

TEUTHID CEPHALOPODS FROM THE LOWER JURASSIC OF YORKSHIRE

by PETER DOYLE

ABSTRACT. Specimens of four teuthid species, *Loligosepia aalensis* (Zieten), *Jeletzkyteuthis agassizi* (Deslongchamps), *Teudopsis schuebleri* (Quenstedt) and *T. subcostata* (Münster), are described from the Whitby Mudstone Formation (Toarcian) of North Yorkshire. *Jeletzkyteuthis* nom. nov. is erected to replace *Loliginites* Quenstedt which is nomenclaturally invalid. This teuthid fauna is found to be similar to that of southern England, Normandy and southern Germany.

THE initial phase of fossil teuthid research took place during the first half of the nineteenth century. Most of the species' names still in use were first applied by workers such as Zieten (1830–32), Deslongchamps (1835), Buckland (1836), Quenstedt (1839, 1845–49), d'Orbigny (1842, 1845), and Münster (1843). Many of these authors directly compared their fossil specimens with the 'pens' of recent squid, and the genus *Loligo* was used for some of the named species (e.g. Zieten 1830–32; Buckland 1836).

Recently, interest in fossil teuthids has been rekindled by a number of works from the Tübingen school (e.g. Reitner and Engeser 1981, 1982; Engeser and Reitner 1983, 1985, 1986; Riegraf and Zügel 1984). However, despite the encouragement provided by Jeletzky (1966, p. 42) and Donovan (1977), little has been written on British teuthids in recent years. In this paper, I redescribe the teuthid specimens discussed by Simpson (1855, 1884) and Tate and Blake (1876) (see also Crick 1922, p. 288) from Yorkshire, figuring the type specimens of Simpson's species for the first time. Well-preserved teuthid specimens are rare due to their fragility and so new material is not readily available, requiring the re-examination of older collections. Fortunately, both Simpson and Blake carefully localized their material, and matrix lithologies allow reasonable stratigraphical control.

Interest in fossil teuthids in Britain probably began with Buckland (1836). He figured several specimens from the Lower Jurassic of Dorset which he assigned to *Loligo*, suggesting that they were similar to Zieten's (1830–32) *Loligo aalensis*. Voltz (1840) was later to reassign these forms to a new species, *Belopeltis bucklandi*. This is one of the oldest known species of *Loligosepia* (Sinemurian-Pliensbachian: Jeletzky 1966, p. 42), although earlier forms are known from Germany (Reitner 1978; Reitner and Engeser 1981). The majority of British nineteenth century discoveries were from southern England, as shown by Morris (1854, p. 303), Moore (1867) and Smithe (1877). Smithe (1877, p. 400) described a new species, *Beloteuthis glevensis*, from the sands overlying the Marlstone Rock Bed in North Gloucestershire which may represent the basal Toarcian (see Howarth 1980). Engeser and Phillips (1986) and Engeser (1988) have interpreted this as a species of *Teudopsis*. A revision of teuthids from the Fish and Insect beds (Toarcian) of southwest England was given by Crick (1921) who recorded two species, *Geoteuthis agassizi* (Deslongchamps) and *Teuthopsis [sic] brunelli [sic]* (Deslongchamps). These species may now be assigned to *Loligosepia aalensis* (Zieten) and *Teudopsis bunelii* Deslongchamps, respectively. A third species from the same horizon in Gloucestershire, *Teudopsis subcostata* (Münster), may be added to this list (BMNH C.5252). Moore (1867, p. 183) indicated that these teuthids were extremely common in southern England, and was able to suggest that they formed the stable diet of the contemporary ichthyosaurs, an idea supported by Pollard (1968) from the examination of ichthyosaur gastric masses.

Simpson (1855, 1884) was the first author to describe teuthids from Yorkshire. He erected four new species, *Sepia obtusalis*, *S. cuspidata*, *S. haustum* and *S. incomposita*. Blake (in Tate and Blake

1876) re-examined Simpson's material, assigning *S. cuspidata* to the genus *Teudopsis*, and considering the nominal species *S. obtusalis* and *S. haustum* junior synonyms of *Geoteuthis coriaceus* (Quenstedt). The types of these species are preserved in the Whitby Museum (WM). The fourth species, *S. incomposita*, is not mentioned in the WM catalogue, but Blake (*in* Tate and Blake 1876, p. 257) suggested that these specimens were in the York Museum collections. In any case, this species is actually based on fragments of fish vertebrae (Tate and Blake 1876, p. 257) and is therefore not dealt with here. Blake's specimens of this fish (*Gyrosteus mirabilis*) are certainly in the York Museum (Pyrah 1979, p. 417). Blake added two more species with his own *Beloteuthis leckenbyi* (now in the Sedgwick Museum), and a single specimen of *Beloteuthis subcostata* Münster (now in the British Museum (Natural History)) (see Crick 1922). These Yorkshire specimens were all collected from the Jet Rock (= Upper Lias Division 6 of Simpson, 1884) which is equivalent to the Jet Rock *sensu stricto* (*exaratum* Subzone) as defined by Howarth (1962, p. 386), and the lower part of the Jet Rock Member of Powell (1984). This original published information (Simpson 1855, 1884; Blake *in* Tate and Blake, 1876) is confirmed by the examination of the fossil matrices.

SYSTEMATIC PALAEOLOGY

All specimens are housed in Whitby Museum (WM), the British Museum (Natural History) (BMNH) and the Sedgwick Museum, Cambridge (SM). The descriptions given below are based purely on Yorkshire material and so little can be added to the original diagnoses. Most of the type specimens of the species described below are preserved in the Geologisches und Paläontologisches Institut, Tübingen (GPIT), West Germany.

The terms used below are discussed by Jeletzky (1966) (text-fig. 1). Recently, Engeser (1986, 1988) and Berthold and Engeser (1987) have suggested a revised taxonomy of the Coleoidea based on phylogenetic systematics. Jeletzky's (1966) less controversial classification is used below, however, as discussion of higher taxa is beyond the scope of this study, and as taxa of low rank remain unaffected. The synonymy lists follow the convention of Matthews (1973).

Subclass COLEOIDEA Bather, 1888

Order TEUTHIDA Naef, 1916

Suborder LOLIGOSEPIINA Jeletzky, 1965

Family LOLIGOSEPIIDAE Van Regteren Altena, 1949

(= Belopeltidae Naef, 1921)

Genus LOLIGOSEPIA Quenstedt, 1839

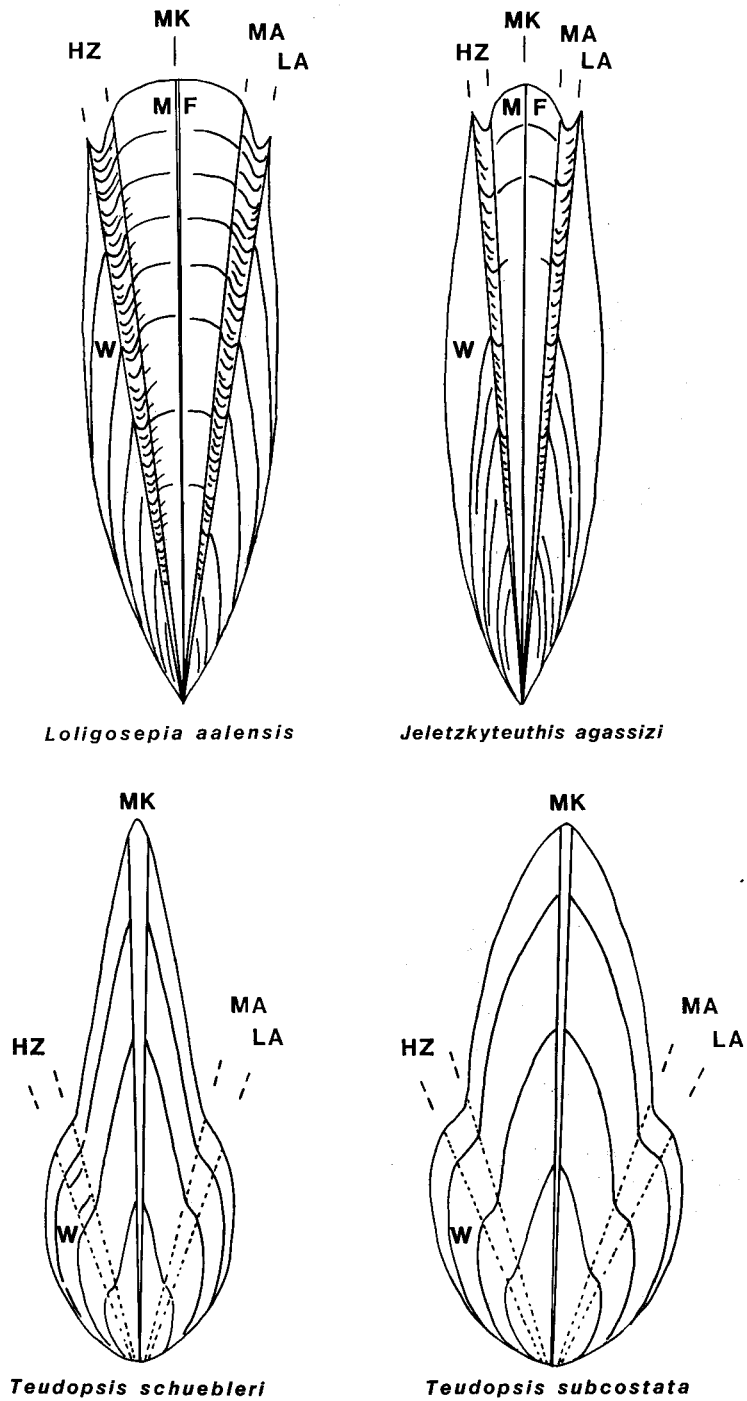
(= *Belopeltis* Voltz, 1840, (objective synonym); *Palaeosepia* Theodori, 1844, *Geoteuthis* Münster, 1843 (subjective synonyms))

Type species. *Loligo aalensis* Zieten, 1832, by monotypy.

Diagnosis. Large Loligosepiidae with gladius comprising relatively broad, smooth median field with central well-defined median keel and parallel striations; narrow hyperbolar fields with markedly anterior-concave growth lines; wings of parabolic form and with pointed anterior ends, generally extending for not less than one-third of the length of the median field. Large ink-sac present.

Range. This genus is known primarily from the Lower Jurassic (Sinemurian-Toarcian) of Europe (Jeletzky 1966; Reitner and Engeser 1981). However, Reitner (1978) has reported this genus from the Upper Triassic of Bavaria, although the specimens illustrated by him have markedly reduced wings.

Remarks. On the basis of the reconstructions given by Naef (1922, p. 129), specimens of *Loligosepia* may be distinguished from the similar genus *Parabelopeltis* Naef which has smaller hyperbolar zones with less anteriorly concave growth lines, and from *Jeletzkyteuthis* nom. nov. which has a narrower, elongate gladius with a narrow median field (text-fig. 1).



TEXT-FIG.1. Diagrammatic reconstructions of the four teuthid species under discussion, not to scale. Abbreviations: HZ, hyperbolar zone; LA, lateral asymptote; MA, median asymptote; MF, median field; MK, median keel; W, wing.

Loligosepia aalensis (Zieten, 1832)

Text-figs. 1, 2A–C, 3B, C

- *. 1832 *Loligo Aalensis* Zieten, p. 34, pl. XXV, fig. 4.
- . 1832 *Loligo Bollensis* Zieten, p. 34, pl. XXV, fig. 5. [Lectotype, here selected, Lower Toarcian, Posidonienschiefer, Boll, Southern Germany. Original in the GPIT].
- non 1832 *Loligo Bollensis* Zieten, p. 49, pl. XXXVII, fig. 1. [= *Teudopsis schuebleri* (Quenstedt)].
- . 1849 *Loliginites Bollensis* Zieten; Quenstedt, p. 508, pl. 32, figs. 11–13; pl. 33, figs. 1–5. [pl. 33, fig. 1 is Zieten's pl. XXV, fig. 5 specimen refigured].
- v. 1855 *Sepia haustum* Simpson, p. 21.
- v. 1876 *Geoteuthis coriaceus* Quenstedt; Blake (in Tate and Blake), p. 313, pl. IV, fig. 1.
- v. 1884 *Sepia haustum* Simpson; Simpson, p. 19.
- . 1920 *Geoteuthis Bollensis* (Schübler) Zieten; Bülow-Trummer, p. 253. [Full early synonymy].
- . 1921 *Geoteuthis agassizi* (Deslongchamps); Crick, p. 251, pl. A.
- . 1922 *Geoteuthis coriaceus* (Quenstedt); Crick, p. 288.
- . 1922 *Belopeltis Aalensis* (Zieten); Naef, p. 125, text-fig. 47b.
- . 1949 *Loligosepia aalensis* (Zieten); Van Regteren Altena, p. 58.
- . 1981 *Loligosepia aalensis* (Zieten); Reitner and Engeser, p. 427, text-fig. 2.
- . 1984 *Loligosepia aalensis* (Zieten); Riegraf *et al.*, p. 37.
- . 1988 *Loligosepia aalensis* (Schübler in Zieten); Engeser, p. 9. [Full synonymy].

Type specimen. Holotype, the original of Zieten (1832, p. 34, pl. XXV, fig. 4), from the Lower Toarcian of Aalen, southern Germany. Original in the GPIT.

Material. Nine specimens: WM 2, 3, 5; BMNH C.651, C.2699, C.2698, C.37529, C.46828 and C.12047 (the original of Tate and Blake 1876, pl. IV, fig. 1), all from the Jet Rock Member, Whitby Mudstone Formation (*falciferum* Zone), of Whitby, North Yorkshire.

Notes on Simpson's material. Simpson's (1855) nominal species *Sepia haustum* is a junior subjective synonym of *Loligosepia aalensis*. Two specimens are available in the Whitby Museum labelled *Sepia haustum* in Simpson's handwriting, namely WM 2 and 3 (text-fig. 2A, B). Specimen WM 2 is here designated lectotype (text-fig. 2B). Both specimens are preserved in concretions and are from Simpson's Upper Lias 6 division, equivalent to the Jet Rock *sensu stricto* of Howarth (1962).

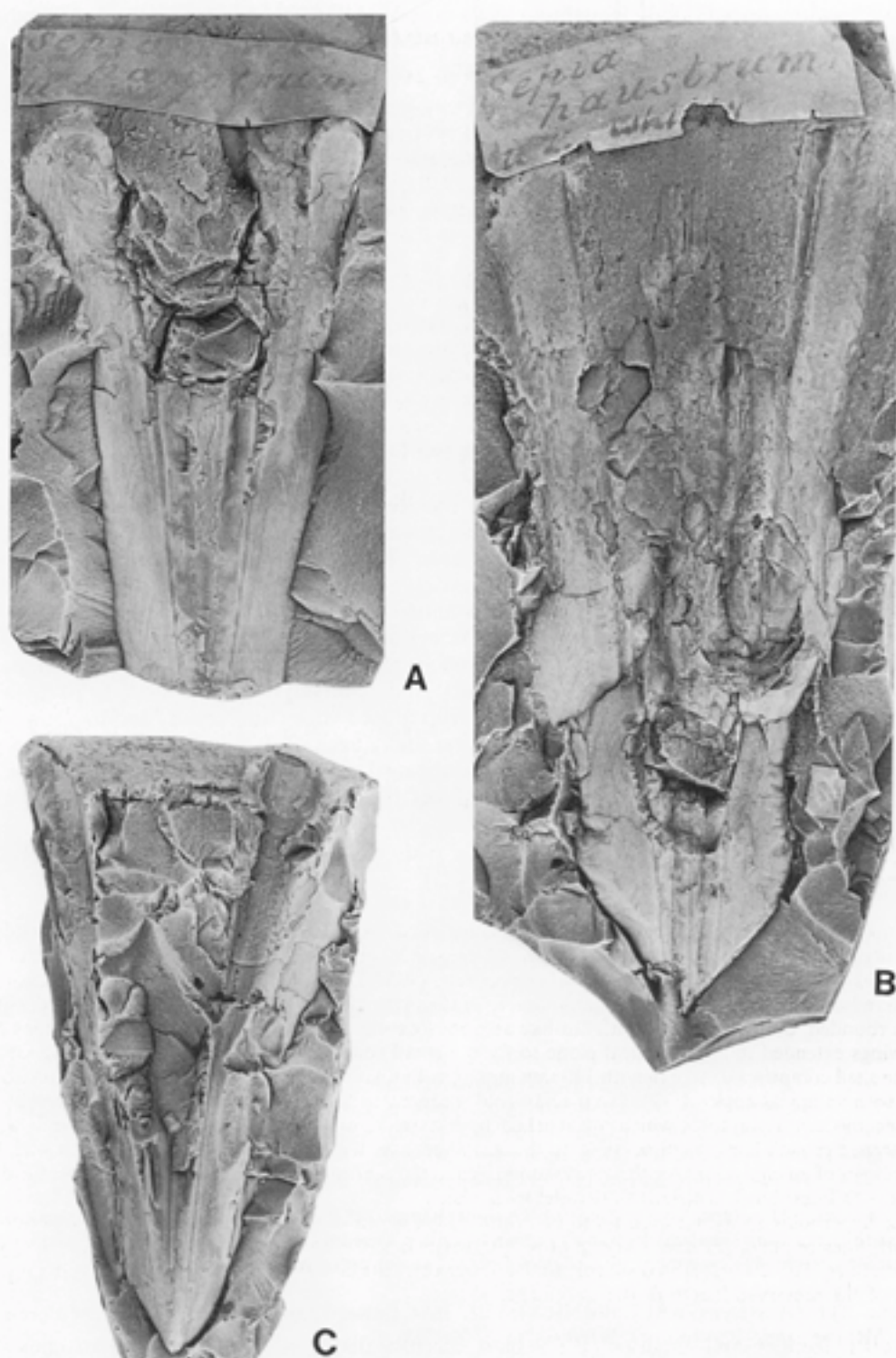
Diagnoses. See Quenstedt (1849, p. 508; '*Loliginites Bollensis*'), Naef (1922, p. 25; '*Belopeltis aalensis*') and Reitner and Engeser (1981, p. 427).

Description. Several specimens of this species have been recovered from the Toarcian of Yorkshire. The majority (BMNH C.651, C.2698, C.2699, C.12047, C.46828) are crushed and generally unrepresentative of the actual in-life gladius. However, two of the specimens (WM 5, text-fig. 2C; BMNH C.37529: text-fig. 3B, C) preserved in concretions are more representative of the original form of the shell. When flattened, the gladius has a rounded, obtuse posterior with fan-like anterior (text-fig. 2B). In concretions, the posterior is acute with the wings extended into the vertical plane to form a small conus (e.g. BMNH C.37529: text-fig. 3B).

The shell comprises a large (length 140 mm max.) gladius with a regular anteriorly-diverging, broad, median field with an apical angle of 18°. The median field is separated from the narrow hyperbolic zones by sharply-defined median asymptotes which are marked by a narrow, well-defined groove which expands anteriorly. Transverse growth lines are discernible on the lateral parts of the median field. A sharp median keel, bounded by grooves of an equivalent width, is accommodated in the central third of the median field. This third displays no growth lines, but has striations parallel to the keel.

The hyperbolic zones are each up to one-third of the width of median field, and display anterior-concave growth lines bounded by sharp asymptotes. The wings are parabolic in shape with correspondingly-formed growth lines. These are deflected sharply to the posterior at the lateral asymptotes. The wings are present along most of the preserved length of the specimens.

Remarks. Reitner and Engeser (1981) have recently discussed the differential diagnosis of this species within the genus *Loligosepia*. It can be distinguished from the coexisting species



TEXT-FIG. 2. *Loligosepia aalensis* (Zieten), ventral views $\times 1$. A. WM 3, paralectotype of *Sepia haustrum* Simpson. B. WM 2, lectotype of *Sepia haustrum* Simpson. C. WM5.

Jeletzkyteuthis agassizi (Deslongchamps) by its broad median field and well-developed median keel. Riegraf (1987) recently described a large isolated ink-sac from southern Germany that he interpreted as belonging to *Loligosepia aalensis*.

Genus JELETZKYTEUTHIS nom. nov.
(nom. nov. for *Loliginites* Quenstedt, 1849)

Type species. *Teudopsis agassizi* Deslongchamps, 1835.

Derivation of name. In memory of Dr J. A. Jeletzky, 1915–1988.

Diagnosis. Large Loligosepiidae with smooth, narrow and elongate gladius comprising a narrow median field with median keel; hyperbolar zones equivalent in width to the median field with anterior-concave growth lines; wings of parabolic form similar to those of *Loligosepia*. Ink-sac present.

Range. Lower Jurassic (Toarcian) of Europe (Naef 1922).

Remarks. *Jeletzkyteuthis* is erected here as a replacement name for *Loliginites* Quenstedt, 1849, which Engeser (1988, p. 50) found was unavailable for the Principle of Priority under Article 20 of the *International Code of Zoological Nomenclature*, being originally used for fossil species of the Recent genus *Loligo* (Quenstedt 1849). Engeser (1988) further suggested that the type species of *Loliginites*, *L. coriaceus* Quenstedt (= *Teudopsis agassizi* Deslongchamps), was actually a plesiotoothid of the genus *Romaniteuthis* Fischer and Riou, 1982. However, forms formerly attributed to the genus *Loliginites* have much greater affinity to the Loligosepiidae than Plesiotoothidae, having well-developed wings, and relatively broad median fields with simple keels. *Romaniteuthis* is distinguished by its much reduced wings and conus, and its rounded, well-developed, keel (Fischer and Riou 1982; Riegraf and Zügel 1984). In consequence *Jeletzkyteuthis* nom. nov. is erected here for those narrow, elongate Loligosepiidae characterized by the species *Jeletzkyteuthis agassizi* (Deslongchamps) (see Naef 1922, text-fig. 47 and text-fig. 1 herein).

Jeletzkyteuthis agassizi (Deslongchamps, 1835)

Text-figs. 1 and 3A

- *.1835 *Teudopsis Agassizi* Deslongchamps, p. 72, pl. 5, fig. 15.
- .1849 *Loliginites coriaceus* Quenstedt, p. 512, pl. 34, figs. 5–8.
- v.1855 *Sepia obtusalis* Simpson, p. 20.
- non 1876 *Geoteuthis coriaceus* Quenstedt; Blake (*in* Tate and Blake), p. 313, pl. IV, fig. 1 [= *Loligosepia aalensis*].
- v.1884 *Sepia obtusalis* Simpson; Simpson, p. 18.
- .1920 *Geoteuthis coriacea* Quenstedt; Bülow-Trummer, p. 253.
- non 1921 *Geoteuthis agassizi* Deslongchamps; Crick, p. 251, pl. A [= *Loligosepia aalensis* (Zieten)].
- .1922 *Loliginites coriaceus* Quenstedt; Naef, p. 130, text-fig. 47c.
- .1984 *Loliginites agassizi* (Deslongchamps); Riegraf *et al.*, p. 37.
- .1988 *Romaniteuthis agassizi* (Eudes-Deslongchamps); Engeser, p. 51. [Full synonymy].

Type specimen. Holotype, the original of Deslongchamps (1835, p. 72, pl. 5, fig. 15), Toarcian, Curcy, Normandy, northern France. It is not known whether Deslongchamps's specimen still exists. However, Quenstedt's (1846–49) specimens of *Loliginites coriaceus* are preserved in GPIT.

Material. Three specimens, WM 1, BMNH 83685, C.3654, Lower Toarcian, Whitby Mudstone Formation, Jet Rock Member, (*falciferum* Zone), Whitby, North Yorkshire.

Notes on Simpson's specimens. Simpson's (1855) nominal species *Sepia obtusalis*, is a junior subjective synonym of *Jeletzkyteuthis agassizi*. Two specimens bear this name in the Whitby Museum Catalogue. Specimen WM 1 has a distinct well-preserved ink-sac, and is undoubtedly the specimen referred to by Simpson (1855, p. 20). This specimen is here designated lectotype of *Sepia obtusalis* (text-fig. 3A). It is preserved in bituminous shale and is undoubtedly from the Jet Rock Member. A second specimen, WM 5, bears no label, but is noted as *Sepia obtusalis* in the Whitby Museum catalogue. This is actually a representative of the species *Loligosepia aalensis* (Zieten) (text-fig. 2C; see above).

Diagnoses. See Quenstedt (1849, p. 512; *Loliginites coriaceus*) and Naef (1922, p. 130; *Loliginites coriaceus*).

Description. Few specimens of this species have been recovered from the Yorkshire Toarcian. The single WM specimen (text-fig. 3A) is fragmentary and worn, but comprises a posterior portion (length 50 mm) of a gladius slightly offset from a large, elongate ink-sac. The gladius fragment is flattened and narrow with a maximum preserved width of 19 mm. A central median field commences with an acute apex and remains narrow for its total length. The median field is slightly crushed and worn, but a narrow median keel can be discerned in its mid-part. The greater part of the width of the specimen is taken by the wings which are each up to three times the width of the median field. Preservation of this specimen is such that no growth lines can be discerned on the wings, and the hyperbolar zones cannot be identified, although the lateral asymptotes can be seen. Slightly oblique from the gladius is an elongate, flask-shaped ink-sac with a total length of 75 mm.

Specimen BMNH 83685 is rather better preserved, and comprises a narrow, elongate gladius 180 mm long. The median field is largely unornamented with a weak median keel. The hyperbolar zones are so narrow in its posterior as to be barely discernable; in the anterior they display anterior concave growth lines. The wings are three times as wide as the median field, extending for at least one half of the length of the gladius, and possess parabolic growth lines.

Remarks. These specimens are representative of the species *Jeletzkyteuthis agassizi*. Simpson's specimen, WM 1, is very close to Quenstedt's (1849, pl. 34, fig. 5). The specimen illustrated by Blake (in Tate and Blake 1878, pl. IV, fig. 1: BMNH C.12047) is more properly assigned to *Loligosepia aalensis* (Zieten) as it possesses a broader and more ornamented median field. *Jeletzkyteuthis agassizi* is clearly distinguished from *Loligosepia aalensis* (Zieten) by possessing a narrow, elongate and less ornamented gladius as illustrated by Naef (1922, text-fig. 47).

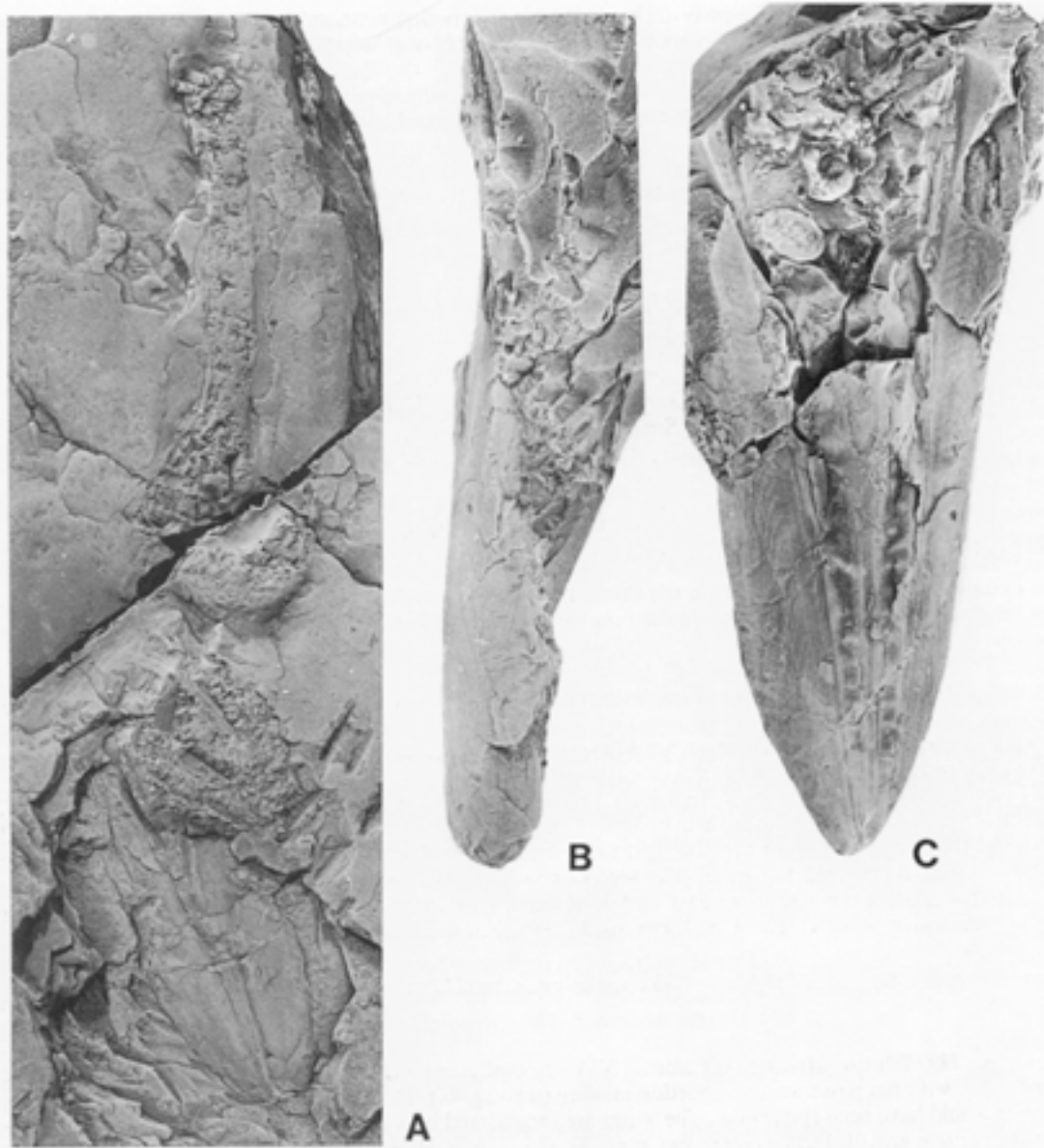
Suborder MESOTEUTHINA Naef, 1921
Family PALAEOLOLIGINIDAE Naef, 1921
Genus TEUDOPSIS Deslongchamps, 1835
(= *Beloteuthis* Münster, 1843 (Subjective synonym))

Type species. *Teudopsis bunelii* Deslongchamps, 1835, by subsequent designation (Woodward 1851–56, p. 69).

Diagnosis. Small to large, rhomboid to pyriform Palaeololiginidae comprising spoon-like gladius with posterior blade-like extension and rounded elliptical wings; median field restricted to well-developed keel or mid rib; hyperbolar zones developed as weak deflection of the growth lines.

Range. Lower Jurassic (Toarcian) to Middle Jurassic (Callovian) of Europe (Naef 1922; Fischer and Riou 1982). The species *Teudopsis brodiei* Caruthers reported from the Upper Jurassic of Dorset has recently been redescribed as an indeterminate plant fragment by Engeser and Phillips (1986).

Remarks. The nominal genus *Beloteuthis* Münster is a junior subjective synonym of *Teudopsis* Deslongchamps. Van Regteren Altena (1949) subsequently designated the species *Loligo bollensis* Zieten, 1832 as type of *Beloteuthis*. This is not without complication, however, as the nominal genera *Geoteuthis* Münster, 1843 and *Palaeosepia* Theodori, 1844 (junior subjective synonyms of *Loligosepia* Quenstedt) also share this type species. Although actually based on a different syntype



TEXT-FIG. 3. A, *Jeletzkyteuthis agassizi* (Deslongchamps), WM 1, $\times 1$. Ventral view of gladius and ink-sac. Lectotype of *Sepia obtusalis* Simpson. B, C, *Loligosepia aalensis* (Zieten), BMNH C.37529, $\times 1$. B, lateral view showing wings in lateral plane. C, ventral view.

of *Loligo bollensis*, they are junior objective synonyms of *Beloteuthis*. Fortunately, as already discussed, *Teudopsis* is the senior synonym. In addition, the lectotype of *Loligo bollensis* Zieten selected above is a specimen of *Loligosepia aalensis* (Zieten), thus making *L. bollensis* a junior subjective synonym of the same (see below).

Teudopsis was first recorded from Britain by Moore (1867, p. 303) and from Yorkshire, by Blake (in Tate and Blake 1876, p. 314). Crick (1921) described the type species *Teudopsis brunelli* [sic] from the 'Saurian and Fish Bed' (Lower Toarcian, *falciferum* Zone) of Alderton Hill in Gloucestershire.

This species is unknown in Yorkshire, but a single crushed specimen has been recovered from the Lower Toarcian (*falciferum* Zone) of Lincolnshire (BMNH C.46971).

Teudopsis schuebleri (Quenstedt, 1849)

Text-figs. 1 and 4A, C

- non 1832 *Loligo Bollensis* Zieten, p. 34, pl. XXV, fig. 4. [= *Loligosepia aalensis* (Zieten)].
 .1832 *Loligo Bollensis* Zieten, p. 49, pl. XXXVII, fig. 1.
 * .1843 *Loligo Schübleri* Quenstedt, p. 254.
 .1845 *Teudopsis ampullaris* Münster; d'Orbigny, p. 156, pl. 14, figs. 1, 2.
 .1845 *Teudopsis Bollensis* Zieten; d'Orbigny, p. 187, pl. 14, fig. 3.
 .1849 *Loliginites Schübleri* Quenstedt; Quenstedt, p. 499, pl. 32, figs. 14, 15.
 v. 1855 *Sepia cuspidata* Simpson, p. 21.
 .1858 *Loliginites Schübleri* Quenstedt; Quenstedt, p. 243, pl. 34, fig. 9.
 v. 1876 *Teudopsis cuspidatus* Simpson; Blake (*in* Tate and Blake), p. 314, pl. IV, fig. 3.
 v. 1884 *Sepia cuspidata* Simpson; Simpson, p. 19.
 1920 *Beloteuthis Schübleri* Zieten; Bülow-Trummer, p. 260. [Full early synonymy].
 .1922 *Teudopsis cuspidatus* (Simpson); Crick, p. 288.
 .1922 *Beloteuthis Bollensis* (Zieten); Naef, p. 144, text-fig. 53b.
 1949 *Teudopsis schübleri* (Quenstedt); Van Regteren Altena, p. 60.
 pars 1988 *Teudopsis bunelii* Eudes-Deslongchamps; Engeser, p. 77. [Includes *T. schuebleri* in synonymy].

Type specimen. Lectotype, here designated, the original of Quenstedt (1849, p. 499, pl. 32, fig. 15), from the Toarcian Posidonienschiefer of Holzmaden, southern Germany. The original is housed in the GPIT.

Material. Two specimens, WM 4 and SM J.35013 (the original of Blake *in* Tate and Blake 1876, pl. IV, fig. 3), from the Whitby Mudstone Formation, Jet Rock Member (*falciferum* Zone), of Whitby, North Yorkshire.

Notes on Simpson's specimens. Simpson's (1855) species *Sepia cuspidata* is a junior subjective synonym of *Teudopsis schuebleri*. Two specimens exist in the Whitby Museum that bear the label *Sepia cuspidata*. The first, WM 4 (text-fig. 4A), bears a label in Simpson's handwriting that reads '*Sepia cuspidata*, UL, Whitby'. This specimen is preserved in bituminous shale typical of the Jet Rock Member, and Simpson (1884, p. 19) recorded this species from his Upper Lias division 6 equivalent to the Jet Rock *sensu stricto* of Howarth (1962). This specimen is here designated lectotype. The second specimen, WM 682 (text-fig. 4B) is also labelled *Sepia cuspidata*, but close examination reveals that it is actually a skull of the fish *Saurorhynchus brevirostris* (Woodward) similar to that figured by Woodward (1899, text-fig. 1).

Diagnoses. See Quenstedt (1849, p. 499; *Loliginites Schübleri*) and Naef (1922, p. 144; *Teudopsis bollensis*).

Description. The Whitby Museum specimen (WM 4) consists of an elongate, conical, leaf-shaped gladius 120 mm long, with the posterior-most portion missing (text-fig. 4A). The gladius is flattened, but it is clear that the conus would have been spoon-like. The wings are represented by a slight lateral expansion in the posterior area with arcuate growth lines. Hyperbolar zones bounded by indistinct asymptotes are just discernible, and the growth lines are only slightly flexuous rather than notably anterior-concave. A relatively broad median keel, slightly displaced by compression in the posterior, is present for the length of the gladius and expands anteriorly to a maximum width of 4 mm. The keel is surrounded by an anterior blade-like extension with a posterior angle of divergence of 29°. Growth lines are discernible on the anterior extension, and mirror its leading edge.

The Sedgwick Museum specimen (SM J.35013) is a juvenile with a maximum length of 76 mm, preserved in three dimensions in a pyrite-skinned concretion (text-fig. 4C). The wings extend anteriorly for 34 mm from the spoon-like conus, and hyperbolar zones similar to the other specimen are seen on this example (text-fig. 4C). The median keel is well-developed with a relief of approx. 1 mm above the gladius, and it expands anteriorly to a width of 1.5 mm. The anterior blade-like extension consists of a platform containing the keel which has a border with a sub-relief of < 1 mm (text-fig. 4C). The anterior extension diverges posteriorly at an angle of 21°, and displays growth lines similar to those preserved on the WM example.

Remarks. Zieten (1832, pl. XXXVII, fig. 1) figured a specimen of this species from the Posidonienschiefer of southern Germany under the name *Loligo Bollensis*. Earlier in his monograph Zieten had used this name for a *Loligosepia*-like form now considered identical to his *Loligo aalensis* of the same work. The latter specimen is designated lectotype of *Loligo Bollensis* above, leaving the former specimen, a different species, without a name. Quenstedt (1839, p. 163, footnote) was aware of these problems, and later (Quenstedt 1843, p. 254) erected the name *Loliginites Schübleri* for the *Teudopsis*-like specimen of *Loligo Bollensis*.

Engeser (1988) considered the nominal species *Teudopsis schuebleri* a junior synonym of *Teudopsis bunelii* Deslongchamps. However, *T. schuebleri* can be readily distinguished from *T. bunelii* (syntype BMNH 74009, original of Deslongchamps 1835, pl. 3, fig. 3) by its elongate wing area, and its sharp, blade-like anterior extension which has a less regular form in *T. bunelii*. Both species can be distinguished from *T. subcostata* (Münster) in possessing a smaller form and less rhomboid shape (text-fig. 1).

Teudopsis subcostata (Münster, 1843)

Text-figs. 1 and 5A–C

- *.1843 *Beloteuthis subcostata* Münster, p. 61, pl. V, fig. 2; pl. VI, fig. 2.
- .1845 *Beloteuthis subcostata* Münster; d'Orbigny, p. 364, pl. 22, figs. 1–3.
- .1849 *Loliginites subcostatus* Münster; Quenstedt, p. 501, pl. 32, figs. 7, 8.
- v.1876 *Beloteuthis subcostatus* Münster; Blake (in Tate and Blake), p. 313.
- v.1876 *Beloteuthis Leckenbyi* Blake (in Tate and Blake), p. 314, pl. IV, fig. 2.
- .1920 *Beloteuthis subcostata* Münster; Bülow-Trummer, p. 261. [Full early synonymy].
- .1922 *Beloteuthis subcostata* Münster; Naef, p. 142, text-fig. 53a.

Type specimen. Lectotype, here designated, the original of Münster (1843, pl. 5, fig. 2) from the Toarcian Posidonienschiefer of Ohmden, southern Germany. The original of this specimen is believed to have been destroyed during the Second World War (W. Riegraf, pers. comm., 1988). However, Quenstedt's (1846–49) specimens from the same area are available in the GPIT for neotype selection.

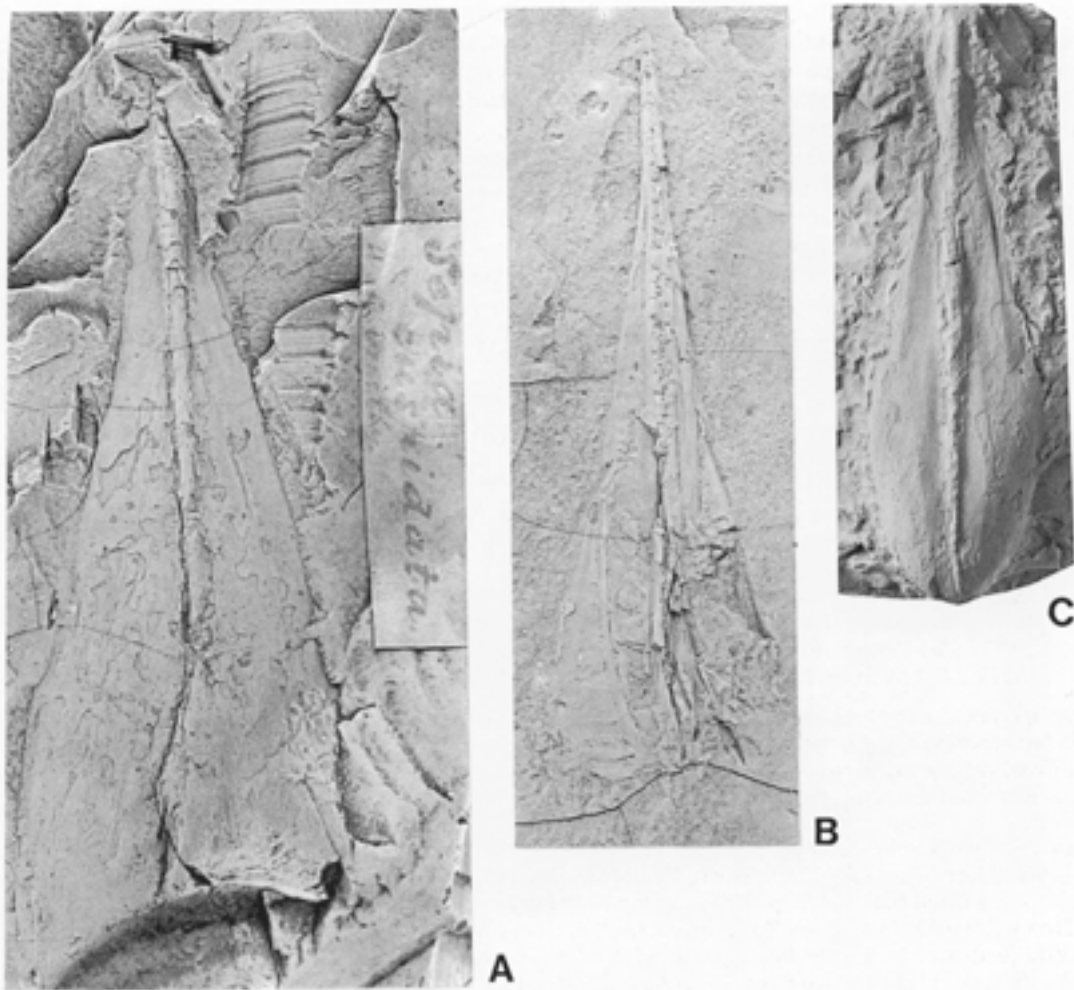
Material. Two specimens from the Toarcian Jet Rock Member (Whitby Mudstone Formation, *falciferum* Zone) of the environs of Whitby, North Yorkshire. The first, BMNH C.12046 (text-fig. 5A), was recorded by Blake (in Tate and Blake 1878, p. 314) from the *Serpentinus* Beds of Kettlewell. Only the Jet Rock *sensu stricto* of Howarth (1962) (*falciferum* Zone, *exaratum* Subzone) is exposed on the foreshore there. The second, SM J.35012 (text-fig. 5B, C) is the holotype of *Beloteuthis Leckenbyi* Blake. It was recorded by Blake (in Tate and Blake 1876, p. 314) as also from the *Serpentinus* Beds, and the specimen bears the label 'Whitby'. It is preserved in a small pyrite concretion or dogger, typical of the Jet Rock *sensu stricto* (Howarth 1962).

Diagnoses. See Münster (1843, p. 61; *Beloteuthis subcostata*), d'Orbigny (1845, p. 364; *Beloteuthis subcostata*), Quenstedt (1849, p. 501; *Loliginites subcostatus*) and Naef (1922, p. 142; *Beloteuthis subcostata*).

Description. The Yorkshire material comprises two specimens. The first, BMNH C.12046 (text-fig. 5A), is a large (length 240 mm), almost complete gladius of rhomboid shape, and is flattened. The second, SM J.35012 (text-fig. 5B, C), is smaller (length 100 mm), probably a juvenile, and is preserved in three dimensions.

The larger specimen (BMNH C.12046) is flattened with most of the gladius preserved, but with the wings present only as impressions. The wings are represented as small lateral extensions of the rhomb, and are present for almost half of the length of the gladius. Growth lines curve posteriorly, changing direction sharply at the lateral asymptotes, becoming almost straight in the hyperbolar zones and extending anteriorly to the median keel with a divergent angle of 54°. A broad, triangular anterior extension is present, with slightly curving leading edges (text-fig. 5A). A very broad median keel, reaching 10 mm at its widest, is central to the extension, and the surface of the central portion of the gladius is ornamented by lesser ridges and depressions that gradually diverge from the posterior (text-fig. 5A).

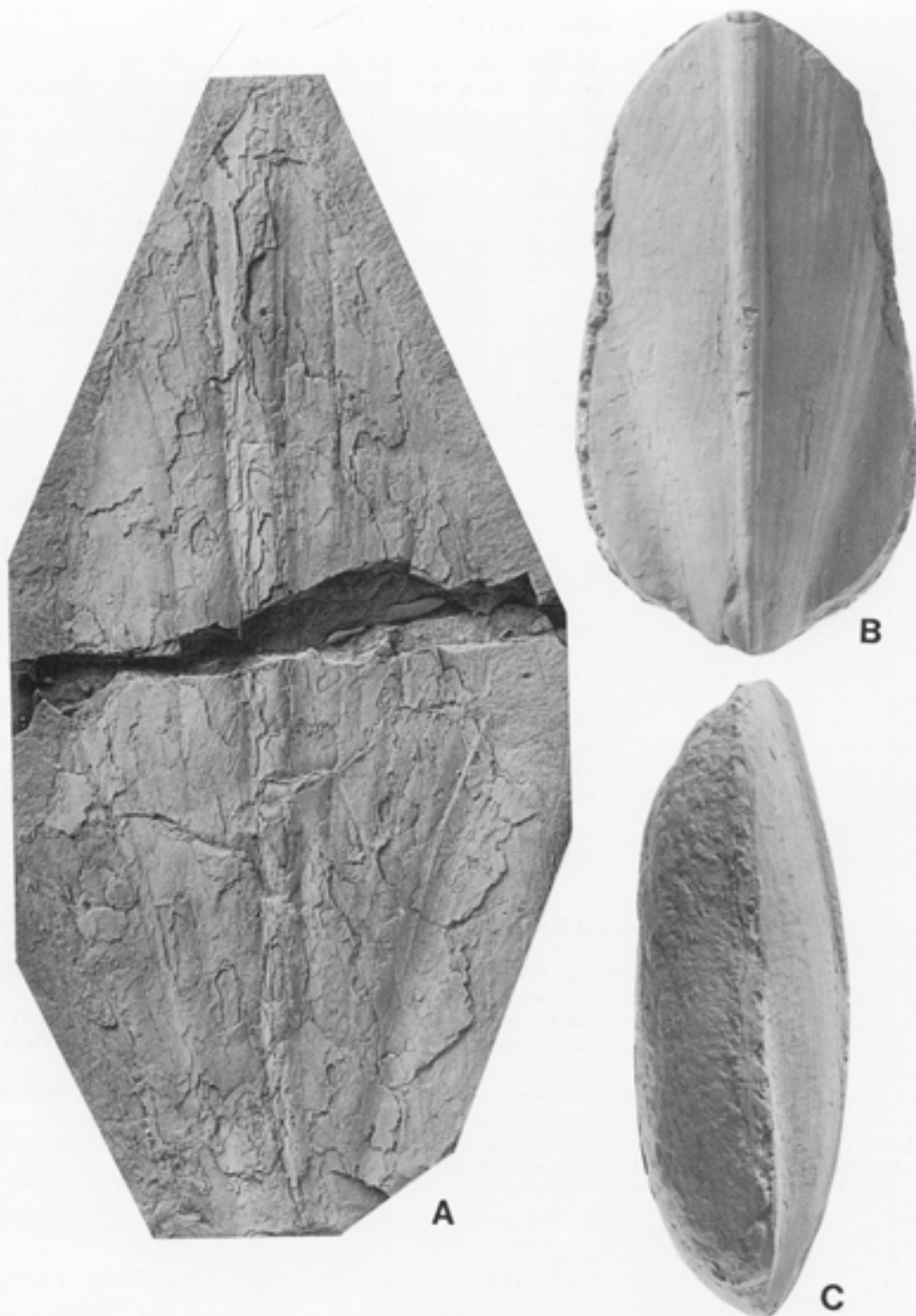
The smaller specimen (SM J.35012), has a similar morphology to the larger specimen, and is obviously a juvenile of the same species. It is preserved in three dimensions, with the hyperbolar zones falling as the



TEXT-FIG. 4. A, *Teudopsis schuebleri* (Quenstedt), WM 4, $\times 1$. Ventral view, posterior part missing. Lectotype of *Sepia cuspidata* Simpson. B, *Saurorhynchus brevirostris* (Woodward), WM 682, $\times 1$. View of skull in same orientation as 4A. This specimen was labelled *Sepia cuspidata* in the WM catalogue. C, *Teudopsis schuebleri* (Quenstedt), SM J.35013, $\times 1$. Ventral view.

curvature between the laterally extended wings and the main body of the gladius (text-fig. 5b). The median keel has a relief of 2 mm above the rest of the gladius (text-fig. 5c). The leading edges of the anterior extension of this specimen are curved giving a spatulate appearance. This obviously misled Blake (*in* Tate and Blake 1876), who used this specimen as holotype of his new species *Beloteuthis leckenbyi*. However, that this spatulate form is an artifact of the preservation is indicated by the growth lines on the surface of the gladius which reveal the typical rhomboid form of *Teudopsis subcostata* (text-fig. 5b).

Remarks. This species is very clearly distinguished from both *Teudopsis bunellii* Deslongchamps and *Teudopsis schuebleri* (Quenstedt) by its larger size and regular rhomboid form (text-fig. 1).



TEXT-FIG. 5. *Teudopsis subcostata* (Münster), A, BMNH C.12056, $\times 0.75$. Ventral view. B, C, SM J.35012, holotype of *Beloteuthis leckenbyi* Blake, $\times 1$. B, ventral view. C, left lateral view.

INTER-REGIONAL COMPARISONS

Inter-regional comparisons of fossil teuthid faunas are difficult because of their fragility and hence scarcity in the fossil record. Preservation of such delicate features as ink-sacs requires immediate burial (see Lyell 1878, p. 350) and/or a lack of scavengers. Thus, many teuthid finds are from deposits renowned for their exceptionally preserved faunas (fossil Lagerstätten; see Seilacher *et al.* 1985 for a review).

Fortunately, the Toarcian was a period of widespread anoxia in the shelf-seas of Europe (e.g. Riegraf *et al.* 1984) and elsewhere. Close similarities exist between the Yorkshire and southern England teuthids and those of Normandy and southern Germany (e.g. Deslongchamps 1835; d'Orbigny 1842, 1845; Quenstedt 1846–49; Riegraf *et al.* 1984, p. 36) in these adjacent shelf seas. Local differences do occur however, with, for example, the apparent absence of *Teudopsis bunelii* from Yorkshire, and similarly the absence of *Jeletzkyteuthis agassizi* from southern England. However, these are most probably artifactual differences, a result of the imperfect teuthid record. Nagy (1958) described a specimen of *Teudopsis* from the Lower Jurassic of Hungary which Engeser (1988) subsequently referred to *T. bunelii*. However, Nagy's figures illustrate a specimen too poorly preserved to be reliably identified to specific level.

In addition to the species described above, Riegraf *et al.* (1984) listed *Lioteuthis problematica* Naef (unknown outside Germany), *Geopeltis emarginata* (Voltz) and *Parabelopeltis flexuosa* (Münster). None of these species are known to occur in Britain. Riegraf *et al.* (1984) also listed the pliosoteuthids *Paraplesiotheuthis sagitata* (Münster) and *P. hastata* (Münster). Again, neither of these teuthids are known in Britain, but Hall (1985) has recorded the latter species from the Toarcian bituminous shales of Alberta, Canada. This is the only Lower Jurassic squid recorded outside Europe.

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PETER DOYLE

Nature Conservancy Council
Northminster House
Peterborough PE1 1UA, UK

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Note added in proof. Hall and Neuman (1989) have recorded a new species of *Teudopsis*, close to *T. schuebleri*, from the lower Jurassic (*falciferum* Zone) of Alberta, Canada, suggesting close faunal links with Europe.

HALL, R. L. and NEUMAN, A. G. 1989. *Teudopsis cadominensis*, a new teuthid squid from the Toarcian (Lower Jurassic) of Alberta. *Journal of Paleontology*, **63**, 324–327.