, p. 28.

Type specimens. Holotype, WM 11, "*communis*" Zone (=*bifrons* Zone), Whitby, North Yorkshire.

Material BMNH, 1 specimen, ?*bifrons* Zone, Upper Lias Clay, Cheltenham, Gloucestershire; 2 specimens, *bifrons* Zone, Alum Shale Member, Whitby Mudstone Formation, North Yorkshire. OUM, 10 specimens, *falciferum* Zone and Subzone, Jet Rock Member, and *bifrons* Zone, Alum Shale Member, Whitby Mudstone Formation, North Yorkshire. WM, 8 specimens, *bifrons* Zone, Alum Shale Member, North Yorkshire.

Diagnosis. Medium to large, robust, cylindriconical *Parapassaloteuthis*. Outline symmetrical, cylindriconical. Profile asymmetrical, but otherwise similar. Transverse sections subquadrate. Apex recurved. Well-developed dorso-lateral apical grooves and lateral lines.

Description. Large, robust rostra that are cylindrical to cylindriconical in form, with a total length of approximately five times Dv. The outline is symmetrical and cylindriconical. The apex is moderately acute, with moderate to strong divergence at the apex, the flanks becoming parallel in the stem region. The profile is asymmetrical and cylindriconical and has a flattened venter that becomes more inflated adapically. The apex in profile is moderately acute and recurved. The transverse sections are subquadrate and slightly compressed.

There are two moderate to strongly incised dorso-lateral apical grooves which develop adorally into broad and deep lateral depressions. A strong dorsally placed "levee" is also present, overprinting the ventro-lateral line. There is no ventral groove. The details of the phragmocone of this species are unknown due to its comparative rarity. However, the phragmocone does appear to penetrate approximately one third of the rostrum. Its similarity in form to *P. zieteni* suggests the presence of a cyrtolineate apical line in this species.

Specimen	*L*	*l*	*Dv*	*Dl*
WM 11	194·6	68·5	35·2	29·5
BMNH C6906	99·8	55·7	20·3	20·6
C59338	110·4	61·0	21·1	19·2
C59413	79·8	46·2	17·6	15·6

Table 5. Measurements of *Parapassaloteuthis robusta* (Simpson, 1855).

Remarks. Parapassaloteuthis robusta is a very distinct species, which differs from *P. zieteni* (Mayer-Eymar) by its much larger and robust rostrum, its deeper lateral lines and its stronger apical grooves. It is distinguished from *P. polita* (Simpson) by its robust, cylindriconical form.

Occurrence. Lower Toarcian (*falciferum* Zone and Subzone) of Britain.

Parapassaloteuthis polita (Simpson, 1866) Pl. 5, figs 3–9

non 1831 *Belemnites acuminatus* (Schubler MS) Zieten, p. 26, pl. XX, fig. 2 [=*Megateuthis acuminatus*].
v. 1855 *Belemnites acuminatus* Simpson, p. 29 [Lectotype, here designated, WM. 449, "*communis*" Zone, Whitby, North Yorkshire].
v*. 1866 *Belemnites politus* Simpson; Simpson, p. 216.
v. 1867 *Belemnites acuminatus* Simpson; Phillips (*pars*), p. 56, pl. IX, figs 21, 22 [excluding *Belemnites ferreus* Simpson from synonomy].
. 1876 *Belemnites acuminatus* Simpson; Blake (*in* Tate & Blake) (*pars*), p. 320 [same exception as Phillips 1867].
v. 1884 *Belemnites acuminatus* Simpson; Simpson, p. 39.
v. 1884 *Belemnites politus* Simpson; Simpson, p. 39.
1920 *Dactyloteuthis acuminata* (Simpson); Bülow-Trummer, p. 96.
1925 *Hastites acuminatus* (Simpson); Lissajous, p. 51.
1925 *Passaloteuthis politus* (Simpson); Lissajous, p. 122.
1970 *Brachybelus* (*Brachybelus*) *acuminatus* (Simpson); Saks & Naln'yaeva, p. 21.

Holotype. WM 2047, "*communis* Zone" of High Whitby, North Yorkshire. This stratigraphic location was added to the wooden tablet attached to the specimen by later museum workers. Simpson regarded this species as a form from "the bed immediately above Jet Rock" (1866, p. 216) and "Upper Lias 5, High Whitby" (1884, p. 40). Upper Lias division 5 is equivalent to beds 42–46 (Howarth 1962) of the Jet Rock Member, *falciferum* Zone and Subzone.

Material. BMNH, 20 specimens; WM, 8 specimens, both collections from Jet Rock Member (*falciferum* Zone and Subzone) to Alum Shale Member (*commune* Subzone, *bifrons* Zone), North Yorkshire.

Diagnosis. Medium sized, cylindrical to weakly subhastate *Parapassaloteuthis*. Outline symmetrical, cylindrical or weakly subhastate. Profile similar, but asymmetrical. Transverse sections rounded subquadrate. Apex commonly mucronate. Apical grooves weak to moderately developed.

Description. Medium sized rostra which are generally cylindrical in form, becoming subhastate in some individuals, with a total length of about five times Dv. The outline is symmetrical and cylindrical, becoming subhastate with a bulbous stem region and mucronate apex. The profile is

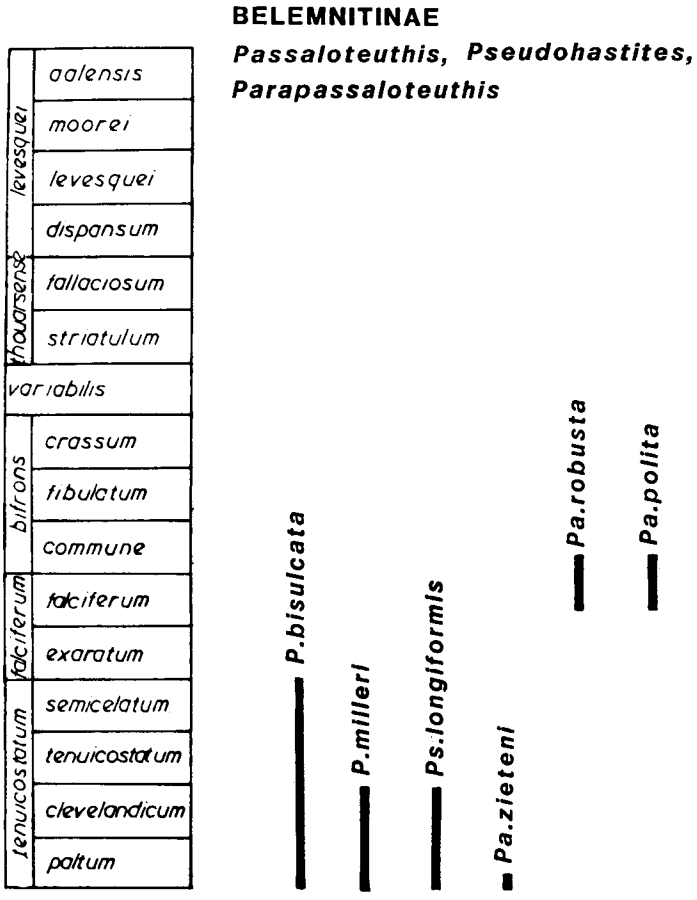
more asymmetrical with a bulbous stem region and mucronate apex. The profile is more asymmetrical and less hastate than the outline, generally being cylindriconical in form. The apex is inflated and mucronate. The transverse sections are moderately compressed and rounded subquadrate in form. However, the apical sections may be more depressed than those of the stem region.

There are two moderately well-developed dorso-lateral apical grooves, but there is no ventral groove. The venter and dorsum may display short striae. The lateral lines are developed as a broad depression continuing adorally from the dorso-lateral apical grooves, flanked by a weak ridge and a narrow, shallow depression below it. However, in more robust individuals these details may be lost. The phragmocone penetrates one half of the rostrum, and is ventrally deflected. The apical line is weakly cyrtolineate to curved goniolineate.

Specimen		*L*	*l*	*x*	*Dv*	*Dl*	*Dv max*	*Dl max*
WM 2047		93·7	60·5	36·0	17·1	15·7	17·8	16·8
BMNH	C59334	87·3	57·8	37·7	17·6	15·3	17·1	15·7
	C59335	72·1	44·9	26·9	15·0	13·6	14·2	13·4
	C59337	79·5	44·6	27·6	14·7	14·2	14·5	–

Table 6. Measurements of *Parapassaloteuthis polita* (Simpson, 1866).

Remarks. Juveniles of *Parapassaloteuthis polita* (Simpson) may be confused with those of co-occurring species of *Acrocoelites* (*Odontobelus*), but they are distinguished by their mucronate apices and lack of a ventral groove. *P. polita* differs from *P. zieteni* (Mayer-Eymar) which is smaller and more depressed, and from *P. robusta* which is larger and less hastate.



TEXT-FIG. 14. Stratigraphic ranges of the British Toarcian Belemnitinae (*Passaloteuthis*, *Pseudohastites* and *Parapassaloteuthis*) plotted against the ammonite zones and subzones.

Subfamily MEGATEUTHIDINAE Saks & Nal'nyaeva, 1967

Genus **ACROCOELITES** Lissajous, 1915

Type species. *Belemnites oxyconus* Zieten, 1831, by original designation.

Diagnosis. Small and delicately formed, to large and robust, cylindrical, cylindriconical or conical Megateuthidinae. Outline symmetrical, cylindriconical to conical. Profile asymmetrical or almost symmetrical, conical to cylindriconical, with a commonly inflated venter. Apex characterized by two well-developed dorso-lateral apical grooves, and a single ventral apical groove that is incised in some species and reduced in others. A short epirostrum may be developed, commonly bearing the characteristic grooves and numerous striae. Lateral lines consist of two broad depressions separated by a weak ridge or weal. The phragmocone penetrates one quarter to one half of the rostrum and is ventrally displaced. The apical line is goniolineate, and the alveolar angle is commonly 25°–70°

Range. Lower Toarcian to Aalenian of Britain, mainland Europe, North America, east Greenland, ?Svalbard and the USSR.

Remarks. *Acrocoelites* bears a superficial resemblance to *Passaloteuthis*, but differs in the possession of a single ventral apical groove. *Acrocoelites* resembles *Simpsonibelus* gen. nov. (see below) in possessing three incised apical grooves, but the latter differs in possessing a distinct hastate form.

There are three subgenera of *Acrocoelites*: *Acrocoelites* (*Acrocoelites*) Lissajous, 1915; *Acrocoelites* (*Toarcibelus*) Riegraf, 1980 and *Acrocoelites* (*Odontobelus*) Naef, 1922.

Subgenus **ACROCOELITES** Lissajous, 1915

Type species. As for genus.

Other species. *A.* (*A.*) *subtenuis* (Simpson); *A.* (*A.*) *strictus* Lissajous; *A.* (*A.*) *bobeti* Lissajous; *A.* (*A.*) *subgracilis* Kolb; *A.* (*A.*) *longiconus* (Schwegler).

Diagnosis. Slender, small to medium sized, cylindriconical to conical *Acrocoelites*. Outline symmetrical, conical to cylindriconical. Profile similar. Transverse sections compressed elliptical to compressed subquadrate. Apex characterized by well-defined ventral groove, usually better developed than the dorso-lateral apical grooves. Short, striated epirostrum may occur, bearing characteristic grooves. Phragmocone penetrates one quarter of the rostrum.

Range. Lower Toarcian to Aalenian of Britain, mainland Europe, North America, USSR and East Greenland.

Remarks. This subgenus is represented by the slender, compressed, conical to cylindriconical species of *Acrocoelites* referred to as 'graciles' by Phillips (1866). Species of this subgenus could be confused with small, slender species of genera such as *Youngibelus* (e.g. *Y. simpsoni* (Mayer)) and *Holcobelus* (e.g. *H. blainvillei* (d'Orbigny)). However, the former has no apical grooves, and the latter possesses an extremely long ventral apical groove, lacking dorso-lateral grooves.

Acrocoelites (*Acrocoelites*) can be distinguished from *Acrocoelites* (*Toarcibelus*) which has more robust elongate species, and from *Acrocoelites* (*Odontobelus*) which is characteristically short, robust and conical.

Acrocoelites (Acrocoelites) oxyconus (Zieten, 1831) Pl. 6, figs 1–4, ?6

v* 1831 *Belemnites oxyconus* [Hehl MS] Zieten, p. 27, pl. XXI, fig. 5

v. 1848 *Belemnites tripartitus oxyconus*; Quenstedt [*pars*], p. 419, pl. XXVI, fig. 19 [*non* fig. 20 = *Acrocoelites subtricissus* Kolb].

v? 1855 *Belemnites telum* Simpson, p. 27 [Lectotype, here designated, WM 20, '*communis*' Zone, Whitby, North Yorkshire].

. 1856 *Belemnites oxyconus* Zieten; Oppel, p. 361.

v? 1858 *Belemnites tripartitus oxyconus* Quenstedt; Quenstedt, p. 255, pl. XXXVI, fig. 10.

1863 *Belemnites oxyconus* Hehl; Mayer, p. 184.

v *non* 1867 *Belemnites oxyconus* Quenstedt; Phillips, p. 87, fig. 23 [=*Nannobelus cricki* (Lissajous), syntypes BMNH C7034–6].

1883 *Belemnites oxyconus* Hehl; Mayer-Eymar, p. 641.

v? 1884 *Belemnites telum* Simpson; Simpson, p. 32.

. 1902 *Belemnites oxyconus* Zieten; Janensch, p. 117.
. 1912 *Belemnites oxyconus* Zieten; Werner, p. 127.
1915 *Acrocoelites oxyconus* (Hehl *in* Zieten); Lissajous, p. 17.
1920 *Cuspiteuthis oxycona* (Zieten); Bülow-Trummer [*pars*], p. 104.
1925 *Acrocoelites oxyconus* (Hehl *in* Zieten); Lissajous, p. 116.
?1967 *Salpingoteuthis oxycona* (Zieten); Činčurová, p. 5, pl. I, fig. 3.
v. 1969 *Belemnites oxyconus* Zieten; Schwegler, p. 164, fig. 78.
?1971 *Salpingoteuthis oxyconus* (Zieten); Činčurová, p. 66, pl. IV, fig. 10
1975 *Acrocoelites oxyconus* (Hehl *in* Zieten); Saks & Nal'nyaeva, p. 10.
v. 1980 *Acrocoelites* (*Acrocoelites*) *oxyconus* (Zieten); Riegraf, p. 148.
v. 1984 *Acrocoelites* (*Acrocoelites*) *oxyconus* (Hehl *in* Zieten); Riegraf *et al.*, p. 154, pl. 10, figs 4, 10.

Type specimens. Holotype, the original of Zieten (1831, pl. XXI, fig. 5), from Upper Lias of Boll, Württemberg, Germany, preserved in the Staatliches Museum für Naturkunde, Stuttgart (no registration number).

Material. BMNH, 13 specimens, Alum Shale Member to Blea Wyke Sandstone Formation (*bifrons-levesquei* zones), North Yorkshire.

Diagnosis. Medium sized, conical *Acrocoelites* (*Acrocoelites*). Outline symmetrical, cylindriconical to conical. Profile symmetrical, conical. Apex acute. Transverse sections subquadrate. Apical grooves well-developed.

Description. Medium sized, robust conical rostra with a total length approximately six times Dv. The outline is symmetrical and conical or cylindriconical with weak to moderate divergence adorally from the acute apex. The profile is symmetrical and regularly conical, with no inflation. The apex is sometimes found eroded suggesting the possibility of an epirostrum being present. The transverse sections are compressed subquadrate, becoming rounded and even pyriform in individuals.

The apex is commonly striated and bears three well-developed apical grooves, one ventral and two dorso-lateral. The ventral groove may vary in development in individuals. The lateral lines are somewhat indistinct, but consist of a narrow, shallow ventro-lateral depression, with a thinner dorso-lateral depression above, and a weak ridge between them. The phragmocone penetrates approximately one third of the rostrum. The apical line is slightly curved, but otherwise goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59419	81·7	52·2	15·4	12·8
C59433	86·4	40·2	14·0	12·5
C59456	66·6	31·1	12·4	11·0

Table 7. Measurements of *Acrocoelites* (*Acrocoelites*) *oxyconus* (Zieten, 1831).

Remarks. Acrocoelites (*Acrocoelites*) *oxyconus* is the most robust of its subgenus, and in consequence may be confused with some members of *Acrocoelites* (*Odontobelus*). However, it may be distinguished by its almost symmetrical profile, as all members of *Acrocoelites* (*Odontobelus*) possess asymmetrical profiles with inflated venters. *A.* (*A.*) *oxyconus* most closely resembles *A.* (*A.*) *longiconus* (Schwegler), but this species is generally weakly subhastate, and possesses a short epirostrum. Some individuals of *A.* (*A.*) *strictus* Lissajous approach *A.* (*A.*) *oxyconus*, but most are smaller, less conical, and with a more inflated apex. Both *A.* (*A.*) *bobeti* Lissajous and *A.* (*A.*) *subtenuis* (Simpson) are smaller and more delicate than *A.* (*A.*) *oxyconus*.

Occurrence. Uppermost Lower Toarcian (*bifrons* Zone) to Upper Toarcian (*levesquei* Zone) of Britain and mainland Europe.

Acrocoelites (Acrocoelites) subtenuis (Simpson, 1855) Pl. 6, figs 5, 7–14; Pl. 7, figs 1–3; Text-fig. 15

v*. 1855 *Belemnites subtenuis* Simpson, p. 26.
v. 1867 *Belemnites subtenuis* Simpson; Phillips [*pars*], p. 60 [*non* pl. X, fig. 27 =juvenile *Acrocoelites* (*Toarcibelus*) *trisulculosus* (Simpson)].

v. 1867 *Belemnites striolatus* Phillips [*pars*], p. 59, pl. X, fig. 25l [*non* fig. 25v = *Youngibelus simpsoni* (Mayer)].
v. 1874 *Belemnites stimulis* Dumortier, p. 38, pl. 4, figs 8–10.
. 1875 *Belemnites subtenuis* Simpson; Phillips [*pars*], p. 263, pl. 27, fig. 6.
v. 1876 *Belemnites subtenuis* Simpson; Blake (*in* Tate & Blake), p. 324.
1883 *Belemnites subtenuis* Simpson; Mayer-Eymar, p. 641.
v. 1912 *Belemnites striolatus* Phillips; Werner, p. 128, pl. 12, fig. 3.
1920 *Cuspiteuthis subtenuis* (Simpson); Bülow-Trummer, p. 109.
1925 *Acrocoelites subtenuis* (Simpson); Lissajous, p. 142.
v. 1969 *Belemnites striolatus* Phillips; Schwegler, p. 196, fig. 79.
?1975 *Acrocoelites subtenuis* (Simpson); Saks & Nal'nyaeva, p. 14, pl. 11, figs 1–3.
1975 *Acrocoelites stimulus* (Dumortier); Saks & Nal'nyaeva, p. 10.
?1975 *Mesoteuthis striolatus* (Phillips); Saks & Nal'nyaeva, p. 38, pl. VII, figs 6–8.
v. *1980* *Acrocoelites* (*Acrocoelites*) *subtenuis* (Phillips); Riegraf, p. 149.

Type specimens. Lectotype (here designated), WM 445c; paralectotypes, WM 445a and WM 445b, from the '*communis*' Zone (=*bifrons* Zone) of Whitby, North Yorkshire.

Material. BMNH, 132 specimens, *falciferum* Zone and Subzone, Jet Rock Member and *commune* Subzone, *bifrons* Zone, Alum Shale Member, Whitby Mudstone Formation, North Yorkshire; 15 specimens, *commune* Subzone, Raasay Ironstone, Raasay. BGS, 4 specimens, *commune* Subzone, *bifrons* Zone, Upper Lias Clay, Grantham, Lincolnshire. CMN, 9 specimens, *falciferum* Zone, Northampton. OUM, 7 specimens, *falciferum* Zone and Subzone, Jet Rock Member, Whitby Mudstone Formation, North Yorkshire.

Diagnosis. Small to medium sized, conical to cylindriconical *Acrocoelites* (*Acrocoelites*). Outline and profile similar, symmetrical and conical. Apex acute to attenuate. Transverse sections compressed subquadrate to elliptical. Apical grooves either well-developed or reduced.

Description. Small, slender, conical to slightly cylindriconical rostrum with a total length approximately 10 times Dv. The outline is symmetrical and conical to cylindriconical. The flanks weakly diverge adorally from the acute apex, becoming parallel in the stem region. The apex is acute to very acute, becoming attenuate in some individuals. The profile is symmetrical and conical with no inflation of venter or dorsum. The transverse sections of the rostrum are compressed and subquadrate to elliptical.

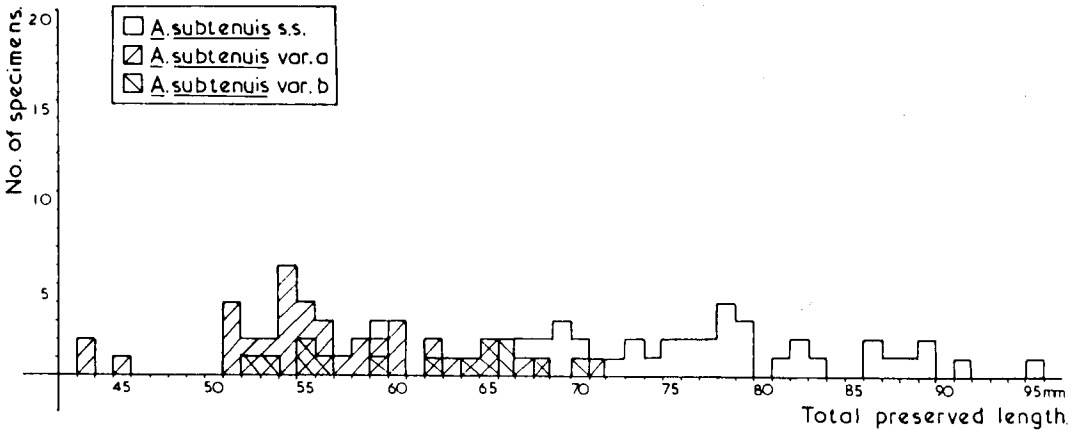
Three well-defined apical grooves (one ventral, two dorso-lateral) are generally present, although variants may possess a longer, more incised groove ('*Belemnites stimulus*'); three equal, well-incised grooves; or, much reduced grooves ('*Belemnites striolatus*'). Lateral lines are usually well developed, and consist of a strong central ridge or weal bounded by two narrow depressions. The phragmocone penetrates approximately one quarter of the rostrum. The apical line is goniolineate, although it may be slightly curved ventrally.

Specimen	*L*	*l*	*Dv*	*Dl*
WM 445c	78·5	61·2	7·6	7·2
BMNH C59321	79·0	58·3	8·1	6·5
C59322	70·0	53·0	7·3	6·2
C59329	79·4	57·5	8·5	7·6
C59330	68·9	48·9	8·4	7·9
C59331	69·8	50·0	8·6	8·3
C59323	57·3	37·1	6·1	5·9
C59415	71·4	45·9	7·3	6·2
C59477	57·8	42·0	6·1	5·7
C59478	58·8	36·8	5·7	4·9

Table 8. Measurements of *Acrocoelites* (*Acrocoelites*) *subtenuis* (Simpson, 1855).

Remarks. *Acrocoelites* (*Acrocoelites*) *subtenuis* is a very variable species. Simpson (1884, p. 33) considered that there were two variants differing from the norm; 'var. a', with no grooves or striae, and 'var. b', which is more robust, again without grooves or striae. Specimens recently collected from Yorkshire also show two variants from the norm. One, which could be regarded as Simpson's 'var. a' is shorter than is usual, and generally has only weakly developed grooves (some

specimens of this variant from Raasay have been found with well-developed grooves). The other (possibly Simpson's 'var. b') is much stouter, with a less compressed rostrum, and well-incised, short apical grooves. Of these, 'var. a' is the most common, 'var. b' occurring rather rarely. The frequency histogram (Text-fig. 15) suggests a bimodal distribution of the variants with respect to their total preserved length. Although the shorter variety is less robust than the norm, it is unlikely to represent simply juveniles of the species as this form is common in Raasay. It is possible that the small variety represents a sexual dimorph ('micro-rostrum') of the 'normal' *A.* (*A.*) *subtenuis* ('macro-rostrum', see Doyle 1985). The robust variety of ('var. b') is much rarer and is probably aberrant.



TEXT-FIG. 15. Frequency histogram of the total preserved length of *Acrocoelites* (*Acrocoelites*) *subtenuis* from North Yorkshire.

A. (*A.*) *subtenuis* most closely resembles *A.* (*A.*) *bobeti* Lissajous, but is distinguished by its acute apex, its well-developed grooves and its conical form. *A.* (*A.*) *strictus* Lissajous is also similar, but it is a robust form with a less compressed transverse section. *A.* (*A.*) *oxyconus* (Zieten) is larger, more robust and possesses a more regular subquadrate transverse section than *A.* (*A.*) *subtenuis*. *A.* (*A.*) *subtenuis* has also been confused with juveniles of *A.* (*Toarcibelus*) *trisulculosus* (Simpson) (see Phillips 1867, pl. X, fig. 27), but juveniles of this species are characteristically more robust and conical with elongate ventral striae.

The species described by Phillips (1867, p. 59) as *Belemnites striolatus* was based on specimens including juveniles of *Youngibelus simpsoni* (Mayer) and weakly grooved members of *A.* (*A.*) *subtenuis* (OUM J15112, 13). Specimen OUM J15113 (a typical *A.* (*A.*) *subtenuis*) is here designated lectotype of *Belemnites striolatus* Phillips, a junior subjective synonym of *A.* (*A.*) *subtenuis* (Simpson).

Occurrence. Lower Toarcian (*falciferum* Zone and Subzone to *bifrons* Zone, *commune* Subzone) of Britain, mainland Europe and possibly USSR.

Acrocoelites (Acrocoelites) strictus Lissajous, 1927 Pl. 7, figs 7, 8, 12

v*. 1927 *Acrocoelites strictus* Lissajous, p. 16, pl. II, figs 2–4.
1975 *Acrocoelites strictus* Lissajous; Saks & Nal'nyaeva, p. 11.

Type specimens. Lectotype (here designated), UCBL 27491; paralectotypes, UCBL 27489, 90, all from the Toarcian ('*bifrons-jurense* zones') of Northampton. Howarth (1978) has proved that the Upper Toarcian ('*jurense* Zone') is not present in Northampton. It is probable that the *stratum typicum* is the Leda Ovum Beds (*bifrons* Zone).

Material. BMNH, 12 specimens; CMN, 24 specimens, all from the *bifrons* Zone, Leda Ovum Beds, Northampton.

Diagnosis. Small to medium sized, cylindriconical to conical *Acrocelites* (*Acrocoelites*). Outline symmetrical, cylindriconical. Profile symmetrical, conical. Apex moderately acute. Transverse sections elliptical. Three well-developed apical grooves.

Description. Small to medium sized, cylindrical rostrum, with a total length approximately seven times Dv. The outline is symmetrical and cylindriconical or very slightly subhastate. The flanks diverge weakly from the apex, becoming parallel in the stem, and the apex is moderately acute. The profile is symmetrical or weakly asymmetrical and conical, with some inflation of both venter and dorsum. Transverse sections of the rostrum are elliptical to compressed elliptical, becoming more robust towards the stem region.

The apex bears three well-developed apical grooves (one ventral and two dorso-lateral). The ventral groove is incised and commonly attains twice the length of the dorso-lateral grooves. The dorso-lateral grooves are close to the dorsum. The lateral lines are reasonably well-developed and comprise a nearly central ridge or 'weal', flanked above and below by two parallel depressions. The phragmocone penetrates approximately one quarter of the rostrum. The apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C46165	85·6	67·5	9·6	8·0
C46166	74·3	57·3	10·3	8·1
C46167	–	52·3	9·2	8·1
C57390	75·6	55·2	10·5	9·2

Table 9. Measurements of *Acrocoelites* (*Acrocoelites*) *strictus* Lissajous, 1927.

Remarks. A. (*A.*) *strictus* is distinguished from *A.* (*A.*) *subtenuis* (Simpson) by its more robust, cylindriconical form, its greater dorso-ventral diameter and more inflated apex. *A.* (*A.*) *bobeti* Lissajous possesses a much smaller, slender, and slightly subhastate rostrum with shorter apical grooves. *A.* (*A.*) *oxyconus* (Zieten) differs *A.* (*A.*) *strictus* in possessing a much larger, more conical rostrum with a subquadrate transverse section.

Occurrence. Lower Toarcian (?*falciferum* to *bifrons* Zones) of Northamptonshire and ?North Yorkshire.

Acrocoelites (Acrocoelites) bobeti Lissajous, 1927 Pl. 7, figs 9–11, 13–15

1925 *Acrocoelites bobeti* Lissajous, p. 60 [*nomen nudum*].
v*. 1927 *Acrocoelites bobeti* Lissajous; Lissajous, p. 19.
v. 1971 *Acrocoelites bobeti* Lissajous; Combémorel, p. 63, pls I–II [figures Lissajous' type specimens for first time].
1975 *Acrcoelites bobeti* Lissajous; Saks & Nal'nyaeva, p. 10.

Type specimens. Lectotype (here designated): UCBL 27.525a; paralectotypes: UCBL 27.525b,c. All from the Lower Aalenian of Brenaux (Vénède), Lozère, France.

Material. BMNH, 98 specimens, Down Cliff Clay (*levesquei* Zone, *moorei* Subzone) and Bridport Sands (*levesquei* Zone, *aalensis* Subzone), Dorset; BGS, 1 specimen, Stowell Park Borehole (*levesquei* Zone); NMW, 1 specimen, Bridport Sands, Dorset.

Diagnosis. Small to medium sized, cylindriconical to weakly subhastate *Acrocoelites* (*Acrocoelites*). Outline symmetrical, cylindriconical to weakly subhastate. Profile symmetrical, conical to weakly subhastate. Apex acute. Apical grooves short.

Description. Small to medium sized cylindriconical or slightly subhastate rostrum with a total length of approximately 10 times Dv. The outline is symmetrical and cylindriconical to slightly subhastate. The apex is acute to moderately obtuse from which the flanks diverge in the apical region, becoming parallel in the stem region, and converging slightly in the alveolar region. The profile is symmetrical and may also be subhastate, although this is generally less apparent than in the outline. The venter and dorsum may be weakly inflated near the apex. Juveniles tend to be more subhastate than the adult specimens. The transverse sections are generally depressed and subquadrate, although they may be rounded in some individuals.

The apex possesses three short and equally developed apical grooves (one ventral and two dorso-lateral). In some cases, however, the ventral groove may be more incised, generally opening adorally into a broad triangular flattened area. The lateral lines are reasonably well-developed and consist of a central ridge or "weal" flanked by two parallel depressions above and below it. The phragmocone penetrates approximately one fifth of the rostrum. The apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59475	60·3	46·8	6·4	5·3
C59480	62·0	44·0	5·8	5·2
C59481	71·8	50·5	7·7	6·6
C59490	63·3	44·0	5·9	4·9
C59491	61·2	44·9	6·7	5·9
C59492	52·1	40·3	4·8	3·1

Table 10. Measurements of *Acrocoelites* (*Acrocoelites*) *bobeti* Lissajous, 1927.

Remarks. *Acrocoelites* (*Acrocoelites*) *bobeti* may easily be distinguished from the other members of its subgenus by its depressed subquadrate section and its slightly subhastate outline and profile. *A.* (*A.*) *subtenuis* (Simpson) most closely resembles it, but has a more conical profile, attenuate apex and compressed section. *A.* (*A*) *strictus* Lissajous is larger, more robust and with longer apical grooves. Both *A.* (*A.*) *oxyconus* (Zieten) and *A.* (*A.*) *longiconus* (Schwegler) are more conical and robust than *A.* (*A.*) *bobeti*.

Occurrence. Upper Toarcian (*levesquei* Zone) to Lower Aalenian of southwest Britain and France.

Acrocoelites (Acrocoelites) longiconus (Schwegler, 1969) Pl. 7, figs 4–6, 17

non 1831 *Belemnites rostratus* Zieten, p. 30, pl. 23, fig. 5 [*?Passaloteuthis rostratus* (Zieten)].
v. 1884 *Belemnites rostratus* Simpson, p. 36 [lectotype, here designated, WM.2048A; paralectotype, WM.2048B, "Upper Lias 4" =beds 47–8, Jet Rock Member, Hawsker Bottoms, North Yorkshire]
1925 *Belemnites rostratus* Simpson; Lissajous, p. 129.
v*. 1969 *Belemnites longiconus* Schwegler, p. 187, text-fig. 73.
1975 *Acrocoelites longiconus* (Schwegler); Saks & Nal'nyaeva, p. 10.
1980 *Acrocoelites* (*Toarcibelus*) *longiconus* (Schwegler); Riegraf, p. 148.
v?1984 *Acrocoelites* (*Acrocoelites*) *longiconus* (Schwegler); Riegraf *et al.*, p. 155, pl. 11.

Holotype. The original specimen of Schwegler (1969, p. 187, Text-fig. 73), GPIT (no registration number), Upper Lias (*bifrons* Zone, *commune* Subzone), Heiningen, Württemberg, southwest Germany.

Material. BMNH, 9 specimens, *bifrons* Zone, Alum Shale Member, Whitby Mudstone Formation, North Yorkshire; Upper Lias Clay, Lincolnshire. OUM, 5 specimens, *bifrons* Zone, Leda Ovum Beds, Wordington, Northampton. CMN, 8 specimens, *bifrons* Zone, Leda Ovum Beds, Northampton. WM, 3 specimens, *bifrons* Zone, Alum Shale Member, North Yorkshire.

Diagnosis. Medium sized, conical to slightly subhastate *Acrocoelites* (*Acrocoelites*) with a short epirostrum. Outline symmetrical, conical to cylindriconical. Profile nearly symmetrical, conical to slightly subhastate. Apex acute to attenuate, commonly striated. Three well-defined apical grooves.

Description. Medium to large sized, conical rostrum, some individuals being subhastate. A short epirostrum is common in this species. The total length of the rostrum is approximately eight times Dv. The outline is symmetrical and conical, in some cases being cylindriconical or subhastate. The apices of both epi- and orthorostra are acute, from which the flanks diverge gradually for the length of the epirostrum, becoming parallel in some cases in the stem region. The profile may be asymmetrical due to irregularities of the epirostrum, but typical specimens have symmetrical uninflated profiles which are conical to subhastate in form. The transverse sections of the rostrum are compressed and subquadrate, subhastate forms generally having a more compressed alveolar region.

The epirostrum bears three long, well-incised grooves (one ventral, two dorso-lateral) and is well-striated. The lateral lines are indistinct, but consist of a broad, shallow, ventro-lateral depression with a very weak ridge and thinner depression above it. Due to the relative rarity of this species, exact details of the phragmocone are unknown. However, the phragmocone penetrates approximately a quarter of the rostrum. The apical line is almost certainly goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59346	95·6	71·7	13·3	11·7
C59347	99·9	74·1	12·1	9·3
C59348	95·5	73·7	10·3	8·4

Table 11. Measurements of *Acrocoelites* (*Acrocoelites*) *longiconus* (Schwegler, 1969).

Remarks. *A.* (*A.*) *longiconus* is larger than most other members of the subgenus, with the exception of *A.* (*A.*) *subgracilis* Kolb. It closely resembles *A.* (*A.*) *oxyconus* (Zeiten), but differs in possessing a short epirostrum and a less conical profile. It is possible that these two forms represent sexual dimorphs of a single species (e.g. Doyle 1985), but more specimens are needed to confirm this. All other species of *Acrocoelites* (*Acrocoelites*) are more slender and regular in shape than *A.* (*A.*) *longiconus*.

Occurrence. Lower Toarcian (*bifrons* Zone, *commune* Subzone) of Britain and Germany.

Acrocoelites (Acrocoelites) subgracilis Kolb, 1942 Pl. 7, fig. 16; Pl. 8, figs 1, 2

v. 1848 *Belemnites tripartitus gracilis* Quenstedt, p. 420, pl. 26, fig. 17 [homonym of *B. gracilis* Zieten, 1831].
v?1848 *Belemnites tripartitus sulcatus* Quenstedt (*pars*), p. 419, pl. 26, fig. 16.
. 1912 *Belemnites tripartitus gracilis* Quenstedt; Werner (*pars*), p. 127
1920 *Cuspiteuthis tripartita gracilis* (Quenstedt); Bülow-Trummer, p. 107.
*. 1942 *Acrocoelites subgracilis*; Kolb, p. 161, pl. 8, figs 5–7.
v. 1969 *Belemnites tripartitus gracilis* Quenstedt; Schwegler, p. 205, text-fig. 86.
1975 *Acrocoelites subgracilis* Kolb; Saks & Nal'nyaeva, p. 10
1980 *Youngibelus gracilis* (Quenstedt); Riegraf, p. 149.
v. 1984 *Salpingteuthis persulcata* (Janensch); Riegraf *et al.*, p. 163, pl. 12, fig. 11.

Holotype. The original of Kolb (1942, pl. 8, fig. 5), GPIE, Toarcian "*radiosus*-Schichten" of Blomenhof, Bavaria, southwest Germany.

Material. BMNH, 7 specimens, Alum Shale Member (*bifrons* Zone, *commune* Subzone) to Blea Wyke Formation (*levesquei* Zone), North Yorkshire; CMN, 4 specimens, Leda Ovum Beds, (*bifrons* Zone), Northampton.

Diagnosis. Large, elongate, slender cylindrical *Acrocoelites* (*Acrocoelites*). Outline symmetrical, cylindrical to cylindriconical. Transverse sections compressed elliptical. Apex acute. Apical grooves well-developed.

Description. Large, elongate, slender rostrum with a total length of approximately seven times Dv. The outline is symmetrical and usually cylindrical to cylindriconical. The apex is acute with the flanks diverging regularly from the apex until the mid-stem region, where they become more parallel. The profile is symmetrical and more conical than the outline, although individuals may be more irregular with greater inflation. Transverse sections of the rostrum are compressed and elliptical, although they are pyriform in some specimens.

The apex of the rostrum bears three grooves (one ventral, two dorso-lateral), the ventral groove commonly being longer and more incised than the dorso-laterals. The tip of the apex is

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59345	90·3	70·5	15·1	13·0
C59444	122·3	91·5	14·6	12·8
C59471	99·6	83·0	–	8·9

Table 12. Measurements of *Acrocoelites* (*Acrocoelites*) *subgracilis* Kolb, 1942.

commonly striated. The lateral lines consist of a broad, shallow, ventro-lateral depression (thinning adapically), with a weak ridge and thinner depression above it. The phragmocone penetrates approximately one quarter of the rostrum. The apical line is goniolineate.

Remarks. *A.* (*A.*) *subgracilis* may be confused with the more slender "gracile" members of *Acrocoelites* (*Toarcibelus*) *ilminsterensis* (Phillips) (e.g. see Werner 1912, and Riegraf *et al.* 1984), but this species has a symmetrical profile and a depressed transverse section. *A.* (*A.*) *subgracilis* resembles *A.* (*A.*) *strictus* Lissajous, but this species has a compressed transverse section and three equally well-developed apical grooves. Both *A.* (*A.*) *subtenuis* (Simpson) and *A.* (*A.*) *bobeti* Lissajous are more slender than *A.* (*A.*) *subgracilis*, while *A.* (*A.*) *oxyconus* (Zieten) and *A.* (*A.*) *longiconus* (Schwegler) are more acutely conical with robust transverse sections.

Quenstedt (1848) was the first author to describe this species, giving it the name *Belemnites tripartitus gracilis*. However, this name is a junior primary homonym of both *Belemnites gracilis* Zieten, and *Belemnites tripartitus* Schlotheim, 1820. The valid name for this species is therefore *Acrocoelites subgracilis* Kolb.

Occurrence. Lower to Upper Toarcian (*bifrons* Zone, *commune* Subzone to *levesquei* Zone, *dispansum* Subzone) of Britain, Germany and east Greenland (*GMC 700.1983*, Rosenkrantz Collection, Jameson Land).

Subgenus **TOARCIBELUS** Reigraf, 1980

Type species. *Belemnites quenstedti* Oppel, 1856, by original designation.

Other species. *A.* (*T.*) *trisulculosus* (Simpson), *A.* (*T.*) *ilminsterensis* (Phillips), *A.* (*T.*) *inaequistriatus* (Simpson).

Diagnosis. Large, robust, cylindriconical to conical *Acrocoelites*. Outline symmetrical, cylindriconical to conical. Profile asymmetrical, cylindriconical to conical. Apex acute, a short epirostrum may be developed. Transverse sections subquadrate to rounded subquadrate. Three well-defined apical grooves (one ventral, two dorso-lateral) are present, although the ventral groove is reduced in some species. Apex commonly striated. Phragmocone penetrates one quarter of the rostrum.

Range. Lower Toarcian to Aalenian of Britain, mainland Europe and USSR.

Remarks. Members of the subgenus include the most primitive, robust and cylindriconical species of *Acrocoelites*. Some species may be confused with those of *Passaloteuthis* Lissajous and *Megateuthis* Bayle, but both these genera lack ventral apical grooves. *A.* (*Toarcibelus*) differs from *A.* (*Acrocoelites*) in its larger size and relatively uncompressed transverse sections, while it differs from *A.* (*Odontobelus*) in its elongate cylindriconical form.

A. (*Toarcibelus*) is here restricted, to exclude the squat, conical forms (which are more properly assigned to *A.* (*Odontobelus*)) and the slender compressed species (belonging to *A.* (*Acrocoelites*)) included within it by Riegraf (1980).

Acrocoelites (Toarcibelus) quenstedti (Oppel, 1856) Pl. 8, figs 3, 5–7

. 1848 *Belemnites compressus paxillosus* Quenstedt, p. 423, pl. 27, figs 2, 3 [homonym of both *B. compressus* Stahl, 1822 and *B. paxillosus* Lamarck, 1801].
*. 1856 *Belemnites Quenstedti* Oppel, p. 363.
. 1858 *Belemnites opalinus* Quenstedt, p. 308, pl. 24, fig. 13.
1863 *Belemnites Quenstedti* Oppel; Mayer, p. 185.
?1874 *Belemnites Quenstedti* Oppel; Dumortier (*pars*), p. 35, pl. III, figs 1, 2 [*non* 3, 4, 9=*A.* (*Odontobelus*) sp.].
. 1878 *Megateuthis Quenstedti* (Oppel); Bayle & Zeiller, pl. XXVI, figs 2, 3.
1883 *Belemnites Quenstedti* Oppel; Mayer-Eymer, p. 641.
?*non* 1898 *Belemnites Quenstedti* Oppel; Benecke, p. 46, pl. IV, fig. 3 [?=*A.* (*Odontobelus*) *vulgaris* Young & Bird].
. 1902 *Belemnites Quenstedti* Oppel; Janensch, p. 109, pl. XII, figs 1, 2.
. 1905 *Belemnites Quenstedti* Oppel; Benecke, p. 288.
. 1912 *Belemnites opalinus* Quenstedt; Werner, p. 133, pl. XII, fig. 4
1920 *Megateuthis opalina* (Quenstedt); Bülow-Trummer (*pars*), p. 115.
1920 *Megateuthis Quenstedti* (Oppel); Bülow-Trummer, p. 116.
1925 *Mesoteuthis Quenstedti* (Oppel); Lissajous, p. 126.

?1931 *Mesoteuthis quenstedti* (Oppel); Krimhol'z, p. 13, pl. 1, figs 6–8.
non 1942 *Acrocoelites quenstedti* (Oppel); Kolb, p. 158, pl. 8, figs 3, 8 [=*Acrocoelites* (*Odontobelus*) *tricissus* (Janensch)].
v. 1969 *Belemnites quenstedti* Oppel; Schwegler (*pars*), p. 188, text-fig. 74.
?1971 *Mesoteuthis quenstedti* (Oppel); Činčurová, p. 72, pl. V, fig. 5.
1975 *Acrocoelites quenstedti* (Oppel); Saks & Nal'nyaeva, p. 11.
1980 *Acrocoelites* (*Toarcibelus*) *quenstedti* (Oppel); Riegraf, p. 148.

Type specimens. The originals of Quenstedt (1848, pl. 27, figs 2, 3) are the valid syntypes of this species. These specimens are not in GPIT and are apparently lost. Werner's (1912, pl. 12, fig. 4) figured topotype is also lost (W. Riegraf, *pers. comm.* 1984). However, Schwegler's (1969, p. 188, text-fig. 74) topotype is extant in GPIT (no registered number), and is herein selected as neotype of *Belemnites quenstedti* Oppel, from the Aalenian ("Mittlerer Jura Alpha") of Boll, Württemberg, southwest Germany.

Material BMNH, 23 specimens, *levesquei* Zone, Bridport Sands, Dorset; Cephalopod Bed, Wotton Hill, Gloucestershire; Bredon Hill, Hereford and Worcester; Aalenian Terebratula Bed, Blea Wyke, North Yorkshire. CMN, 2 specimens, Aalenian Northampton Sand, Northampton.

Diagnosis. Medium sized cylindriconical *Acrocoelites* (*Toarcibelus*). Outline and profile similar, symmetrical and cylindriconical. Apex moderately acute. Transverse sections subcircular. Apical grooves incised, short. Ventral groove expands adorally.

Description. Medium sized, cylindriconical rostrum with a total length of approximately six times Dv. The outline is symmetrical and cylindriconical. The apex is reasonably acute, and the flanks diverge moderately in the apical region, with weaker divergence in the stem region. The profile is similar, but it is generally more conical than the outline, and individuals may have asymmetrical profiles with inflated venters. Transverse sections are subcylindrical, becoming elliptical in more compressed specimens.

The apex of the rostrum bears three well-developed apical grooves (one ventral, two dorso-lateral), with the ventral groove generally longer and more incised than the dorso-laterals. Often this groove expands adorally into a broad, triangular flattened region. The lateral lines are indistinct, but commonly consist of a broad, ventro-lateral flattened region, with a ridge, and thinner dorso-lateral depression above. The phragmocone penetrates approximately one third of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59474	91·5	58·6	16·1	14·1
C59482	75·5	50·5	15·9	15·2
C59496	88·9	54·6	16·4	14·8
C59497	98·5	53·0	17·7	15·2

Table 13. Measurements of *Acrocoelites* (*Toarcibelus*) *quenstedti* (Oppel, 1856).

Remarks. Acrocoelites (*Toarcibelus*) *quenstedti* has been confused with *A.* (*Odontobelus*) *tricissus* (Janensch), which it resembles (e.g. Kolb 1942, pl. 8, figs 3, 4, and synonymies in Werner 1912 and Schwegler 1969). However, *A.* (*O.*) *tricissus* is distinguished by its shorter rostrum, its very acute apex and its less inflated venter. Within its subgenus, *A.* (*T.*) *quenstedti* differs from *A.* (*T.*) *trisulculosus* (Simpson) by its more cylindriconical form and its rounded section, and from *A.* (*T.*) *ilminsterensis* (Phillips) by its more conical form and compressed rather than depressed section.

Occurrence. Upper Toarcian (*?thouarsense* Zone) to Lower Aalenian of Britain and mainland Europe.

Acrocoelites (Toarcibelus) trisulculosus (Simpson, 1855) Pl. 8, fig. 4; Pl. 9, figs 1–3, ?4, 5, 6; Pl. 10, figs 1–3; Pl. 11, figs 1–3

v*. 1855 *Belemnites trisulculosus* Simpson, p. 26.
v. 1855 *Belemnites incisus* Simpson, p. 27 [Lectotype, here designated, WM. 122, '*serpentinus*' Zone, Whitby, North Yorkshire].
v. 1855 *Belemnites distortus* Simpson, p. 26 [Lectotype, here designated, WM. 34b, '*serpentinus*' Zone, Jet Rock, Whitby, North Yorkshire. Has a pathological apex].

v. 1855 *Belemnites substriatus* Simpson, p. 27 [Lectotype, here designated, WM. 2646, U.L. 6 (=Beds 41–42), Jet Rock, Saltwick, North Yorkshire].
v? 1855 *Belemnites spicatus* Simpson, p. 29 [Lectotype, here designated, WM. 21, '*serpentinus*' Zone, Whitby, North Yorkshire].
v? 1855 *Belemnites validus* Simpson, p. 28 [Lectotype, here designated, WM. 2407, '*serpentinus*' Zone, Whitby, North Yorkshire].
v. 1867 *Belemnites tripartitus* v. Schlotheim; Phillips, p. 62, pl. II, fig. 28.
. 1867 *Belemnites subaduncatus* Voltz; Phillips (*pars*), p. 63, pl. XI, fig. 29l[vi] only.
. 1867 *Belemnites subtenuis* Simpson; Phillips (*pars*), p. 60, pl. X, fig. 27 only [juvenile].
v. 1876 *Belemnites tripartitus* v. Schlotheim; Blake (*in* Tate & Blake), p. 325.
v. 1884 *Belemnites trisulculosus* Simpson; Simpson, p. 30.
v. 1884 *Belemnites incisus* Simpson; Simpson, p. 31.
v. 1884 *Belemnites substriatus* Simpson; Simpson, p. 32.
v? 1884 *Belemnites spicatus* Simpson; Simpson, p. 33.
v? 1884 *Belemnites validus* Simpson; Simpson, p. 41.
. 1912 *Belemnites Raui* Werner, p. 130, pl. XI, fig. 7.
1920 *Cuspiteuthis oxycona* (Zieten); Bülow-Trummer (*pars*), p. 106.
1920 *Cuspiteuthis Raui* (Werner); Bülow-Trummer, p. 106.
1925 *Acrocoelites trisulculosus* (Simpson); Lissajous, p. 148.
v. 1969 *Belemnites raui* Werner; Schwegler, p. 185, text-fig. 72.
. 1971 *Salpingoteuthis carpaticus* Činčurová, p. 62, pl. 5, fig. 1.
?1975 *Acrocoelites trisulculosus* (Simpson); Saks & Nal'nyaeva, p. 17, pl. II, fig. 4; pl. III, figs 1–5.
1975 *Mesoteuthis raui* (Werner); Saks & Nal'nyaeva, p. 30.
1980 *Acrocoelites (Toarcibelus) raui* (Werner); Riegraf, p. 148.
v. 1983 *Acrocoelilte s (Toarcibelus) raui* (Werner); Reitner & Urlichs, p. 451, figs 1–3.
. 1983 *Salpingoteuthis carpaticus* Činčurová; Činčurová, p. 17, text-fig. 1, pl. I, fig. 10.
v. 1984 *Acrocoelites (Toarcibelus) raui* (Werner); Riegraf *et al.*, p. 150, pl. 9, fig. 9.

Type specimens. Lectotype (here designated): WM 36, Jet Rock ((*falciferum* Zone, *exaratum* Subzone), Saltwick Bay, North Yorkshire. Paralectotype: WM 31, Jet Rock (*falciferum* Zone, *exaratum* Subzone), Hawsker Bottoms, North Yorkshire.

Material. BMNH, 97 specimens, Jet Rock Member (*exaratum* Subzone, *falciferum* Zone), North Yorkshire; OUM, 1 specimen, Jet Rock Member, North Yorkshire; CMN, 1 specimen, *exaratum* Zone, Bugbrooke, Northampton; WM, 19 specimens, Jet Rock Member, (*exaratum* Subzone, *falciferum* Zone), North Yorkshire.

Diagnosis. Large, robust, cylindriconical to cylindrical *Acrocoelites* (*Toarcibelus*). Outline and profile similar, symmetrical and cylindriconical. Apex acute. Transverse sections quadrate. Ventral groove reduced.

Description. Large, elongate and robust, cylindrical or cylindriconical rostra with a total length of approximately eight times Dv. The outline is symmetrical and cylindrical to cylindriconical with parallel flanks. The apex is acute to very acute, with weak divergence of the flanks in the apical region, which become parallel in the stem and alveolar regions. The profile is asymmetrical to almost symmetrical, and is commonly cylindriconical to very slightly subhastate. The venter may be slightly inflated, and the apex may be recurved.

The apex is marked by two well-developed dorso-lateral apical grooves, and a single ventral

Specimen	*L*	*l*	*Dv*	*Dl*
WM 36	162·5	133·2	17·7	15·1
BMNH C59344	215·5	174·9	26·3	21·6
C59376	146·8	110·7	17·9	15·7
C59377	122·4	82·0	19·6	16·4
C59378	177·5	141·7	20·8	18·7
C59379	178·0	134·2	20·0	16·5
C59380	65·7j	45·8	10·0	9·5
C59381	65·4j	42·5	8·4	8·2

Table 14. Measurements of *Acrocoelites* (*Toarcibelus*) *trisulculosus* (Simpson, 1855). Abbreviation: j, juvenile.

apical groove which may be very shallow, or reduced in some specimens. The apex is commonly striated, in some cases strongly, probably leading Simpson (1855) to separate extreme examples under the name *Belemnites substriatus*. The lateral lines consist of a broad ventro-lateral flattened region generally overlain by a weak ridge and narrower depression. The phragmocone penetrates approximately one quarter of the rostrum. The apical line is goniolineate.

ONTOGENY. *Acrocoelites* (*Toarcibelus*) *trisulculosus* is very common within the Jet Rock (*falciferum* Zone, *exaratum* Subzone) of North Yorkshire, where juveniles of all sizes are found associated with adults. Comparison of these immature rostra with prepared sections of adult specimens enables one to complete the picture of the ontogeny of this species. Three arbitrary growth stages are recognized (see *Passaloteuthis bisulcata* (Blainville), above).

1. *Nepionic*. The nepionic rostrum is short, robust and conical (at approximately 5 mm total length). Rostra become successively more elongate with age, becoming cylindriconical, with a subquadrate transverse section, at 35 mm total length. The apex of these rostra is acute, and may be recurved. Two dorso-lateral apical grooves are developed, and these are unstriated. A third, ventral, groove is also seen, but this is characterized by a series of elongated striae (see Phillips 1867, pl. X, fig. 27). Elongation of the rostrum continues throughout this stage.
2. *Neanic*. The neanic stage corresponds approximately to a period of more rapid increase in size (length and diameter) at 70 mm approximate total length. The neanic rostrum is cylindriconical to conical, and possesses an acute apex. In this stage the apical sculpture is similar to that of the nepionic stage, but with slightly more incised grooves. The ventral groove is still characterized by its elongate striae. Phillips' (1867, pl. X, fig. 27) *Belemnites subtenuis* is probably a juvenile neanic rostrum of *A.* (*T.*) *trisulculosus*, as the figure clearly displays the characteristic striation.
3. *Ephebic-Gerontic*. The adult stage is commenced by the gradual increase of length and width to produce the characteristic cylindriconical rostrum with a subquadrate section typical of *A.* (*T.*) *trisulculosus*. Some adult specimens may be more conical than the norm, generally with a larger dorso-ventral diameter. Such variants were specifically separated by Simpson (1855) as *Belemnites incisus* and *Belemnites spicatus*. In addition, some examples of *A.* (*T.*) *trisulculosus* may attain a very large size (up to 200 mm long and 30 mm in diameter). Such specimens were also separated by Simpson (1855) from the main stock of *A.* (*T.*) *trisulculosus* (as *Belemnites validus*).

Remarks. Due to its stratigraphic position (in the *falciferum* Zone, *exaratum* Subzone) above the last occurrence of *Passaloteuthis bruguieriana*, and its overall similarity in form, *A.* (*T.*) *trisulculosus* has often been confused with this species (e.g. Hallam 1967, p. 419). However, it is readily distinguished by its regular, subquadrate section, and its three well-developed apical grooves. *A.* (*T.*) *trisulculosus* bears a great resemblance to *A.* (*T.*) *ilminsterensis* (Phillips). However, this species can be distinguished by its more depressed transverse section and its more symmetrical profile. Simpson (1855, 1884) described a great number of species from the Jet Rock of North Yorkshire which are here considered as variants of *A.* (*T.*) *trisulculosus* (e.g. *Belemnites incisus*, *B. spicatus*, *B. substriatus* and *B. validus*; see plates for figures of the lectotypes).

Occurrence. Lower Toarcian (*falciferum* Zone) of Britain, mainland Europe and the USSR.

Acrocoelites (Toarcibelus) ilminsterensis (Phillips, 1867) Pl. 12, figs 1–7; ?Pl. 28, fig. 6

v. 1847 *Belemnites tripartitus paxillosus* Quenstedt, p. 420, pl. 26, figs 25–26 [homonym of both *B. tripartitus* Schlotheim, 1820 and *B. paxillosus* Lamarck, 1801].
v. 1858 *Belemnites tripartitus paxillosus* Quenstedt; Quenstedt, p. 255, pl. 36, fig. 10.
v*. 1867 *Belemnites ilminsterensis* Phillips, p. 64, pl. XII, fig. 30.
v. 1867 *Belemnites microstylus* Phillips (*pars*), p. 66, pl. XIII, fig. 31o [partially obscured by matrix] [*non* figs $31g^{i}$, $31g^{iii}$ = *Hastites microstylus* (Phillips), lectotype, here designated].

' *1883* *Belemnites ilminsterensis* Phillips; Mayer-Eymar, p. 641.
. 1906 *Belemnites* (*Megateuthis*) *ilminsterensis* Phillips; Lissajous, p. 54, pl. 5, fig. 3.
v. 1912 *Belemnites iuvensis* Werner, p. 136 [junior objective synonym].
1920 *Cuspiteuthis ilminsterensis* (Phillips); Bülow-Trummer, p. 103.
1925 *Acrocoelites ilminsterensis* (Phillips); Lissajous, p. 102.
v. 1969 *Belemnites tripartitus paxillosus* Quenstedt; Schwegler, p. 159, text-fig. 70.
v? 1969 *Belemnites juvensis* Werner; Schwegler, p. 184, text-fig. 71a–c.
1980 *Acrocoelites* (*Toarcibelus*) *tripartitus* (Schlotheim); Riegraf, p. 148.
v. 1984 *Acrocoelites* (*Toarcibelus*) *ilminsterensis* (Phillips); Riegraf *et al.*, p. 155, pl. 10.

Type specimens. Lectotype: GMB M.1216A, here designated (=Phillips 1867, pl. XII, fig. 30l). Paralectotypes: GMB M.1216, M.1216B, C, F, G, all from the 'Upper Lias' (Junction Bed) of Somerset. Specimen M.1216C is a juvenile and syntype of Werner's (1912) species *Belemnites iuvensis*. It is here designated lectotype of this species.

Material. BMNH, 25 specimens; BGS, 14 specimens, all from the *falciferum* and *bifrons* zones of North Yorkshire (Whitby Mudstone Formation), and southeast England (Junction Bed). CMN, 24 specimens, *falciferum* Zone, Cephalopod Bed, and *bifrons* Zone, Leda Ovum Beds, Northampton. WM, 1 specimen, *falciferum* Zone and Subzone, Jet Rock Member, Whitby Mudstone Formation, North Yorkshire. GMB, 24 specimens, *falciferum* Zone, Junction Bed, Ilminster, Somerset.

Diagnosis. Medium sized, slender, cylindriconical to cylindrical *Acrocoelites* (*Toarcibelus*). Outline and profile similar, symmetrical. Apex acute. Transverse sections depressed subquadrate. Ventral groove usually well-developed.

Description. Medium sized, slender cylindriconical to cylindrical rostrum with a total length of approximately 10 times Dv. The outline is symmetrical and cylindrical to cylindriconical with only slight divergence in the acute apical region, the flanks becoming parallel in the stem. The profile is nearly symmetrical and cylindriconical, with little inflation of the venter or dorsum. The transverse sections of the rostrum are depressed quadrate in the stem region, becoming more compressed and subquadrate in the alveolar region. Juveniles of this species are commonly very depressed in their stem regions (i.e. *Belemnites iuvensis* Werner).

There are three well-developed apical grooves (one ventral, two dorso-lateral), and the ventral groove is commonly longer and more incised than the dorso-laterals. The lateral lines are reasonably well-developed in this species, and consist of two parallel, narrow depressions separated by a well-developed ridge or 'weal'. The phragmocone penetrates one third of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C20777d	94·0	67·8	9·5	10·2
C6956	77·7	51·1	10·5	10·3
C59500	72·8j	52·5	8·7	8·2
C59501	62·2j	41·6	7·9	7·4

Table 15. Measurements of *Acrocoelites* (*Toarcibelus*) *ilminsterensis* (Phillips, 1867). Abbreviation: j, juvenile.

Remarks. A. (*T.*) *ilminsterensis* is a very variable species, and the name has been widely applied. There are two basic variants within it. The first is that typified by the type specimens figured by Phillips (1867, pl. XII, fig. 30) and those figured by Quenstedt (1847, pl. 26, figs 25, 26) as *Belemnites tripartitus paxillosus*, which are conical and relatively short. The second variant is typified by specimens in the OUM mentioned by Phillips (1867, p. 64; OUM J17042, J17045). These are generally more compressed and slender and resemble *A.* (*Acrocoelites*) *subgracilis* Kolb. A typical example of this variant was figured by Phillips (1867, pl. XIII, fig. 31o) as '*Belemnites microstylus*' from the Dumbleton Insect Bed (=Alderton Fish Bed, *exaratum* Subzone) of Gloucestershire. This figure showed a dorsal outline of a slender *A.* (*T.*) *ilminsterensis*, although the other specimens of this species figured by Phillips (1867) are typical hastitids of the Lower Lias. Robust members of

A. (*T.*) *ilminsterensis* approach *A.* (*T.*) *trisulculosus* (Simpson) in form, but the former species can be distinguished by its symmetrical profile and generally regular shape. *A.* (*T.*) *ilminsterensis* may also resemble some species of *A.* (*Acrocoelites*), but in general, species of this subgenus are less depressed, more slender, shorter and more conical than *A.* (*T.*) *ilminsterensis*.

Quenstedt (1847) was first to describe this species, under the name *Belemnites tripartitus paxillosus*. This nominal species is identical to *Belemnites ilminsterensis* Phillips, 1867, but although the senior synonym, Quenstedt's (1847) older trinomial name is a junior homonym of both *Belemnites tripartitus* Schlotheim, 1820 and *Belemnites paxillosus* Lamarck, 1801. Therefore Phillips' later name is the valid one for this species. Werner's (1912) species *Belemnites iuvensis* was in part based on the specimens figured by Phillips (1867) as juveniles of *A.* (*T.*) *ilminsterensis*. Examination of these specimens indicates that Phillips' assumption is correct, and therefore *Belemnites iuvensis* Werner is a junior objective synonym of *A.* (*T.*) *ilminsterensis*.

Occurrence. Lower Toarcian (*exaratum* Subzone, *falciferum* Zone, to *crassum* Subzone, *bifrons* Zone) of Britain and mainland Europe.

Acrocoelites (Toarcibelus) inaequistriatus (Simpson, 1855) Pl. 13, figs 1–5; Pl. 14, figs 1–3, 7

non 1824 *Belemnites compressus* Stahl, p. 33, pl. II, fig. 4 [=*Gastrobelus compressus* (Stahl)].
v. 1828 *Belemnites compressus* Young & Bird, p. 276, pl. XV, fig. 5.
v*. 1855 *Belemnites inaequistriatus* Simpson, p. 24.
v. 1855 *Belemnites concavus* Simpson, p. 24 [Lectotype, here designated, WM. 41, '*serpentinus*' Zone, Saltwick, North Yorkshire].
v. 1855 *Belemnites compressus* Young & Bird; Simpson, p. 24.
v. 1867 *Belemnites inaequistriatus* Simpson; Phillips, p. 83, pl. XIX, fig. 48.
. 1874 *Belemnites longisulcatus* Voltz; Dumortier, p. 39, pl. II, figs 9, 10.
. 1876 *Belemnites inaequistriatus* Simpson; Blake (*in* Tate & Blake), p. 325.
v. 1876 *Belemnites crossotelus* Blake (*in* Tate & Blake) (*pars*), p. 326.
1883 *Belemnites iniquistriatus* Simpson; Mayer-Eymar, p. 641.
v. 1884 *Belemnites compressus* Young & Bird; Simpson, p. 26.
v. 1884 *Belemnites inaequistriatus* Simpson; Simpson, p. 27.
v. 1884 *Belemnites limatulus* Simpson; Simpson (*pars*), p. 28.
v. 1884 *Belemnites concavus* Simpson; Simpson, p. 29.
v. 1884 *Belemnites cinereus* Simpson, p. 33 [Lectotype, here designated, WM. 1996, '*communis*' Zone, Whitby, North Yorkshire].
1920 *Cuspiteuthis inaequistriata* (Simpson); Bülow-Trummer, p. 109.
1925 *Salpingoteuthis inaequistriatus* (Simpson); Lissajous, p. 98.

Holotype. WM 454, 'Upper Lias 6' (=beds 41–42 of the Bituminous Shales), Saltwick, North Yorkshire.

Material. BMNH, 34 specimens; OUM, 5 specimens; WM, 10 specimens. All from the *bifrons* Zone to *variabilis* Zone, Alum Shale and Peak Mudstone members, North Yorkshire.

Diagnosis. Large sized, cylindrical to cylindriconical *Acrocoelites* (*Toarcibelus*), with short epirostrum. Outline and profile similar, symmetrical and cylindriconical. Transverse sections compressed elliptical to pyriform. Apex very striated, with three well-developed apical grooves.

Description. Large, cylindrical to cylindriconical rostrum, frequently with a short epirostrum developed. The total length of the rostrum complete with epirostrum is commonly seven times Dv. The outline is symmetrical and cylindriconical, although individuals may be cylindrical. In outline the apex may be acute to attenuated, with weak divergence of the flanks from the apex. The profile is generally similar, but may be more irregular in form due to the development of the epirostrum, and the slightly more inflated apex of the orthorostrum. The different states of preservation of the epirostrum in this species have led to excessive taxonomic splitting. Thus the names *Belemnites concavus* Simpson and *B. limatulus* Simpson have been applied to specimens with eroded apices, while the name *Belemnites compressus* Young & Bird has been given to those with crushed epirostra.

The epirostrum bears three (one ventral, two dorso-lateral) apical grooves that are well-developed, and in addition it is commonly strongly striated. In some cases, the ventral groove may be less well-developed than the two dorso-laterals. Lateral lines are very indistinct in this species, but commonly take the form of a ventro-lateral broad depression, with a weak ridge and thinner depression above. The phragmocone penetrates approximately one third of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
WM 454	161·7e	129·4	16·2	13·1
BMNH C59340	124·9e	93·2	17·4	15·0
C59349	111·6d	74·6	20·5	17·2
C59423	119·5d	87·8	19·3	15·2
C59462	118·8e	87·9	17·3	15·7

Table 16. Measurements of *Acrocoelites* (*Toarcibelus*) *inaequistriatus* (Simpson, 1855). Abbreviations: d, epirostrum destroyed; e, epirostrum present.

Remarks. A. (*T.*) *inaequistriatus* is a fairly long-ranging species (*falciferum* to *thouarsense* Zone). Later forms approach *A.* (*O.*) *brevisulcatus* (Quenstedt), but this species has a more conical orthorostrum. *A.* (*T.*) *inaequistriatus* also resembles *Megateuthis longisulcata* (Voltz) and *Youngibelus gigas* (Quenstedt). It differs from both in the possession of three well-developed apical grooves, and a strongly striated epirostrum. *Y. gigas* also possesses an ortholineate apical line and a longer epirostrum. *A.* (*T.*) *inaequistriatus* most closely resembles *A.* (*T.*) *ilminsterensis* (Phillips), but is distinguished by its compressed section and epirostrum.

Occurrence. Lower to Upper Toarcian (*falciferum* Zone and Subzone, to *thouarsense* Zone) of Britain and mainland Europe.

Subgenus **ODONTOBELUS** Naef, 1922

Type species. Belemnites pyramidalis Zieten, 1831; by original designation.

Other species. A. (*O.*) *vulgaris* (Young & Bird), *A.* (*O.*) *levidensis* (Simpson), *A.* (*O.*) *tricissus* (Janensch), *A.* (*O.*) *subtricissus* Kolb, *A.* (*O.*) *wrighti* (Oppel).

Diagnosis. Medium sized, robust to very robust, conical to cylindriconical *Acrocoelites*. Outline symmetrical, cylindriconical to conical. Profile asymmetrical, conical to cylindriconical, venter commonly inflated. Apex reasonably acute or obtuse. Three well-defined apical grooves are present (one ventral, two dorso-lateral), although the ventral groove may be reduced in some species. A short epirostrum may be present, bearing the apical grooves, and it is commonly well-striated. Lateral lines consist of weakly defined flattened areas or depressions separated by a ventro-laterally placed weak ridge. The phragmocone is weakly displayed ventrally, and penetrates one half of the rostrum. The apical line is goniolineate, and the alveolar angle is commonly 25°–30°.

Range. Lower Toarcian (*falciferum* Zone and Subzone) to Aalenian of Britain, mainland Europe and the USSR.

Remarks. Acrocoelites (*Odontobelus*) contains the squat, conical species of *Acrocoelites*. Smaller species of this subgenus may be confused with those of *Brevibelus* gen. nov. (see below) while some of the smoother species resemble those of *Dactyloteuthis*. Species of both these genera may be distinguished, however, by their absence or reduced number of apical grooves. *A.* (*Odontobelus*) differs from *A.* (*Toarcibelus*) and *A.* (*Acrocoelites*) by its squat, conical form, generally with an inflated apex. *A.* (*Odontobelus*) as defined here differs from the usuage of Riegraf (1980) in including much larger species with more inflated venters than he considered typical (e.g. *A.* (*O.*) *levidensis*).

Acrocoelites (Odontobelus) pyramidalis (Zieten, 1831) Pl. 10, figs 4–8; Pl. 11, figs 4, 5

*. 1831 *Belemnites pyramidalis* (Münster M.S.) Zieten, p. 31, pl. XXIV, fig. 5.
. 1836 *Belemnites pyramidalis* Münster; Roemer, p. 172.

v. 1848 *Belemnites tripartitus brevis* Quenstedt, p. 420, pl. 26, fig. 18; pl. 27, fig. 32.
v. 1855 *Belemnites curtus* Simpson, p. 29 [junior homonym of *Belemnites curtus* d'Orbigny, 1842].
. *1856* *Belemnites pyramidalis* Münster; Oppel, p. 241.
1863 *Belemnites pyramidalis* Münster; Mayer, p. 184.
. 1874 *Belemnites pyramidalis* Zieten; Dumortier, p. 36, pl. V, figs 6, 7.
1883 *Belemnites pyramidalis* Münster; Mayer-Eymar, p. 641.
v. 1884 *Belemnites curtus* Simpson; Simpson, p. 39.
v. 1884 *Belemnites urbanus* Simpson (*pars*), p. 39.
?1898 *Belemnites tripartitus* v. Schlotheim; Benecke, p. 46, pl. iv, fig. 4.
. 1902 *Belemnites tripartitus* v. Schlotheim; Janensch, p. 118, pl. XI, figs 6–8.
. 1906 *Belemnites* (*Pachyteuthis*) *pyramidalis* Zieten; Lissajous, p. 52.
. 1912 *Belemnites pyramidalis* Zieten; Werner, p. 135.
1920 *Megateuthis pyramidalis* (Zieten); Bülow-Trummer, p. 116.
. 1922 *Odontobelus pyramidalis* (Zieten); Naef, p. 238.
?1924 *Belemnites* (*Odontobelus*) *Janenschi* Ernst, p. 85, pl. XII, figs 9–11.
1925 *Acrocoelites pyramidalis* (Münster); Lissajous, p. 126.
. 1942 *Acrocoelites pyramidalis* (Zieten); Kolb, p. 159, pl. 10, figs 8, 9; pl. 11, fig. 4.
?1967 *Megateuthis pyramidalis* (Zieten); Činčurová, p. 7, pl. 1, fig. 5.
v. 1969 *Belemnites pyramidalis* Zieten; Schwegler, p. 198, fig. 81.
?1971 *Salpingoteuthis pyramidalis* (Zieten); Činčurová, p. 67, pl. IV, fig. 11.
. 1975 *Mesoteuthis pyramidalis* (Zieten); Saks & Nal'nyaeva, p. 42, pl. IV, figs 5–7.
1980 *Acrocoelites* (*Odontobelus*) *pyramidalis* (Zieten); Riegraf, p. 149.
v. 1984 *Acrocoelites* (*Odontobelus*) *pyramidalis* (Münster *in* Zieten); Riegraf *et al.*, p. 156, pl. 10, fig. 7.

Type specimen. Holotype; BSfP AS XX 7, the original of Zieten (1831, pl. 24, fig. 5) from the Upper Lias of Boll, Württemberg, southwest Germany.

Material. BMNH, 47 specimens; BGS, 1 specimen; OUM, 11 specimens; WM, 11 specimens. From the *falciferum* to *variabilis* Zones, Jet Rock to Peak Mudstone members, North Yorkshire.

Diagnosis. Small to medium sized conical *Acrocoelites* (*Odontobelus*). Outline symmetrical and conical. Profile nearly symmetrical and conical. Apex acute. Transverse sections subquadrate to compressed elliptical. Ventral groove reduced, dorso-lateral grooves well-developed.

Description. Small to medium sized, delicately formed, conical to slightly cylindriconical *Acrocoelites*, its length about four times Dv. The outline is conical to slightly cylindriconical, and symmetrical, with only moderate divergence from the acute apex. The profile is conical and nearly symmetrical, as the venter is only slightly inflated. Transverse sections of the rostrum are compressed and subquadrate to elliptical.

The apex bears two well-defined dorso-lateral apical grooves and a third, ventral apical groove may be present, but less incised. This ventral apical groove may be replaced by striae in some individuals. The lateral lines take the form of a broad ventro-lateral depression separated by a weak ridge from a thinner, dorso-lateral line which joins the dorso-lateral apical groove. The phragmocone penetrates one half of the rostrum. The apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59325	63·8	39·6	15·9	14·4
C59356	68·2	44·8	14·6	12·4
C59412	62·3	37·1	13·1	12·4
C59437	55·1	29·4	12·8	11·2
C59449	67·7	38·2	15·2	13·6

Table 17. Measurements of *Acrocoelites* (*Odontobelus*) *pyramidalis* (Zieten, 1831).

Remarks. Acrocoelites (*Odontobelus*) *pyramidalis* is a conical species, resembling *A.* (*Acrocoelites*) *oxyconus*. However the latter is more regularly conical and slender. *A.* (*O.*) *vulgaris* (Young & Bird) also resembles *A.* (*O.*) *pyramidalis*, but is distinguished by its more inflated venter and cylindrical form. Simpson's (1855) species *Belemnites curtus* (lectotype, here designated, WM 2063, Upper Lias, Whitby) is a junior subjective synonym of this species.

Occurrence. Lower Toarcian (*falciferum* Zone and Subzone) to Lower Aalenian of Britain, mainland Europe and USSR.

Acrocoelites (Odontobelus) vulgaris (Young & Bird, 1822) Pl. 11, figs 6–8; Pl. 13, figs 6, 7; Pl. 14, figs 4–6; Pl. 15, figs 2, 3

*. 1822 *Belemnites vulgaris* Young & Bird, p. 258, pl. XIV, fig. 1.
. 1828 *Belemnites vulgaris* Young & Bird; Young & Bird, p. 275, pl. XV, fig. 1.
v. 1855 *Belemnites vulgaris* Young & Bird; Simpson, p. 28
1863 *Belemnites vulgaris* Young & Bird; Mayer, p. 184.
v. 1867 *Belemnites vulgaris* Young & Bird; Phillips, p. 73, pl. XVI, figs 40, 41.
v. 1867 *Belemnites regularis* Phillips; p. 75, pl. XV, fig. 38.
v. 1875 *Belemnites vulgaris* Young & Bird; Phillips, p. 263, pl. 27, fig. 11.
v. 1876 *Belemnites vulgaris* Young & Bird; Blake (*in* Tate & Blake), p. 322.
1883 *Belemnites vulgaris* Young & Bird; Mayer-Eymar, p. 641.
v. 1884 *Belemnites urbanus* Simpson, p. 39 [Lectotype, here designated, WM 2610, "*communis*" Zone, Saltwick, North Yorkshire].
. 1905 *Belemnites incurvatus* Zieten; Benecke, p. 297, pl. XXV, figs 5, 9, 10; pl. XXVI, figs 1–4.
. 1912 *Belemnites tripartitus crassus* Werner, p. 135, pl. XIII, fig. 5.
1920 *Dactyloteuthis vulgaris* (Young & Bird); Bülow-Trummer, p. 101.
1925 *Acrocoelites vulgaris* (Young & Bird); Lissajous, p. 152.
. 1969 *Belemnites tripartitus crassus* Werner; Schwegler, p. 199, text-fig. 82.
? 1971 *Dactyloteuthis wrighti* (Oppel); Činčurová, p. 58, pl. IV, fig. 5.
1975 *Mesoteuthis vulgaris* (Young & Bird); Saks & Nal'nyaeva, p. 31.
1980 *Acrocoelites* (*Odontobelus*) *crassus* (Werner); Riegraf, p. 149.

Type specimens. Young & Bird (1822) figured a single specimen to represent their new species. It is shown in lateral view (pl. XIV, fig. 1), and it is preserved with most of the phragmocone intact. Many of Young & Bird's specimens are preserved in Whitby Museum, but the only specimen to approach the one figured by them is the type of *Belemnites densus* Simpson (Lectotype, WM 443). This specimen is clearly labelled by Simpson as coming from the "Upper Lias 7" (=Jet Rock), unlike *Belemnites vulgaris* which is commonest in the Alum Shales. It can therefore be assumed that Young & Bird's type is lost, as Simpson was aquainted with their work and is unlikely to have used the type specimen of their species for his own *Belemnites densus*. Three specimens of *Belemnites vulgaris* from the Alum Shales of Whitby figured by Phillips (1867, pl. XVI, figs 40s, 40a, 41) are preserved at Oxford (OUM J15321, J14766, J15397). Specimen J15397 (Phillips 1867, pl. XVI, fig. 41) is typical of the species, and is here designated neotype.

Material. BMNH, 119 specimens; BGS, 15 specimens; OUM, 20 specimens; WM, 1 specimen. From the *falciferum* Zone to *levesquei* Zone, Jet Rock Member to Blea Wyke Sandstone Formation, North Yorkshire, and the *bifrons* Zone of the North Midlands; CNM, 27 specimens, Leda Ovum Beds, *bifrons* Zone, Northampton.

Diagnosis. Medium sized, cylindriconical *Acrocoelites* (*Odontobelus*). Outline symmetrical, cylindriconical to weakly subhastate. Profile asymmetrical, cylindriconical to weakly subhastate, venter generally inflated. Apex moderately acute. Transverse sections compressed, elliptical to pyriform. Three well-developed apical grooves are present.

Description. Medium sized, robust cylindriconical rostrum, with a total length of approximately five times Dv. The outline is symmetrical and cylindriconical, becoming weakly subhastate in some individuals (those originally separated as *Belemnites regularis*). Divergence of the flanks from the apex is moderate, and the apex itself is moderately acute. The profile is asymmetrical, generally cylindriconical or conical, but sometimes slightly subhastate (as in *Belemnites regularis*). The venter is characteristically inflated in profile. Transverse sections of the rostrum are compressed, and generally elliptical to pyriform. Individuals may be more compressed in their alveolar region.

There are three well-defined apical grooves, one ventral and two dorso-lateral, but in some cases, the ventral groove may be replaced by fine striae. The lateral lines are indistinct, but consist of a broad, short, ventro-lateral depression separated by a weak ridge from a narrow, elongate depression above it. This dorso-lateral depression then joins the dorso-lateral apical grooves. The phragmocone penetrates approximately one half of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59357	86·7	56·1	19·1	16·0
C59360	86·0	52·6	18·6	16·1
C59361	83·6	58·3	17·2	15·1
C59417	139·5	55·5	19·5	16·9
C59424	96·8	53·0	16·9	14·0
C59451	103·5	53·2	17·8	16·3

Table 18. Measurements of *Acrocoelites* (*Odontobelus*) *vulgaris* (Young & Bird, 1822).

Remarks. Acrocoelites (*Odontobelus*) *vulgaris* is a variable species that is common in the Lower Toarcian of Britain. Variants include the slightly subhastate *Belemnites regularis* Phillips (lectotype, here designated, OUM J17066; paralectotype, OUM J17056). Other examples are more regularly conical or more elongate than is typical. It is feasible that such variants represent sexual dimorphs manifested as short and elongate rostra (see Delattre 1956; Doyle 1985), but further detailed collecting is needed to test this.

A. (*O.*) *vulgaris* may be distinguished by its asymmetrical profile from other species of this subgenus which commonly have less inflated venters (e.g. *A.* (*O.*) *pyramidalis* (Zieten), *A.* (*O.*) *tricissus* (Janensch) and *A.* (*O.*) *subtricissus* Kolb). *A* (*O.*) *levidensis* (Simpson) approaches *A.* (*O.*) *vulgaris* in form, but this species is much larger and more robust.

Occurrence. Lower Toarcian (*falciferum* Zone and Subzone) to Aalenian of Britain and mainland Europe.

Acrocoelites (Odontobelus) levidensis (Simpson, 1855) Pl. 14, fig. 8; Pl. 15, figs 4–7

non 1827 *Belemnites brevis* var. C (*meta*) Blainville, p. 87, pl. III, fig. 3 [=*Brevibelus* sp.].
v*. 1855 *Belemnites levidensis* Simpson, p. 20.
v*. 1876 *Belemnites levidensis* Simpson; Blake (*in* Tate & Blake), p. 322, pl. 3, figs 3, 7 [BMNH C11864, Upper Lias, Whitby, North Yorkshire].
v. 1884 *Belemnites levidensis* Simpson; Simpson, p. 41.
. 1898 *Belemnites meta* Blainville; Benecke [*pars*], p. 36, pl. II, fig. 9; pl. III, fig. 1.
? 1898 *Belemnites crassus* Voltz; Benecke, p. 41, pl. III, fig. 4.
. 1902 *Belemnites meta* Blainville; Janensch, p. 111, pl. XII, figs 3, 4.
?1905 *Belemnites meta* Blainville; Benecke, p. 299.
v. 1912 *Belemnites meta* Blainville; Werner, p. 138, pl. XII, figs 5–7.
1920 *Holcoteuthis* (?) *levidensis* (Simpson); Bülow-Trummer, p. 84.
. 1924 *Belemnites* (*?Homaloteuthis*) *meta* Blainville; Ernst, p. 81, pl. XII, fig. 6.
1925 *Dactyloteuthis levidensis* (Simpson); Lissajous, p. 109.
?1942 *Dactyloteuthis* cf. *meta* (Blainville); Kolb, p. 155, pl. 7, fig. 8.
v *non* 1969 *Belemnites meta* Blainville; Schwegler, p. 191, text-fig. 76 [=*Acrocoelites trisulculosus*, "*Belemnites validus*" form].
. 1969 *Belemnites* cf. *meta* Blainville; Schwegler, p. 192, text-fig. 77.

Type specimen. Lectotype, here designated, WM 2059 from the "*communis*" Zone (=*bifrons* Zone) of Peak (Ravenscar), North Yorkshire.

Material. BMNH, 44 specimens; OUM, 5 specimens; WM, 3 specimens. From the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire.

Diagnosis. Medium sized, robust, cylindriconical *Acrocoelites* (*Odontobelus*). Outline symmetrical, cylindriconical to cylindrical. Profile asymmetrical, conical, venter inflated, apex moderately acute. Transverse sections subcircular or slightly compressed and elliptical. Three well-developed apical grooves present.

Description. Medium sized, very robust cylindriconical or conical rostrum with a total length of approximately four times Dv. The outline is symmetrical and cylindriconical, with only weak to moderate divergence from the moderately acute apex. The profile is asymmetrical and conical or cylindriconical, commonly with an inflated venter. Transverse sections of the rostrum are subcircular or moderately compressed and elliptical. Some of the more compressed individuals approach *Dactyloteuthis crossotela* (Blake).

The apex bears three well-developed apical grooves, one ventral, and two dorso-lateral in position, although in some cases the ventral groove may be reduced. Striae may be present at the apex, but they are uncommon. Lateral lines are indistinct, and consist of a broad, lateral depression extending from the dorso-lateral grooves, becoming more ventral in position adorally. There is little evidence of a median weak lateral ridge as in other megateuthids. The phragmocone penetrates one third of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
WM 2059	66·5	38·1	18·8	16·3
BMNH C11864	84·0	50·1	23·9	20·5
C59369	85·2	54·0	23·1	20·8
C59438	87·0	47·9	21·1	18·6
C59442	87·4	53·0	20·9	18·0
C59450	98·3	60·5	20·8	19·5

Table 19. Measurements of *Acrocoelites* (*Odontobelus*) *levidensis* (Simpson, 1855).

Remarks. Acrocoelites (*Odontobelus*) *levidensis* resembles *Dactyloteuthis crossotela* (Blake) in its robust form and general morphology, but is distinguished by its well-developed apical grooves, which the latter species lacks. Within its own subgenus, *A.* (*O.*) *levidensis* most closely resembles *A.* (*O.*) *vulgaris* (Young & Bird) (see especially Blake's (*in* Tate & Blake 1876) pl. 3, fig. 3)). However, *A.* (*O.*) *vulgaris* is generally smaller, less robust and more cylindriconical than *A.* (*O.*) *levidensis*. Most other species of *A.* (*Odontobelus*) are smaller and less inflated than that described above.

Simpson (1884, p. 41) considered that Blake's (*in* Tate & Blake 1876) specimen of *Belemnites levidensis* was typical of his species. Indeed, Simpson's type specimen is rather eroded, but from collecting it is evident that both forms are typical of this species. Corrosion of typical *A.* (*O.*) *levidensis* leads to the production of a *Dactyloteuthis crossotela*-like rostrum (see above), while uncorroded forms resemble a large *A.* (*O.*) *vulgaris*.

Occurrence. Lower Toarcian (*commune* Subzone, *bifrons* Zone) to Lower Aalenian of Britain, mainland Europe and east Greenland.

Acrocoelites (Odontobelus) tricissus (Janensch, 1902) Pl. 16, figs 1–5

. 1831 *Belemnites trisulcatus* (Hartman M.S.) Zieten, p. 31, pl. 24, fig. 3.
*. 1902 *Belemnites tricissus* Janensch, p. 113, pl. 12, fig. 7.
1920 *Megateuthis* (?) *tricissa* (Janensch); Bülow-Trummer, p. 119.
1925 *Acrocoelites tricissus* (Janensch); Lissajous, p. 146.
. 1931 *Mesoteuthis tricissa* (Janensch); Krimhol'z p. 12, pl. 1, figs 4, 5.
. 1942 *Acrocoelites tricissus* (Janensch); Kolb, p. 157, pl. 9, figs 3, 6.
. 1942 *Acrocoelites quenstedti* (Oppel); Kolb, p. 158, pl. 8, fig. 3.
?1942 *Mesoteuthis banzensis*; Kolb, p. 157, pl. 11, figs 1, 2, 7.
. 1956 *Acrocoelites tricissus* (Janensch); Delattre, p. 37.
. 1975 *Acrocoelites tricissus* (Janensch); Saks & Nal'nyaeva (*pars*), p. 20, pl. V, figs 1–3.

Type specimen. Holotype, the original of Janensch (1902, pl. 12, fig. 7), from the Jurensisschicten (=Upper Toarcian) of Schillersdorf, Alsace-Lorraine, France.

Material. BMNH, 49 specimens; BGS, 1 specimen; OUM, 6 specimens. From the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire; *thouarsense* Zone, Cephalopod Bed, Gloucestershire.

Diagnosis. Medium sized, slender, conical *Acrocoelites* (*Odontobelus*). Outline symmetrical, cylindriconical. Profile asymmetrical, conical, venter weakly inflated. Apex acute to attenuated. Transverse sections compressed, elliptical to subcircular. Three apical grooves, ventral groove may be reduced.

Description. Medium sized, almost slender, conical rostrum with a total length of approximately six times Dv. The outline is symmetrical and cylindriconical or weakly subhastate, with moderate divergence from the apex. The apex is acute or attenuated in some individuals. The

profile is asymmetrical and cylindriconical to conical, commonly with a very slightly inflated venter and a recurved apex. Transverse sections of the rostrum are compressed, generally elliptical, but also pyriform. The apical region commonly is less compressed with a subcircular section.

Three apical grooves are found in this species (one ventral and two dorso-lateral), but often the ventral groove is reduced or replaced by striae. Lateral lines are weak, but are present as a broad ventro-lateral depression or flattened area which thins adapically, overlain by a thinner depression that joins the dorso-lateral apical grooves. The phragmocone penetrates one half of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59416	78·3	58·1	14·0	13·1
C59425	91·7	53·9	14·9	13·1
C59426	88·0	54·6	12·9	11·5
C59457	100·4	56·1	15·7	14·5
C59495	78·3	58·1	14·0	13·1

Table 20. Measurements of *Acrocoelites* (*Odontobelus*) *tricissus* (Janensch, 1902).

Remarks. Acrocoelites (*Odontobelus*) *tricissus* has not previously been recognized in Britain, perhaps being included in the range of variation of *A.* (*O.*) *vulgaris* (Young & Bird). However, the latter species is distinguished by its inflated venter and more robust form. *A.* (*O.*) *tricissus* differs from all other species of its subgenus in possessing a more acutely conical rostrum with an almost attenuated apex.

Belemnites trisulcatus Zieten is identical to *Belemnites tricissus*, but is a junior homonym of *Belemnites* [=*Salpingoteuthis*] *trisulcatus* Blainville (1827, p. 83, pl. 5, fig. 13), a fact recognized by Janensch (1902). Delattre (1956) considered *A. tricissus* to be a sexual dimorph of *A. conoideus* (Oppel). However, this species is so far unrecorded in Britain.

Occurrence. Lower to Upper Toarcian (*commune* Subzone, *bifrons* Zone to *dispansum* Subzone, *levesquei* Zone) of Britain, mainland Europe and USSR.

Acrocoelites (Odontobelus) subtricissus Kolb, 1942 Pl. 16, figs 6–8; Pl. 17, figs 1–3

*. 1942 *Acrocoelites subtricissus* Kolb, p. 160, pl. 11, figs 6, 8.
. 1942 *Mesoteuthis tricissiformis* Kolb, p. 164, pl. 11, figs 3, 9.
1975 *Acrocoelites subtricissus* Kolb; Saks & Nal'nyaeva, p. 11.

Type specimen. Holotype, the original of Kolb (1942, pl. 11, fig. 6) from the *Hircinus*-Schichten (*levesquei* Zone) of Berg, northern Bavaria, Germany.

Material. BMNH, 39 specimens; BGS, 2 specimens; OUM, 8 specimens; WM, 1 specimen. From the *bifrons* Zone to the *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire.

Diagnosis. Medium to large sized, conical *Acrocoelites* (*Odontobelus*). Outline symmetrical, conical or cylindriconical. Profile nearly symmetrical, conical, with some ventral and dorsal inflation. Apex acute. Three well-developed apical grooves.

Description. Medium to large sized, robust conical rostrum with a total length of approximately five times Dv. The outline is symmetrical and cylindriconical or conical, and divergence from the acute apex is strong. The profile is almost symmetrical and conical. However, it may be 'pinched' slightly in the alveolar region giving it a subhastate form. Both venter and dorsum are inflated to the same degree. Transverse sections of the rostrum are only weakly compressed, and rounded elliptical to subcircular. However, the alveolar region may be more compressed.

The apex bears three well-defined apical grooves, one ventral and two dorso-lateral, which are only rarely reduced. In addition, the apex may be weakly striated. The weak lateral lines consist of a broad ventro-lateral depression or flattened region, with a subparallel and weaker depression above, which joins the dorso-lateral apical grooves. On more robust specimens the lateral lines

are very indistinct. The phragmocone commonly penetrates one half of the rostrum, and the apical line is goniolineate.

Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59320	96·9	60·4	18·1	15·9
C59339	98·8	62·6	20·6	17·5
C59350	95·2	53·0	18·7	17·5
C59427	99·5	62·1	22·1	20·4
C59470	80·4	59·6	19·2	17·4

Table 21. Measurements of *Acrocoelites* (*Odontobelus*) *subtricissus* Kolb, 1942.

Remarks. Like *A.* (*O.*) *tricissus* (Janensch), *A.* (*O.*) *subtricissus* has not previously been recorded in Britain, perhaps being included in the range of variation of *A.* (*O.*) *vulgaris* (Young & Bird). Indeed, this species is close to *A.* (*O.*) *subtricissus*, but may be distinguished by its asymmetrical profile with inflated venter and its generally more cylindrical form. *A.* (*O.*) *subtricissus* is distinguished from the conical members of its subgenus (*A.* (*O.*) *tricissus* (Janensch) and *A.* (*O.*) *pyramidalis* (Zieten)) by its large size and inflated venter and dorsum.

Occurrence. Lower Toarcian (*falciferum* Subzone and Zone) to Lower Aalenian of Britain and mainland Europe.

Acrocoelites (Odontobelus) wrighti (Oppel, 1856) Pl. 17, figs 4–7

v. 1848 *Belemnites digitalis tripartitus* Quenstedt, p. 418, pl. XXVI, figs 14, 31.
v*. 1856 *Belemnites Wrighti* Oppel, p. 240.
1863 *Belemnites Wrighti* Oppel; Mayer, p. 184.
1883 *Belemnites Wrighti* Oppel; Mayer-Eymar, p. 641.
1912 *Belemnites Wrighti* Oppel; Werner, p. 125.
1920 *Dactyloteuthis Wrighti* (Oppel); Bülow-Trummer, p. 101.
1925 *Dactyloteuthis Wrighti* (Oppel); Lissajous, p. 153.
v. 1971 *Belemnites wrighti* Oppel; Schwegler, p. 84, text-fig. 99.
1980 *Dactyloteuthis* (*Dactyloteuthis*) *wrighti* (Oppel); Riegraf, p. 151.

Type specimens. The originals of Quenstedt's (1848) *Belemnites digitalis tripartitus*. The specimen in pl. 26, fig. 14 is lost, but that of pl. 26, fig. 31 from the 'Zone of *Amm. Jurensis*' (=*variabilis* to *levesquei* Zones) of Lyme Regis (more properly of the Lyme Regis district), Dorset is preserved in GPIT (no registered number) and is here designated lectotype.

Material. BMNH, 14 specimens; OUM, 1 specimen. From the *bifrons* Zone to the *thouarsense* Zone, Alum Shale to Peak Mudstone members, North Yorkshire.

Diagnosis. Medium sized, cylindriconical or cylindrical *Acrocoelites* (*Odontobelus*). Outline symmetrical, cylindriconical or cylindrical. Profile nearly symmetrical, cylindriconical. Apex moderately acute. Transverse sections weakly compressed and elliptical in the stem region, strongly compressed and elliptical or subquadrate in the apical region. Three well-developed apical grooves present.

Description. Medium sized, cylindriconical to cylindrical rostrum with a total length of approximately six times Dv. The outline is symmetrical and cylindriconical with weak to moderate divergence of the flanks from the apex, which approaches obtuse. The profile is nearly symmetrical and is generally more conical than the outline. The venter and dorsum are both inflated, the venter slightly more so, and the alveolar region is slightly flared accentuating its conical form. The transverse sections of the rostrum are weakly compressed in the stem and alveolar regions, and are rounded elliptical to slightly pyriform. The apical region is more compressed and elliptical or subquadrate.

The apex bears three apical grooves (one ventral and two dorso-lateral) that are reasonably well-developed. It is a common occurrence for the ventral groove to be more incised than the dorso-laterals. Lateral lines are indistinct on the rounded flanks of this species, but take the form of shallow ventro-lateral and dorso-lateral depressions separated by a weak ridge. The phragmocone penetrates approximately one quarter of the rostrum, and the apical line is goniolineate.

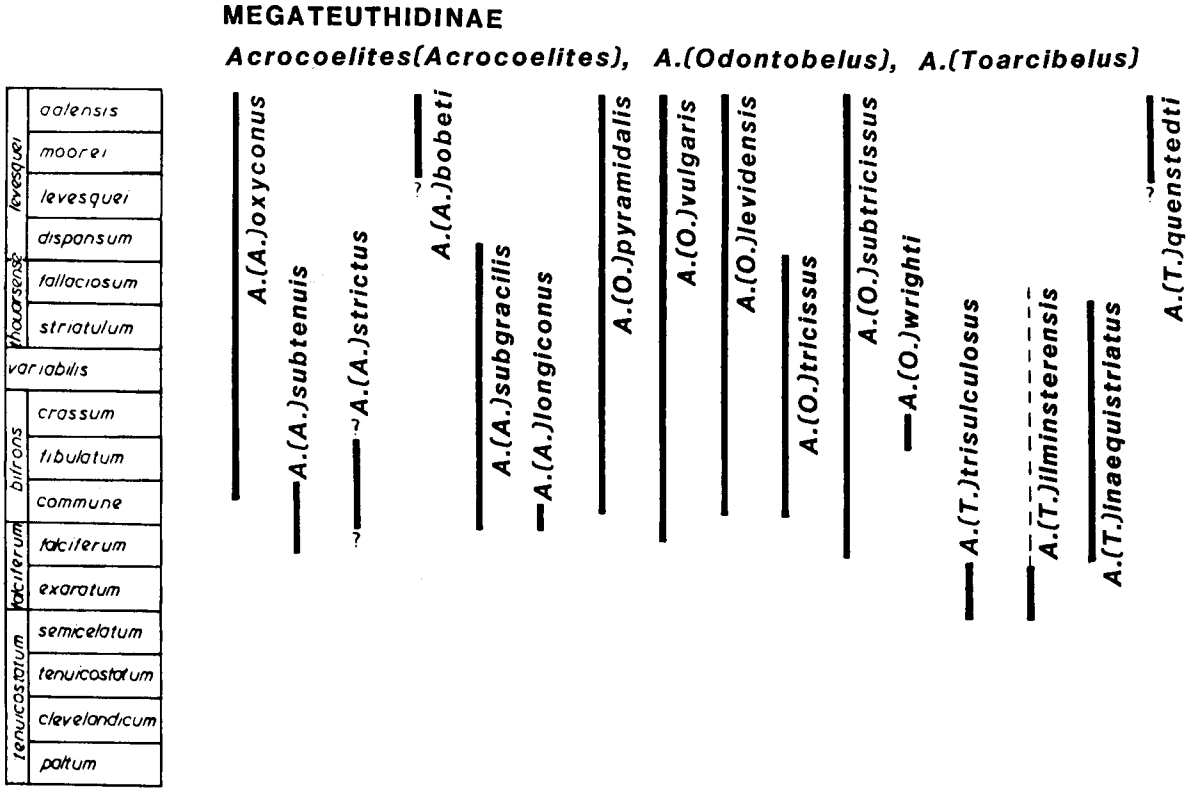
Specimen	*L*	*l*	*Dv*	*Dl*
BMNH C59439	109·2	67·1	15·7	14·1
C59440	88·7	59·0	15·1	13·8
C59441	82·7	53·3	16·6	14·4
C59443	80·8	47·1	12·2	11·6

Table 22. Measurements of *Acrocoelites* (*Odontobelus*) *wrighti* (Oppel, 1856).

Remarks. Acrocoelites (*Odontobelus*) *wrighti* is a very distinctive species characterized by its unique apical compression. However, robust individuals of *Simpsonibelus lentus* (Simpson) approach *A.* (*O.*) *wrighti*, but are distinguished by their more compressed stem region and slender form. *A.* (*O.*) *wrighti* differs from most other members of its subgenus with its possession of a cylindriconical form, a regular profile and a compressed apical region.

Quenstedt (1848) first described this form under the trinomial name *Belemnites digitalis tripartitus*. However, both of his specific names are junior homonyms of earlier specific names (*Belemnites digitalis* Blainville, 1827 and *Belemnites tripartitus* Schlotheim, 1820), and should be replaced by the specific name *Belemnites wrighti* Oppel, which was based on Quenstedt's interpretation of this species (Oppel, 1856). Most subsequent authors have included *Belemnites wrighti* in *Dactyloteuthis* Bayle (e.g. Bülow-Trummer 1920; Lissajous 1925; Riegraf 1980), following Quenstedt's (1848) original grouping, based primarily on the characteristic compression of this species, and ignoring the apical grooves. The presence of three well-developed apical grooves on a squat conical to cylindriconical rostrum indicates that *Belemnites wrighti* is more properly a species of *Acrocoelites* (*Odontobelus*).

Occurrence. Lower to Upper Toarcian (*crassum* Subzone, *bifrons* Zone to *variabilis* Zone) of Britain, mainland Europe and east Greenland.



TEXT-FIG. 16. Stratigraphic ranges of the British Toarcian Megateuthidinae (*Acrocoelites*) plotted against the ammonite zones and subzones.

PLATE EXPLANATIONS

All figures are natural size except where stated otherwise, and have been whitened with ammonium chloride prior to photography. Unless stated to the contrary, two views are illustrated, a ventral outline and left profile (venter to left). For locality details see pages 4–11; bed numbers are given in Text-figs 3–10. Martin Simpson's types are located where possible using his eight divisions of the Upper Lias (Simpson 1884), which are interpreted as follows: UL 8, Grey Shale Member; UL 7, beds 33–40, Jet Rock Member; UL 6, beds 41–42, Jet Rock Member; UL 5b, beds 43–44, Jet Rock Member; UL 5a, beds 44–46, Jet Rock Member; UL 4, beds 47–48, Jet Rock Member; UL 3, beds 49–50, Alum Shale Member; UL 2, beds 51–52, Alum Shale Member; UL 1, bed 53 and above, Alum Shale Member to Peak Mudstone Member (at Fox Cliff).

PLATE 1

Fig. Page

Passaloteuthis bisulcata (Blainville, 1826) 19

1. Variety a. Lectotype of *Belemnites cylindricus* Simpson, 1855, WM 1981, Spinatus Beds [Cleveland Ironstone Formation], Kettleness, North Yorkshire.

2. Variety a. Lectotype of *Belemnites modestus* Simpson, 1884, WM 2712, Upper Lias [probably Grey Shale Member], Sandsend, North Yorkshire.

3. Left profile and ventral outline. BMNH C59373, bed 29, Grey Shale Member, Hawsker Bottoms, North Yorkshire.

4. Juvenile with pathological ventral groove. BMNH C59375, bed 32, Grey Shale Member, same locality.

5. Large juvenile. BMNH C59406, bed 19c, Grey Shale Member, East Kettleness, North Yorkshire.

6. Juvenile. BMNH C59398, bed 4, Grey Shale Member, same locality.

7. Juvenile. BMNH C59395, bed 1, Grey Shale Member, same locality.

8. Juvenile. BMNH C59407, bed 19c, Grey Shale Member, same locality.

DOYLE, Toarcian belemnites

Plate 1

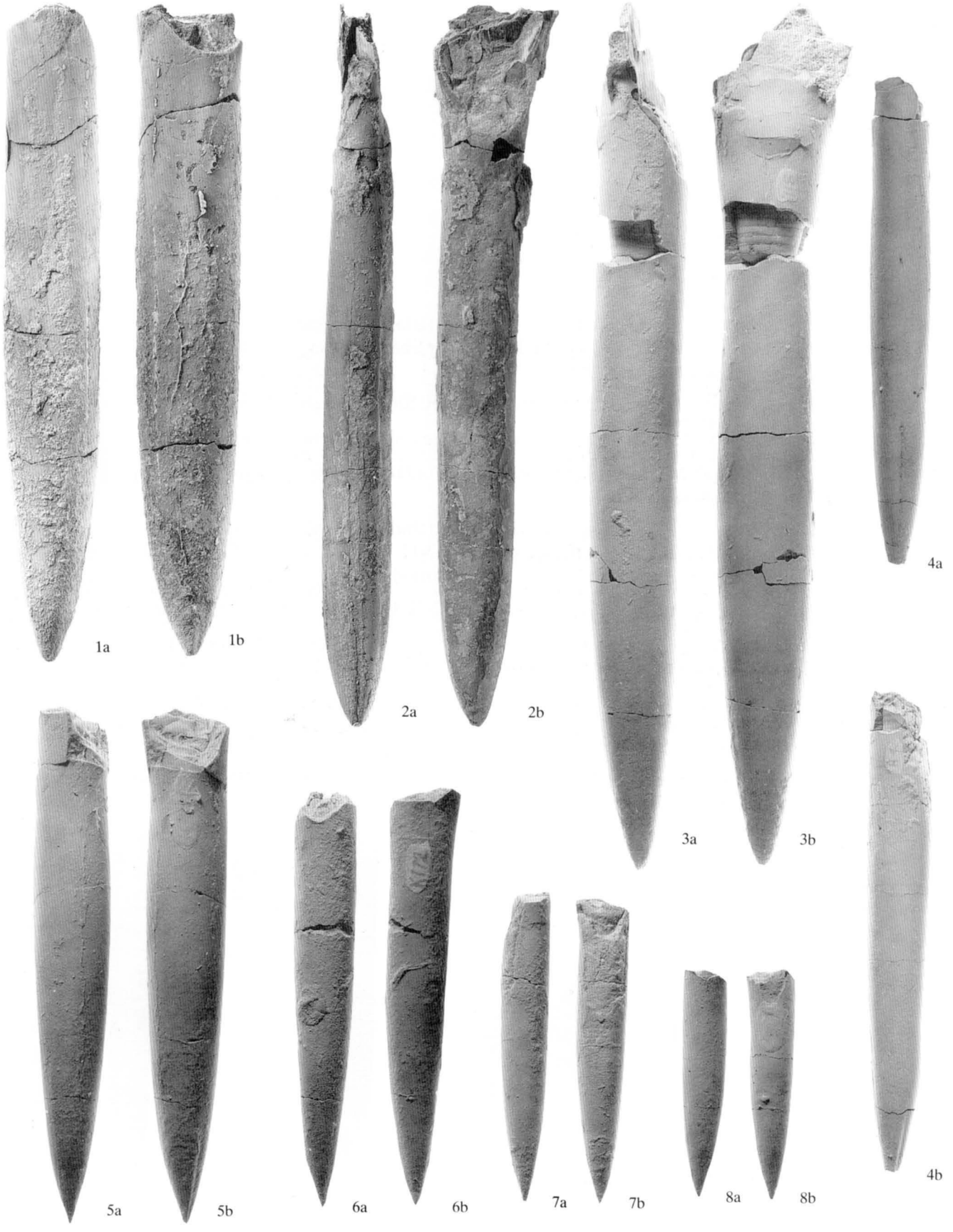


PLATE 2

Fig. | Page

Passaloteuthis bisulcata (Blainville, 1827) 19

1. Variety a. BMNH C59404, bed 19c, Grey Shale Member, East Kettleness, North Yorkshire.

2. Variety b. BMNH C59409, bed 31, Grey Shale Member, same locality.

3. Variety b. BMNH C59405, bed 19c, Grey Shale Member, same locality.

4. Juvenile. NMW 26.135.G353, layer P (Jackson 1926), Junction Bed, Watton Cliff, Dorset.

Passaloteuthis milleri (Phillips, 1867) 22

5. Ventral outline and right profile. BMNH C59396, bed 2, Grey Shale Member, East Kettleness, North Yorkshire.

6. Ventral outline and right profile. BMNH C59401, bed 10, Grey Shale Member, same locality.

7. Ventral outline and right profile. BMNH C59402, same horizon and locality.

8. Ventral outline and right profile. BMNH C59382, bed 4, Grey Shale Member, Staithes, North Yorkshire.

9. Longitudinal section, venter to right. BMNH C59388, bed 27, Cleveland Ironstone Formation, East Kettleness, North Yorkshire.

DOYLE, Toarcian belemnites

Plate 2

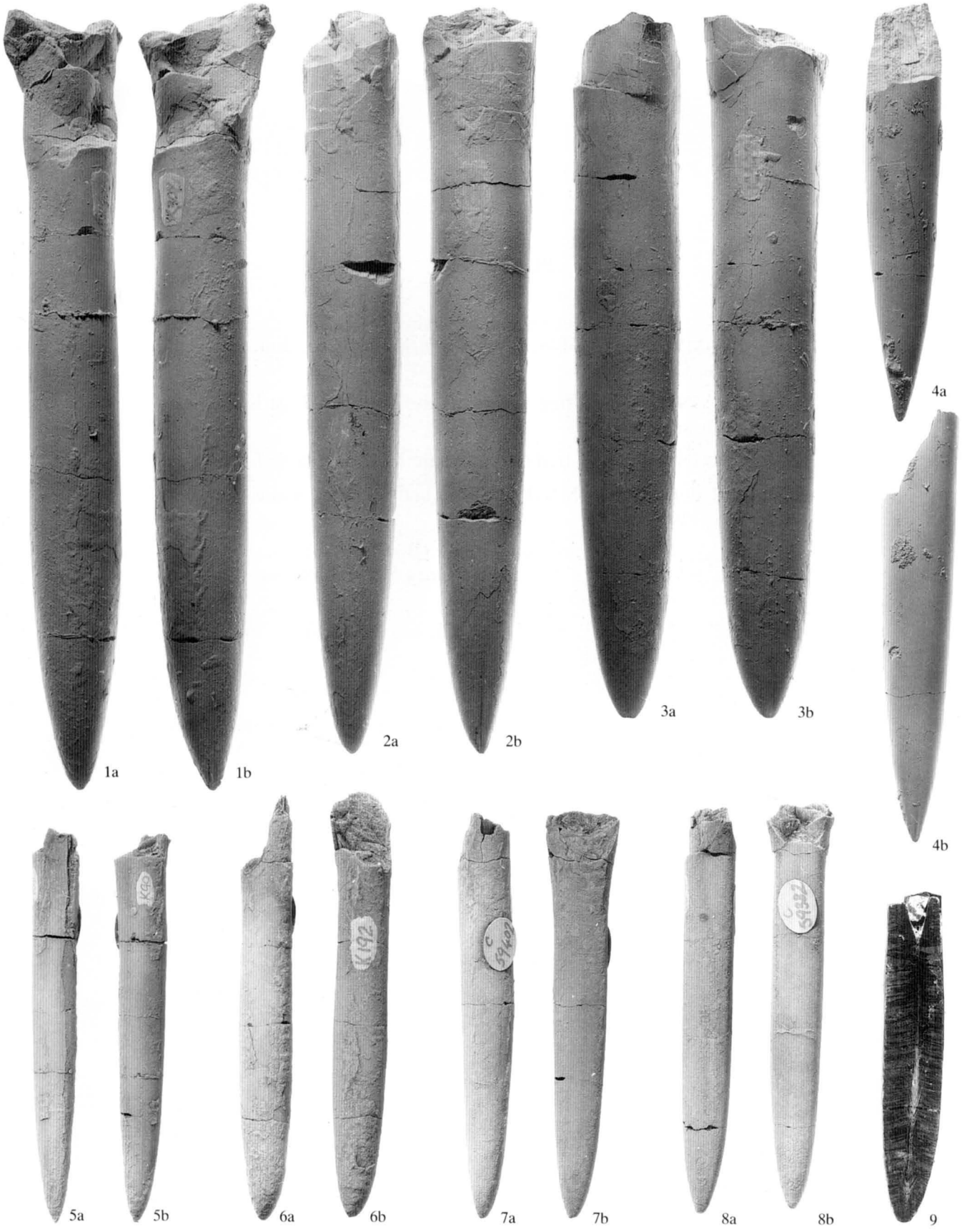


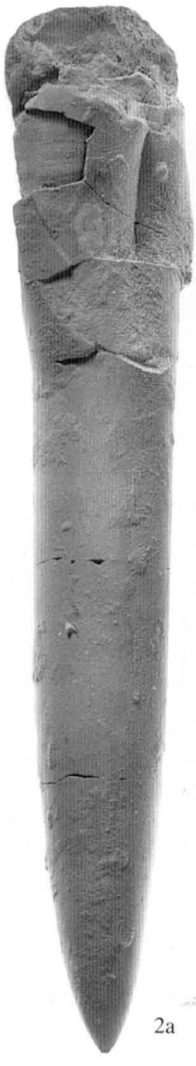
PLATE 3

Fig.		Page
	Passaloteuthis bisulcata (Blainville, 1827)	19
1.	Variety c. NMW 26.135.G146, layer P (Jackson 1926), Junction Bed, Doghouse Cliff, Dorset.	
2.	Variety c. BMNH C59392, bed 1, Grey Shale Member, East Kettleness, North Yorkshire.	
3.	Variety c. BMNH C59400, bed 6 Grey Shale Member, same locality.	
4.	Pathological deformity. BMNH C59394, bed 1, Grey Shale Member, same locality.	
	Pseudohastites longiformis (Blake, 1876)	24
5.	Short form. BMNH C59372, bed 25, Grey Shale Member, Hawsker Bottoms, North Yorkshire.	
6.	Robust form. BMNH C59386, bed 27, Cleveland Ironstone Formation, East Kettleness, North Yorkshire.	
7.	BMNH C59399, bed 6, Grey Shale Member, same locality.	
8.	Lectotype, *Belemnites tenuis* Simpson, 1855, WM 2004, '*annulatus*' Zone, UL 8 [Grey Shale Member], Hawsker Bottoms, North Yorkshire.	
9.	Longitudinal section, venter to right. BMNH C59403, bed 19a, Grey Shale Member, East Kettleness, North Yorkshire.	

DOYLE, Toarcian belemnites

Plate 3

1a



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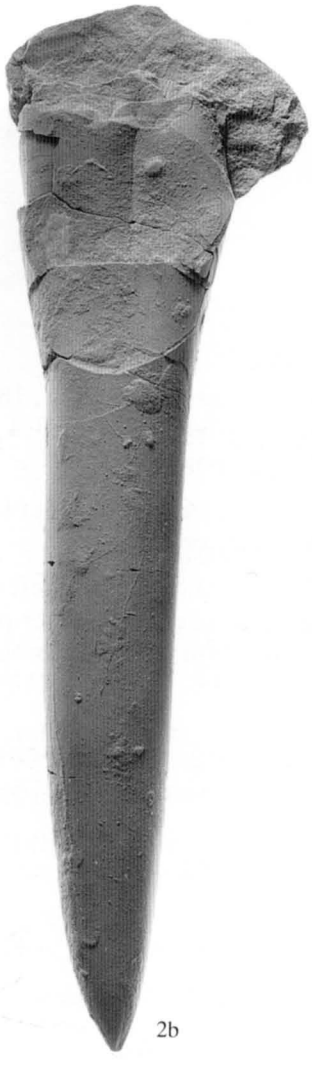

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8b

9

PLATE 4

Fig.		Page
	Parapassaloteuthis robusta (Simpson, 1855)	26
1.	Lectotype, left profile and ventral outline, WM 11, UL 5 [beds 43–46, Jet Rock Member], Whitby, North Yorkshire.	
4.	Left profile and ventral outline. BMNH C6906, Upper Lias [?*falciferum* or *bifrons* zones], Cheltenham, Gloucestershire.	
6.	Lectotype of *Belemnites latisulcatus* Phillips, 1866, left profile and ventral outline, OUM J1874, Upper Lias [probably upper part of the Jet Rock Member, or lower part of the Alum Shale Member], Whitby, North Yorkshire.	
	Parapassaloteuthis zieteni (Mayer-Eymar, 1884)	25
2.	Juvenile, left profile and ventral outline. BMNH C59389, bed 27, Cleveland Ironstone Formation, East Kettleness, North Yorkshire.	
3.	Juvenile, longitudinal section, venter to right. BMNH C59387, same horizon and locality.	
5.	Left profile and ventral outline. BMNH C59493, same horizon and locality.	
7.	Left profile and ventral outline. BMNH C59389, same horizon and locality.	
8.	Left profile and ventral outline. BMNH C59385, same horizon and locality.	
9.	Left profile and ventral outline. BMNH C59384, same horizon and locality.	

DOYLE, Toarcian belemnites

Plate 4

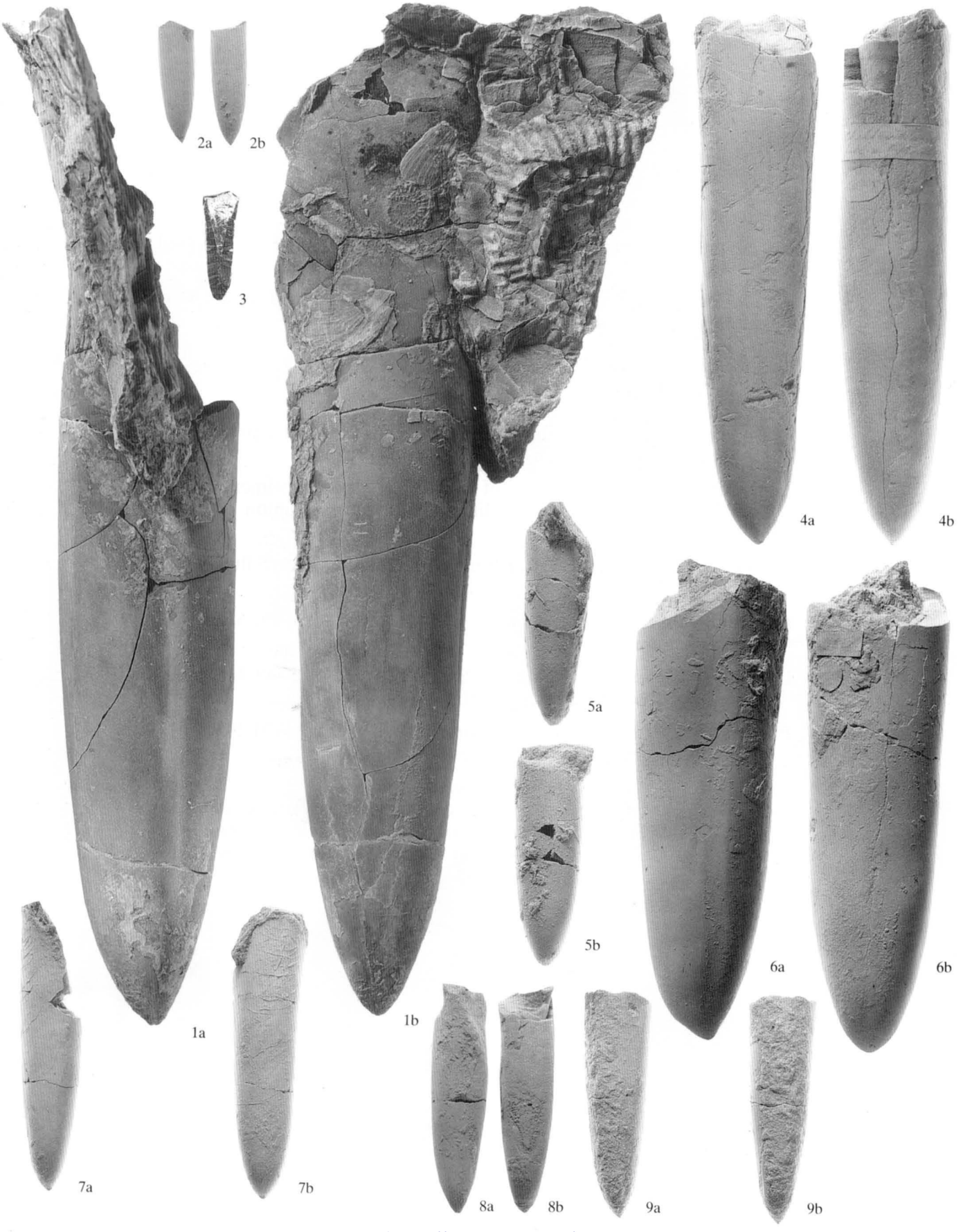


PLATE 5

Fig.		Page
	Parapassaloteuthis robusta (Simpson, 1855)	26
1.	Lectotype of *Belemnites obtusus* Simpson, 1855, WM 119, UL 5 [beds 43–46, Jet Rock Member], Whitby, North Yorkshire.	
2.	Ventral outline and right profile. BMNH C59413, bed xvi, Alum Shale Member, Ravenscar, North Yorkshire.	
	Parapassaloteuthis polita (Simpson, 1866)	27
3.	BMNH C59334, bed 45, Jet Rock Member, Saltwick Bay, North Yorkshire.	
4.	Lectotype, ventral outline and right profile, WM 2047, UL 5 [beds 43–46, Jet Rock Member], High Whitby, North Yorkshire.	
5.	Left profile and ventral outline of slightly deformed specimen. BMNH C20746a, Upper Lias, Minchinhampton Common, Stroud, Gloucestershire.	
6.	BMNH C59324, bed 48 (Ovatum Band), Jet Rock Member, Saltwick Bay, North Yorkshire.	
7.	Longitudinal section, venter to right. BMNH C59342, bed 49, Alum Shale Member, same locality.	
8.	Lectotype of *Belemnites acuminatus* Simpson, 1855, WM 449, UL 5 [beds 43–46, Jet Rock Member], Whitby, North Yorkshire.	
9.	Paralectotype of *Belemnites acuminatus* Simpson, 1855, WM 2054, UL 3 [beds 49–50, Alum Shale Member], same locality.	
	Parapassaloteuthis sp.	26
10.	Pathologically deformed specimen, comparable to *Parapassaloteuthis robusta* Simpson, 1855. Lectotype of *Belemnites pollex* Simpson, 1855, WM 14, UL 5 [beds 43–46, Jet Rock Member], Whitby, North Yorkshire.	

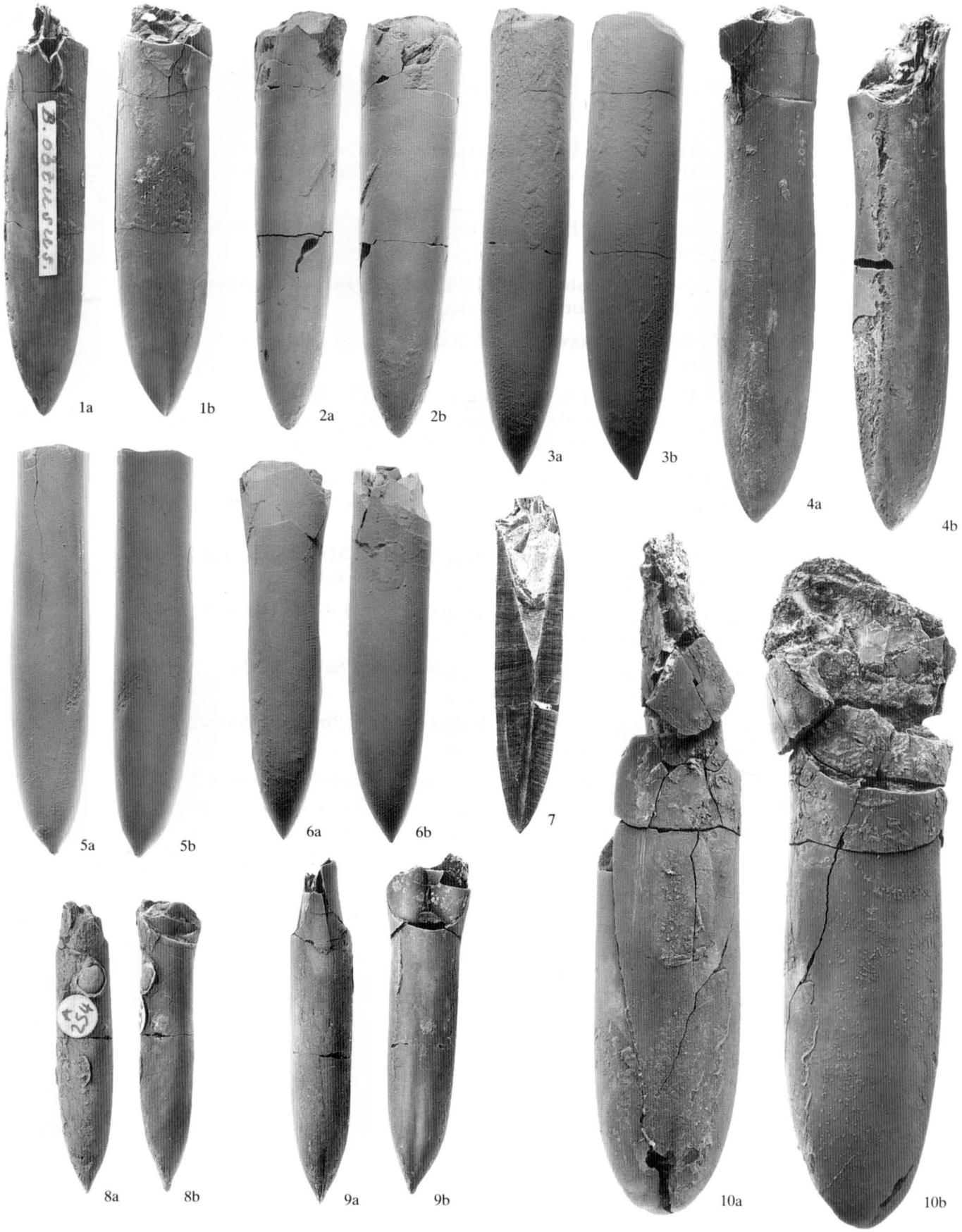


PLATE 6

Fig. Page

Acrocoelites (*Acrocoelites*) *oxyconus* (Zieten, 1831) 29

1. BMNH C59419, bed xxxviii, Alum Shale Member, Ravenscar, North Yorkshire.

2. BMNH C59456, bed 13, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.

3. Longitudinal section, venter to right. BMNH C59353, bed 54, Alum Shale Member, Whitby, North Yorkshire.

4. BMNH C59433, bed xxxviii, Alum Shale Member, Ravenscar, North Yorkshire.

?*Acrocoelites* (*Acrocoelites*) *oxyconus* (Zieten, 1831) 29

6. Lectotype of *Belemnites telum* Simpson, 1855, WM 20, UL 1 [beds 53 and above, Alum Shale Member], Whitby, North Yorkshire.

Acrocoelites (*Acrocoelites*) *subtenuis* (Simpson, 1855) 30

5. Variety b. BMNH C59330, bed 45, Jet Rock Member, Saltwick Bay, North Yorkshire.

7. Paralectotype, ventral outline and right profile, WM 445b, UL 4, 5 [beds 43–48, Jet Rock Member], Whitby, North Yorkshire.

8. Lectotype, ventral outline and right profile, WM 445c, UL 4, 5 [beds 43–48, Jet Rock Member], same locality.

9. BMNH C59329, bed 47, Jet Rock Member, Saltwick Bay, North Yorkshire.

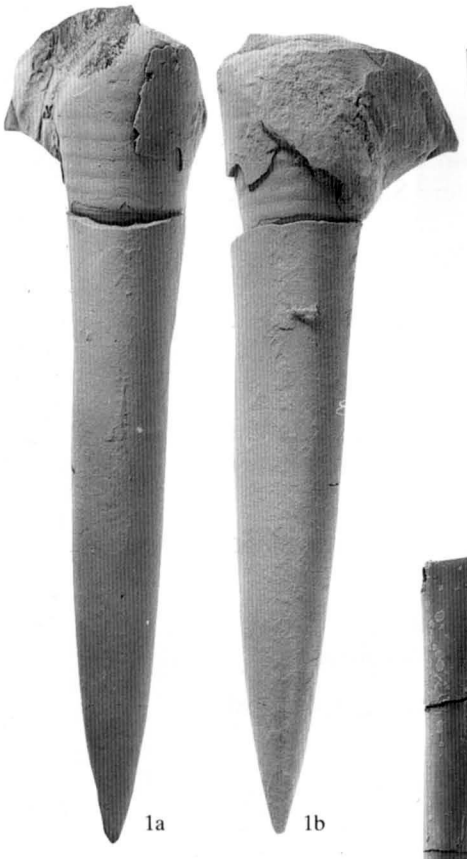
10. Ventral outline and right profile. BMNH C59321, bed 49, Alum Shale Member, same locality.

11. Variety a. BMNH C59478, bed 4, Raasay Ironstone, Inverarish Burn, Raasay.

12. Variety a. BMNH C59477, same horizon and locality.

13. Variety a. BMNH C59323, bed 49, Alum Shale Member, Saltwick Bay, North Yorkshire.

14. BMNH C59415, Bed xiv, Alum Shale Member, Ravenscar, North Yorkshire.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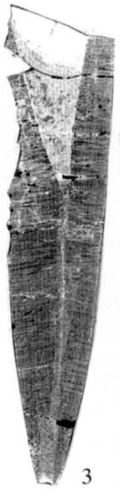
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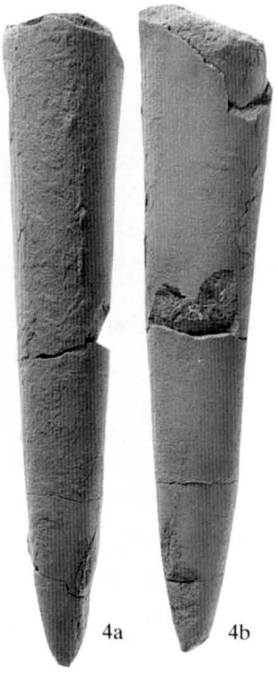
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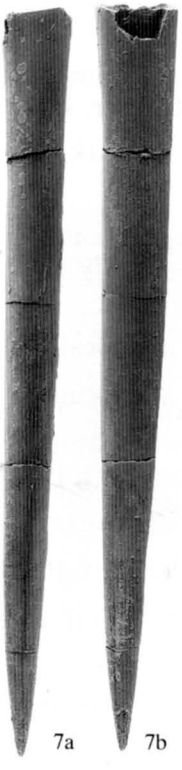
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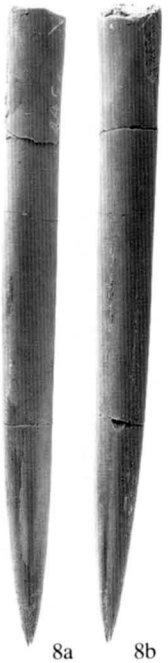
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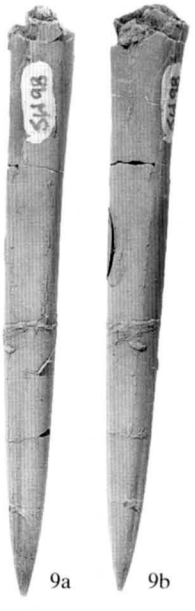
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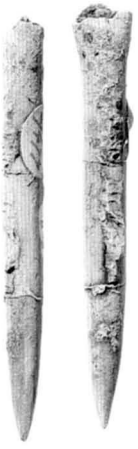
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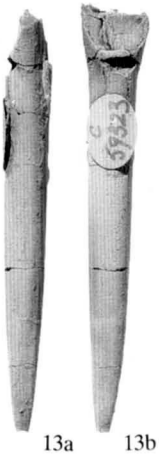
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PLATE 7

Fig.		Page
	Acrocoelites (*Acrocoelites*) *subtenuis* (Simpson, 1855)	30
1.	Variety b. BMNH C59331, bed 45, Jet Rock Member, Saltwick Bay, North Yorkshire.	
2.	BMNH C59322, bed 49, Alum Shale Member, same locality.	
3.	Longitudinal section, venter to right. BMNH C59343, same horizon and locality.	
	Acrocoelites (*Acrocoelites*) *longiconus* (Schwegler, 1969)	34
4.	Lectotype of *Belemnites rostratus* Simpson, 1855, ventral outline and right profile, WM 2048, UL 4 [beds 47–48, Jet Rock Member], Hawsker Bottoms, North Yorkshire.	
5.	Ventral outline and right profile. BMNH C59346, bed 51, Alum Shale Member, Whitby, North Yorkshire.	
6.	Specimen with crushed epirostrum, ventral outline and right profile. BMNH C 59347, bed 53, Alum Shale Member, same locality.	
17.	Ventral outline and right profile. BMNH C59348, same horizon and locality.	
	Acrocoelites (*Acrocoelites*) *strictus* Lissajous, 1927	32
7.	Lectotype, UCBL 27491, *bifrons* Zone [probably Leda Ovum Beds], Northampton.	
8.	Paralectotype, UCBL 27490, same horizon and locality.	
12.	Paralectotype, UCBL 27489, same horizon and locality.	
	Acrocoelites (*Acrocoelites*) *bobeti* Lissajous, 1927	33
9.	BMNH C59491, bed 11, Bridport Sands, East Cliff, Bridport, Dorset.	
10.	BMNH C59480, Down Cliff Clay, Down Cliff, Dorset.	
11.	BMNH C59490, bed 11, Bridport Sands, East Cliff, Bridport, Dorset.	
13.	BMNH C59481, bed 16, Bridport Sands, Burton Cliff, Burton Bradstock, Dorset.	
14.	BMNH C59480, Down Cliff Clay, Down Cliff, Dorset.	
15.	Juvenile. BMNH C59492, bed 11, Bridport Sands, East Cliff, Bridport, Dorset.	
	Acrocoelites (*Acrocoelites*) *subgracilis* Kolb, 1942	35
16.	BMNH C59471, bed 80, Grey Sandstone Member, Blea Wyke Point, North Yorkshire.	

DOYLE, Toarcian belemnites

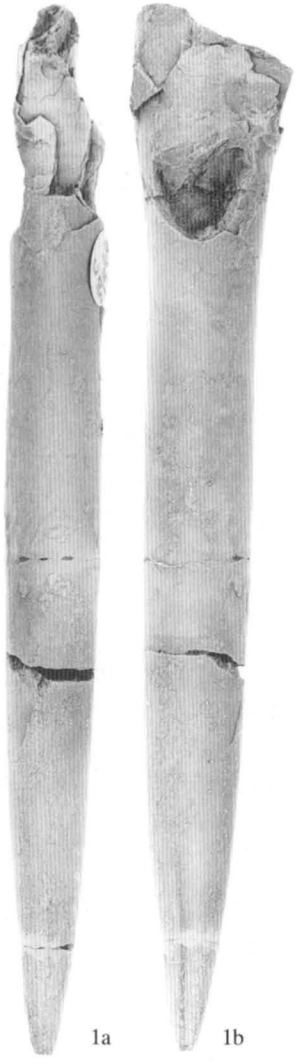
Plate 7

PLATE 8

Fig.		Page
	Acrocoelites (*Acrocoelites*) *subgracilis* Kolb, 1942	35
1.	Ventral outline and right profile. BMNH C59444, bed 9, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	
2.	Ventral outline and right profile. BMNH C59345, bed 51, Alum Shale Member, Whitby, North Yorkshire.	
	Acrocoelites (*Toarcibelus*) *quenstedti* (Oppel, 1856)	36
3.	BMNH C59497, limestone capping Upper Lias Clay, Bredon Hill, Hereford and Worcester.	
5.	Short form. BMNH C59482, Bridport Sands, Burton Cliff, Burton Bradstock, Dorset.	
6.	BMNH C59474, Terebratula Bed (Aalenian), Blea Wyke Point, North Yorkshire.	
7.	BMNH C59496, bed 15, Cephalopod Bed, Wotton Hill, Wotton-under-Edge, Gloucestershire.	
	Acrocoelites (*Toarcibelus*) *trisulculosus* (Simpson, 1855)	37
4.	Large adult (='*Belemnites validus*' Simpson), left profile. BMNH C59344, bed 41, Jet Rock Member, North Yorkshire.	

DOYLE, Toarcian belemnites

Plate 8



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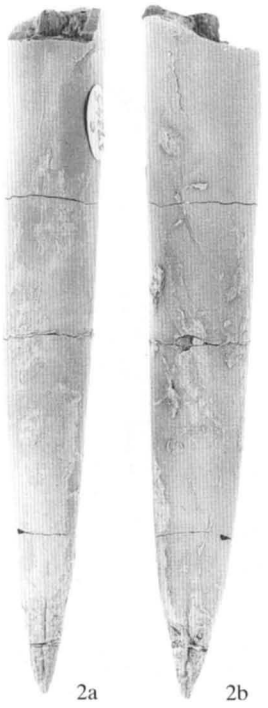

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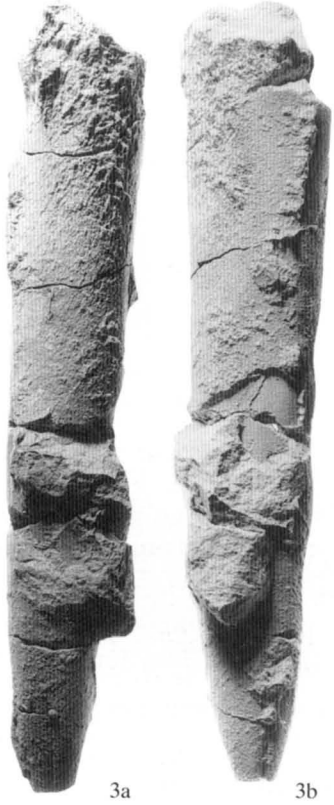

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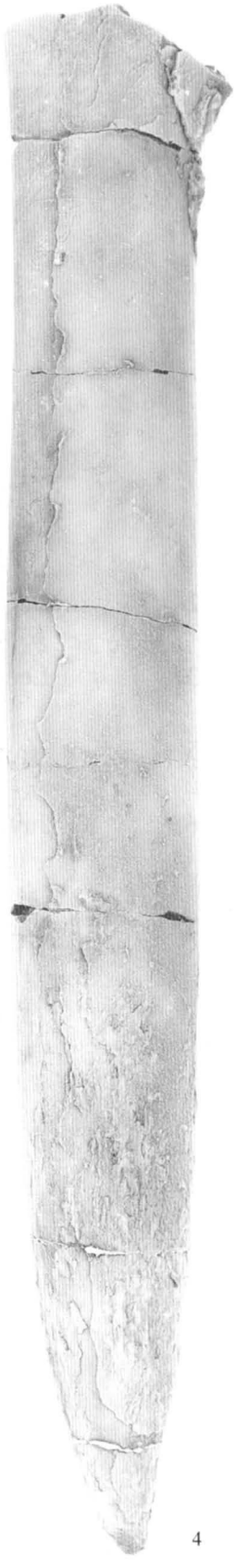

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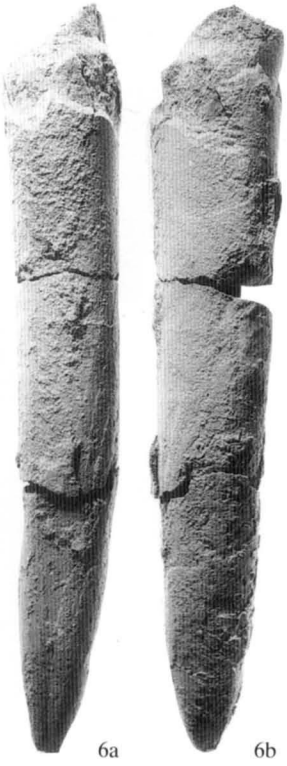

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PLATE 9

Fig.		Page
	Acrocoelites (*Toarcibelus*) *trisulculosus* (Simpson, 1855)	37
1.	Lectotype, ventral outline and right profile, WM 36, UL 7 [beds 33–40, Jet Rock Member], Saltwick Bay, North Yorkshire.	
2.	Lectotype of *Belemnites distortus* Simpson, 1855, ventral outline and right profile, WM 34a, Jet Rock Member, Whitby, North Yorkshire.	
3.	Lectotype of *Belemnites substriatus* Simpson, 1855, WM 2646, UL 6 [beds 41–42, Jet Rock Member], Saltwick Bay, North Yorkshire.	
5.	Juvenile, ventral outline and right profile. BMNH C59380, bed 38, Jet Rock Member, Hawsker Bottoms, North Yorkshire.	
6.	Juvenile, ventral outline and right profile. BMNH C59381, same horizon and locality.	
	Acrocoelites (*Toarcibelus*) ?*trisulculosus* (Simpson, 1855)	37
4.	Lectotype (here designated) of *Belemnites mulgravius* Simpson, 1855, WM 2614, UL 6 [beds 41–42, Jet Rock Member], Sandsend, North Yorkshire.	

DOYLE, Toarcian belemnites

Plate 9

PLATE 10

Fig.		Page
	Acrocoelites (*Toarcibelus*) *trisulculosus* (Simpson, 1855)	37
1.	Lectotype of *Belemnites validus* Simpson, 1855, WM 2607, '?*annulatus*' Zone [more probably Jet Rock Member], Whitby, North Yorkshire.	
2.	Lectotype of *Belemnites incisus* Simpson, 1855, WM 122, Jet Rock Member, Whitby, North Yorkshire.	
3.	Lectotype of *Belemnites bituminosus* Simpson, 1884, WM 2707, UL 7 [beds 33–40 Jet Rock Member], Saltwick Bay, North Yorkshire.	
	Acrocoelites (*Odontobelus*) *pyramidalis* (Zieten, 1831)	42
4.	BMNH C59356, bed 55, Alum Shale Member, Whitby, North Yorkshire.	
5.	BMNH C59449, bed 11, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	
6.	BMNH C59325, bed 49, Alum Shale Member, Saltwick Bay, North Yorkshire.	
7.	Longitudinal section, venter to right. BMNH C59420, bed xiv, Jet Rock Member, Ravenscar, North Yorkshire.	
8.	Lectotype of *Belemnites curtus* Simpson, 1855, right profile and ventral outline, WM 2063, UL 4 [beds 47–48, Jet Rock Member], Whitby, North Yorkshire.	

DOYLE, Toarcian belemnites

Plate 10

PLATE 11

Fig.		Page
	Acrocoelites (*Toarcibelus*) *trisulculosus* (Simpson, 1855)	37
1.	Paralectotype, ventral outline and right profile, WM 31, Jet Rock Member, Hawsker Bottoms, North Yorkshire.	
2.	Lectotype of *Belemnites spicatus* Simpson, 1855, WM 21, Jet Rock Member, Whitby, North Yorkshire.	
3.	BMNH C59377, bed 35, Jet Rock Member, Hawsker Bottoms, North Yorkshire.	
	Acrocoelites (*Odontobelus*) *pyramidalis* (Zieten, 1831)	42
4.	BMNH C59412, bed xiv, Jet Rock Member, Ravenscar, North Yorkshire.	
5.	BMNH C59437, bed xliv, Alum Shale Member, Ravenscar, North Yorkshire.	
	Acrocoelites (*Odontobelus*) *vulgaris* (Young & Bird, 1822)	44
6.	BMNH C59357, bed 55, Alum Shale Member, Whitby, North Yorkshire.	
7.	Paralectotype of *Belemnites regularis* Phillips, 1867, OUM J17066, Upper Lias Clay, Badby near Banbury, Oxfordshire.	
8.	Longitudinal section, venter to right. BMNH C59365, bed 63, Alum Shale Member, Whitby, North Yorkshire.	

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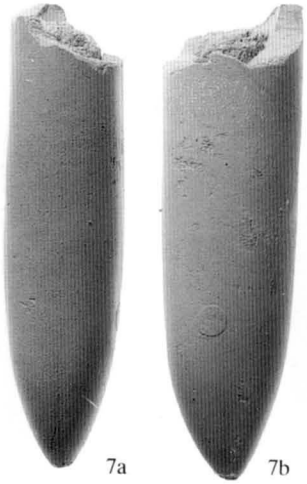

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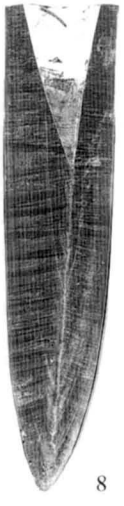

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PLATE 12

Fig. Page

Acrocoelites (*Toarcibelus*) *ilminsterensis* (Phillips, 1867) 39

1. Lectotype, ventral outline and right profile, GMB M1216a, Upper Lias [Junction Bed], Ilminster, Somerset.

2. Paralectotype, ventral outline and right profile, GMB M1216, same horizon and locality.

3. BGS GSM53878, Upper Lias [?Junction Bed], Nailsworth, Avon.

4. BMNH C59411, bed 37, Jet Rock Member, Port Mulgrave, North Yorkshire.

5. Juvenile, ventral outline and right profile. Lectotype of *Belemnites iuvensis* Werner, 1912, GMB M1216c, Upper Lias [Junction Bed], Ilminster, Somerset.

6. Paralectotype, ventral outline and right profile, GMB M1216b, same horizon and locality.

7. Juvenile. BMNH C59501, upper 1.7 m of the Junction Bed, Stocklinch Reservoir, Somerset.

DOYLE, Toarcian belemnites

Plate 12

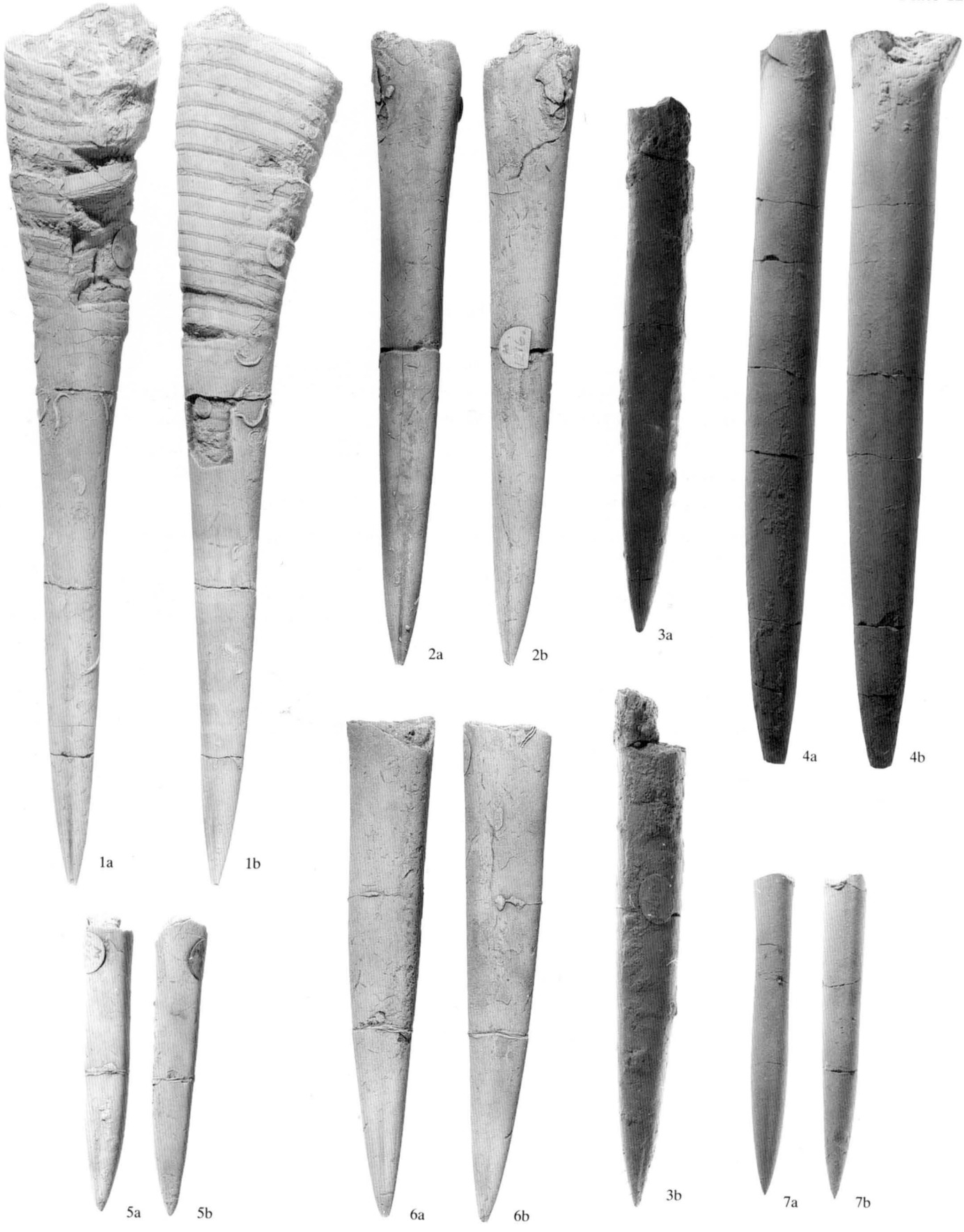

PLATE 13

Fig.		Page
	Acrocoelites (*Toarcibelus*) *inaequistriatus* (Simpson, 1855)	41
1.	Lectotype, WM 454, Jet Rock Member, Whitby, North Yorkshire.	
2.	BMNH C59462, bed 17, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	
3.	Pathologically deformed specimen. BMNH C59340, bed 43, Jet Rock Member, Saltwick Bay, North Yorkshire.	
4.	Possible type specimen of *Belemnites compressus* Young & Bird, 1828, closely resembling their specimen figured in pl. XV, fig. 3 (and presumed to be in the Whitby Museum). WM 14, Jet Rock Member, Sandsend, North Yorkshire.	
5.	Lectotype of *Belemnites concavus* Simpson, 1855, WM 41, '*serpentinus*' Zone (=*falciferum* Zone), Saltwick Bay, North Yorkshire.	
	Acrocoelites (*Odontobelus*) *vulgaris* (Young & Bird, 1822)	44
6.	BMNH C59360, bed 56, Alum Shale Member, Whitby, North Yorkshire.	
7.	Lectotype (here designated) of *Belemnites regularis* Phillips, 1867, OUM J17056, Upper Lias Clay, Badby near Banbury, Oxfordshire.	

DOYLE, Toarcian belemnites

Plate 13

PLATE 14

Fig. | Page

Acrocoelites (*Toarcibelus*) *inaequistriatus* (Simpson, 1855) 41

1. Adult lacking epirostrum. BMNH C59349, bed 53, Alum Shale Member, Whitby, North Yorkshire.

2. Adult with epirostrum partly destroyed. BMNH C59423, bed xxx, Alum Shale Member, Ravenscar, North Yorkshire.

3. Lectotype of *Belemnites cinereus* Simpson, 1884, WM 1996, UL 1 [bed 53 and above, Alum Shale Member], Whitby, North Yorkshire.

7. Longitudinal section, venter to right. BMNH C59359, bed 56, Alum Shale Member, Whitby, North Yorkshire.

Acrocoelites (*Odontobelus*) *vulgaris* (Young & Bird, 1822) 44

4. BMNH C59417, bed xxiv, Alum Shale Member, Ravenscar, North Yorkshire.

5. BMNH C59361, bed 56, Alum Shale Member, Whitby, North Yorkshire.

6. BMNH C59451, bed 15, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.

Acrocoelites (*Odontobelus*) *levidensis* (Simpson, 1855) 45

8. Lectotype, ventral outline and right profile, WM 2059, Alum Shale Member, Peak [Ravenscar], North Yorkshire.

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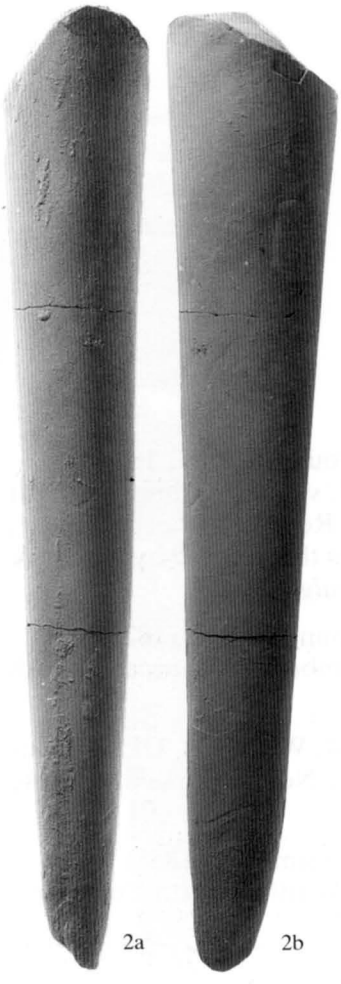

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3a 3b

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8a 8b

PLATE 15

Fig.		Page
	?Acrocoelites (*Odontobelus*) *vulgaris* (Young & Bird, 1822)	44
1.	Lectotype of *Belemnites densus* Simpson, 1855, ventral outline and right profile, WM 443, UL 7 [beds 33–40, Jet Rock Member], Whitby, North Yorkshire. This specimen approaches that figured by Young & Bird (1822, pl. XIV, fig. 1) as *Belemnites vulgaris*.	
	Acrocoelites (*Odontobelus*) *vulgaris* (Young & Bird, 1822)	44
2.	BMNH C59424, bed xxx, Alum Shale Member, Ravenscar, North Yorkshire.	
3.	Lectotype of *Belemnites urbanus* Simpson, 1884, WM 2610, UL 5a [beds 45–46, Jet Rock Member], Saltwick Bay, North Yorkshire. Note pathological groove in the stem region.	
	Acrocoelites (*Odontobelus*) *levidensis* (Simpson, 1855)	45
4.	BMNH C59369, bed 70, Alum Shale Member, Whitby, North Yorkshire.	
5.	Ventral outline and right profile. BMNH C59438, bed xliv, Alum Shale Member, Ravenscar, North Yorkshire.	
6.	BMNH C59442, bed lii, Alum Shale Member, locality as above.	
7.	BMNH C59450, bed 11, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	

PLATE 16

Fig.		Page
	Acrocoelites (*Odontobelus*) *tricissus* (Janensch, 1902)	46
1.	BMNH C59457, bed 13, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	
2.	BMNH C59416, bed xxiv, Alum Shale Member, Ravenscar, North Yorkshire.	
3.	BMNH C59426, bed xxxii, Alum Shale Member, locality as above.	
4.	BMNH C59425, horizon and locality as above.	
5.	BMNH C59495, bed 15, Cephalopod Bed, Wotton Hill, Gloucestershire.	
	Acrocoelites (*Odontobelus*) *subtricissus* Kolb, 1942	47
6.	BMNH C59470, bed 70, Grey Sandstone Member, Blea Wyke Point, North Yorkshire.	
7.	BMNH C59427, bed lii, Alum Shale Member, Ravenscar, North Yorkshire.	
8.	Longitudinal section, venter to right. BMNH C59341, bed 49, Alum Shale Member, Saltwick Bay, North Yorkshire.	

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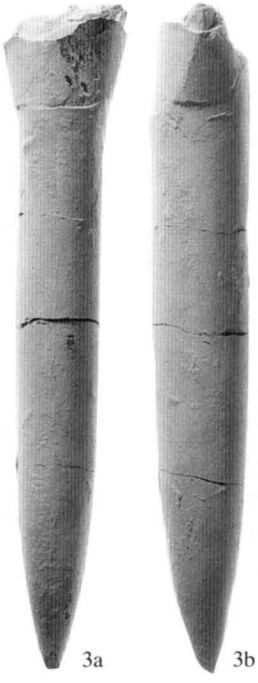

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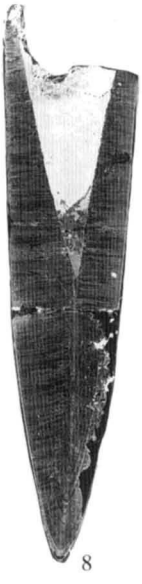

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PLATE 17

Fig.		Page
	Acrocoelites (*Odontobelus*) *subtricissus* Kolb, 1942	47
1.	BMNH C59350, bed 53, Alum Shale Member, Whitby, North Yorkshire.	
2.	BMNH C59320, bed 51, Alum Shale Member, Saltwick Bay, North Yorkshire.	
3.	BMNH C59339, bed 43, Jet Rock Member, locality as above.	
	Acrocoelites (*Odontobelus*) *wrighti* (Oppel, 1856)	48
4.	Ventral outline and right profile. BMNH C59439, bed xliv, Alum Shale Member, Ravenscar, North Yorkshire.	
5.	Ventral outline and right profile. BMNH C59441, bed xl, Alum Shale Member, locality as above.	
6.	Ventral outline and right profile. BMNH C59443, bed 9, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.	
7.	Ventral outline and right profile. BMNH C59440, bed xliv, Alum Shale Member, Ravenscar, North Yorkshire.	

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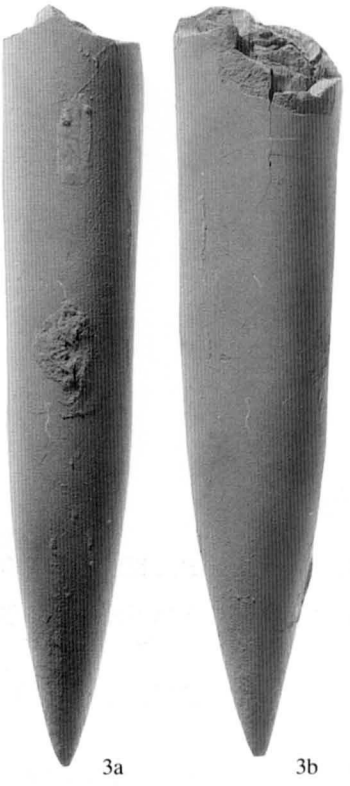

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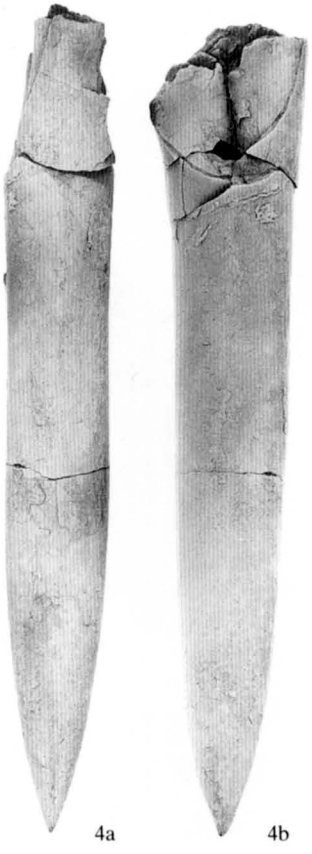

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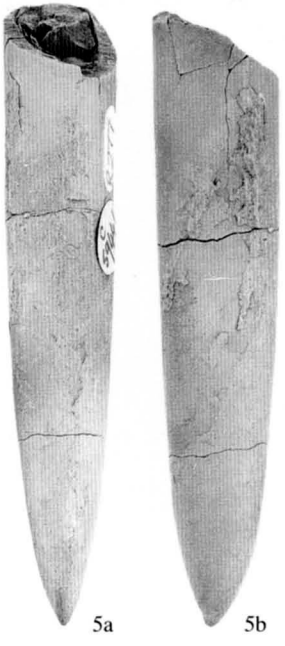

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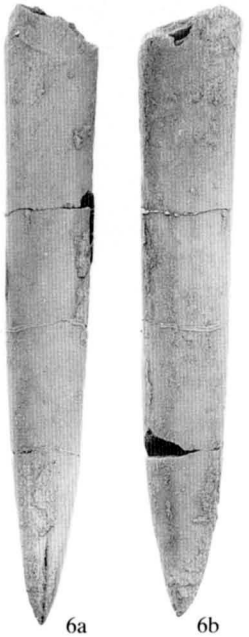

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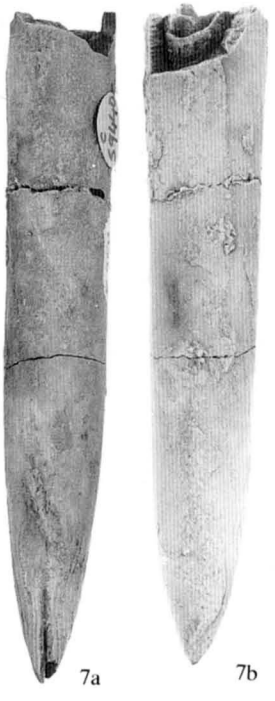

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