

THE BRITISH TOARCIAN  
(LOWER JURASSIC)  
BELEMNITES

P. DOYLE

PART 2

Pages 50–79; Plates 18–28  
with Title Page, Contents and Index

MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

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1990 – 1992

The Palaeontographical Society issues an annual volume of serially numbered publications; these may either be a single complete monograph or part of a continuing monograph.

Publication No. 587, issued as part of  
Volume 145 for 1991

Recommended reference to this publication:

DOYLE, P. 1992. The British Toarcian (Lower Jurassic) belemnites. Part 2. *Monograph of the Palaeontographical Society* London: 50–79, pls 18–28. (Publ. No. 587, part of vol. 144 for 1991).

ABSTRACT

Part 2 includes descriptions of 13 species belonging to 5 genera (including *Simpsonibelus* gen. nov. and *Brevibelus* nom. nov.) of the Belemnitidae d'Orbigny; 3 species belonging to one genus of the Salpingoteuthididae fam. nov.; and one species belonging to one genus of the Belemnoteuthididae Zittel.

RÉSUMÉ

La 2ème partie comprend les descriptions de 13 espèces appartenant à 5 genres des Belemnitidae d'Orbigny (y compris *Simpsonibelus* gen. nov. et *Brevibelus* nom. nov.). Sont également décrites 3 espèces appartenant à un genre des Salpingoteuthididae fam. nov., et une espèce appartenant à un genre des Belemnoteuthididae Zittel.

ZUSAMMENFASSUNG

Teil 2 enthält Beschreibungen von 13 Arten, die zu 5 Gattungen der Belemnitidae d'Orbigny gehören (einschließlich *Simpsonibelus* n. gen. und *Brevibelus* n. gen.), 3 Arten einer Gattung der Salpingoteuthididae n. fam. sowie 1 Art einer Gattung der Belemnoteuthididae Zittel.

РЕЗЮМЕ

Часть 2 включает описание 13 видов, принадлежащих 5 родам (включая *Simpsonibelus* gen. nov. и *Brevibelus* nom. nov.) Belemnitidae d'Orbigny, 3 вида одного рода Salpingoteuthididae fam. nov. и один вид рода, входящего в состав Belemnoteuthididae Zittel.

Edited by R. M. OWENS

*Originated and printed in Great Britain  
by Michael Heath Limited, Reigate, Surrey*

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| PART<br>NO.                                | PAGES | PLATES | ISSUED IN<br>VOL. FOR YEAR | PUBL.<br>NO. | PUBLISHED                 |
|--|-------|--------|----------------------------|--------------|---------------------------|
| 1  | 1-49  | 1-17   | 144                        | 1990         | 584      20 December 1990 |
| 2  | 50-79 | 18-28  | 145                        | 1991         | 587      January 1992     |
| incl. Title-page,<br>Contents and<br>Index |       |        |                            |              |                           |

Recommended reference to this publication:

DOYLE, P. 1990-92. The British Toarcian (Lower Jurassic) Belemnites. *Monograph of the Palaeontographical Society*, London: Part 1, 1-49, pls 1-17 (Publ. No. 584, part of vol. 144 for 1990); Part 2, 50-79, pls 18-28 (Publ. No. 587, Part of vol. 145 for 1991).

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# THE BRITISH TOARCIAN (LOWER JURASSIC) BELEMNITES

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Genus **YOUNGIBELUS** Riegraf, 1980

*Type species.* *Belemnites tubularis* Young & Bird, 1822.

*Other species.* *Y. gigas* (Quenstedt), *Y. simpsoni* (Mayer-Eymar).

*Diagnosis.* Small to large, elongate slender, cylindriconal Megateuthidinae. Outline and profile similar, symmetrical or almost symmetrical and cylindrical to cylindriconal. An epirostrum is commonly developed, generally extending the total length of the rostrum to three times that of the orthorostrum. Transverse sections weak to moderately compressed, elliptical, subquadrate or pyriform. Apical grooves are absent or residual, although the apices of both epi- and orthorostra are commonly well-striated. Lateral lines consist of a weak ridge or weal separating two narrow depressions that extend for the length of the rostrum. The phragmocone is central with a slight ventral deflection at its apex, commonly penetrating one quarter of the rostrum. The apical line is ortholineate and the alveolar angle is in the region of 27°.

*Range.* Lower Toarcian of Britain, mainland Europe and possibly the USSR.

*Remarks.* *Youngibelus* is a distinctive elongate symmetrical genus, characteristically with a long epirostrum. It differs from *Dactylosteuthis* by its slender cylindrical rather than digit-like orthorostrum and its ortholineate apical line, and from *Salpingoteuthis* by its greater size and its lack of elongate grooves on its flanks.

**Youngibelus tubularis** (Young & Bird, 1822) Pl. 18, figs 1–5, 7

- \* . 1822 *Belemnites tubularis* Young & Bird, p. 259, pl. XIV, fig. 6.
- . 1829 *Belemnites tubularis* Young & Bird; Phillips, p. 163, pl. XII, fig. 20.
- . 1831 *Belemnites longissimus* Miller; Zieten, p. 28, pl. XXI, figs 10, 11.
- . 1838 *Belemnites tubularia* Phillips; Brown, p. 43, pl. XXIX, fig. 17.
- v non 1848 *Belemnites acuarius tubularis* Quenstedt, p. 411, pl. XXV, figs 9, 10 [=Acrocoelites (*Toarcibelus*) *gracilis* (Quenstedt)].
- v . 1855 *Belemnites tubularis* Young & Bird; Simpson, p. 23.
- v . 1866 *Belemnites productus* Simpson, p. 216 [Lectotype, here designated, WM 975, 'serpentinus' Zone, Whitby, North Yorkshire]
- v . 1867 *Belemnites tubularis* Young & Bird; Phillips (*pars*), p. 68, pl. XIV, fig. 36, *non* fig. 36p"-p" [=*Youngibelus gigas* (Quenstedt)].
- v . 1876 *Belemnites tubularis* Young & Bird; Blake (*in Tate & Blake*), p. 325.
- 1883 *Belemnites tubularis* Young & Bird; Mayer-Eymar, p. 641.
- v . 1884 *Belemnites productus* Simpson; Simpson, p. 26.
- . 1906 *Belemnites (Dactylosteuthis) tubularis* Young & Bird; Lissajous, p. 56, pl. 5, fig. 1.
- 1912 *Belemnites tubularis* Young & Bird; Werner (*pars*), p. 128.
- 1920 *Cuspiteuthis tubularis* (Young & Bird); Bülow-Trummer, p. 107.
- 1925 *Dactylosteuthis tubularis* (Young & Bird); Lissajous, p. 125.
- v non 1969 *Belemnites tubularis* Young & Bird; Schwegler, p. 206, text-fig. 87.
- ? non 1971 *Salpingoteuthis tubularis* (Young & Bird); Činčurová, p. 71, pl. V, fig. 4.
- 1980 *Youngibelus tubularis* (Young & Bird); Riegraf, p. 149.
- v . 1984 *Youngibelus tubularis* (Young & Bird); Riegraf *et al.*, p. 158, pl. 11, figs 7, 8, *non* fig. 6 [=Acrocoelites (*Toarcibelus*) *ilmminsterensis* (Phillips)].
- v . 1984 *Youngibelus gigas* (Quenstedt); Riegraf *et al.* (*pars*), p. 158, pl. 11, fig. 11 only.
- v . 1985 *Youngibelus tubularis* (Young & Bird); Doyle, p. 136, pl. 1, figs 1–5.

*Type specimen.* Neotype (designated Doyle 1985, p. 136), BMNH C59185, from bed 43 of the Bituminous Shales (*falciferum* Subzone and Zone), Saltwick Bay, North Yorkshire.

*Diagnosis.* Large, elongate, cylindrical *Youngibelus* with epirostrum. Outline and profile symmetrical and cylindrical. Apex acute. Transverse sections of orthorostrum pyriform to elliptical, of epirostrum almost circular. No apical grooves, rostral surface wrinkled in alveolar region.

*Material.* BMNH, 104 specimens; BGS, 7 specimens; OUM, 7 specimens; WM, 6 specimens. All from the *falciferum* Zone, Jet Rock Member, North Yorkshire.

*Description.* Very elongate and slender cylindrical rostra in which the length of the orthorostrum is approximately nine times Dv. The epirostrum commonly extends for twice

the length of the orthorostrum. The outline is symmetrical and cylindrical, with a slight adoral flaring, and the apex of the epirostrum is very acute where preserved. The apex of the orthorostrum is generally mucronate. The profile is less symmetrical than the outline, with a slightly inflated venter, and cylindrical. Where the epirostral wall leaves the orthorostrum, there is a tendency to produce a slight constriction in both outline and profile. Transverse sections of the orthorostrum are compressed and pyriform, or more rarely, elliptical, whereas those of the uncrushed epirostrum are almost circular.

No apical grooves are found in this species, but apical striae are commonly well-developed, restricted to the very posterior end of the orthorostrum, but extending almost for its length in the epirostrum. Wrinkles on the surface of the rostrum have been found in the alveolar region, and more extreme cases have led to the separation of the 'species' *Belemnites productus* Simpson. However, this is not regarded as a taxonomic feature of any weight. The lateral lines are developed as long, narrow depressions separated by a weak ridge or weal for the length of the orthorostrum. The phragmocone penetrates approximately one third of the orthorostrum, and the apical line is ortholineate.

*Ontogeny.* The ontogeny of this species has been fully discussed elsewhere (Doyle 1985).

| Specimen    | L      | l     | lo   | Dv   | Dl  |
|-------------|--------|-------|------|------|-----|
| BMNH C42213 | 185.3u | 136.0 | —    | 10.6 | 8.9 |
| C59185      | 200.4u | 171.6 | —    | 10.3 | 8.2 |
| C59200      | 241.3u | 211.0 | —    | 9.7  | 8.1 |
| C59186      | 112.2c | 87.5  | 54.2 | 10.3 | 9.1 |
| C59187      | 100.7c | 83.6  | 55.8 | 8.7  | 6.9 |

Table 23. Measurements of *Youngibelus tubularis* (Young & Bird, 1822).

Abbreviations: lo, distance from apex of orthorostrum to adapical tip of protoconch; c, epirostrum crushed; u, epirostrum uncrushed.

*Remarks.* *Y. tubularis* resembles *Acrocoelites (Toarcibelus) gracilis* (Zieten), and has often been confused with it (e.g. Quenstedt 1848, Werner 1912; Schwegler 1969; Riegraf *et al.* 1984). However, *A. (T.) gracilis* may be easily distinguished by its quadrate section and well-defined apical grooves. *Y. tubularis* differs from *Y. gigas* (Quenstedt) which posses a more robust and massive orthorostrum, and generally a longer epirostrum (the specimen figured by Phillips 1867 in pl. XIV, fig. 36p"-p" is a typical *Y. gigas*). *Y. tubularis* resembles *Y. simpsoni* (Mayer-Eymar) in the form of its orthorostrum, but the latter differs by its more robust rostrum with a rounded pyriform section. *Y. simpsoni* (=*Y. levis*) was considered to be a sexual dimorph of *Y. tubularis* by Doyle (1985).

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

#### **Youngibelus simpsoni** (Mayer-Eymar, 1883) Pl. 18, fig. 6; Pl. 19, figs 1–10.

- non 1836 *Belemnites laevis* Roemer, p. 165 [=*Megateuthis laevis* (Roemer)].  
 v. 1855 *Belemnites levis* Simpson, p. 25.  
 v. 1867 *Belemnites laevis* Simpson; Phillips, p. 57, pl. X, figs 23, 25.  
 v. 1876 *Belemnites laevis* Simpson; Blake (*in Tate & Blake*), p. 325.  
 v\* 1883 *Belemnites simpsoni* Mayer-Eymar, p. 641.  
 v. 1884 *Belemnites levis* Simpson; Simpson, p. 35.  
 v. 1884 *Belemnites aptus* Simpson, p. 36. [Lectotype, here designated, WM 1990A, ?'communis' Zone, Saltwick, North Yorkshire. More probably *falciferum* Zone and Subzone].  
 1920 *Cuspiteuthis laevis* (Simpson); Bülow-Trummer, p. 103.  
 1925 *Acrocoelites laevis* (Simpson); Lissajous, p. 103.  
 1975 *Mesoteuthis laevis* (Simpson); Saks & Nal'nyaeva, p. 31.  
 v. 1984 *Acrocoelites (Toarcibelus) laevis* (Phillips); Riegraf *et al.*, p. 153, pl. 10, fig. 6.  
 v. 1985 *Youngibelus levis* (Simpson); Doyle, p. 138, pl. 15, figs 1–6.

*Type specimens.* Lectotype (designated Reigraf *et al.* 1984; Doyle 1985), WM 453a; paralectotypes, WM 453b, 453c, all from 'division 5b' (=bed 43 Bituminous Shales, *falciferum* Subzone and Zone), Saltwick, near Whitby, North Yorkshire.

*Diagnosis.* Medium sized, cylindrical *Youngibelus* without epirostrum. Outline symmetrical, profile nearly symmetrical, both cylindrical. Transverse sections rounded pyriform.

*Material.* BMNH, 111 specimens; BGS, 10 specimens; OUM, 10 specimens; WM, 16 specimens. All from the *falciferum* Zone, Jet Rock Member, North Yorkshire.

*Description.* Medium sized, generally slender, cylindrical rostrum with a total length of approximately seven times  $D_v$ . The outline is symmetrical and cylindrical, with divergence from the moderately obtuse apex being terminated rapidly (0·2 of total length from apex), leaving the outline cylindrical. The profile is less symmetrical than the outline, with a slightly inflated venter, and it tends to be more cylindriconal than the outline. Transverse sections are compressed and rounded pyriform, with a broad venter.

The apex possesses no definite apical grooves, but the presence of slight depressions give the impression of dorso-lateral grooves (specimens with pathologically deepened grooves have been separated previously as *Belemnites aptus* Simpson). The apex is, however, usually striated, striations being confined to the apical-most tip of the rostrum. The apex may be found compressed, either as an incipient epirostrum, or more likely, due to 'resorption'. The lateral lines are present as broad lateral depressions subdivided by a weak weal or ridge. The phragmocone penetrates a third of the rostrum, and the apical line is ortholineate.

*Ontogeny.* The ontogeny of this species has been discussed in detail elsewhere (Doyle 1985).

| Specimen    | <i>L</i> | <i>l</i> | <i>Dv</i> | <i>Dl</i> |
|-------------|----------|----------|-----------|-----------|
| BMNH C59188 | 85·7     | 52·8     | 11·8      | 10·0      |
| C59196      | 93·8     | 54·9     | 12·0      | 10·5      |
| C59197      | 86·0     | 50·0     | 12·8      | 10·7      |
| C59198      | 85·0     | 53·5     | 13·1      | 11·1      |

Table 24. Measurements of *Youngibelus simpsoni* (Mayer-Eymar, 1883).

*Remarks.* *Y. simpsoni* has been placed previously in several genera (e.g. *Acrocoelites*, *Mesoteuthis*), no doubt due to its relatively nondescript form. However, its lack of apical grooves, its ortholineate apical line and cylindrical form with a pyriform section allies it with *Youngibelus*. Doyle (1985) considered this species to be a sexual dimorph of *Y. tubularis* (Young & Bird), but described it under the name *Y. levis* (Simpson), believing the one letter difference between Simpson's later (1855) and Roemer's earlier (1836) species validated it. However, according to Article 58 of the *International Code of Zoological Nomenclature*, Simpson's species is a junior homonym of Roemer's, and therefore Mayer-Eymar's (1883) replacement is the valid name for this species.

*Y. simpsoni* differs from both *Y. tubularis* (Young & Bird) and *Y. gigas* (Quenstedt) in lacking an epirostrum, and is distinguished by its rounded pyriform transverse section.

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

#### Genus SIMPSONIBELUS gen. nov.

*Type species.* *Belemnites expansus* Simpson, 1855.

*Other species.* *S. latus* (Simpson), *S. dorsalis* (Phillips).

*Derivation of name.* In recognition of the work of Martin Simpson (1800–1892).

*Diagnosis.* Medium sized, hastate to subhastate Megateuthidinae. Outline symmetrical, hastate to subhastate. Apex acute to attenuate. Profile asymmetrical, often arched, hastate. The position of maximum inflation of the rostrum is in the stem third of the rostrum. Transverse sections are depressed to compressed and subquadrate in the alveolar region, becoming rounded adapically. The apex is characterised by a well-defined ventral apical

groove that is restricted to the apical-most tip of the rostrum, but which opens adorally into a wide triangular depression. Dorso-lateral apical grooves are also present, but less well-defined. A short mid-dorsal alveolar groove may be developed, but it is neither underlain by a splitting surface, nor does it attain the anterior border of the rostrum. Lateral lines are present as two parallel, narrow, depressions separated by a weak to moderately strong ridge. The phragmocone is ventrally displaced and penetrates one quarter to a fifth of the rostrum. The apical line is cyrtolineate, and the alveolar angle is in the region of 24–25°.

*Occurrence.* Lower to Upper Toarcian of Britain, mainland Europe and east Greenland.

*Remarks.* Representatives of this genus in Europe have previously been included within *Acrocoelites* Lissajous because of their three well-developed apical grooves. In form, *Simpsonibelus* most closely resembles *Lenobelus* Gustomesov from the Toarcian-Aalenian of the Arctic regions. However, *Lenobelus* has a well-developed dorsal alveolar groove with an incipient splitting surface that extends a short distance from the anterior border of the rostrum; that of *Simpsonibelus* is less well-developed. In addition, *Lenobelus* possesses a long ventral groove which extends past the apical region and lacks dorso-lateral apical grooves (Saks & Nal'nyaeva 1975; Jeletzky 1980; Doyle & Kelly 1988). *Simpsonibelus* also resembles *Parahastites* Nal'nyaeva in the form of its lateral lines, and in the presence of weak dorsal alveolar grooves in some specimens, but *Parahastites* lacks apical grooves. The presence of weak dorsal alveolar grooves in unrelated, hastate, taxa has been recorded by Stevens (1965, p. 41), and is thought to be of little taxonomic significance.

### **Simpsonibelus expansus** (Simpson, 1855) Pl. 20, figs 1–10

- v\*. 1855 *Belemnites expansus* Simpson, p. 31.
- v. 1855 *Belemnites repandus* Simpson, p. 31 [Lectotype, here designated, WM 1998, ‘communis’ Zone, Whitby, North Yorkshire].
- . 1867 *Belemnites subaduncatus* Voltz; Phillips (*pars*), p. 63, pl. XI, fig. 29, *non* fig. 29<sup>1</sup><sup>iv</sup> [= *Acrocoelites (Toarcibelus) trisulculosus* (Simpson)].
- v. 1876 *Belemnites subaduncatus* Voltz; Blake (*in* Tate & Blake), p. 324.
- . 1883 *Belemnites subaduncatus* Voltz; Mayer-Eymar, p. 641.
- v. 1884 *Belemnites expansus* Simpson; Simpson, p. 35.
- v. 1884 *Belemnites repandus* Simpson; Simpson, p. 35.
- . 1902 *Belemnites blainvillei* Voltz; Janensch, p. 122, pl. XI, fig. 3.
- . 1925 *Acrocoelites expansus* (Simpson); Lissajous, p. 86.
- v. 1984 *Dactyloteuthis* (*Cataleuthis*) aff. *inaudita* (Voronez); Riegraf *et al.*, p. 161, pl. 12, fig. 9.

*Type specimen.* Lectotype, WM 2685, ‘Upper Lias 1’ (= *bifrons* Zone, *fibulatum* to *crassum* Subzones) of Whitby, North Yorkshire.

*Diagnosis.* Medium sized, subhastate *Simpsonibelus*. Outline symmetrical, subcylindrical to subhastate. Profile asymmetrical, subhastate. Apex moderately acute. Alveolar transverse section subquadrate, stem sections subcircular.

*Material.* BMNH, 221 specimens; BGS, 1 specimen; OUM, 15 specimens; WM, 4 specimens. All from the *falciferum* Zone to *levesquei* Zone, Jet Rock Member to Blea Wyke Sandstone Formation, North Yorkshire. CMN, 15 specimens, Leda Ovum Beds, *bifrons* Zone, Northampton.

*Description.* Medium sized, slender or robust subhastate rostra with a total length of about seven times Dv. The outline is symmetrical, subcylindrical to subhastate. Divergence from the acute and attenuated, or relatively obtuse and blunt, apex is moderate. The profile is asymmetrical and weak to moderately subhastate, depending on the inflation of the venter, which is usually greater than that of the dorsum. However, in some individuals the reverse is true. The alveolus may flare adorally. The position of maximum inflation of the rostrum is generally in the stem third of the rostrum. The transverse sections of the rostrum are generally equidimensional, the stem section is subcircular to subquadrate and the alveolar section is subquadrate.

The apex bears three apical grooves; the ventral groove is usually deeply incised, expanding into a broader triangular region (although restricted to the apex), while the dorso-lateral grooves are shallow and extend for only two thirds of the ventral groove's length. A short, shallow, median dorsal alveolar groove may occasionally be developed. Lateral lines are not well-defined in this species due to its robustness, but consist of two narrow depressions separated by a weak ridge or weal. The phragmocone penetrates a third of the rostrum, and the apical line is cyrtolineate.

| Specimen    | <i>L</i> | <i>l</i> | <i>x</i> | <i>Dv</i> | <i>Dl</i> | <i>Dvmax</i> | <i>Dlmax</i> |
|-------------|----------|----------|----------|-----------|-----------|--------------|--------------|
| WM2685      | 60.5     | 48.4     | 27.4     | 7.8       | 7.8       | 8.8          | 8.1          |
| BMNH C59354 | 62.7     | 43.5     | 28.2     | 9.6       | 9.5       | 9.7          | —            |
| C59362      | 79.0     | 59.5     | 34.6     | 11.4      | 11.1      | 11.5         | 11.5         |
| C59363      | 75.6     | 53.5     | 30.6     | 11.5      | 11.0      | 13.0         | 11.7         |
| C59364      | 62.9     | 42.6     | 24.9     | 12.5      | 12.3      | 12.7         | 12.7         |
| C59366      | 73.0     | 56.9     | 31.0     | 9.5       | 8.8       | 9.6          | 9.5          |
| C59367      | 77.0     | 56.4     | 28.5     | 10.6      | 9.0       | 11.7         | 10.6         |

Table 25. Measurements of *Simpsonibelus expansus* (Simpson, 1855).

*Remarks.* *Simpsonibelus expansus* has in the past been confused with '*Brachybelus (Parabrachybelus) subaduncatus*' (Voltz) (e.g. Phillips 1867; Tate & Blake 1876), but is easily distinguished from this species, which is more robust, and possesses only two short dorso-lateral grooves without a ventral groove. Within its own genus, *S. expansus* may be distinguished from *S. dorsalis* (Phillips) which is smaller, with an attenuated apex and a depressed transverse section, and from *S. lentus* (Simpson), which is more slender, with a notably compressed section (Text-fig. 17).

Simpson (1855, 1884) listed two varieties of *Belemnites expansus*; one with an attenuated apex (=*Belemnites repandus* Simpson) and the other with an obtuse apex (=*Dactyloleuthis aff. inaudita* (Voronez) of Riegraf *et al.* 1984); both are commonly found in Yorkshire.

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

***Simpsonibelus dorsalis* (Phillips, 1867)** Pl. 20, figs 11–16; Pl. 21, fig. 8

- v\*. 1867 *Belemnites dorsalis* Phillips, p. 58, pl. X, fig. 24.
- v. 1875 *Belemnites dorsalis* Phillips; Phillips, p. 262, pl. 27, fig. 2.
- v. 1876 *Belemnites dorsalis* Phillips; Blake (*in Tate & Blake*), p. 324.
- 1883 *Belemnites dorsalis* Phillips; Mayer-Eymar, p. 641.
- v. 1884 *Belemnites dorsalis* Phillips; Simpson, p. 34.
- 1920 *Cuspiteuthis dorsalis* (Phillips); Bülow-Trummer, p. 103.
- 1925 *Acrocoelites dorsalis* (Phillips); Lissajous, p. 81.
- ?non 1931 *Mesoteuthis dorsalis* (Phillips); Krimhol'z, p. 18, pl. 1, figs 9, 10 [=?*Hastites* sp.].
- v. 1984 *Acrocoelites (Acrocoelites) dorsalis* (Phillips); Riegraf *et al.* (*pars*), p. 156, pl. 11, fig. 4.

*Type specimens.* Lectotype (designated Riegraf *et al.* 1984), OUM J15203 (=original of Phillips 1867, pl. X, fig. 24*l*'); Paralectotypes, OUM J15201, J15202 (=originals of pl. X, figs 24*l'*, 24*d*), all from the Upper Lias (probably Bituminous Shales, *falciferum* Zone and Subzone) of Saltwick, near Whitby, North Yorkshire.

*Diagnosis.* Small, subhastate *Simpsonibelus*. Outline symmetrical, weakly subhastate. Profile asymmetrical, strongly subhastate. Apex attenuated. Transverse sections depressed, quadrate to subquadrate.

*Material.* BMNH, 356 specimens; BGS, 4 specimens; OUM, 6 specimens; WM, 22 specimens. All from the *falciferum* Zone to *levesquei* Zone, Jet Rock Member to Blea Wyke Sandstone Formation, North Yorkshire. CMN, 8 specimens, Leda Ovum Beds *bifrons* Zone, Northampton.

*Description.* Small, delicate, subhastate rostra with a total length of approximately 11 times *Dv*. The outline is symmetrical and subhastate, frequently with its apex attenuated to

a fine point. The profile is asymmetrical and more hastate than the outline. The venter is arched, with a recurved apex, and the alveolar region is constricted in profile giving the impression of an inflated dorsum. The position of maximum inflation is in the apical third of the rostrum. The transverse sections are depressed throughout the rostrum, generally quadrate or subquadrate in the alveolar region, becoming more rounded adapically.

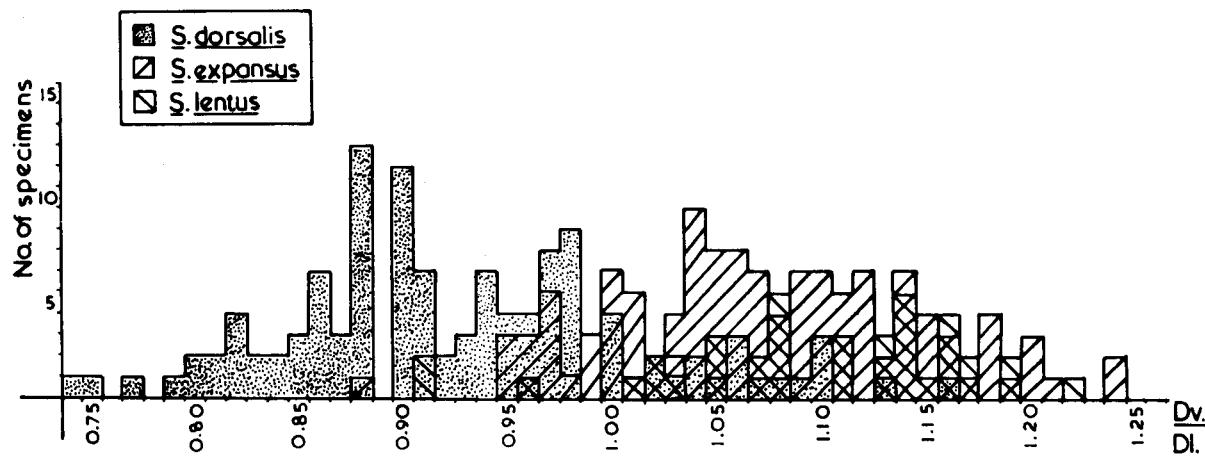
The apex bears a ventral groove that is short and relatively well-incised, broadening adorally, and two dorso-lateral grooves of similar length that are less well-developed. A short, median alveolar groove is invariably present, situated in the centre of the alveolar third, occupying the position of Dvmin. This groove is without a splitting surface and bifurcates at its adoral tip, never reaching the anterior border. Lateral lines are well-developed in this species, accentuated by its depressed section, and consist of two parallel narrow depressions separated by a weal or ridge. The phragmocone penetrates a third of the rostrum, and the apical line is cyrtolineate.

| Specimen    | <i>L</i> | <i>l</i> | <i>x</i> | <i>Dv</i> | <i>Dl</i> | <i>Dvmax</i> | <i>Dlmax</i> |
|-------------|----------|----------|----------|-----------|-----------|--------------|--------------|
| OUM J175202 | 64.8     | 49.0     | 24.8     | 5.2       | 6.1       | 6.0          | 6.2          |
| BMNH C59327 | 61.7     | 42.5     | 23.3     | 5.7       | 6.1       | 6.3          | 6.6          |
| C59328      | 76.5     | 50.8     | 24.0     | 5.9       | 6.7       | 6.8          | 6.9          |
| C59332      | 56.9     | 39.7     | 20.7     | 5.3       | 5.8       | 6.0          | 5.8          |
| C59352      | 50.8     | 32.8     | 23.2     | 6.9       | 7.2       | 7.8          | 7.4          |
| C59448      | 41.2     | 29.2     | 15.3     | 4.7       | 4.9       | 5.0          | 5.1          |

Table 26. Measurements of *Simpsonibelus dorsalis* (Phillips, 1867).

*Remarks.* *Simpsonibelus expansus* may be confused with *Parahastites subclavatus* (Voltz), which has a similar shape and size and is reported with dorsal alveolar grooves (Jeletzky 1966, p. 144), but is distinguished by its apical grooves, as *P. subclavatus* has a smooth apex devoid of grooves. Within its own genus, *S. dorsalis* is distinguished from both juveniles (comparable in size to *S. dorsalis*) and adults of *S. expansus* (Simpson) which are robust with an equidimensional transverse section, and *S. latus* (Simpson) which are slender with a compressed transverse section (Text-fig. 17).

The interpretation of this species by Riegraf *et al.* (1984) is only partially applicable, as they included specimens of *Belemnites striolatus* Phillips *sensu* Werner (=*Acrocoelites subtenuis* (Simpson)) in their synonymy. However, their figured specimen bears some resemblance to this species, and appears to possess traces of a dorsal groove.



TEXT-FIG. 17. Frequency histogram of the ratio *Dv:Dl* in the three species of *Simpsonibelus* gen. nov. from North Yorkshire.

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

**Simpsonibelus latus** (Simpson, 1855) Pl. 21, figs 1–7

- v\*. 1855 *Belemnites latus* Simpson, p. 31.
- v. 1875 *Belemnites subaduncatus* Voltz; Blake (*in Tate & Blake*) (*pars*), p. 324.
- v. 1884 *Belemnites latus* Simpson; Simpson, p. 34.  
1920 *Holcoteuthis subaduncata* (Voltz); Bülow-Trummer (*pars*), p. 87.
- 1925 *Acrocoelites latus* (Simpson); Lissajous, p. 106.
- v. 1984 *Dactyloteuthis (Cataeuthis) inaudita* (Voronez); Riegraf *et al.*, p. 159, pl. 12, figs 5–8.

*Type specimen.* Holotype, WM 54, ‘*communis* Zone’ (= *bifrons* Zone), Whitby, North Yorkshire.

*Diagnosis.* Medium sized, slender subhastate *Simpsonibelus*. Outline symmetrical, weakly subhastate. Profile nearly symmetrical, subhastate. Apex acute. Transverse sections compressed, subquadrate in alveolar region, elliptical in the stem region.

*Material.* BMNH, 64 specimens; BGS, 1 specimen; OUM, 6 specimens; WM, 2 specimens. All from the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire. CMN, 8 specimens, *bifrons* Zone, Northampton.

*Description.* Medium sized, slender subhastate rostrum with a total length of approximately 9 times Dv. The outline is symmetrical and slightly subhastate or even cylindrical, and the apex is acute although not attenuated. The profile is nearly symmetrical, the venter and dorsum both being weakly inflated, and is more hastate than the outline. The position of maximum inflation of the rostrum is in the apical-most part of the stem region. Transverse sections of the rostrum are moderate to strongly compressed throughout. The alveolar section is compressed subquadrate in form, while the stem section is compressed elliptical to subquadrate.

The apex bears three well-developed apical grooves. The ventral apical groove is moderately incised, and although confined to the apical third, broadens adorally into a triangular region. The two dorso-lateral apical grooves are generally less well-developed than the ventral. Median dorsal alveolar grooves are rarely developed in this species, but do occur. Lateral lines are subdued, typically consisting of two narrow depressions separated by a weak swelling or ridge. The phragmocone penetrates a third of the rostrum, and the apical line is cyrtolineate.

| Specimen    | L    | l    | x    | Dv   | Dl  | Dvmax | Dlmax |
|-------------|------|------|------|------|-----|-------|-------|
| WM54        | 81·2 | 68·3 | 39·1 | 8·8  | 7·0 | 9·0   | 7·9   |
| BMNH C59429 | 87·0 | 58·2 | 29·2 | 9·2  | 8·1 | 9·8   | 9·3   |
| C59453      | 80·0 | 62·0 | 33·8 | 8·7  | 7·8 | 9·1   | 8·1   |
| C59454      | 90·0 | 68·5 | 32·1 | 9·4  | 8·7 | 10·5  | 8·8   |
| C59455      | 82·2 | 65·5 | 33·7 | 9·5  | 8·1 | 10·2  | 8·9   |
| C59459      | 79·2 | 61·3 | 32·2 | 9·0  | 7·1 | 9·8   | 8·5   |
| C59460      | 83·8 | 64·4 | 33·5 | 10·1 | 8·9 | 10·9  | 9·4   |

Table 27. Measurements of *Simpsonibelus latus* (Simpson, 1855).

*Remarks.* This species somewhat resembles *Pseudohastites longiformis* (Blake) in its similar compression and subhastate profile, but *Simpsonibelus latus* is easily distinguished from the older species by its ventral apical groove. *S. latus* may be distinguished from *S. expansus* (Simpson), which has a robust rostrum and an equidimensional section, and from *S. dorsalis* (Phillips) which is smaller with a depressed section (Text-fig. 17).

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

Genus **DACTYLOTEUTHIS** Bayle, 1878[=*Cuspiteuthis* Abel, 1916]

*Type species.* *Belemnites irregularis* Schlotheim, 1820, by subsequent designation (Douville 1879, p. 91).

*Other species.* *D. digitalis* (Blainville); *D. similis* (Seebach); *D. ventricosa* (Quenstedt); *D. hebetata* (Ernst); *D. cossotela* (Blake).

*Diagnosis.* Medium to large sized, cylindrical and digit-like Megateuthidinae. Epirostrum may be present, extending total length of the rostrum to three or four times that of the orthorostrum. Outline symmetrical, cylindrical, apex obtuse and blunt, sometimes mucronate. Profile symmetrical or nearly symmetrical with inflated venter, and cylindrical. Transverse sections very compressed, with narrow venter and dorsum, and elliptical. Apex of orthorostrum may be completely smooth or bear a single incised ventral apical groove, but true dorso-lateral apical grooves are absent. Apex of epirostrum very commonly striated. Lateral lines indistinct, but consist of two parallel depressions, one broad and ventro-lateral in position, the other narrow and in a dorso-lateral position. Phragmocone slightly ventrally displaced, penetrating approximately one half of the orthorostrum. Apical line weakly cyrtolineate or curved goniolineate. Alveolar angle approximately 24–26°.

*Occurrence.* Upper Lower Toarcian to Upper Toarcian of Britain, Europe and the USSR. Especially common in France and western Germany, rare in Britain and USSR. Doyle (1987) has suggested that *Dactyloteuthis* is of Tethyan origin.

*Remarks.* *Dactyloteuthis* is a very distinctive genus easily distinguished from all other Megateuthidinae by its smooth, digit-like rostrum and blunt apex. It is closest to *Brevibelus* nom. nov. (=*Brachybelus* Naef, see p. 62), and this has led to some confusion (e.g. Stevens 1965, p. 63; Saks & Nal'nyaeva 1967, 1970). Species of *Brevibelus* are characterized by their smooth groove-less, conical depressed rostra.

Formerly, species of *Acrocoelites* (*Odontobelus*) have been included in *Dactyloteuthis* (e.g. *A. (O.) incurvatus* (Zieten) and *A. (O.) wrighti* (Oppel); Stolley 1919; Bülow-Trummer 1920; Lissajous 1925; Riegraf 1980), despite the fact that the type species clearly lacks dorso-lateral apical grooves. In future, compressed species bearing three apical grooves should properly be included in *Acrocoelites*. Bayle (1878) made no distinction between epirostrate and non-epirostrate forms of his genus, yet epirostrate species with digit-like orthorostra have been removed to genera such as *Cuspiteuthis* Abel and *Salpingoteuthis* Lissajous. Such genera have become ‘catch-all’ for belemnites with epirostra, and it is clear from examination of orthorostra that species of many genera are represented in them. The taxonomic rank of epirostra is low, and attention should be paid to the form of the orthorostrum to determine the true affinity of epirostrate species. The use of *Cuspiteuthis* Abel as a subgenus of *Dactyloteuthis* to contain epirostrate species is therefore considered superfluous (see Riegraf 1980). The interpretation by Riegraf *et al.* (1984) of *Cataleuthis* Nal'nyaeva as a subgenus of *Dactyloteuthis* is erroneous, as Nal'nyaeva's genus possesses dorso-lateral apical grooves and no ventral groove. The specimens figured by Riegraf *et al.* are typical of *Simpsonibelus* (see above).

**Dactyloteuthis digitalis** (Blainville, 1827) Pl. 21, figs 9–14

- \*. 1827 *Belemnites digitalis* Faure-Biguet; Blainville, p. 88, pl. 3, figs 5–6.
- . 1830 *Belemnites digitalis* Faure-Biguet, var. A; Voltz, p. 46; pl. 2, fig. 5.
- . 1831 *Belemnites digitalis* Faure-Biguet; Zieten, p. 31, pl. XXIII, fig. 9.
- v. 1842 *Belemnites irregularis* Schlotheim; d'Orbigny, p. 74, pl. IV, figs 2–5.
- v. 1848 *Belemnites digitalis* Blainville; Quenstedt (*pars*), p. 416, pl. 26, fig. 8.
- v. 1867 *Belemnites irregularis* v. Schlotheim; Phillips, p. 72, pl. XV, figs 31, 39.
- . 1878 *Dactyloteuthis irregularis* (v. Schlotheim); Bayle (*pars*), pl. XXVIII, fig. 5.
- . 1912 *Belemnites irregularis* v. Schlotheim; Werner (*pars*), p. 124.
- 1920 *Dactyloteuthis irregularis* (v. Schlotheim); Bülow-Trummer (*pars*), p. 97.
- . 1924 *Belemnites* (*Dactyloteuthis*) *digitalis* Blainville *emend.* Voltz; Ernst, p. 168, pl. XI, figs 3–5.

- 1925 *Dactylosteuthis digitalis* (Faure-Biguet); Lissajous, p. 80.  
 . 1942 *Dactylosteuthis digitalis* Voltz; Kolb, p. 155, pl. 6, fig. 4; pl. 7, fig. 13.  
 . 1960 *Dactylosteuthis digitalis* (Blainville); Stürz-Kowing, p. 4, pl. 1, figs 2–8.  
 v. 1971 *Belemnites irregularis* v. Schlotheim; Schwegler (*pars*), p. 85, text-fig. 100a.  
 1980 *Dactylosteuthis* (*Dactylosteuthis*) *irregularis* (v. Schlotheim); Riegraf (*pars*), p. 154.  
 v. 1984 *Dactylosteuthis* (*Dactylosteuthis*) *irregularis* (v. Schlotheim); Riegraf *et al.*, p. 162, pl. 11, fig. 5.

*Type specimens.* Lectotype (here designated), the original of Blainville (1827), pl. 3, fig. 5 from the Calcaires de Jura of Nancy, France. As it is unlikely that this specimen survives, a neotype should be selected.

*Diagnosis.* Small to medium sized, cylindrical *Dactylosteuthis*. Outline symmetrical, cylindrical. Profile similar but more inflated and slightly asymmetrical. Apex blunt and obtuse. Transverse sections very compressed, elliptical. Apex with single ventral groove.

*Material.* BMNH, 6 specimens, *?variabilis* Zone to *levesquei* Zone, Cotswold Cephalopod Bed and equivalents, Gloucestershire. GMB, 1 specimen, *levesquei* zone, Yeovil Sands, Somerset.

*Description.* Small to medium sized, elongate cylindrical digit-like rostrum with a total length of approximately five times Dv. The outline is symmetrical and cylindrical with only slight divergence from the apex. The apex itself is relatively acute in outline though obtuse and blunt in profile, and is commonly mucronate. The profile is broadly symmetrical and cylindrical, with a rounded, blunt apex giving it a digit-like appearance. The venter rarely may be inflated more than the dorsum, making the profile asymmetrical. The width of the profile is commonly twice that of the outline. The transverse sections of the rostrum are very compressed and elliptical in form, although some individuals may be pyriform.

The apex of the rostrum is commonly devoid of grooves, but a single ventral groove may be developed. Lateral lines are indistinct, but consist of two parallel and broad depressions. The phragmocone penetrates approximately one half of the rostrum, and the apical line is curved goniolineate.

| Specimen   | L    | l    | Dv   | Dl   |
|------------|------|------|------|------|
| BMNH C7827 | 57.3 | 38.1 | 13.8 | 11.0 |
| C59234     | 54.8 | 35.6 | 14.9 | 12.1 |
| C59235     | 65.5 | 43.5 | 13.7 | 10.7 |
| C59236     | 59.7 | 36.8 | 13.4 | 11.4 |
| C59237     | 62.8 | 37.7 | 12.8 | 9.9  |
| C59499     | 71.3 | 37.8 | 14.4 | 11.7 |

Table 28. Measurements of *Dactylosteuthis digitalis* (Blainville, 1827).

*Remarks.* *Dactylosteuthis digitalis* is easily distinguished from compressed species of other Megateuthidinae (e.g. *Acrocoelites* (*Odontobelus*) *incurvatus* (Zieten)) by its digit-like form and lack of apical grooves. Within *Dactylosteuthis*, it may be distinguished from *D. irregularis* (Schlotheim) which has a squat, robust rostrum, and from *D. similis* (Seebach) which is more elongate and cylindrical (see Stürz-Kowing 1960). In addition, *D. crossotela* (Blake) is robust and cylindriconal and *D. ventricosa* (Quenstedt) is more compressed, and possesses an epirostrum. It is probable that *D. digitalis* and *D. ventricosa* are sexual dimorphs of the same species (see Doyle 1985), but the rarity of the both species in Britain prevents further comment. The few examples of *D. digitalis* known from southern England are slightly smaller than their more numerous mainland European counterparts.

Blainville (1827) and some later authors (Voltz 1830; Zieten 1831) attributed this species to the authorship of Faure-Biguet (Biguet 1819). However, there is no description of a *Belemnites digitalis* in this work, although there is a *Belemnites digitulus*, of unknown affinity.

*Occurrence.* Upper Toarcian (*variabilis* and *levesquei* Zones) of southern England (rare) and mainland Europe (common).

**Dactyloteuthis crossotela** (Blake in Tate & Blake, 1876) Pl. 21, fig. 15; Pl. 22, figs 1–5;  
 v. 1848 *Belemnites digitalis acutus* Quenstedt, p. 428, pl. 26, fig. 11 [junior homonyms of both *B. digitalis* Blainville, 1827 and *B. acutus* Miller, 1826].  
 v? 1855 *Belemnites erosus* Simpson, p. 42 [Lectotype here designated, WM 66, 'communis' Zone (=bifrons Zone), Whitby, North Yorkshire].

- v\*. 1876 *Belemnites crossotela* Blake (in Tate & Blake), p. 326.  
 v. 1884 *Belemnites dactylus* Simpson, p. 42 [Lectotype, here designated, WM 324b, U.L.1. (=Bed 54 and above), bifrons Zone, Whitby, North Yorkshire].  
 ? 1898 *Belemnites meta* Blainville; Benecke (*pars*), p. 56, pl. 11, fig. 5.  
 . 1898 *Belemnites* sp.; Benecke, p. 47, pl. IX, fig. 10.  
 1920 *Cuspiteuthis crossotela* (Tate & Blake); Bülow-Trummer, p. 108.  
 1925 *Dactyloteuthis crossotela* (Blake); Lissajous, p. 76.  
 v? 1971 *Belemnites digitalis acutus* Quenstedt; Schwegler, p. 88, text-fig. 101.  
 1980 *Dactyloteuthis* (*Dactyloteuthis*) *acuta* (Quenstedt); Riegraf, p. 151.

*Type specimen.* Lectotype (here designated), BMNH C11868 from the Alum Shales (=bifrons Zone) of Whitby, North Yorkshire.

*Diagnosis.* Large, robust, cylindriconal *Dactyloteuthis*. Outline symmetrical, cylindriconal. Profile asymmetrical and conical. Venter inflated. Apex of epirostrum acute, apex of orthorostrum less acute. No apical grooves.

*Material.* BMNH, 9 specimens; OUM, 4 specimens; WM, 2 specimens. All from the *bifrons* Zone to the *variabilis* Zone, Alum Shale to Peak Mudstone members, North Yorkshire. BGS, 2 specimens, from the *bifrons* Zone, Alum Shale Member, of North Yorkshire, and the *?bifrons* Zone to *?thouarsense* Zone, Nailsworth Sands, Gloucestershire.

*Description.* Large, robust, cylindriconal rostrum, often with an epirostrum. The total length of the orthorostrum is approximately four times Dv, while those specimens with epirostra have a total length of approximately eight times Dv. The outline is symmetrical and cylindriconal with moderate divergence from a reasonably acute apex, which is less obtuse than most members of *Dactyloteuthis* (with the exception of *D. hebetata* (Ernst)). The profile is asymmetrical and conical with a moderately inflated venter. Where epirostra are developed, the profile becomes cylindriconal. Transverse sections of the orthorostrum are moderately compressed and elliptical, and some individuals may have a more depressed section. Sections of the epirostrum are circular.

The apex of the orthorostrum bears no grooves, but the apex of the epirostrum is commonly striated. The lateral lines are difficult to distinguish, but consist of two, broad and parallel depressions along the length of each flank. The phragmocone penetrates one half to three fifths of the orthorostrum, and the apical line is curved goniolineate.

| Specimen    | L      | l     | lo   | Dv   | Dl   |
|-------------|--------|-------|------|------|------|
| BMNH C11868 | 90·0c  | 58·4  | 43·8 | 22·9 | 18·8 |
| C59370      | —      | 85·0  | 55·2 | 19·3 | 16·2 |
| C59430      | 122·3u | 106·3 | —    | 22·2 | 17·3 |
| C59434      | 87·5o  | —     | 59·3 | 24·1 | 21·3 |
| C59435      | 86·5o  | —     | 53·5 | 22·0 | 17·9 |

Table 29. Measurements of *Dactyloteuthis crossotela* (Blake, 1876).

Abbreviations: lo, length from apex of orthorostrum to adapical tip of protoconch; c, epirostrum crushed; o, orthorostrum without epirostrum; u, epirostrum uncrushed.

*Remarks.* The orthorostrum of *D. crossotela* may be confused with more robust specimens of *Acrocoelites* (*Odontobelus*) *levidensis* (Simpson), but is distinct because of its complete absence of apical grooves. *D. crossotela* is distinguished from *Acrocoelites* (*Toarcibelus*) *inaequistriatus* (Simpson) (=*Belemnites compressus* Young & Bird) by its much more robust form and conical orthorostrum. *D. digitalis* is distinguished from other members of its genus by its inflated, relatively uncompressed and conical orthorostrum.

*Belemnites dactylus* Simpson (a junior homonym of *B. dactylus* Biguet) was described using two unrelated syntypes (WM 324a,b). One of these (WM 324b) is here designated lectotype, and is typical of *D. crossotela*. It is probable that those specimens without epirostra and those specimens with epirostra are sexual dimorphs of the same species (see Doyle 1985). In this case both morphotypes are included within the same morphospecies, rather than erect a new name for those rostra without epirostra.

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

**Dactyloteuthis cf. ventricosa** (Quenstedt, 1848) Pl. 23, figs 3–5, 7–9

cf.\* 1848 *Belemnites acuarius ventricosa* Quenstedt, p. 409, pl. 24, fig. 8.

v? 1866 *Belemnites sulci-stylus* Phillips, p. 83, pl. XIX, fig. 49 [has a pathological groove on flank, GMB M12191].

cf. 1912 *Belemnites acuarius ventricosa* Ouenstedt; Werner, p. 129.

cf. 1920 *Cuspitethis acarius ventricosa* (Quenstedt); Bülow-Trummer, p. 101.

cf. 1925 *Dactyloctenius acuarium ventricosa* (Quenstedt); Lissajous, p. 47.

cf. 1942 *Dactyloctenius subtubularis* Kolb, p. 156, pl. 7, fig. 10; pl. 8, fig. 9.

cf.v 1971 *Belemnites acuarius ventricosa* Quenstedt; Schwegler, p. 90, text-fig. 103.

cf. 1980 *Dactyloteuthis (Cuspiteuthis) ventricosa* (Quenstedt); Riegraf, p. 151.

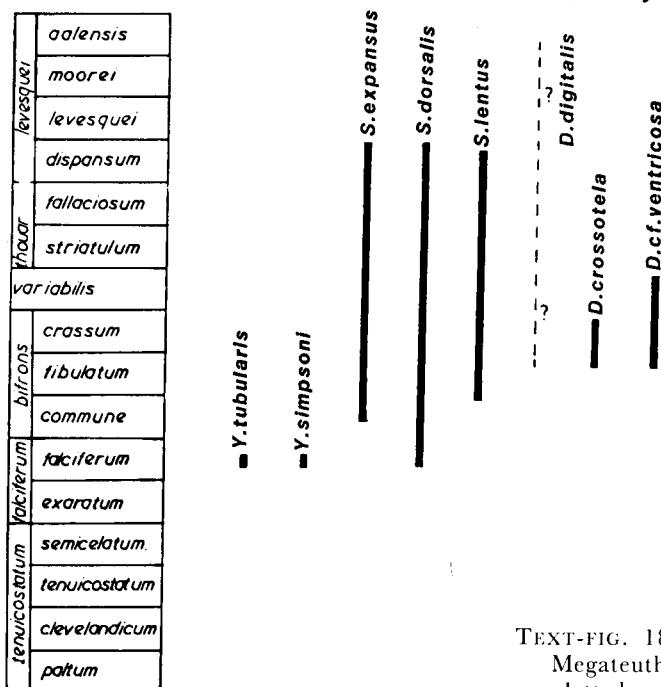
cf. v? 1985 *Dactyloctenius (Cuspiteuthis) semistriata* (Münster); Riegraf et al., p. 163, pl. 12, figs 4, 12.

*Type specimens.* There is no record of Quenstedt's (1848, pl. 25, fig. 8) figured specimen at Tübingen where most of his other types are preserved. Therefore a neotype should be chosen, and as the specimen figured by Schwegler (1971, text-fig. 103 preserved in GPIT, no registration number) from the Upper Toarcian of Ohmden, Württemburg, southwest Germany is typical of this species, it is here selected.

*Diagnosis.* Slender, elongate cylindrical *Dactyloeteuthis* with epirostrum. Outline of the orthorostrum is symmetrical, cylindriconal to cylindrical, profile similar. Transverse sections compressed elliptical.

## MEGATEUTHIDINAE

#### **Youngibelus, Simpsonibelus. Dactyloeteuthis**



TEXT-FIG. 18. Stratigraphic ranges of British Toarcian Megateuthidinae (*Youngibelus*, *Simpsonibelus* and *Dactyloteuthis*) plotted against ammonite zones and subzones.

*Material.* BMNH, 9 specimens, *bifrons* Zone to *variabilis* Zone, Alum Shale Member to Peak Mudstone Member, North Yorkshire. GMB 1 specimen, *levesquei* Zone, Yeovil Sands, Somerset.

*Description.* Slender rostrum with short cylindriconal orthorostrum and elongated cylindrical epirostrum. The total length of the orthorostrum is approximately four times  $D_v$ , while that of the complete rostrum is approximately thirteen times  $D_v$ . The outline of the orthorostrum is symmetrical and cylindriconal to cylindrical, with slight divergence from a moderately acute apex. The apex of the epirostrum is very acute. The profile is symmetrical and generally similar to the outline, although with a greater diameter, and the venter and dorsum are weakly inflated. The transverse sections of the orthorostrum are compressed and elliptical, and those of the epirostrum are similar although smaller.

The apicies of the epi- and orthorostra bear no apical grooves, although the tip of the apex of the epirostrum may bear striae, which in some cases may be deepened into pathological grooves. The lateral lines are difficult to distinguish, but generally occur as two parallel, shallow depressions separated by a weak ridge. The phragmocone penetrates approximately one half of the orthorostrum, and the apical line is curved goniolineate.

| Specimen    | <i>L</i> | <i>l</i> | <i>lo</i> | $D_v$ | $D/l$ |
|-------------|----------|----------|-----------|-------|-------|
| BMNH C59445 | 76.8c    | 60.7     | 26.1      | 9.4   | 7.8   |
| C59446      | 124.7u   | 110.7    | 26.7      | 9.2   | 7.5   |
| C59447      | 51.1o    | —        | 34.1      | 12.0  | 10.2  |
| C59458      | 146.2u   | 124.7    | 29.6      | 10.9  | 8.2   |

Table 30. Measurements of *Dactylotheuthis* cf. *ventricosa* (Quenstedt, 1848).

Abbreviations: *lo*, length from apex of orthorostrum to adapical tip of protoconch; *c*, epirostrum crushed; *o*, orthorostrum without epirostrum; *u*, epirostrum uncrushed.

*Remarks.* This species bears a superficial resemblance to the Lower Toarcian species *Youngibelus tubularis*, but it differs from *D. cf. ventricosa* in the possession of an elongate orthorostrum, an ortholineate apical line and a pyriform section. The specimens here assigned to *D. cf. ventricosa* differ from the true *D. ventricosa* in their overall smaller size and their more compressed section. However, until more specimens are collected this species is not formally named. The orthorostrum of *D. cf. ventricosa* most closely resembles *D. hebetata* Ernst which is of a similar size, but is distinguished by its more cylindrical form and compressed section. All other *Dactylotheuthis* are more robust and digit-like or conical.

*Occurrence.* Lower to Upper Toarcian (*crassum* Subzone, *bifrons* Zone to *variabilis* Zone and possibly *levesquei* Zone) of Britain.

#### Genus **BREVIBELUS** nom. nov.

[pro *Brachybelus* Naef, 1922,

homonym of *Brachybelus* Ståhl, 1869 (Insecta)]

*Type species.* *Belemnites breviformis* Voltz, 1830.

*Other species.* *B. gingensis* (Oppel).

*Derivation of name.* *Brevis* (lat.), short.

*Diagnosis.* Small, short and robust, conical to cylindriconal Megateuthidinae. Outline symmetrical and conical to cylindriconal, profile nearly symmetrical, otherwise similar to the outline. Apex obtuse to moderately acute, often mucronate. Venter inflated in some species. Transverse sections quadrate, compressed in some species, depressed in others. Apex devoid of grooves or striae. Lateral lines may be well-developed, consisting of two weak and parallel depressions separated by a relatively well-developed ridge. The phragmocone is ventrally displaced, penetrating one half of the rostrum. Apical line strongly cyrtolineate, apical angle approximately 27°.

*Occurrence.* Upper Toarcian to Aalenian of Britain, mainland Europe and USSR.

*Remarks.* *Brevibelus* closely resembles *Parapassaloteuthis* Riegraf in both external and internal morphology (see discussion, this monograph, p. 25). However, *Brevibelus* can be distinguished by its more conical rostrum without apical grooves and with weaker lateral lines.

The new name *Brevibelus* is a replacement for the well-known but invalid name *Brachybelus* Naef. Naef's (1922) name is a junior primary homonym of *Brachybelus* Ståhl, 1869 which is an insect genus (see Ståhl 1870). There are no junior synonyms of Naef's genus, and both Saks' (1967, 1970) subgenus *Brachybelus* (*Acobelus*) and Riegraf's (1980) subgenus *Brachybelus* (*Parabrachybelus*) are unsuitable as replacement names, as the former has a type species (*Dactyloteuthis dolosa*) that is probably unrelated, and the latter a type species (*Belemnites subaduncatus* Voltz) of uncertain affinity. Therefore the name *Brevibelus* is here erected as a replacement for *Brachybelus* Naef.

***Brevibelus breviformis* (Voltz, 1830)** Pl. 23, figs 6, 10, 11; Pl. 24, figs 1, 2

- \* . 1830 *Belemnites breviformis* Voltz, p. 42, pl. II, figs 2–4.
- non 1831 *Belemnites breviformis* Voltz, Zieten, p. 27, pl. XXI, fig. 7 [=lectotype of *Parapassaloteuthis zieteni* (Mayer-Eymar)].
- . 1842 *Belemnites abbreviatus* Miller; d'Orbigny (*pars*), p. 92, pl. XI, fig. 7 only.
- v. 1848 *Belemnites breviformis* Voltz; Quenstedt, p. 427, pl. 27, figs 21–27.
- . 1856 *Belemnites brevis* Blainville; Oppel, p. 361.
- v non 1866 *Belemnites breviformis* Voltz; Phillips, p. 41, pl. IV, figs 9–10 [=*Parapassaloteuthis zieteni* (Mayer-Eymar)].
- non 1869 *Belemnites breviformis* Voltz; Dumortier, p. 32, pl. I, figs 9–12 [=*Parapassaloteuthis zieteni* (Mayer-Eymar)].
- ? 1874 *Belemnites breviformis* Voltz; Dumortier, p. 37, pl. VI, figs 11–12.
- v non 1876 *Belemnites breviformis* Voltz; Blake (*in Tate & Blake*), p. 320 [=*Parapassaloteuthis zieteni* (Mayer-Eymar)].
- 1883 *Belemnites breviformis* Voltz; Mayer-Eymar, p. 640.
- . 1906 *Belemnites (Pachyteuthis) breviformis* Voltz; Lissajous, p. 51, pl. 6, fig. 1.
- . 1912 *Belemnites breviformis* Voltz; Werner, p. 111.
- 1920 *Homaloteuthis breviformis* (Voltz); Bülow-Trummer, p. 120.
- 1922 *Brachybelus breviformis* (Voltz); Naef, p. 241.
- . 1924 *Belemnites (Homaloteuthis) breviformis* Voltz; Ernst, p. 78, pl. 12, fig. 8.
- 1925 *Pachyteuthis breviformis* (Voltz); Lissajous, p. 61.
- ? 1931 *Homaloteuthis breviformis* (Voltz); Krimhol'z, p. 19, pl. 1, figs 20, 21.
- . 1942 *Brachybelus breviformis* (Voltz); Kolb, p. 146, pl. 7, fig. 9; pl. 10, fig. 11.
- . 1956 *Brachybelus breviformis* (Voltz); Delattre, p. 38.
- 1970 *Brachybelus (Brachybelus) breviformis* (Voltz); Saks & Nal'nyaeva, p. 36.
- . 1971 *Homaloteuthis breviformis* (Voltz); Činčurová, p. 76, pl. V, fig. 8.
- v. 1971 *Belemnites breviformis* Voltz; Schwegler, p. 95, text-fig. 106.
- 1980 *Brachybelus (Brachybelus) breviformis* (Voltz); Riegraf, p. 151.

*Type specimen.* Voltz (1830) figured eight specimens under the name *Belemnites breviformis* from the Toarcian of Gundersoffen, Württemburg, southwest Germany, but unfortunately all of Voltz's types were destroyed by fire (M. Wolf, Strasbourg, *pers. comm.* 1983). A neotype should therefore be selected for this species.

*Diagnosis.* Small, conical to cylindriconal *Brevibelus*. Outline symmetrical, conical. Profile, nearly symmetrical, cylindriconal. Venter flattened. Transverse sections depressed quadrate.

*Material.* BMNH, 16 specimens, from the *levesquei* Zone, Blea Wyke Sandstone Formation, North Yorkshire; Dun Caan Shale, Raasay; Cotswold Cephalopod Bed, Gloucestershire; equivalent horizons in Wiltshire.

*Description.* Small and robust, cylindriconal to conical rostra with a total length of about four times Dv. The outline is symmetrical and conical, with a rounded, blunt apex which becomes more acute and mucronate in some cases. The profile is less symmetrical than the outline and is generally more cylindriconal than it, with a flat venter. The transverse

sections are generally depressed and subquadrate in the alveolar region, but become more rounded and elliptical in the stem region.

The apex bears no grooves and is generally completely smooth. The lateral lines are weakly developed and consist of two narrow weak depressions on each flank. The phragmocone penetrates approximately one half of the rostrum and the apical line is cyrtolineate.

| Specimen    | <i>L</i> | <i>l</i> | <i>Dv</i> | <i>Dl</i> |
|-------------|----------|----------|-----------|-----------|
| BMNH C59463 | 40·0     | 21·8     | 11·2      | 11·7      |
| C59465      | 46·2     | 21·4     | 12·1      | 13·2      |
| C59473      | 55·4     | 27·7     | 13·2      | 13·3      |
| C59494      | 52·7     | 30·2     | 13·9      | 13·0      |
| C59498      | 45·2     | 28·8     | 12·8      | 13·0      |

Table 31. Measurements of *Brevibelus breviformis* (Voltz, 1830).

*Remarks.* *Brevibelus breviformis* is very similar in appearance to *Parapassaloteuthis zieteni* (Mayer-Eymar), but differs from this species by its more conical shape, its complete lack of apical grooves and its weakly developed lateral lines. Within its genus *B. breviformis* can be easily distinguished from *B. gingensis* (Oppel) which is more robust and conical.

*Occurrence.* Upper Toarcian (*dispansum* Subzone, *levesquei* Zone) to Aalenian of Britain, mainland Europe and possibly the USSR. Its presence in British Columbia, Canada has been noted by the late J. A. Jeletzky (*pers. comm.*, 1987).

### ***Brevibelus* cf. *gingensis* (Oppel, 1856) Pl. 24, fig. 6**

- cf. 1848 *Belemnites breviformis* Voltz; Quenstedt (pars); p. 428, pl. 27, figs 23–26 only.
- cf. 1856 *Belemnites Gingensis* Oppel, p. 362.
- cf. 1866 *Belemnites gingensis* Oppel; Phillips, p. 44, pl. V, fig. 11.
- cf. 1912 *Belemnites gingensis* Oppel; Werner, p. 112, pl. X, fig. 8.
- cf. v 1971 *Belemnites gingensis* Oppel; Schwegler, p. 98, text-fig. 108.
- cf. 1980 *Brachybelus (Brachybelus) gingensis* Oppel; Riegraf, p. 151.

*Type specimens.* Oppel (1856) based his description of *Belemnites gingensis* on the specimens described by Quenstedt (1848) as *Belemnites breviformis* Voltz, from the Middle Jurassic (Brauner Jura) of Giengen. However, there are no records of these specimens in Tübingen or Munich, and they are probably lost. A neotype should be selected for this species, and the most suitable specimen is that figured by Schwegler (1971, p. 98, text-fig. 108) from the Upper Aalenian of Öfingen, Württemburg, southwest Germany.

*Material.* BMNH, 1 specimen, *levesquei* Zone, *dispansum* Subzone of Blea Wyke Point, North Yorkshire.

*Description.* Small, robustly conical rostrum with a maximum length of approximately three times *Dv*. The outline is symmetrical and cylindriconal with moderate divergence from the apex, which is obtuse and blunt. The profile is also symmetrical, but more conical than the outline. Transverse sections of the rostrum are quadrate and moderately compressed.

The apex bears no apical grooves, and lateral lines are not preserved on this specimen. However, there is evidence of lateral flattening corresponding to a broad lateral line. The alveolus penetrates approximately one half of the rostrum, and the apical line is cyrtolineate.

| Specimen    | <i>L</i> | <i>l</i> | <i>Dv</i> | <i>Dl</i> |
|-------------|----------|----------|-----------|-----------|
| BMNH C59466 | 44·6     | 18·6     | 16·2      | 14·2      |

Table 32. Measurements of *Brevibelus* cf. *gingensis* (Oppel, 1856).

*Remarks.* This specimen is close to *Brevibelus gingensis* (Oppel) in the form of its short conical rostrum. However, it cannot definitely be assigned to this species as it has a compressed section. Both *B. cf. gingensis* and *B. gingensis sensu stricto* differ from *B. breviformis* (Voltz), which is more cylindriconal with a less inflated profile.

*Occurrence.* *Brevibelus gingensis* (Oppel) *sensu stricto* is known from the Aalenian to Bajocian of Britain and mainland Europe.

**Genus MEGATEUTHIS Bayle, 1878**  
[=*Mesoteuthis* Lissajous, 1915; *Mucroteuthis* Abel, 1916]

*Type species.* *Belemnites giganteus* Schlotheim, 1820, by subsequent designation (Douville 1879, p. 91).

*Other species.* Include: *M?* *aalensis* (Oppel), *M.* *benecki* (Schwegler), *M.* *elliptica* (Miller), *M.* *glaber* (Simpson), *M?* *longisulcata* (Voltz).

*Diagnosis.* Large, conical to elongate cylindriconal Megateuthidinae, often with epirostrum developed. The outline and profile are symmetrical or nearly symmetrical and conical to cylindriconal. The apex of the rostrum is generally acute, although more obtuse in robust species. Transverse sections are compressed and elliptical, although some species have less compressed and more subcircular sections. The apex bears two dorso-lateral grooves that extend adorally for one fifth of the rostrum. The apex is commonly well striated, and these striations may be deep in large individuals. There is no ventral groove, although deepened striations may give the impression of one. Lateral lines are present as a broad dorso-lateral depression emanating from the dorso-lateral apical grooves, with a thinner, indistinct depression below. The apical line is goniolineate and the phragmocone is ventrally displaced, penetrating one half to one third of the orthorostrum. The alveolar angle is commonly in the range of 25–28°.

*Range.* Lower Toarcian to Upper Bajocian of Britain, mainland Europe and ?North America.

*Remarks.* *Megateuthis* superficially resembles *Passaloteuthis* Lissajous and *Acrocoelites* Lissajous. Like *Passaloteuthis*, *Megateuthis* bears two dorso-lateral apical grooves, but unlike *Acrocoelites*, it does not possess a ventral groove. *Megateuthis* is usually more robust than *Passaloteuthis*, especially in profile, and is frequently more conical than this genus. It differs from *Acrocoelites* which is distinguished by its irregular profile in addition to its ventral groove. It differs from *Paramegateuthis* Gustomesov, which possesses a more conical rostrum in general, with very elongated dorso-lateral apical grooves.

***Megateuthis rhenana* (Oppel, 1856)** Pl. 24, figs 3–5; Pl. 25, figs 1–3; Pl. 26, fig. 1

- non 1824 *Belemnites compressus* Stahl, p. 33, pl. II, fig. 4 [=*Pleurobelus compressus* (Stahl), Pliensbachian].
- . 1827 *Belemnites compressus* Blainville, p. 84, pl. II, fig. 9.
- . 1830 *Belemnites compressus* Voltz, p. 414, pl. V, figs 1, 2.
- v. 1848 *Belemnites compressus gigas* Quenstedt, p. 423, pl. 27, figs 1, 6.
- v? 1855 *Belemnites athleticus* Simpson, p. 28 [Lectotype, here designated, WM 15, 'jurensis' Zone, Blea Wyke Point, North Yorkshire].
- v? 1855 *Belemnites inclusus* Simpson, p. 28 [Lectotype, here designated, WM 2160, 'communis' Zone (=*bifrons* Zone), Whitby, North Yorkshire].
- v.\* 1856 *Belemnites Rhenanus* Oppel, p. 363.
- 1863 *Belemnites Rhenanus* Oppel; Mayer, p. 185.
- ? 1867 *Belemnites Voltzii* Phillips, p. 79, pl. XVII, fig. 43.
- . 1867 *Belemnites inornatus* Phillips, p. 80, pl. XVIII, fig. 46.
- ? 1876 *Belemnites voltzii* Phillips; Blake (in Tate & Blake), p. 326.
- v? 1876 *Belemnites athleticus* Simpson; Blake (in Tate & Blake), p. 326.
- ? 1878 *Megateuthis Rhenana* (Oppel); Bayle, pl. XXVI, fig. 4.
- 1883 *Belemnites Rhenanus* Oppel; Mayer-Eymar, p. 641.
- ? 1898 *Belemnites inornatus* Phillips; Benecke, p. 42, pl. III, fig. 6.
- . 1902 *Belemnites rhenanus* Oppel; Janensch, p. 121.
- . 1905 *Belemnites inornatus* Phillips; Benecke, p. 290, pl. XXVI, figs 5, 6, 9.
- . 1905 *Belemnites rhenanus* Oppel; Benecke, p. 288, pl. XXVI, figs 7, 8.
- . 1906 *Belemnites (Pachyteuthis) voltzii* Phillips; Lissajous, p. 53.

- . 1906 *Belemnites (Pachyteuthis) cf. inornatus* Phillips; Lissajous, p. 53, pl. 6, figs 4, 5.
- v. 1912 *Belemnites rhenanus* Oppel; Werner, p. 136, pl. 13, figs 1–4.
- 1915 *Mesoteuthis rhenanus* (Oppel); Lissajous, p. 129.
- 1920 *Megateuthis Rhenana* (Oppel); Bülow-Trummer, p. 118.
- . 1924 *Belemnites (Megateuthis) coniformis* Ernst, p. 87, pl. XII, figs 7, 8.
- 1925 *Mesoteuthis rhenanus* (Oppel); Lissajous, p. 129.
- ? 1931 *Mesoteuthis rhenana* (Oppel); Krimholz, p. 15.
- ? 1942 *Mesoteuthis cf. rhenana* (Oppel); Kolb, p. 162, pl. 9, fig. 7.
- . 1942 *Mesoteuthis cf. inornata* (Phillips); Kolb, p. 163, pl. 6, figs 11, 12.
- v. 1965 *Belemnites rhenanus* Oppel; Schwegler, pp. 87–89, text-figs 54–56.
- non? 1971 *Mesoteuthis rhenanus* (Oppel); Činčurová, p. 74, pl. V, fig. 6.
- non? 1971 *Mesoteuthis voltzii* (Phillips); Činčurová, p. 75, pl. V, fig. 7.
- 1975 *Mesoteuthis rhenana* (Oppel); Saks & Nal'nyeva, p. 31.
- 1980 *Megateuthis (Mesoteuthis) rhenana* (Oppel); Riegraf, p. 147.
- non? 1983 *Mesoteuthis rhenanus* (Oppel); Činčurová, p. 41, pl. IV, fig. 1 [=?Acrocoelites (*Odontobelus*) sp.].
- v non 1984 *Acrocoelites (*Odontobelus*) voltzi* (Phillips); Riegraf *et al.*, p. 157, pl. 12, figs 1, 2 [=*Acrocoelites (*Odontobelus*)* sp.].
- 1984 *Megateuthis rhenana* (Oppel); Knitter & Riegraf, p. 82.

*Type specimens.* Oppel's (1856) name *Belemnites rhenanus* was apparently a replacement for Quenstedt's (1848) homonym *Belemnites compressus gigas*. As such Quenstedt's specimens are types of Oppel's species, and Oppel cited one specimen in particular (Quenstedt 1848, pl. 27, fig. 1) as typical. Unfortunately there is no record of this specimen either in Tübingen or Munich, although a second specimen from Quenstedt's figured series is available at Tübingen (GPIT, no registration number). This specimen (Quenstedt 1848, pl. 27, fig. 6) from the Aalenian (lowest zone of the Lower Ooliths, or Dogger α) of Gundershoffen, Württemburg, southwest Germany, is here designated lectotype.

*Diagnosis.* Large sized, robust, conical *Megateuthis*. Outline symmetrical, cylindriconal to conical. Profile nearly symmetrical, conical. Transverse sections elliptical. Apex striated with two short dorso-lateral grooves.

*Material.* BMNH, 21 specimens, from the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire; Bridport Sands, Dorset, Cephalopod Bed, Gloucestershire, and equivalent horizons in Worcestershire. OUM, 1 specimen; WM, 15 specimens. From the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire. GMB, 2 specimens, *levesquei* Zone, Somerset. CMN, 3 specimens, *bifrons* Zone, Northampton.

*Description.* Large sized, conical rostrum with a total length of approximately five times Dv. The outline is symmetrical and cylindriconal to conical, the flanks diverging regularly from the acute apex. The profile is nearly symmetrical and conical, with some individuals having inflated venters, with moderate divergence from the apex. Transverse sections of the rostrum are elliptical and rounded with weak to moderate compression.

The apex of the rostrum is characterized by two short, dorso-lateral grooves that generally do not extend adorally for more than 10 mm. There is no ventral apical groove, but there may be short striae on the venter, as well as on the dorsum, of the apex. Because of the robust nature of the rostrum, lateral lines are indistinct, but consist broadly of two, parallel, weak depressions (one dorso-lateral, one ventro-lateral) separated by a weak ridge or weal. The phragmocone is ventrally displaced, penetrating approximately two fifths of the rostrum. The apical line is goniolineate.

| Specimen    | L     | l    | Dv   | Dl   |
|-------------|-------|------|------|------|
| BMNH C59432 | 115·9 | 71·2 | 22·5 | 19·9 |
| C59468      | 112·4 | 74·5 | 24·9 | 21·4 |
| C59469      | 113·1 | 75·1 | 22·4 | 20·5 |
| C59483      | 85·0  | 57·5 | 18·7 | 18·6 |

Table 33. Measurements of *Megateuthis rhenana* (Oppel, 1856).

*Remarks.* *Megateuthis rhenana* may be confused with the earlier occurring species *Passaloteuthis bisulcata* (Blainville) and with several species of *Acrocoelites* (*Toarcibelus*). However, it can be distinguished from the former in possessing a more robust and uncom-pressed rostrum, and from the latter by the absence of a single ventral apical groove. Within *Megateuthis*, *M. rhenana* most closely resembles *M. glaber* (Simpson), although this species is distinguished by its more irregular profile, the greater compression of its rostrum, and by the presence of a short epirostrum.

Simpson (1855) proposed two earlier species names, *B. athleticus* and *B. inclusus* that may be synonyms of *B. rhenana*. However, the former species is based on a single specimen (WM 15) which is poorly preserved and therefore cannot be assigned to Oppel's species with any certainty. The lectotype of *B. inclusus* is slender with an asymmetrical profile and may represent a species of *Acrocoelites* (*Toarcibelus*) rather than *M. rhenana*. Despite this, it is provisionally assigned to *M. rhenana* because of its overall morphology.

*Occurrence.* Lower Toarcian (*bifrons* Zone, *fibulatum* Subzone) to earliest Aalenian of Britain, mainland Europe and possibly the USSR.

***Megateuthis glaber*** (Simpson, 1855) Pl. 25, figs 4, 5; Pl. 26, figs 2, 3; Pl. 27, figs 3, ?5; Pl. 28, fig 1

- v.\*1855 *Belemnites glaber* Simpson, p. 24.
- v? 1866 *Belemnites limatulus* Simpson, p. 215 [Lectotype, here designated, WM 264, 'communis' Zone, Whitby, North Yorkshire].
- v. 1867 *Belemnites ventralis* Phillips (*pars*), p. 80, pl. XVII, fig. 44, non fig. 45 [= *Acrocoelites (Odontobelus)* sp.].
- ? 1876 *Belemnites voltzii* Phillips; Blake (*in Tate & Blake*) (*pars*), p. 326.
- 1883 *Belemnites ventralis* Phillips; Mayer-Eymar, p. 641.
- v. 1884 *Belemnites glaber* Simpson; Simpson, p. 28.
- v? 1884 *Belemnites optatus* Simpson, p. 29. [Lectotype, here designated, WM 2710, Upper Lias, Whitby, North Yorkshire].
- 1925 *Mesoteuthis glaber* (Simpson); Lissajous, p. 93.
- ? 1965 *Belemnites cf. rhenanus* Oppel; Schwegler, p. 90, text-fig. 57.

*Lectotype.* WM 79, from the 'communis' Zone (= *bifrons* Zone, ?*fibulatum* to *crassum* subzones), Alum Shale Member, Peak (Ravenscar), North Yorkshire.

*Diagnosis.* Large, robust cylindriconal to conical *Megateuthis* with short epirostrum. Outline symmetrical, cylindriconal. Profile symmetrical to asymmetrical, cylindriconal to conical. Transverse sections compressed elliptical. Epirostrum striated, with two short dorso-lateral apical grooves. Secondary ventral apical groove may be developed.

*Material.* BMNH, 12 specimens; OUM, 1 specimen; WM, 3 specimens. All from the *bifrons* Zone to *levesquei* Zone, Alum Shale Member to Blea Wyke Sandstone Formation, North Yorkshire.

*Description.* Large, robust, cylindriconal to conical rostrum with a short epirostrum. The total length of the entire rostrum is approximately six times Dv. The outline is symmetrical and generally cylindriconal or conical, the epirostrum producing a more conical outline. The apex is often found eroded, but where entire with an epirostrum it is relatively acute, with weak divergence of the flanks from the apex, becoming parallel adorally. The profile is asymmetrical, with a slightly inflated venter, and cylindriconal. Transverse sections of the rostrum are compressed and generally elliptical.

The epirostrum is usually finely striated with two well-developed dorso-lateral apical grooves stretching adorally for the length of the epirostrum. A third, ventral apical groove may rarely be found, although this can be considered a pathological development. Lateral lines are indistinct due to the robustness of the rostrum, but consist of a broad dorso-lateral depression continuing adorally from the apical grooves, with a weak ridge and similar, parallel ventro-lateral depression below it. The phragmocone is ventrally displaced and penetrates approximately a third of the rostrum. The apical line is goniolineate with an alveolar angle of 28°.

| Specimen    | <i>L</i> | <i>l</i> | <i>Dv</i> | <i>Dl</i> |
|-------------|----------|----------|-----------|-----------|
| WM79        | 135·6    | 96·2     | 25·4      | 20·7      |
| BMNH C59418 | 122·2    | 91·0     | 26·4      | 23·4      |
| C59428      | 131·1    | 86·3     | 25·2      | 21·1      |
| C59472      | 154·0    | 98·0     | 26·6      | —         |
| C59475      | 112·5    | 78·7     | 19·5      | 17·9      |

Table 34. Measurements of *Megateuthis glaber* (Simpson, 1855).

*Remarks.* *Megateuthis glaber* may be confused with some more robust and conical individuals of *Acrocoelites (Toarcibelus) inaequistriatus* (Simpson) which also occur in the *variabilis* Zone. However, this species is smaller than *M. glaber*, and has a less robust form, a slightly more inflated venter and three well-developed apical grooves. *M. glaber* differs from *M. rhenana* (Oppel) in having a more compressed transverse section and more cylindricconical form, and from *M? longisulcata* (Voltz) which is much more slender and compressed with very long apical grooves. It may be possible that *M. glaber* and *M. rhenana* represent sexual dimorphs of a single biological species; however, the two names are retained to denote differing morphologies (morphospecies; see Doyle 1985).

Simpson (1855, 1884) described a number of belemnite species with ‘imperfect apices’ (*Belemnites glaber*, *B. inclusus*, *B. opatus*). In essence, as perusal of their type specimens shows, these ‘species’ represent specimens of *M. glaber* (= *Belemnites ventralis* Phillips) which have lost their epirostra.

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

### ***Megateuthis?* *longisulcata* (Voltz, 1830) Pl. 22, fig. 6**

- \*. 1830 *Belemnites longisulcatus* Voltz, p. 57, pl. VI, fig. 1.
- v non 1848 *Belemnites acuarium longisulcatus* Quenstedt, p. 413, pl. 25, figs 11, 12, 23 [= *Salpingoteuthis macer* (Quenstedt)].
- . 1856 *Belemnites longisulcatus* Voltz; Oppel, p. 239.
- . 1863 *Belemnites longisulcatus* Voltz; Mayer, p. 184.
- . 1867 *Belemnites longisulcatus* Voltz; Phillips, p. 82, pl. XIX, fig. 47.
- non 1874 *Belemnites longisulcatus* Voltz; Dumortier, p. 39, pl. II, figs 9, 10 [= *Acrocoelites (Toarcibelus) inaequistriatus* (Simpson)].
- ? 1876 *Belemnites longisulcatus* Voltz; Blake (*in Tate & Blake*), p. 325.
- 1883 *Belemnites longisulcatus* Voltz; Mayer-Eymar, p. 641.
- . 1898 *Belemnites acuarium* Schlotheim; Benecke, p. 49, pl. 1, figs 7, 8.
- . 1902 *Belemnites longisulcatus* Voltz; Janensch, p. 115.
- . 1912 *Belemnites longisulcatus* Voltz; Werner, p. 131.
- . 1920 *Cuspiteuthis longisulcata* (Voltz); Bülow-Trummer, p. 109.
- . 1925 *Salpingoteuthis longisulcatus* (Voltz); Lissajous, p. 107.
- . 1942 *Salpingoteuthis longisulcatus* (Voltz); Kolb, p. 152, pl. 7, fig. 14; pl. 8, fig. 1; pl. 10, fig. 1.
- v non 1969 *Belemnites longisulcatus* Voltz; Schwager, p. 211, text-fig. 90 [= *Salpingoteuthis macer* (Quenstedt)].
- non ? 1975 *Salpingoteuthis longisulcatus* (Voltz); Cinćurová, p. 43, pl. 1, fig. 1.
- non 1980 *Salpingoteuthis longisulcata* (Voltz); Riegraf, p. 151 [= *Salpingoteuthis macer* (Quenstedt)].
- ? 1984 *Salpingoteuthis longisulcata* (Voltz); Knitter & Riegraf, p. 82.

*Type specimen.* Voltz’s (1830) type and figured specimens have been destroyed by fire (M. Wolf, *pers. comm.* 1983). A neotype, from the ‘Marnes du Lias Supérieur, Wasseraalfingen, Gundershoffen and Boll’ is therefore required to stabilise this species.

*Diagnosis.* Elongate, slender cylindricconical *Megateuthis?* with long epirostrum. Outline symmetrical, cylindricconical. Profile almost symmetrical, cylindricconical. Transverse sections elliptical to almost pyriform, compressed. Epirostrum striated, bearing elongate dorso-lateral grooves.

*Material.* BMNH, 6 specimens, *bifrons* Zone to *variabilis* Zone, Alum Shale to Peak Mudstone members, North Yorkshire. BGS, 2 specimens, *?thouarsense* to *?levesquei* Zones, Nailsworth Sands, Avon.

*Description.* Medium sized, elongate slender cylindriconal rostrum with epirostrum. The total length of the rostrum is approximately nine times Dv. The outline is cylindriconal and symmetrical, with moderate divergence of the flanks adorally from an acute apex. The profile is similar to the outline, although generally asymmetrical due to the form of the epirostrum, although venter and dorsum are uninflated. The transverse sections are compressed and elliptical, although some sections are pyriform with a broader venter than dorsum.

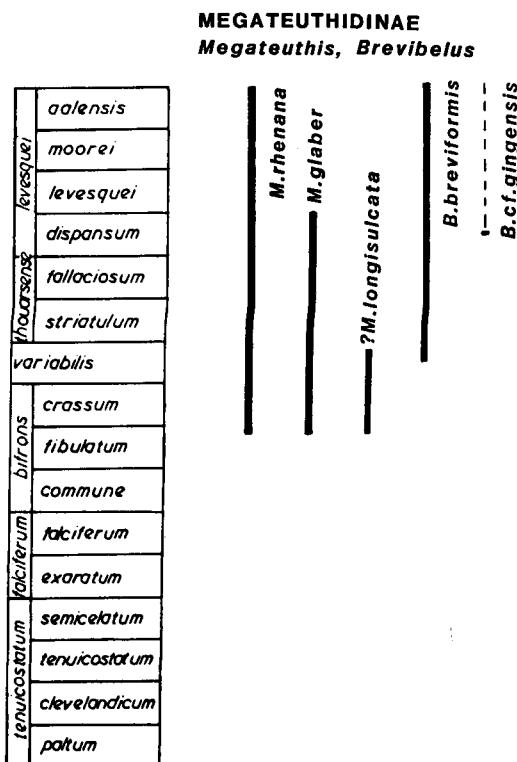
The epirostrum is commonly striated at its apex, dorsal striae extending adorally for some distance. There are two dorso-lateral apical grooves that extend for the length of the epirostrum. There is no ventral apical groove. The lateral lines are present as a broad and shallow dorso-lateral depression emanating from the apical grooves, underlain by a weaker ventro-lateral depression. The phragmocone is ventrally displaced and penetrates approximately one third of the rostrum. The apical line is goniolineate with an apical angle of 25°.

| Specimen   | L     | l     | Dv   | Dl   |
|------------|-------|-------|------|------|
| BMNH C7017 | 170·4 | 112·2 | 19·4 | 16·4 |
| C59452     | —     | 101·6 | 17·7 | 14·9 |

Table 35. Measurements of *Megateuthis? longisulcata* (Voltz, 1830).

*Remarks.* This species is assigned to *Megateuthis* with question because of its dorso-lateral grooves and compressed section, as well as its general morphological similarity to later species such as *M. elliptica* (Schlotheim). However, it cannot definitely be assigned to this genus because of its long dorso-lateral apical grooves and very slender form, which distinguish it from most other species of *Megateuthis* (including *M. rhenana* (Oppel) and *M. glaber* (Simpson)).

*M? longisulcata* resembles *Acrocoelites (Toarcibelus) inaequistriatus* (Simpson) and *Salpingoteuthis macer* (Quenstedt). The former of these two species can be distinguished from



TEXT-FIG. 19. Stratigraphic ranges of British Toarcian Megateuthidinae (*Megateuthis* and *Brevibelus*) plotted against ammonite zones and subzones.

*M? longisulcata* by its three apical grooves and more rounded section, and the latter can be distinguished by its sheath-like orthorostrum and very elongate ventral and dorso-lateral grooves.

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

#### Family SALPINGOTEUTHIDIDAE fam. nov.

*Type genus.* *Salpingoteuthis* Lissajous, 1915.

*Diagnosis.* Belemnitina with sheath-like orthorostra and elongate epirostra bearing multiple canal-like apical grooves not underlain by splitting-surfaces. Phragmocone apparently belemnitid, with spherical protoconch.

*Range.* Lower Toarcian (?*commune* Subzone, *bifrons* Zone) to Aalenian of southern England and mainland Europe.

*Remarks.* *Salpingoteuthis* Lissajous formerly occupied a solitary position within the Belemnitidae. The presence of multiple canal-like grooves is unknown in any other members of this family, usually being confined only to members of the Belemnopseina. However, unlike belemnopseine belemnites, the canal-like grooves of *Salpingoteuthis* lack splitting surfaces, and are truly apical grooves indicating that *Salpingoteuthis* is a representative of the Belemnitina. It is for this reason that a new family, albeit monogeneric, is erected to contain this genus. The Salpingoteuthididae resemble members of the Belemnoteuthididae and Diplobelidae in the sheath-like covering of the phragmocone, but neither of the last named families has a grooved epirostrum, although Reitner & Engeser (1983) have recorded the presence of an epirostrum in the belemnoteuthid *Chitinobelus* Fischer.

Gustomesov (1977) erected two genera, *Hartmannibelus* and *Orbignybelus*, here considered junior synonyms of *Salpingoteuthis*, and included them in a new subfamily, the Holcobelinae (type genus *Holcobelus* Stolley), of his new family, the Mesoteuthidae (type genus *Mesoteuthis* Lissajous). Both *Holcobelus* and *Mesoteuthis* are typical Belemnitidae, having short, apical grooves and 'normal' rostra (e.g. see Saks & Nal'nyaeva 1975), and therefore Gustomesov's (1977) new family taxa cannot be considered senior synonyms of the Salpingoteuthididae.

#### Genus SALPINGOTEUTHIS Lissajous, 1915

[=*Hartmannibelus* Gustomesov, 1977; *Orbignybelus* Gustomesov, 1977]

*Type species.* *Belemnites trisulcatus* Blainville, 1827, by original designation.

*Other species.* *S. tessoniana* (Orbigny); *S. dorsetensis* (Oppel); *S. macer* (Quenstedt) and *S. hartmanni* Lissajous.

*Diagnosis.* Small to medium sized, slender conical to elongate cylindriconal Salpingoteuthididae. Outline symmetrical, profile generally symmetrical, both cylindriconal to conical. Orthorostrum consists of sheath-like covering of phragmocone. Transverse sections generally subcircular to subquadrate and weakly compressed. Multiple ventral and dorsal canal-like grooves extend adorally from apex. Apical line of orthorostrum undefinable, alveolar angle 23°.

*Range.* As for family.

*Remarks.* *Salpingoteuthis* is distinct from other belemnitines in the possession of its unique, multiple, elongate canal-like grooves. It does resemble homeomorphically the Tertiary sepiid *Vasseuria*, as like this taxon it possesses longitudinal canals and a contorted central mass to its epirostrum. However, *Vasseuria* is a sepiid (Curry 1955; Jeletzky 1966), and as such has no 'orthorostrum', possesses a different phragmocone structure, and was constructed from aragonite.

*Salpingoteuthis* is here restricted to its original diagnosis based on its type species *Belemnites trisulcatus* Blainville. Many authors (e.g. Bülow-Trummer 1920; Naef 1922; Roger 1952; Činčurová 1967, 1971, 1974, 1975; Riegraf 1980) have misused this name, including within it several unrelated species united in their possession of an epirostrum, which should

be assigned to the genera *Youngibelus* Riegraf, *Dactylosteuthis* Bayle, *Acrocoelites* Lissajous and *Megateuthis* Bayle (e.g. *M? longisulcata* (Voltz), see above). Gustomesov (1977) recently erected *Hartmannibelus* (type species *Hartmannibelus equisites* Lissajous) and *Orbignybelus* (type species *Belemnites tessoniana* d'Orbigny), but both may be considered junior synonyms of *Salpingoteuthis*, as they are based on species typical of this genus.

**Salpingoteuthis tessoniana** (d'Orbigny, 1842) Pl. 28, figs 7–9, 11

- v.\* 1842 *Belemnites Tessonianus* d'Orbigny, p. 102, pl. 11, figs 13–18.  
 v non 1848 *Belemnites Tessonianus* d'Orbigny; Quenstedt, p. 413, pl. 25, fig. 18 [= *Micropassaloteuthis fistula* Riegraf, 1984].  
 v. 1869 *Belemnites quadricanaliculatus* var. *obsoletus* Phillips, p. 89, text-fig. 25.  
 v non 1912 *Belemnites Tessonianus* d'Orbigny; Werner, p. 133 [= *Micropassaloteuthis fistula* Riegraf, 1984].  
 1920 *Cuspiteuthis Tessoniana* (d'Orbigny); Bülow-Trummer, p. 110.  
 1922 *Salpingoteuthis Tessonii* (d'Orbigny); Naef, p. 236, text-fig. 86h.  
 1925 *Salpingoteuthis Tessonianus* (d'Orbigny); Lissajous, p. 144.  
 v non 1969 *Belemnites tessonianus* d'Orbigny; Schwegler, p. 208 [= *Micropassaloteuthis fistula* Riegraf, 1984].  
 v. 1977 *Orbignybelus tessonianus* (d'Orbigny); Gustomesov, p. 112, pl. 1, fig. 7.  
 non 1980 *Youngibelus?* *tessonianus* (d'Orbigny); Riegraf, p. 149 [= *Micropassaloteuthis fistula* Riegraf, 1984]

*Type specimens.* Syntypes, BMNH 73976, C58934, C58935, Toarcian, Amaye-Sur-Orne (Calvados), France. A lectotype is to be designated by Dr A. Gauthier.

*Diagnosis.* Very small, cylindriconal *Salpingoteuthis*. Outline symmetrical, cylindrical to cylindriconal. Profile generally asymmetrical, cylindriconal. Transverse sections compressed, subquadrate to pyriform. Venter bears pair of elongate, apical grooves for its whole length.

*Material.* BMNH, 23 specimens; BGS, 7 specimens. From the *bifrons* Zone, Oxfordshire, Worcestershire, Somerset, Gloucestershire, Northamptonshire. CMN, 14 specimens, *bifrons* Zone, Northampton. GMB, 26 specimens, *bifrons* Zone, Junction Bed, Somerset.

*Description.* Small ( $L=25$ ), cylindriconal rostrum which flares adorally, with a total length of approximately seven times  $Dv$ . The outline is symmetrical and cylindrical to cylindriconal, the tip of the apex being relatively blunt, although the flanks are almost parallel for most of their length. The profile is asymmetrical, often displaying a convexity of the dorsum, and it is generally more cylindriconal with a slightly inflated dorsum. In both aspects the alveolar region may flare adorally. The transverse sections are generally compressed and subquadrate, with a flat venter caused by the ventral grooves.

The apex bears apical striae and dorso-lateral depressions that are restricted to the apical region. The species is characterised by its ventral pair of parallel canal-like grooves that extend adorally from the apex, fading out on the flared apical region. Details of the phragmocone are unavailable due to the scarcity of specimens, but it is ventrally displaced, penetrating one sixth of the rostrum.

| Specimen   | <i>L</i> | <i>l</i> | <i>Dv</i> | <i>Dl</i> |
|------------|----------|----------|-----------|-----------|
| BMNH C6083 | 25·3     | 15·3     | 3·0       | 3·0       |
| C43008     | 20·0     | 15·0     | 3·6       | 3·2       |
| C59220     | 19·7     | 13·7     | 2·7       | 2·8       |
| C59221     | 21·8     | 14·0     | 3·0       | 3·1       |

Table 36. Measurements of *Salpingoteuthis tessoniana* (d'Orbigny, 1842).

*Remarks.* *S. tessoniana* is a distinct form that can easily be distinguished from other belemnites and members of its genus by its paired ventral grooves. Gustomesov (1977) designated this species the type of his genus *Orbignybelus*, but due to the general similarity of *S. tessoniana* to other members of *Salpingoteuthis* (sheath-like orthorostrum, multiple grooves), it is retained within this genus.

Phillips (1869, p. 89, text-fig. 24) described a series of minute belemnites occurring with *Belemnites quadricanaliculatus* var. *obsoletus* (= *S. tessoniana*) as the new species *Belemnites*

*minutus* (GMB M1221). It is possible that these small, smooth and conical belemnites represent the orthorostra of *S. tessoniana*, but this cannot be easily tested due to the size and rarity of these forms. It is also possible that these small belemnites are the rostra of the belemnoteuthid *Chondroteuthis wunnenbergi* Böde (see below).

*Occurrence.* Lower Toarcian (?*falciferum* or *commune* Subzones, *bifrons* Zone) to Upper Toarcian (?*thouarsense* Zone) of southern England and mainland Europe.

**Salpingoteuthis trisulcata** (Blainville, 1827) Pl. 28, figs 2–5, 10

- \*. 1827 *Belemnites trisulcatus* Blainville, p. 83, pl. 5, fig. 13.
- non 1831 *Belemnites trisulcatus* (Hartmann M.S.) Zieten, p. 31, pl. 24, fig. 3 [= *Acrocoelites (Odontobelus) triscissus* (Janensch)].
- . 1831 *Belemnites tricanaliculatus* (Hartmann M.S.) Zieten, p. 32, pl. 24, fig. 10.
- . 1831 *Belemnites quadricanaliculatus* (Hartmann M.S.) Zieten, p. 32, pl. 24, fig. 11.
- . 1842 *Belemnites tricanaliculatus* Hartmann; d'Orbigny, p. 99, pl. 11, figs 1–5.
- v. 1848 *Belemnites acuarius tricanaliculatus* Quenstedt, p. 414, pl. 25, figs 13, 14, non fig. 15 [= *Salpingoteuthis dorsetensis* (Oppel)].
- 1863 *Belemnites tricanaliculatus* Hartmann; Mayer, p. 184.
- . 1874 *Belemnites tricanaliculatus* Hartmann; Dumortier, p. 245, pl. XLIX, figs 4–6.
- 1883 *Belemnites tricanaliculatus* Hartmann; Mayer-Eymar, p. 641.
- 1920 *Cuspiteuthis tricanaliculata* Hartmann; Bülow-Trummer (*pars*), p. 110 [includes some *S. dorsetensis* in synonymy].
- 1925 *Salpingoteuthis trisulcatus* Blainville; Lissajous, p. 148.
- non 1942 *Salpingoteuthis tricanaliculata* (Hartmann); Kolb, p. 153, pl. 5, fig. 19 [=? *Salpingoteuthis dorsetensis* (Oppel)].
- v. 1969 *Belemnites tricanaliculatus* Zieten; Schwegler, p. 216, text-fig. 95.
- 1980 *Salpingoteuthis trisulcata* (Blainville); Riegraf, p. 150.

*Type specimens.* The specimen figured by Blainville (1827, pl. 5, fig. 13) from the Upper Lias of Calvados, northern France is selected as lectotype. However, as it is improbable that the original specimen is preserved, a neotype from the type locality is required.

*Diagnosis.* Small to medium sized, slender *Salpingoteuthis*. Outline and profile similar, symmetrical, cylindriconical with slight adoral flaring. Apex bears a single ventral groove, two dorso-lateral grooves and often a single dorsal groove.

*Material.* BMNH, 38 specimens; OUM, 1 specimen; NMW, 1 specimen. All from the *levesquei* Zone, Bridport Sands and Down Cliff Clay, Dorset.

*Description.* Small to medium sized, slender elongate conical to cylindriconical rostrum with a total length of approximately nine times Dv. The outline is generally symmetrical and cylindriconical, with an acute apex. The flanks are weakly divergent adorally until the alveolar region which flares out. The profile is essentially similar to the outline. Transverse sections of the rostrum are subcircular (with incised 'nicks' caused by the grooves) and only weakly depressed, although they may have a flattened dorsum.

The rostrum bears multiple grooves extending adorally from the apex. The venter bears a single, central groove running into the alveolar region, and the dorsum may also bear a single, unpaired groove. In addition, there are two long dorso-lateral grooves of similar length, which are usually more incised than either the ventral or dorsal grooves. The phragmocone is only slightly ventrally placed, and it is covered by the thin sheath of the orthorostrum. The phragmocone penetrates approximately one sixth of the total rostral length. There is no structured apical line present.

| Specimen    | L    | l    | Dv  | Dl  |
|-------------|------|------|-----|-----|
| BMNH C59484 | 45.5 | 34.3 | 4.9 | 4.9 |
| C59485      | 57.8 | 42.8 | 6.0 | 5.9 |
| C59488      | 45.6 | 33.3 | 5.7 | 5.1 |

Table 37. Measurements of *Salpingoteuthis trisulcata* (Blainville, 1827).

*Remarks.* *S. trisulcata* is very distinctive, differing from *S. tessoniana* (d'Orbigny) by its transverse section and the form of its apical grooves, and from *S. dorsetensis* (Oppel) by its

more slender, cylindronical form. *S. macer* (Quenstedt) and *S. hartmanni* Lissajous are both much more elongate than *S. trisulcata*. Zieten (1831) erected two new species, *Belemnites tricanaliculatus* and *B. quadricanaliculatus*, which he separated on the presence of an unpaired dorsal groove in the latter. Both species are identical to *S. trisulcata*, the dorsal groove of which is not always apparent.

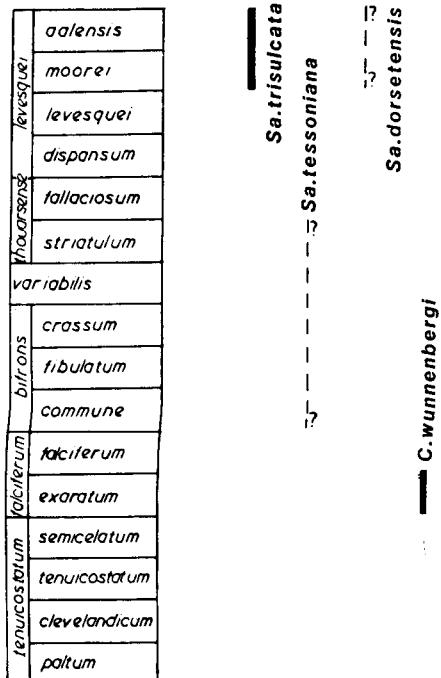
*Occurrence.* Upper Toarcian (*levesquei* Zone) to ?Aalenian of southern England and mainland Europe.

***Salpingoteuthis dorsetensis* (Oppel, 1856)** Pl. 27, figs 1, 2

- v . 1848 *Belemnites acuarius tricanaliculatus* Quenstedt, p. 414, pl. 25, fig. 15, non figs 13, 14 [=*Salpingoteuthis trisulcata* (Blainville)].
- v .\* 1856 *Belemnites Dorsetensis* Oppel, p. 362.  
1863 *Belemnites Dorsetensis* Oppel; Mayer, p. 184.
- v . 1867 *Belemnites quadricanaliculatus* Quenstedt; Phillips, p. 68, pl. XIII, fig. 35.  
. 1874 *Belemnites Dorsetensis* Oppel; Dumortier, p. 246, pl. XLIX, figs 2, 3.  
1883 *Belemnites Dorsetensis* Oppel; Mayer-Eymar, p. 641.  
. 1912 *Belemnites tricanaliculatus* Zieten; Werner, p. 132.  
1920 *Cuspiteuthis tricanaliculata* (Zieten); Bülow-Trummer, p. 110 (*par*) [includes some *S. trisulcata* in synonymy].  
1925 *Salpingoteuthis Dorsetensis* (Oppel); Lissajous, p. 82.  
? 1931 *Mesoteuthis dorsetensis* (Oppel); Krimholz, p. 17, pl. 1, figs 12, 13.  
? 1942 *Salpingoteuthis tricanaliculata* (Hartmann); Kolb, p. 153, pl. 5, fig. 19.
- v . 1969 *Belemnites dorsetensis* Oppel; Schwager, p. 217, text-fig. 96.
- v . 1977 *Hartmannibelus equisites* Gustomesov, p. 109, pl. 1, fig. 5 [based on Phillips 1867, pl. XIII, fig. 35].  
1980 *Salpingoteuthis dorsetensis* Oppel; Riegraf, p. 150.

*Type specimens.* Oppel (1856, p. 362) erected this species using material from the Dorset Coast near Bridport. There is apparently no record of Oppel's specimens in Munich, and

**SALPINGOTEUTHIDIDAE/  
CHONDROTEUTHIDINAE**  
***Salpingoteuthis, Chondroteuthis***



TEXT-FIG. 20. Stratigraphic ranges of British Toarcian *Salpingoteuthidinae* (*Salpingoteuthis*) and *Chondroteuthidinae* (*Chondroteuthis*) plotted against ammonite zones and subzones.

therefore the original of Phillips' (1867, pl. XIII, fig. 35v', l, d') (BGS GSM118048) from the Bridport Sands of Chideock, Bridport, is here designated neotype.

*Diagnosis.* Small, squat and robust *Salpingoteuthis*. Outline and profile symmetrical and conical with no pronounced alveolar flaring. Transverse sections subcircular. Grooves similar to those of *S. trisulcata*.

*Material.* BMNH, 2 specimens; BGS, 3 specimens. From the *levesquei* Zone, Bridport Sands, Dorset.

*Description.* Small, squat and robust conical rostrum with a total length ( $L=46$ ) of approximately six times Dv. The outline is symmetrical and conical with an acute apex, the flanks moderately diverging in a regular pattern, with no alveolar flaring. The profile is essentially similar in form to the outline. The transverse sections of the rostrum are subcircular (with 'nicks' caused by the grooves), but like *S. trisulcata* may have a somewhat flattened dorsum.

The pattern of grooves of this species matches that of *S. trisulcata* in possessing a single ventral groove, incised dorso-lateral grooves and frequently a single dorsal groove in addition. All these grooves extend from the apex to the alveolar region. The phragmocone is slightly ventrally placed and penetrates one fifth of the total rostrum length.

*Remarks.* *S. dorsetensis* can be distinguished from the other *Salpingoteuthis* species by its squat, conical form. *S. trisulcata* (Blainville), *S. macer* (Quenstedt) and *S. hartmanni* Lissajous are all more elongate and cylindriconal than *S. dorsetensis*, and *S. tessoniana* (d'Orbigny) has a different groove pattern.

*Occurrence.* Upper Toarcian (*levesquei* Zone, *aalensis* Subzone) to Aalenian of southern England and mainland Europe.

#### Family BELEMNOTEUTHIDIDAE Zittel, 1885

*Remarks.* Reitner & Engeser (1982, p.158) suggested that the belemnoteuthids are sufficiently distinct morphologically to warrant a new order of belemnoids. Their proposal was based on observations which suggested that the belemnoteuthid rostrum was aragonitic, and that its protoconch had a cup-like morphology. Bandel & Kulicki (1988) subsequently confirmed the aragonite mineralogy of the rostrum, but suggested that the cup-like protoconch found in some specimens (see Reitner & Engeser (1982) for discussion) was a purely preservational artifact. Based on these new observations, the aragonite mineralogy of the rostrum alone is not sufficient to warrant a new order, and therefore the family Belemnoteuthididae, as emended by Jeletzky (1966), is employed here for belemnites with sheath-like aragonitic rostra. The simple conical form of these belemnites and the presence of apical grooves, in its type genus at least, confirms placement of the family within the Belemnitina (see Jeletzky 1966, p.145).

#### Subfamily CHONDROTEUTHIDINAE Jeletzky, 1965

*Remarks.* Jeletzky (1965, 1966) considered that *Chondroteuthis* Böde was sufficiently distinct to warrant a new family. The pro-ostracum of this genus is unusual being extremely elongate, and as discussed by Jeletzky (1966) and Doyle (1986), in morphology it approaches the pro-ostraca of the earliest known Sepiida (e.g. *Naefia*, Upper Cretaceous). However, although elongate, the pro-ostracum of *Chondroteuthis* is still essentially spatulate and Belemnitida-like. The mineralogy of the *Chondroteuthis* rostrum has not been confirmed, but it possesses a conical sheath-like rostrum with faint striae or weak grooves, and is therefore sufficiently *Belemnoteuthis*-like to warrant inclusion within the Belemnoteuthididae. However, the subfamily Chondroteuthidinae is retained because of the unique form of the pro-ostracum.

Genus **CHONDROTEUTHIS** Böde, 1933

*Type species.* *Chondroteuthis wunnenbergi* Böde, 1933.

*Diagnosis.* Small, slender, acutely conical and sheath-like Chondroteuthidinae. Profile and outline similar, symmetrical and acutely conical. Transverse sections compressed and elliptical. Rostrum generally smooth, but it may bear short, weakly defined apical striations and solitary elongate striae. The phragmocone penetrates almost 90% of the rostrum, with an alveolar angle of 13–17°. The pro-ostracum is spatulate and elongate.

*Range.* Lower Toarcian (*falciferum* Zone, *exaratum* Subzone) of southern England and western Germany.

*Remarks.* *Chondroteuthis* is similar to *Belemnoteuthis* Pearce as both possess acute phragmocones (20–22° in *Belemnoteuthis*) and sheath-like rostra. However, *Belemnoteuthis* is distinguished by its strongly incised dorsal apical grooves. *Belemnoteuthis* was constructed from aragonite, but the original shell material of *Chondroteuthis* has not been deduced in the present study. Riegraf (1983) considered *Sueviteuthis* Reitner & Engeser (type species *Sueviteuthis zellensis* Reitner & Engeser, 1982) identical to *Chondroteuthis*. However, the former has a more complex ‘pro-ostracum’ (Reitner & Engeser 1983; T. Engeser *pers. comm.*, 1984) and is possibly a phragmoteuthid rather than a belemnoteuthid. The arm hooks of *Sueviteuthis* also differ from the more curved hook-like *Chondroteuthis* examples.

**Chondroteuthis wunnenbergi** Böde, 1933 Pl. 28, figs 12–15

- \* . 1933 *Chondroteuthis wunnenbergi* Böde, p. 55, pls 9–11, figs 1–13.
- v . 1966 *Chondroteuthis wunnenbergi* Böde; Jeletzky, p. 147, pl. 20, figs 3, 4.
- v . 1983 *Chondroteuthis wunnenbergi* Böde; Riegraf, p. 94, text-figs 1, 2.
- . 1985 *Chondroteuthis wunnenbergi* Böde; Riegraf, p. 253, pl. 17, fig. 4.

*Holotype.* The original of Böde (1933, pl. 9, fig. 1) in the Institute für Geologie und Paläontologie, Clausthal, Germany.

*Diagnosis and description.* As for genus.

*Material.* BMNH, 21 specimens; OUM, 11 specimens, *falciferum* Zone, *exaratum* Subzone, Fish Bed, Gloucestershire.

*Remarks.* *C. wunnenbergi* is easily distinguished from co-occurring belemnites by its sheath-like, almost smooth rostrum. It is a distinctive member of the fauna of the Fish Bed of southern England (*exaratum* Subzone), and occurs at similar horizons in northern and SW Germany (Böde 1933; Riegraf 1983, 1985; and personal observations).

*Occurrence.* As for genus.

#### ADDENDA AND CORRIGENDA

Page 2, line 2: Oppel (1856–58, p.238) also named a new species, *Belemnites whitbyensis*, based on Quenstedt's (1846–49, pl. 24, fig. 1) illustration of a large belemnite from the ‘Middle Lias, England’ (specimen in GPIT, unregistered). Despite Quenstedt's indication to the contrary, Oppel considered this specimen was from the ‘Alum Shales’, but this is inconsistent with its general morphology. This specimen is clearly a large *Passaloteuthis*, which may or may not be closely related to *Passaloteuthis bisulcata* (Blainville), and which is probably Late Domerian to earliest Toarcian in age.

Page 11, Text-fig. 10: Two specimens of *Dactyloteuthis crossotela* (Blake) were collected from bed 6, Inverarish Burn section. This species is indicative of the *bifrons* to *thouarsense* zones of England, supporting the suggestion that the Raasay Ironstone is a condensed deposit (Cope *et al.* 1978, fig. 10B).

Page 15 (References) add:

BAYLE, E. 1878. *Explication de la carte géologique de France. Tome quartrième, première partie. Fossiles principaux des terrains. Atlas.* 176 pl. Paris.

BIGUET, E. 1819. *Considérations sur les Bélemnites, suivies d'un essai de Bélemnitologie synoptique.* 63pp., Lyon.

Page 19: The status of *Belemnites* and the family Belemnitidae. Tubbs (1989) recently reported the progress of the submission by Doyle & Riegraf (1986, 1987) for the use of ICZN plenary powers to suppress the nominal genus *Belemnites* and designate the nominal genus *Passaloteuthis* as type genus of the family Belemnitidae, in order to

maintain current usage. Although a majority of commissioners voted for the proposals, an alternative was proposed by one of them voting in the negative. This suggestion, to retain *Belemnites* as a junior synonym of *Passaloteuthis*, was not accepted by the vast majority of palaeontologists replying to the commission during a second consultation (see Tubbs 1989). However, a second ballot including both proposals was held, producing deadlock with a split vote, and this remains the status at time of writing. It is hoped, given the majority in the initial ballot, that the nominal genus *Belemnites* (and its type species) will at least be suppressed using the plenary powers of the ICZN.

#### Reference.

TUBBS, P.K. 1989. Report on the proposed conservation of the family-group name Belemnitidae d'Orbigny, 1845 (Mollusca, Coleoidea), with suppression of the generic name *Belemnites* Lamarck, 1799 and the designation of *Passaloteuthis* Lissajous, 1915 as the type genus. *Bulletin of Zoological Nomenclature*, **46**, 267–72.

Page 20, line 21: For Bayle & Zeiller, read Bayle.

Page 23, line 13. Insert: *Occurrence*. Upper Domerian and Lower Toarcian (*tenuicostatum* Zone) of Britain and mainland Europe.

Page 24, line 22: For *Passaloteuthis longiconis*, read *Passaloteuthis longiconus*.

Page 26: The following should be added to the synonymy list for *Parapassaloteuthis robusta*: 1883 *Belemnites marcoui* Mayer-Eymar, p. 640 [junior objective synonym of *Belemnites latisulcatus* Phillips, 1866].

Page 31, line 2: for *Belemnites stimulis*, read *Belemnites stimulus*.

Page 34: The nominal species *Belemnites longiconus* Schwegler, 1969 is a junior primary homonym of *Belemnites longiconus* Simpson, 1884 (Pliensbachian, Belemnitiniae). There is no other available name for this species, and the replacement name *Acrocoelites* (*Acrocoelites*) *riegrafi* nom. nov. (in honour of the German palaeontologist Dr W. Riegraf) is erected here. Description and holotype as for *A.(A.) longiconus* (see p. 34).

Page 36, line 18: The nominal subgenus *Toarcibelus* Riegraf, 1980 is a junior objective synonym of the nominal genus *Praepachyteuthis* Gustomesov, 1977 (Gustomesov 1977, p. 111). Gustomesov's name is therefore the valid one for this subgenus.

Page 39, line 34: For *Passaloteuthis bruguieriana*, read *Passaloteuthis bisulcata*.

Page 41, synonymy: Replace *Gastobelus compressus* with *Pleurobelus compressus*.

Pages 46, 47, and captions for Plate 16: for *tricissus*, read *triscissus* throughout (except for Lissajous (1915) synonymy entry).

Pages 47, 48, and captions for Plates 16 and 17: for *subtricissus*, read *subtriscissus* throughout.

Page 47, synonymy list: for *Mesoteuthis tricissiformis*, read *Mesoteuthis triscissiformis*.

Page 50: synonymy list, add: v. 1884 *Belemnites tubularis* Young & Bird; Simpson, p. 26.

Page 51: synonymy list, add: v. 1855 *Belemnites trivialis* Simpson, p. 26 [Lectotype, here designated, WM448A, 'communis' Zone, Whitby, North Yorkshire. Juvenile; original of Phillips 1867, pl. X, fig. 23]; v. 1884 *Belemnites trivialis* Simpson; Simpson, p. 34.

Page 60, line 2, add: The true affinity of Simpson's (1855) species *Belemnites erosus* is unclear, though the single specimen (WM66) has a compressed rostrum similar to epirostrate examples of *D. crossotela*.

#### Plate captions:

Pl. 3, fig. 5: for C59372, read C59391.

Pl. 4, fig. 5: the horizon and locality is Marlstone Rock Bed, Alderton Hill, Gloucestershire (Figs 2, 3, 7–9 as stated).

Pl. 4, fig. 7: for C59389, read C59383.

Pl. 6, fig. 14: for bed xiv read bed xvi.

Pl. 7, fig. 15: for C59480, read C59479.

Pl. 17, fig. 15: for bed xl, read bed xlviii.

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Entries show: pages (major descriptive references in *Systematic Descriptions* in bold); text-figures (in italics); plates (figures in parentheses). Valid taxa are given in Roman type; invalid taxa in italic.

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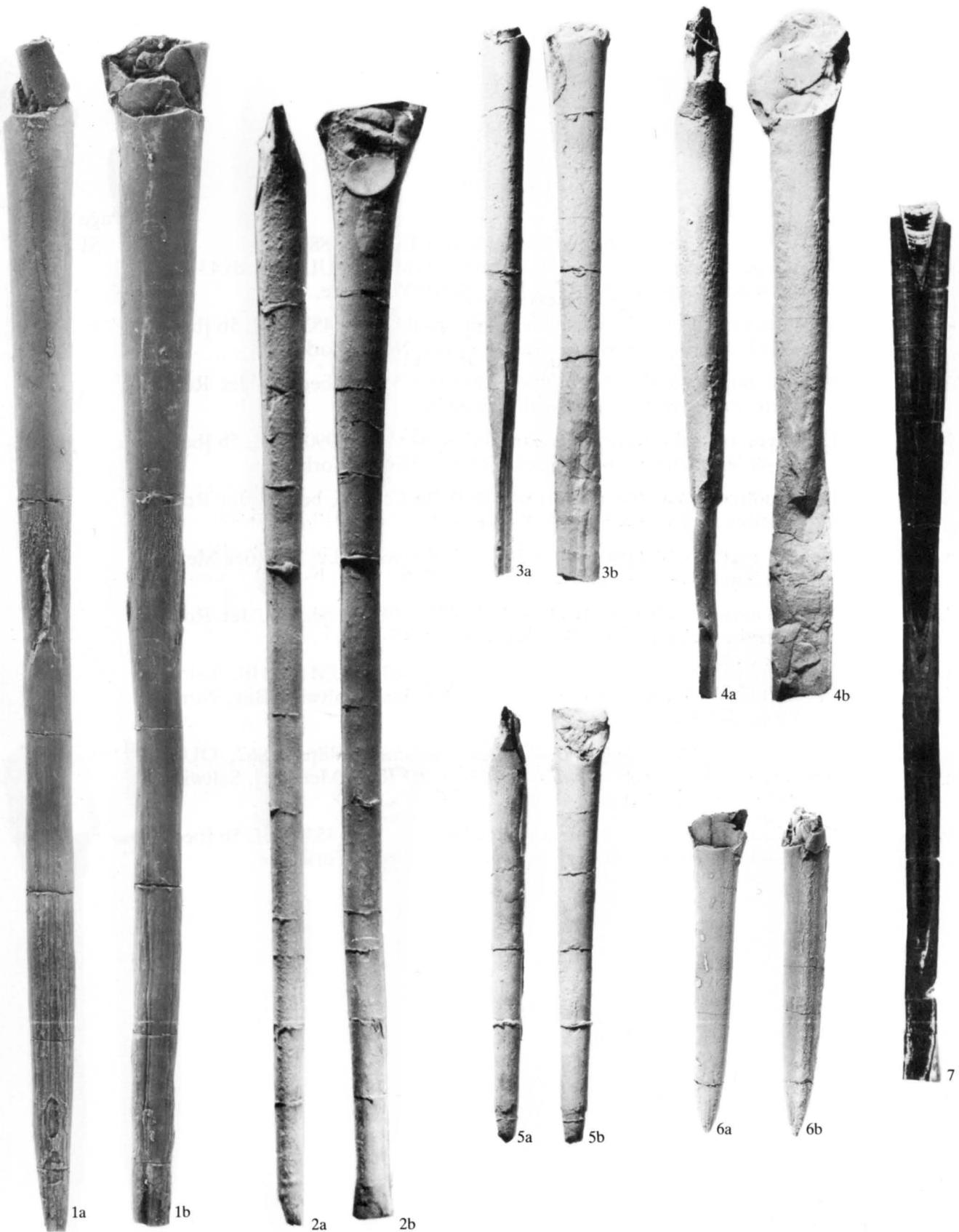
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|      | <i>Youngibelus tubularis</i> (Young & Bird, 1822)  | 50     |
| 1.   | Lectotype of <i>Belemnites productus</i> Simpson, 1866, ventral outline and right profile, WM 975, Jet Rock Member, Whitby, North Yorkshire.   |        |
| 2.   | Neotype, ventral outline and right profile. BMNH C59185, bed 43, Jet Rock Member, Saltwick Bay, North Yorkshire.   |        |
| 3.   | Adult with crushed epirostrum, ventral outline and right profile. BMNH C59200, bed xi, Jet Rock Member, Ravenscar, North Yorkshire.  |        |
| 4.   | Adult with crushed epirostrum, ventral outline and right profile. BMNH C59186, bed 43, Jet Rock Member, Saltwick Bay, North Yorkshire.   |        |
| 5.   | Orthorostrum with epirostral scar, ventral outline and right profile. BMNH C59199, bed xii, Jet Rock Member, Ravenscar, North Yorkshire.   |        |
| 7.   | Longitudinal section, venter to right. BMNH C59192, bed xi, Ravenscar, North Yorkshire.  |        |
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| 3.   | Ventral outline and right profile. BMNH C59188, bed 43, Jet Rock Member, Saltwick Bay, North Yorkshire.   |      |
| 4.   | Lectotype of <i>Belemnites aptus</i> Simpson, 1884, WM 1990a, UL 5b [beds 43–44, Jet Rock Member], Saltwick Bay, North Yorkshire.   |      |
| 5.   | Longitudinal section, venter to left. BMNH C59191, bed xi, Jet Rock Member, Ravenscar, North Yorkshire.   |      |
| 6.   | Ventral outline and right profile. BMNH C59196, bed x, Jet Rock Member, Ravenscar, North Yorkshire.   |      |
| 7.   | Ventral outline and right profile. BMNH C59197, bed 43, Jet Rock Member, Saltwick Bay, North Yorkshire.   |      |
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| 9.   | Juvenile. Paralectotype of <i>Belemnites striolatus</i> Phillips, 1867, OUM J15112, ‘bed with <i>B. tubularis</i> ’ [bed 43, Jet Rock Member], Saltwick Bay, North Yorkshire. |      |
| 10.  | Paralectotype, ventral outline and right profile, WM 453b, UL 5b [beds 43–44, Jet Rock Member], Saltwick Bay, North Yorkshire.  |      |

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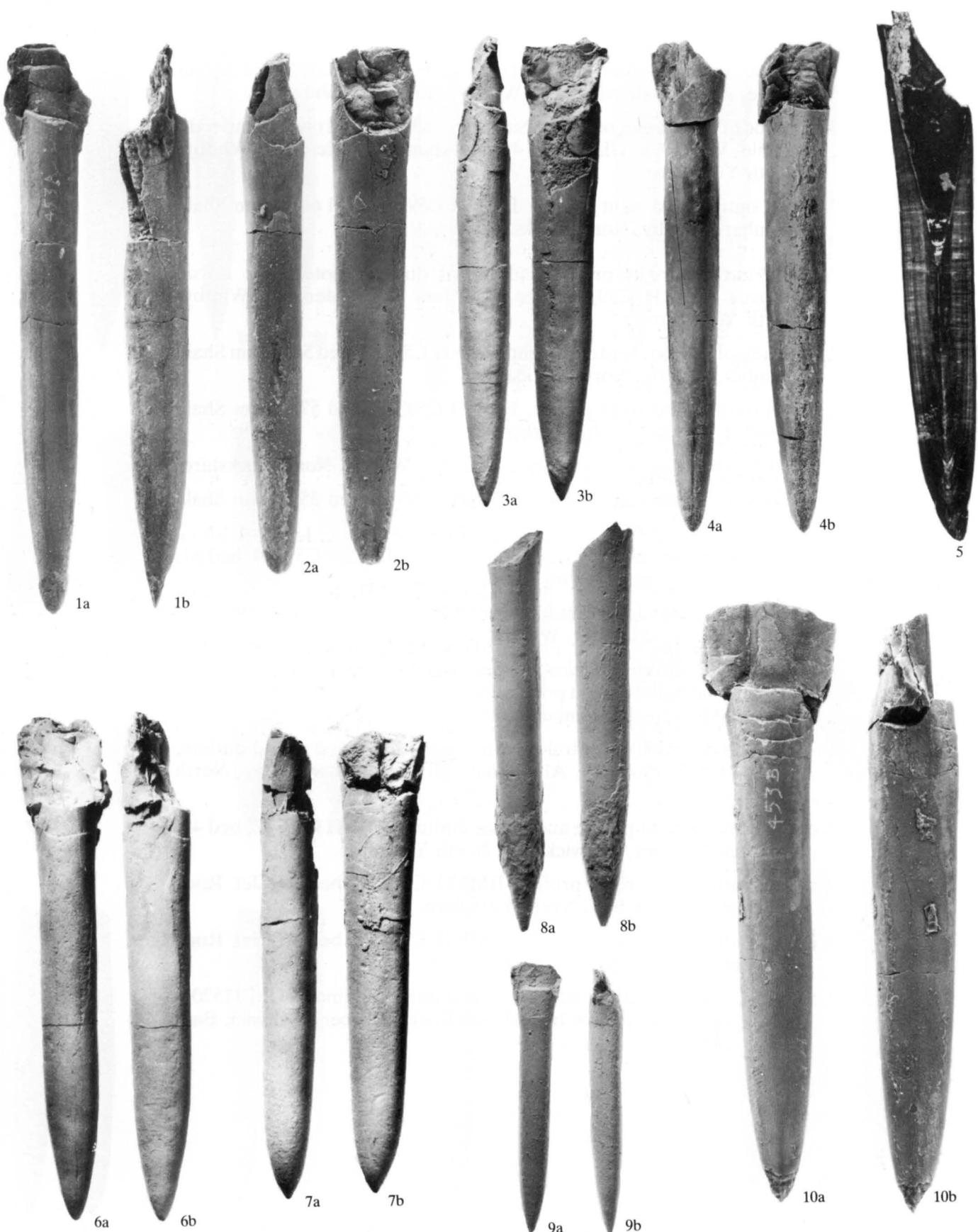


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|      | <i>Simpsonibelus expansus</i> (Simpson, 1855)   | 53   |
| 1.   | Lectotype, ventral outline and right profile, WM 2685, UL 1 [bed 53 and above, Alum Shale Member], Whitby, North Yorkshire.                                       |      |
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| 3.   | Ventral outline and right profile. BMNH C59366, bed 66, Alum Shale Member, Whitby, North Yorkshire.   |      |
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| 5.   | Longitudinal section, venter to right. BMNH C59358, bed 55, Alum Shale Member, Whitby, North Yorkshire.   |      |
| 6.   | Ventral outline and right profile. BMNH C59363, bed 57, Alum Shale Member, Whitby, North Yorkshire.   |      |
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| 15.  | Ventral outline and right profile. BMNH C59328, bed 47, Jet Rock Member, Saltwick Bay, North Yorkshire.   |      |
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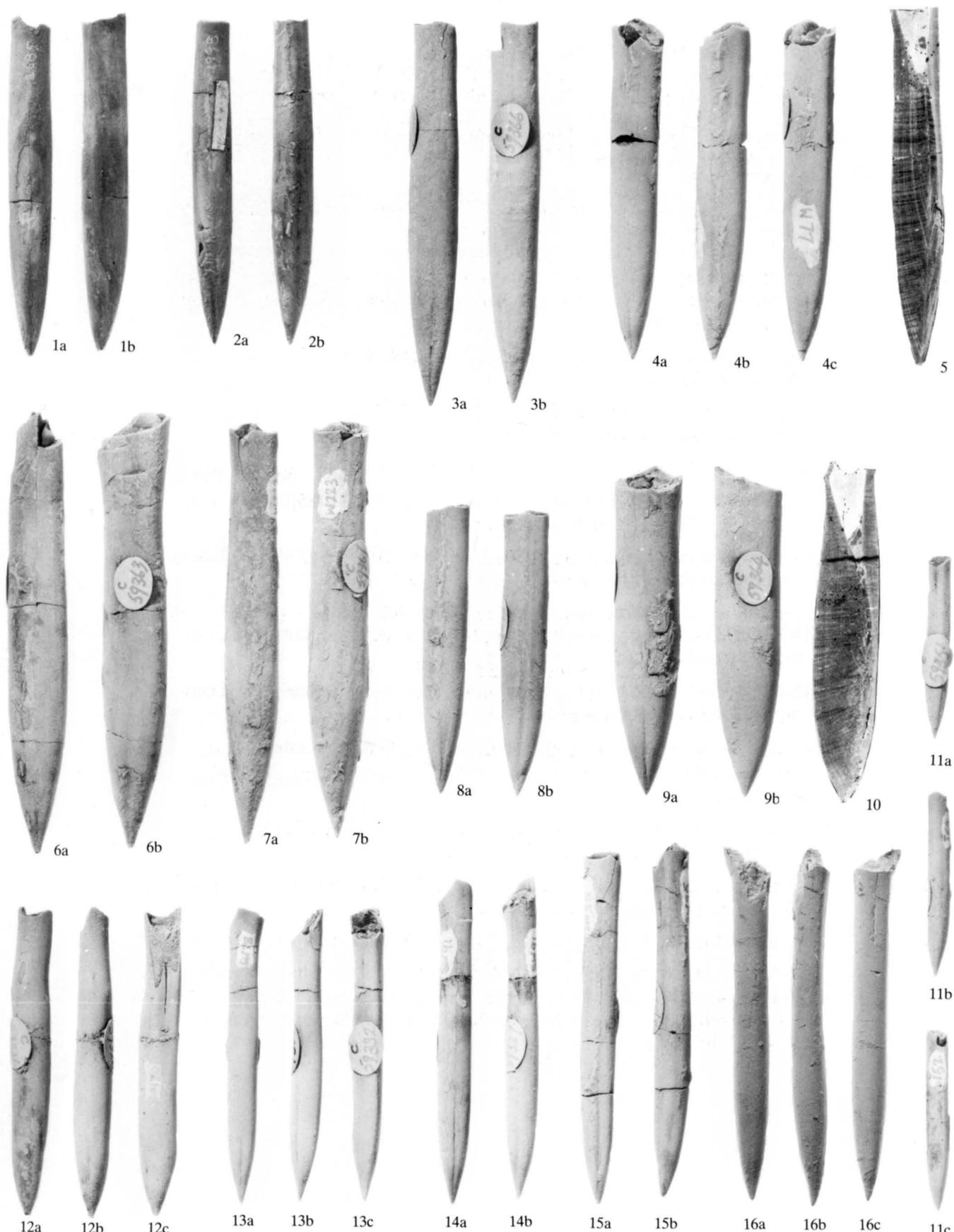


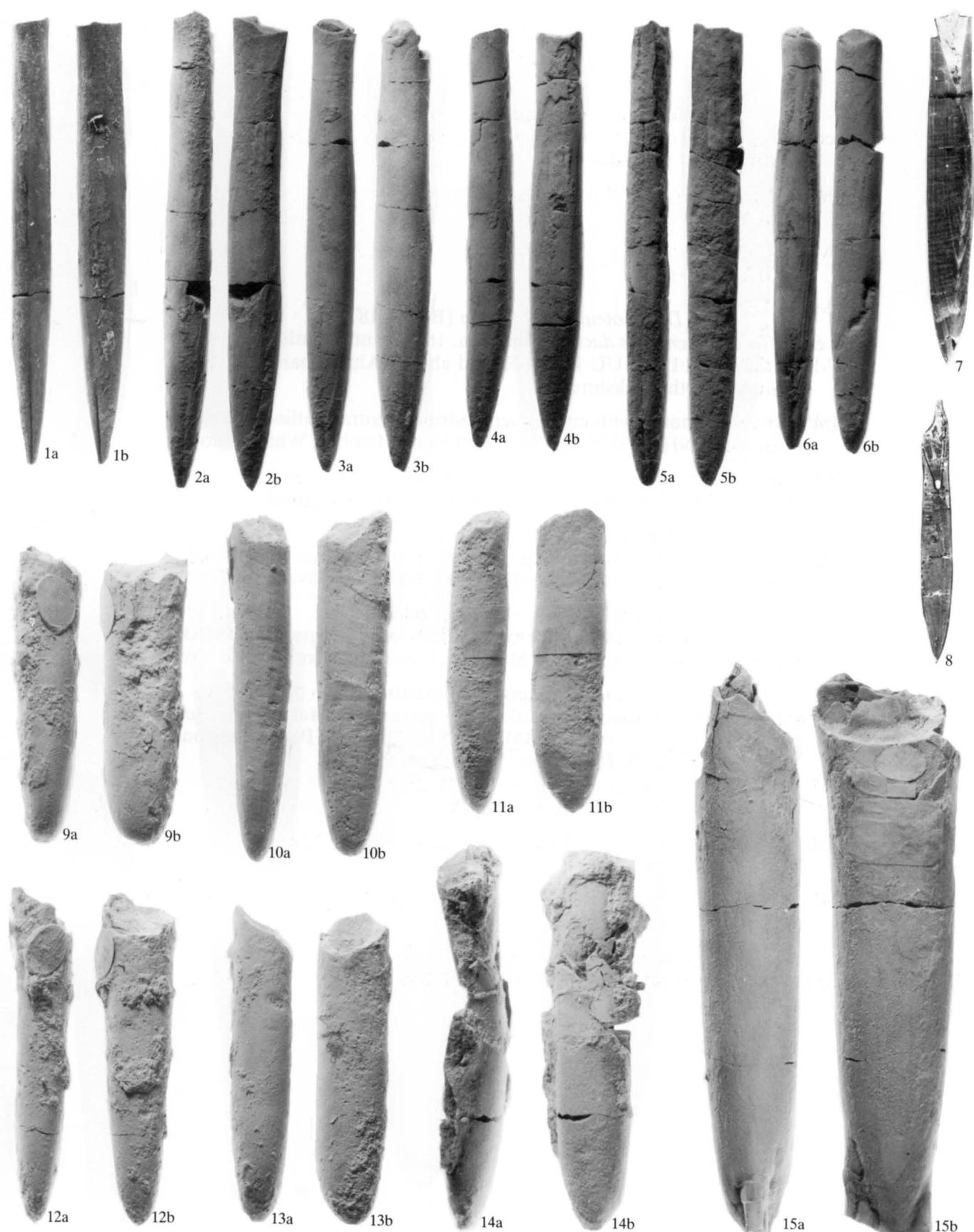
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|      | <i>Simpsonibelus latus</i> (Simpson, 1855)  | 56   |
| 1.   | Lectotype, ventral outline and right profile, WM 54, Alum Shale Member, Whitby, North Yorkshire.                        |      |
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| 3.   | BMNH C59460, bed 19, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.                                       |      |
| 4.   | BMNH C59459, bed 17, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.                                       |      |
| 5.   | BMNH C59467, bed 77, Grey Sandstone Member, Blea Wyke Point, North Yorkshire.   |      |
| 6.   | BMNH C58433, bed 14, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.                                       |      |
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| 9.   | BMNH C59234, Upper Lias [Cephalopod Bed], Minchinhampton Common, Stroud, Gloucestershire.                               |      |
| 10.  | BMNH C59235, Upper Lias [Cephalopod Bed], Minchinhampton Common, Stroud, Gloucestershire.                               |      |
| 11.  | BMNH C7827, Cephalopod Bed, Stinchcombe, Gloucestershire.   |      |
| 12.  | BMNH C59237, Upper Lias [Cephalopod Bed], Minchinhampton Common, Stroud, Gloucestershire.                               |      |
| 13.  | BMNH C59236, Upper Lias [Cephalopod Bed], Minchinhampton Common, Stroud, Gloucestershire.                               |      |
| 14.  | BMNH C59499, limestones overlying Upper Lias Clay, Bredon Hill, Hereford and Worcester.                                 |      |
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| 15.  | Lectotype, epirostrum crushed, BMNH C11868, Alum Shale Member, Whitby, North Yorkshire.                                 |      |

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|      | <i>Dactyloteuthis crossotela</i> (Blake, 1876)   | 59   |
| 1.   | Lectotype of <i>Belemnites dactylus</i> Simpson, 1884, ventral outline and right profile, WM 131b, UL 1 [bed 53 and above, Alum Shale Member], Whitby, North Yorkshire.              |      |
| 2.   | Incomplete specimen with crushed epirostrum, ventral outline and right profile. BMNH C59370, bed 72, Alum Shale Member, Whitby, North Yorkshire.                                     |      |
| 3.   | Specimen without epirostrum, ventral outline and right profile. BMNH C59435, bed xliv, Alum Shale Member, Ravenscar, North Yorkshire.  |      |
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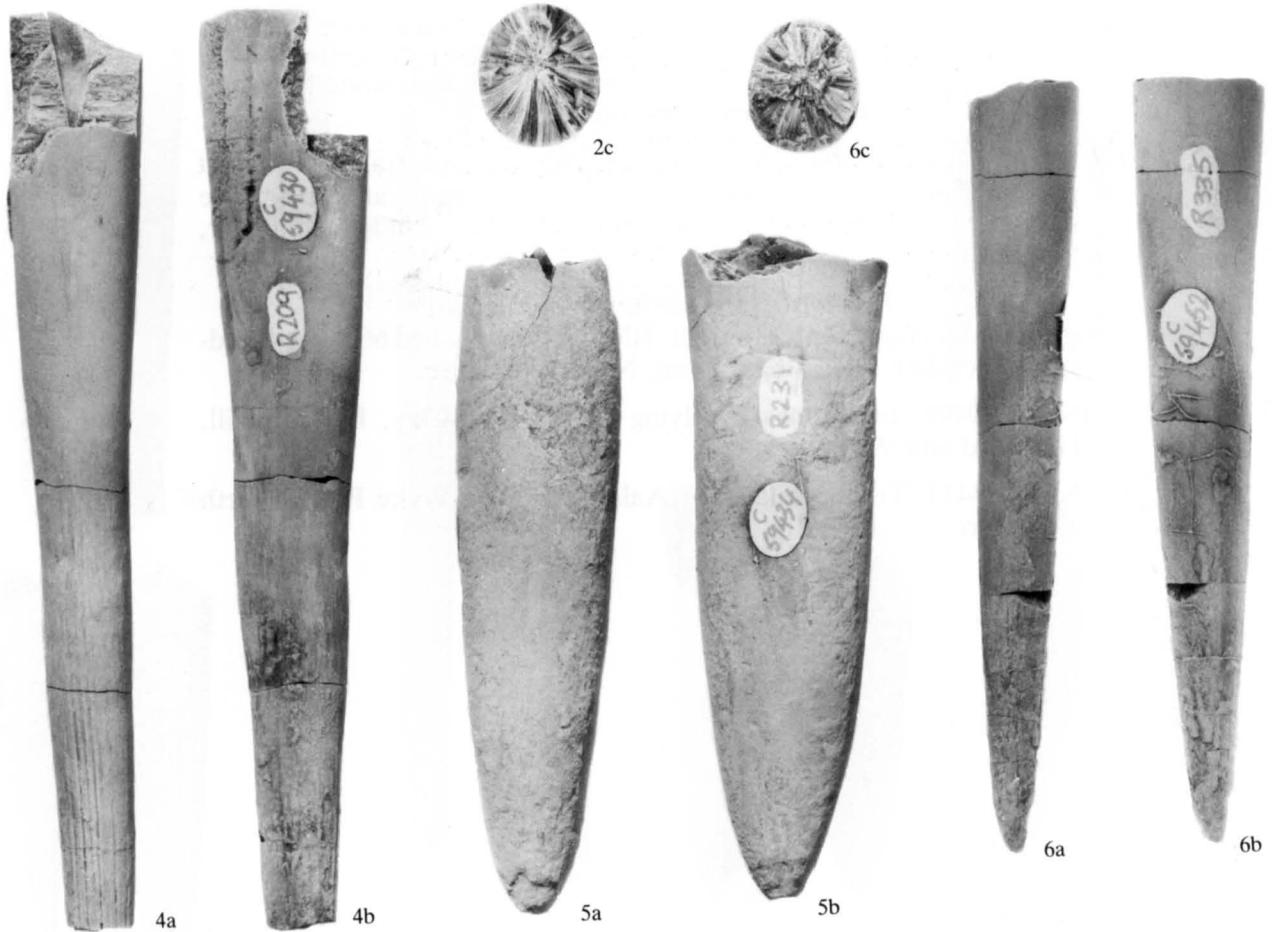
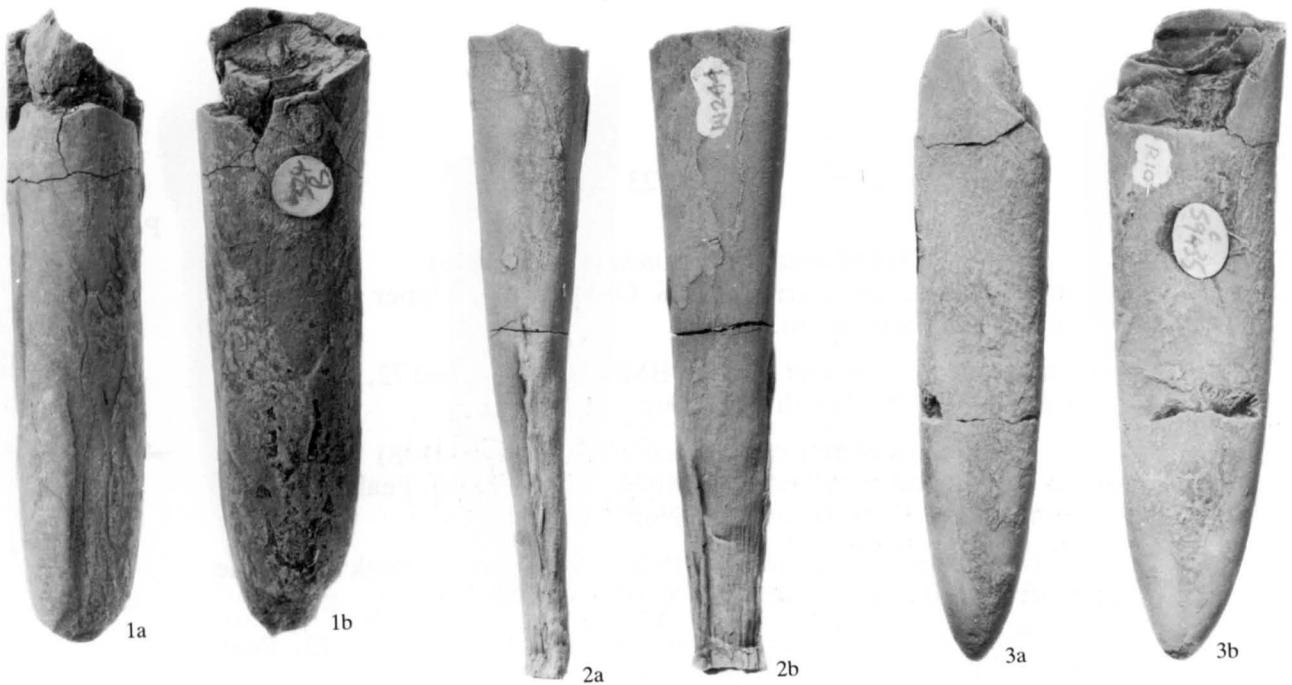


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|      | <i>Dactyloteuthis crossotela</i> (Blake, 1876)  |      |
| 1.   | Specimen without epirostrum. BGS GSM118008, Upper Lias Sand, Nailsworth, Bath, Avon.  | 59   |
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| 7.   | Ventral outline and right profile. BMNH C59445, bed 3, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.   |      |
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| 10.  | BMNH C59498, limestones overlying Upper Lias Clay, Bredon Hill, Hereford and Worcester.   |      |
| 11.  | BMNH C59473, Terebratula Bed (Aalenian), Blea Wyke Point, North Yorkshire.  |      |

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| 4.   | Juvenile. BMNH C59475, bed 5, Peak Mudstone Member, Fox Cliff, Ravenscar, North Yorkshire.  |      |
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| 1.   | <i>Megateuthis rhenana</i> (Oppel, 1856)<br>BMNH C59483, Bridport Sands, Burton Cliff, Burton Bradstock, Dorset.   | 64   |
| 2.   | <i>Megateuthis glaber</i> (Simpson, 1855)<br>Lectotype of <i>Belemnites ventralis</i> Phillips, 1867, OUM J14781, Upper Lias<br>[?Alum Shale to Fox Cliff Mudstone members], Robin Hood's Bay<br>[Ravenscar], North Yorkshire. | 66   |
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| 1.   | Ventral outline, left profile and dorsal outline. BGS GSM118047, Bridport Sands, Chideock, Bridport, Dorset. Specimen figured by Phillips (1867, pl. XIII, figs 35v, 1',d').         |      |
| 2.   | Neotype, ventral outline, left profile and dorsal outline. BGS GSM118048, Bridport Sands, Chideock, Bridport, Dorset. Specimen figured by Phillips (1867, pl. XIII, figs 35v',1,d'). |      |
| 3.   | <i>Megateuthis glaber</i> (Simpson, 1855)  | 66   |
|      | BMNH C59472, bed 80, Grey Sandstone Member, Blea Wyke Point, North Yorkshire.  |      |
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|      | Lectotype of <i>Belemnites erosus</i> Simpson, 1855, ventral outline and right profile, WM 66, Alum Shale Member, Whitby, North Yorkshire.   |      |
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|      | Lectotype of <i>Belemnites optatus</i> Simpson, 1884, WM 2710, UL 1 [bed 53 and above, Alum Shale Member], Whitby, North Yorkshire.  |      |

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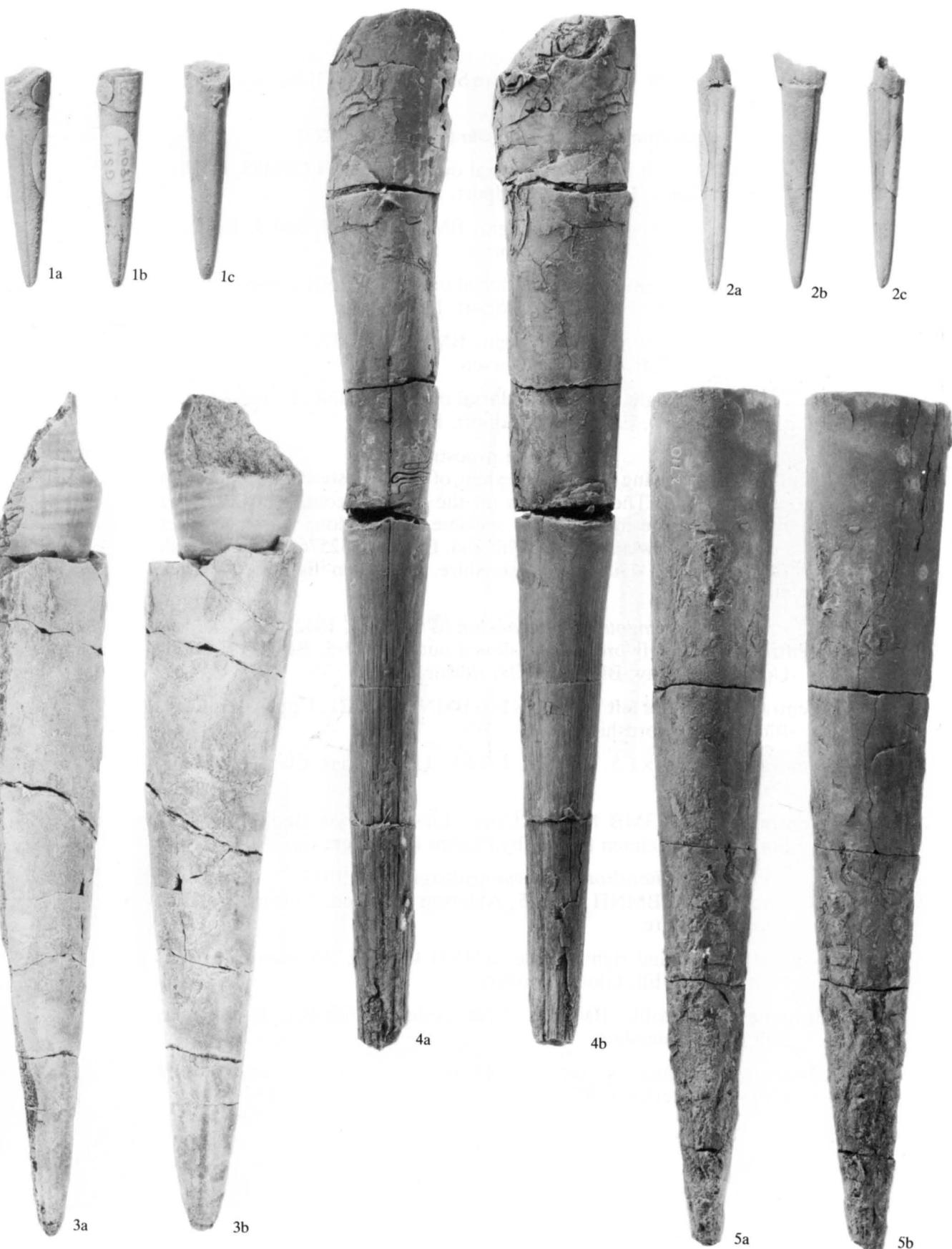


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| Fig. |   | Page |
|------|---|------|
|      | <i>Megateuthis glaber</i> (Simpson, 1855)   | 66   |
| 1.   | Specimen with destroyed epirostrum, ventral outline and right profile.<br>BMNH C59428, bed xxxviii, Alum Shale Member, Ravenscar, North Yorkshire.  |      |
|      | <i>Salpingoteuthis trisulcata</i> (Blainville, 1827)  | 71   |
| 2.   | Ventral outline, left profile and dorsal outline. BMNH C59485, bed 11, Bridport Sands, East Cliff, Bridport, Dorset.  |      |
| 3.   | Longitudinal Section, venter to right. BMNH C59489, bed 5, Bridport Sands, East Cliff, Bridport, Dorset.  |      |
| 4.   | Ventral outline, right profile and dorsal outline. BMNH C59488, bed 9, Bridport Sands, East Cliff, Bridport, Dorset.  |      |
| 5.   | Longitudinal section, venter to right. BMNH C59487, bed 2, Bridport Sands, East Cliff, Bridport, Dorset.  |      |
| 10.  | Ventral outline, right profile and dorsal outline. BMNH C59484, bed 9, Bridport Sands, East Cliff, Bridport, Dorset.  |      |
| 6.   | Belemnite proostracum   | 39   |
|      | Ventral view showing the whole extent of the proostracum and broken phragmocone. The dark stain on the phragmocone represents the remnants of the ink sac. This specimen may belong to <i>Acrocoelites (Toarcibelus) ilminsterensis</i> (Phillips). BMNH C52576, Alderton Fish Bed, Alderton Hill, Gloucestershire. Specimen figured by Crick (1898). |      |
|      | <i>Salpingoteuthis tessoniana</i> (d'Orbigny, 1842)   | 70   |
| 7.   | Ventral outline, left profile and dorsal outline, $\times 1.5$ . BMNH C59220, Upper Lias Clay, Bloxham, Oxfordshire.  |      |
| 8.   | Ventral outline and left profile, $\times 1.5$ . BMNH C59221, Upper Lias Clay, Bloxham, Oxfordshire.  |      |
| 9.   | Ventral outline, $\times 1.5$ . BMNH C6083, Upper Lias Clay, Bloxham, Oxfordshire.  |      |
| 11.  | Ventral outline. GMB M1218, Upper Lias [Junction Bed], Ilminster, Somerset. Specimen figured by Phillips (1869, text-fig. 25).  |      |
|      | <i>Chondroteuthis wunnenbergi</i> Böde, 1933  | 74   |
| 12.  | Arm hooks, $\times 2$ . BMNH C59305, Alderton Fish Bed, Nottingham Hill, Gloucestershire.   |      |
| 13.  | Ventral outline and right profile. BMNH C59293, Alterton Fish Bed, Nottingham Hill, Gloucestershire.  |      |
| 14.  | Juvenile, right profile. BMNH C59296, Alderton Fish Bed, Nottingham Hill, Gloucestershire.  |      |
| 15.  | Rostrum, phragmocone and posterior portion of proostracum. BMNH C59301, Alderton Fish Bed, Nottingham Hill, Gloucestershire.  |      |

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DOYLE, Toarcian belemnites

Plate 28

