

# Maastrichtian *Ceratisepia* and Mesozoic cuttlebone homeomorphs

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The phylogenetics of potential Mesozoic ancestors of cuttlefish of a restricted order Sepiida von Zittel, 1895 (superorder Decabrachia Boettger, 1952) is reviewed. Microstructural studies of Mesozoic homeomorphs of cuttlebones (*Pearceiteuthis* gen. n., *Loligosepia*, *Trachyteuthis*, *Actinosepia*) are consistent with their assignment to the superorder Octobrachia Fioroni, 1981. The discovery of an embryonic *Ceratisepia* shell in the upper Maastrichtian of the Netherlands, indicates that true Sepiida did have a pre-Cenozoic origin. Cretaceous decabrachs of the order Spirulida Stolley, 1919 do not show evidence of the dorso-anterior shell growth vectors seen in Cenozoic spirulids, sepiids and octobrachs. Separate origins of the Sepiida and Spirulida within Cretaceous diplobeliniid belemnites is still the most attractive hypothesis. *Ceratisepia vanknippenbergi* sp. n. from the upper Maastrichtian of the Netherlands and *Pearceiteuthis buyi* gen. et sp. n. from the Callovian of England are described.

Key words: Cephalopods, cuttlefish, ontogeny, biomineralization, Mesozoic.

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## Introduction

Cuttlebones are those dorsally hard and spherulitic, but ventrally soft and septate, aragonitic shells that invade beaches (Cadée 1997) and can be seen being sold to the owners of caged birds in pet shops. They are the expanded and highly modified internal phragmocones of cephalopods (Bandel & von Boletzky 1979) and belong to a diverse group of cuttlefish that appeared in the Rupelian (Szörényi 1934; Hewitt & Pedley 1978; Engeser 1990). Everyone recognises that the older Cenozoic genus *Belosaepia* Voltz, 1830 (Fig. 1) is connected to *Sepia* Linné, 1758 via *Hungarosepia* Doyle *et al.*, 1994 (= *Archaeosepia* Szörényi, 1934, invalid) from the Lutetian–Priabo-

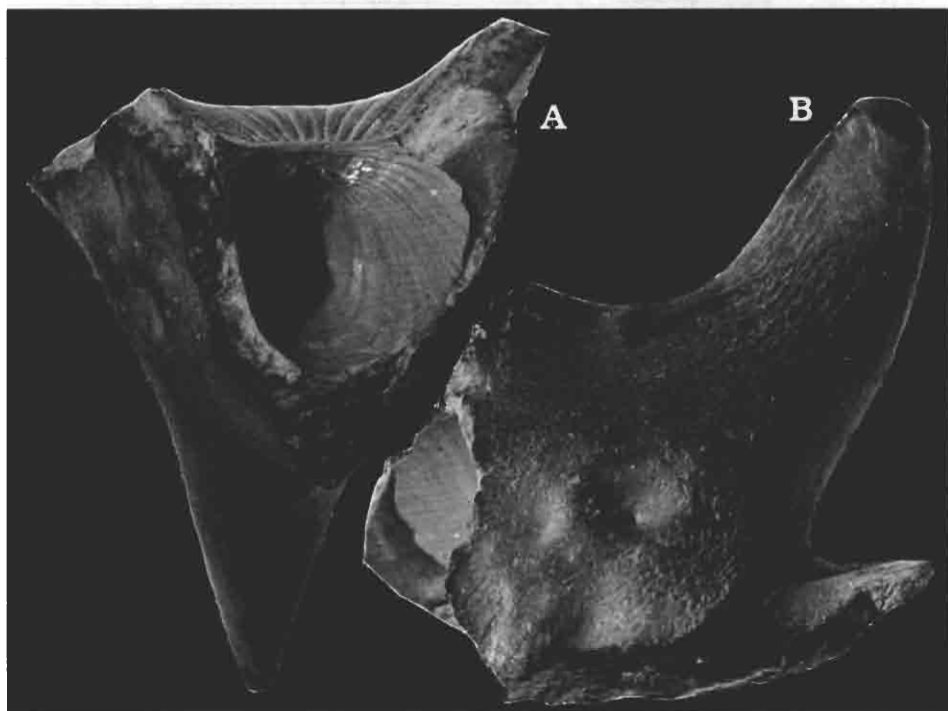


Fig. 1. Posterior end of Bartonian *Belosaepia sepioidea* de Blainville, 1825, NHMM 1997107. **A.** Ventral view of dorsal embryonic septal sutures. **B.** Lateral view, both  $\times 4.6$ .

nian of Hungary (see e.g., nomenclatural changes by Engeser 1990 and Doyle *et al.* 1994). Meyer (1989, 1993) described the Danian genus *Ceratisepia* Meyer, 1989, extending the range of the *Belosaepia* clade.

Haas (1997) and most other modern authors have denied the belemnite affinity of cuttlebones postulated by Meyer (1993), Naef (1922), and Voltz (1830). It is worthwhile to quote here the opinion of Voltz (1830: p. 23): '*Beloptera belemnioidea* et sépiostaires établissent ainsi une chaîne bien naturelle entre les belemnites et les sépiostaires. Je nommerai ce genre *Belosaepia*, et j'appellerai la *Belopt. saepioidea* de Blainv., *Belosaepia Cuvieri*.' [sic].

We here present the first record of a Cretaceous *Ceratisepia*. There are similarities to the breviconic phragmocone of diplobelinid belemnites as well as to *Belosaepia* (Fig. 1A, B) and *Sepia* (Fig. 2B, C). There are also similarities between the longiconic Tithonian *Diplobelus* Naef, 1926 and the Maastrichtian genus *Groenlandibelus* Jeletzky, 1966 of the order Spirulida Stolley, 1919. The difference between the ammonoid-like caecum and prosiphon of *Groenlandibelus* (Jeletzky 1966) and the internal structure of the initial chamber of belemnoids (Jeletzky 1966; Bandel *et al.* 1984), convinced Jeletzky (1966) that *Groenlandibelus* was not derived from the late Jurassic *Diplobelus* and *Belemnotherutis* Pearce, 1842 with which *Groenlandibelus* had previously been compared by Birkelund (1956). It is therefore important to reconstruct the embryonic shell development in *Ceratisepia* and belemnites before making a judgement about affinities.



Fig. 2. Morphological end-members of chambered Sepiida. A, D. Holotype (NHMM 1997106) of the late Maastrichtian *Ceratisepia vanknippenbergi* sp. n. A. Ventral view,  $\times 29$ . D. Dorsal view,  $\times 25$ . B, C. Shell of an unregistered female, subadult *Sepia officinalis* L. B. Ventral view,  $\times 0.47$ . C. Dorsal view,  $\times 0.67$ .

The *Ceratisepia*–*Sepia* clade is the order Sepiida von Zittel, 1895 of Doyle *et al.* (1994), who extended it to the Campanian by inclusion of the American genus *Actinosepia* Whiteaves, 1897. The latter genus might be thought to be an adult stage of *Ceratisepia* with no chambers. But *Actinosepia* is linked to the Jurassic genus *Trachyteuthis* von Meyer, 1846 (Jeletzky 1966; Donovan 1977; Engeser 1990). Donovan (1995) admitted that *Trachyteuthis* was an octobranch (e.g., Recent *Vampyroteuthis* Chun, 1903, plus octopuses) and it is therefore unlikely that either of these two Mesozoic genera could be related to decabranch *Sepia* (Engeser 1990; Young & Vecchione 1996). A new *Sepia*-like form *Pearceiteuthis buyi* gen. et sp. n. from the Callovian of England, described herein, unites the enigmatic family Muensterellidae Roger, 1952, with these two (*Actinosepia* and *Trachyteuthis*) octobranch homeomorphs of cuttlebones.

The soft parts, microstructure of the shell and stratigraphical evidence are in favour of *Sepia* and *Spirula* having the diplobeliniid ancestry as supported by Meyer (1993). Engeser (1990: p. 136) cited the development of the belemnoid ‘closing membrane’ and ‘five-layered shell’ as two synapomorphies which made him place the Diplobelidae at the opposite end (his fig. 2) to *Groenlandibelus* with a similarly slender proostracum.

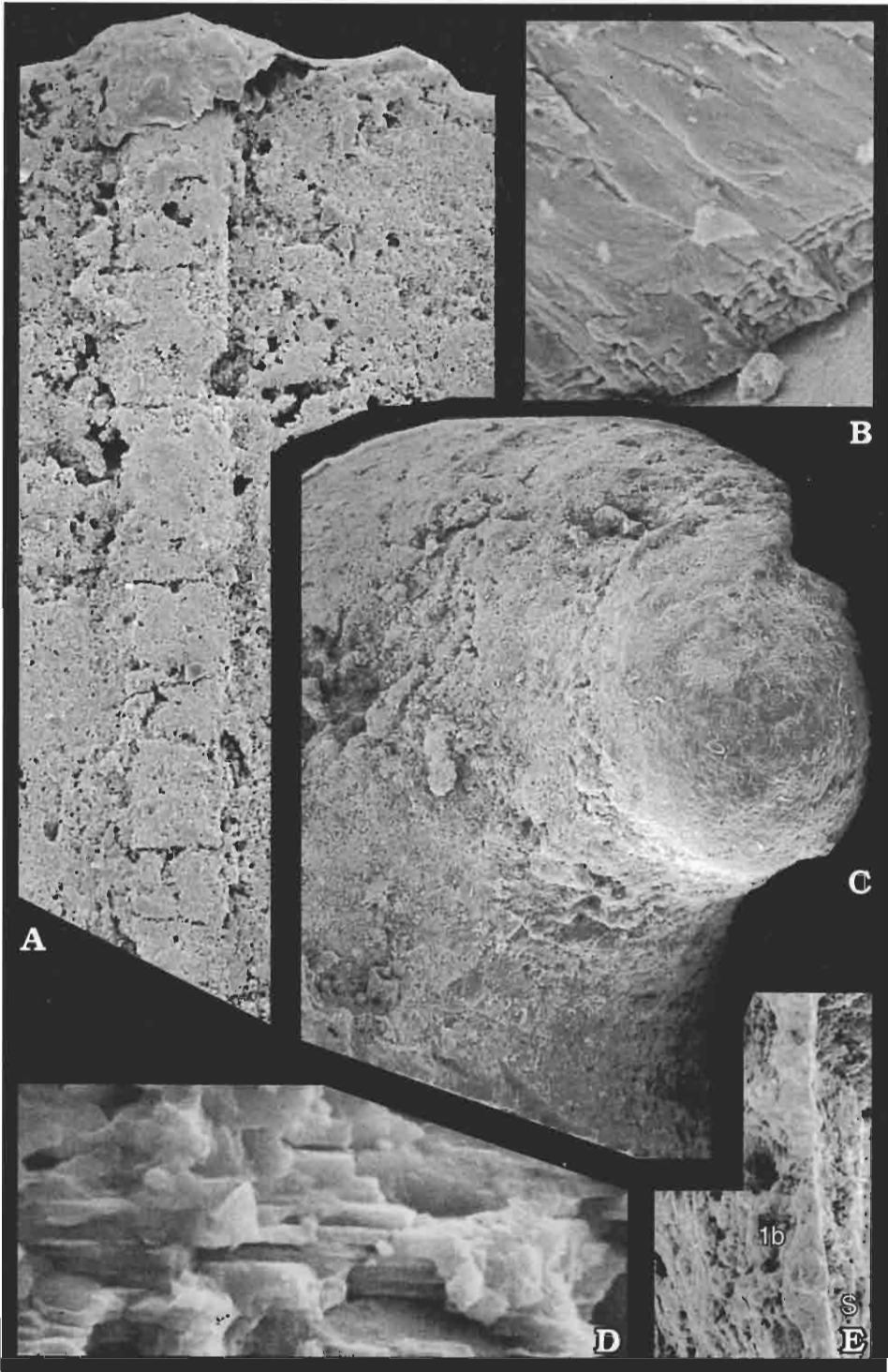
The first section of the present paper shows that Engeser’s (1990) caecum *versus* ‘closing membrane’ dichotomy need not overrule other phylogenetic evidence. After a systematic description of embryonic Belosaepiidae and a new octobranch, the rest of the present paper completes a review of the microstructure of non-belemnoid coleoid skeletons. It is concluded that the second synapomorphy of belemnoids cited by Engeser (1990) is not valid.

**Institutional abbreviations:** BMNH, The Natural History Museum, London (formerly British Museum of Natural History); NHMM, Natuurhistorisch Museum Maastricht, Maastricht.

## Reinterpretation of embryonic evidence

The early Palaeocene (Danian) *Ceratisepia* shows a sudden reduction in the spacing of septa 3 and 4 at a shell length varying between 2.8 and 3.7 mm (Meyer 1993: pl. 2: 8, 9). In embryonic and early juvenile shells it is useful to measure a ‘cap height’ of the dorsal shield normal to the length of the apertural septal sutures. The total length of the late Maastrichtian *Ceratisepia* specimen (Fig. 2A, D) is 3.64 mm and suggests that it died shortly after hatching from a 5 mm-diameter capsule. The relatively large embryonic shell (Denton & Gilpin-Brown 1966; Bandel & von Boletzky 1979) and egg capsules of *Sepia* (Kozłowski 1965) and *Nautilus* (Arnold *et al.* 1987) correlate with bottom feeding (demersal) habits. Recent *Spirula* is thought to hatch with a single septum inside a spherical apex. *Groenlandibelus* has a slight constriction over septum 4; it probably hatched at a shell length of 1.1 mm with two septa inside the conical ‘body

Fig. 3. Comparison of wall microstructures of Cretaceous Sepiida (A, C, E) and Spirulida (B, D). A, C, E. Upper Maastrichtian *Ceratisepia vanknippenbergi* sp. n. (NHMM 1997106). B, D. Campanian *Naefia neogaia* Wetzel, 1930 (K1098, transferred to Royal Ontario Museum). A. Keel at dorsal aperture (top),  $\times 175$ . B. Dorsal wall with laminated septal margin,  $\times 830$ . C. Apex with ventral aperture below,  $\times 95$ . D. Sheet nacre,  $\times 6460$ . E. Chipped anterior margin with dorsal spherulites (1b) and septum (S),  $\times 110$ .



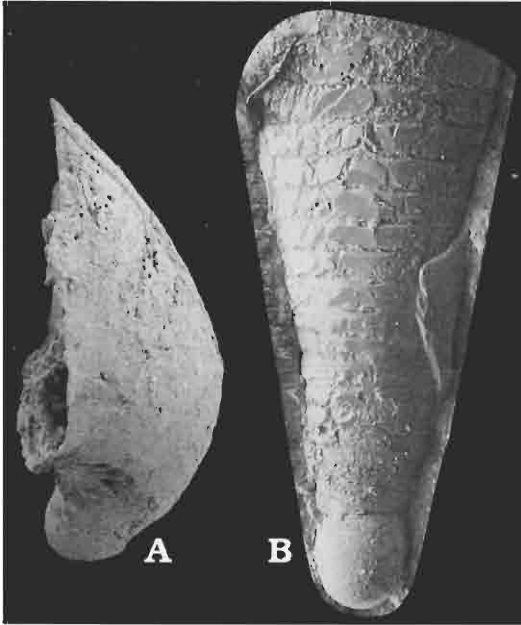


Fig. 4. Lateral apical views of Sepiida and Belemnnoidea. A. Late Maastrichtian *Ceratisepia vanknippenbergi* sp. n. (NHMM 1997106), with dorsal on right,  $\times 17$ . B. Early Callovian *Cylindroteuthis* sp. (NHMM 1997108) with ventral on right,  $\times 31$ .

chamber' defined by this constriction (Jeletzky 1966: pl. 20: 1a). The *Ceratisepia* egg may form part of a trend from pelagic habits and small floating eggs in all the Mesozoic coleoids to the relatively large eggs, fins and ink sac seen in *Sepia*.

A comparison of this embryonic shell of late Maastrichtian *Ceratisepia* and a *Cylindroteuthis* sp. from the middle Brora Shale Member (*Kosmoceras jason* Zone, middle Callovian) in Scotland (NHMM 1997108) is attempted in Fig. 4A, B. The *Cylindroteuthis* Bayle, 1878 is shown with ventral on the opposite (right) side at a magnification of 1.8 times the *Ceratisepia* illustration. There is a ventral thickening and dorsal shift in the axis of the belemnite around the 8th calcified septum at a shell length of 1.3 mm (i.e. this includes 0.1 mm representing the primordial rostrum seen at the hemispherical end of the initial chamber). Hatching is also defined by the ventrally retracted nature of the smallest septum and closing membrane at the neck of the initial chamber. The dorsal spacing of the sutures declines from 120  $\mu\text{m}$  between calcified septa 1 and 2, to 80  $\mu\text{m}$  in chambers 3 and 4, before increasing to 100  $\mu\text{m}$  with the development of lateral saddles on suture 5. It is therefore deduced that *Cylindroteuthis* hatched with a conical and presumably internal body chamber ( $28^\circ$  apical angle) at the septum 2 or 3 stage. This interpretation differs from the hatching with one weak cameral membrane (uncalcified septum, closing membrane) stage from a 0.6 mm long egg interpretation, implied by Bandel *et al.* (1984) and Engeser (1990).

A 'prosiphon' is formed by the concentration of the wettest cameral membranes around the caecum during initial drying of the chamber. A caecum is a stronger form of siphuncle apex than the blunt termination on the ventral side of the 'closing membrane' reviewed as a synapomorphy of belemnoids by Engeser (1990: p. 136). It is quite possible that ammonoids and spirulids hatched in deeper water than belemnoids and developed a caecum by adaptive convergence.

The number of oblique embryonic and early juvenile septal sutures of *Cylindroteuthis* increased in breviconic diplobeliniids with a *Ceratisepia*-like apex on a constriction at a shell length of 4 mm (Jeletzky 1981: pl. 24). This 'unstressed laboratory' for the development of oblique and flat septa also operated in the Sepiida.

Recent *Sepia* grows seven septa and a shell length of 8 mm within the egg (Denton & Gilpin-Brown 1966). Eocene *Belosaepia* is deduced to have hatched at a shell length of 5.3 mm in chamber 4 and it continued to grow progressively narrower spaces between the dorsal septal sutures until chamber 6. The obliquity of the septa enlarges the size of the embryonic shell composed of the same number of septa. A spherical initial chamber need not correspond to the diameter of the egg capsule. The low reticulate ornament on the apex is surrounded by concentric ridges that appear to result from growth and calcification from the inside of the aperture. The reticulate ornament probably results from calcification of an initially uncalcified apex by prisms of the type postulated by Bandel *et al.* (1984) in belemnoids and by Kulicki & Doguzhaeva (1994) in ammonoids. But Cenozoic spirulids and cuttlebones display a second type of remote calcification of protein-chitin sheets, that produces a rugose ornament of spherulitic prisms over the whole dorso-posterior surface. This texture is not observed in Cretaceous spirulids (see below) but it is present on the apertural margins of embryonic *Ceratisepia* (Fig. 3A, C, E).

A diagnostic difference between the similarly smooth and rapidly expanding dorsal appearance of the Maastrichtian *Ceratisepia* (Fig. 2D) and the Aptian diplobeliniid *Conoteuthis* d'Orbigny, 1842 (Jeletzky 1981: pl. 21; Mutterlose 1984) is that the dorso-median keel developed within the embryo of *Ceratisepia*.

## Systematic palaeontology

### Superorder Decabrachia Boettger, 1952

#### Order Sepiida von Zittel, 1895

#### Family Belosaepiidae Dixon, 1850

#### Genus *Belosaepia* Voltz, 1830

Type species: *Beloptera sepioidea* de Blainville, 1825, by original designation.

#### *Belosaepia sepioidea* (de Blainville, 1825)

Figs 1A, B, 5B.

**Material.** — Several specimens from Eocene (Ypresian) London Clay and Bartonian 'Barton Beds' of England.

**Description.** — Three largely intact Ypresian specimens (BMNH 39915, BMNH 68941 and W.J. Quayle Coll.) all have an adult shell length of 90 to 100 mm and show no trace of the septa or siphuncle reconstructed from one of them by Edwards (1849). Their interior was probably similar to the small American 'sepiamorph sepiid' illustrated by Squires (1988) and they show a narrowing of chambers 5 to 7 at a shell length of up to 8 mm.

This embryonic stage of incomplete specimens from the Bartonian Bed A3 at Chewton Bunny (NHMM 1997107, leg. A.J. Totham) and the 'Middle Barton' of

Table 1. Comparison of the length, width and cap height of *Belosaepia* specimens and the major growth increments of the single Maastrichtian specimen of *Ceratisepia* (numbered from the apex of the initial chamber). All dimensions in mm, with the total length of the shell only indicated when it is significantly greater than the anterior-posterior septum length. Abbreviations: TL, total length in septum plane; IL, internal length; IW, internal width; CH, cap height.

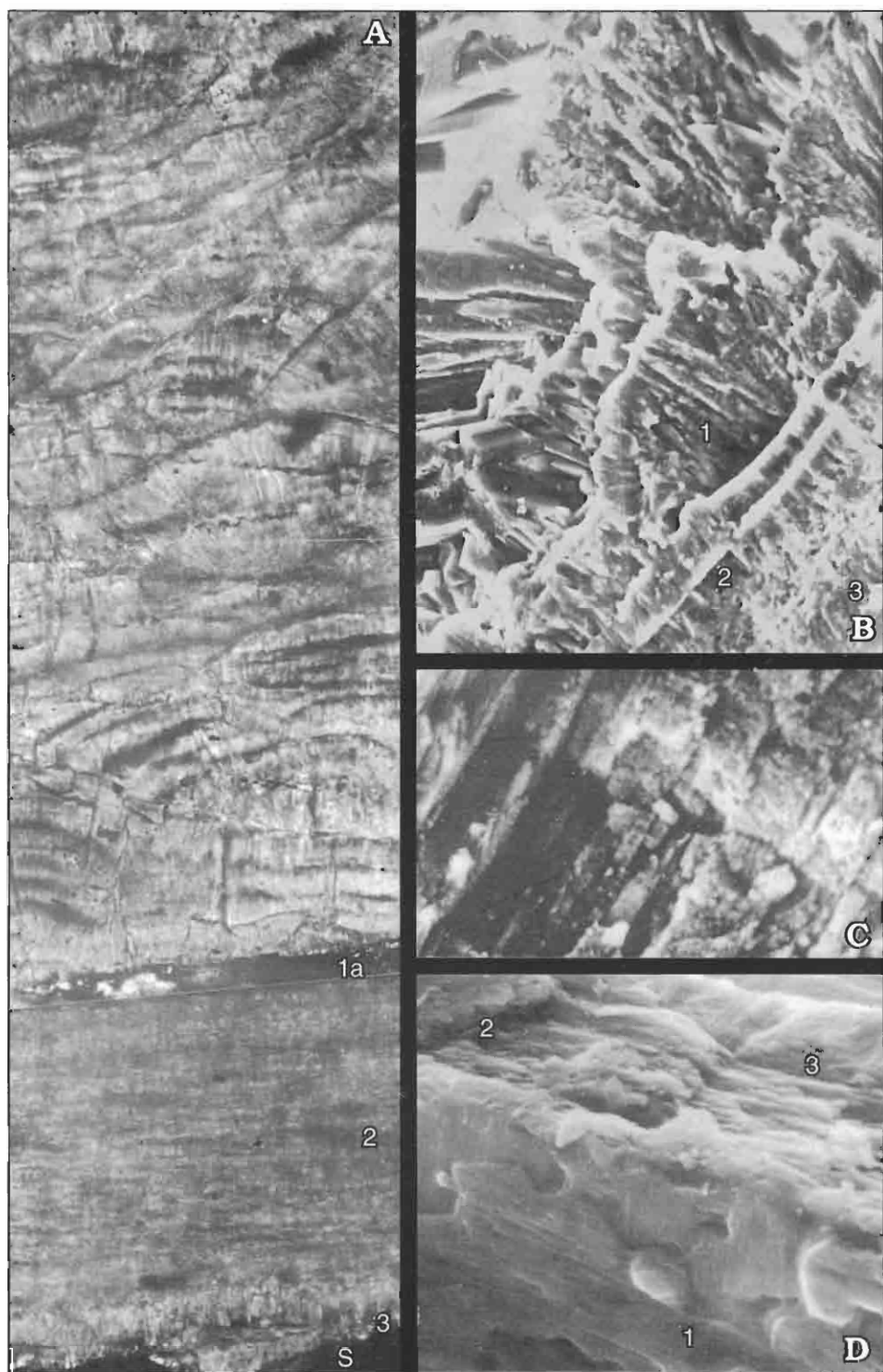
Genus	reg. number	increment number	TL	IL	IW	CH
<i>Belosaepia</i>	BMNH 39915	1 suture	–	0.90	–	–
	NHMM 1997107	1 suture	–	1.64	1.21	0.40
	<b>BMNH CC.393</b>	<b>1 suture</b>	–	<b>1.64</b>	<b>1.48</b>	0.80
	<b>BMNH CC.393</b>	<b>2 suture</b>	–	4.33	3.67	2.00
	NHMM 1997107	2 suture	–	4.66	3.17	2.10
	NHMM 1997107	6 suture	–	–	5.00	–
	BMNH 39915	8 suture	–	7.60	–	–
	BMNH CC.393	6 suture	–	9.50	6.50	4.83
	BMNH 68941	c. 30 suture	c. 100	86.70	51.00	–
<i>Ceratisepia</i>	NHMM 1997106	1	–	<b>0.38</b>	<b>0.46</b>	0.08
	NHMM 1997106	3	–	<b>0.56</b>	<b>0.48</b>	0.36
	<b>NHMM 1997106</b>	11	2.48	1.88	1.64	<b>0.85</b>
	NHMM 1997106	14	3.64	2.58	2.32	1.56

Barton (BMNH CC.393, collected by A.G. Davis, presumably from beds E or F), are compared with the Maastrichtian *Ceratisepia* in Table 1.

Fig. 1A illustrates the generally smooth concavity formed by the ventral side of the dorsal shield covered by the 15 mm long, adult posterior rostrum. The 20 µm thick and 20 µm high flanges, formed by the breakage of the embryonic septa, are easily distinguished from the minor ridges of growth formed on the inner prismatic layer of the dorsal shield. The initial chamber of BMNH CC.393 shows the fine cancellate, internal ornament replaced by a smooth and oval dorsal muscle scar (length 0.42 mm, width 0.22 mm) lying on the posterior side of the first septal suture. *Spirula* displays a similar-sized, ventral muscle scar (Tanabe *et al.* 1998). A scanning electron microscope study of specimen NHMM 1997107 showed that this layer 3 of *Sepia* (see below) had a thickness of 30 µm. Layer 2 is subdivided into 16 µm thick granular and 17 µm thick laminated sublayers (Fig. 5B). The laminae were covered by a membrane (1a) nucleat-

Fig. 5. **A.** Numbered layers of unregistered *Sepia officinalis* L. inner plate, septum (S) and dorsal spherulites (for further explanations see p. 320). Thin section, × 175. **B.** Fractured embryonic wall of Eocene *Belosaepia* Voltz, 1830 (NHMM 1997107, see Fig. 1) showing the same layers, × 632. **C.** Layer 2 of 40 day old *Sepia* (26 µm thickness) which developed nacreous sheets after starvation for five days, × 6100. **D.** Septal layers in 21 µm thick last septum of unregistered, subadult *Sepia* caught off Cornwall, × 1346.





ing the dorsally grown layer 1b composed of 150  $\mu\text{m}$  of yellow coloured spherulites. The post-embryonic layer 1c (1 mm) is formed of laminated and white, prismatic aragonite, grown contemporaneously with the rostrum.

**Remarks.** — English Eocene specimens of *Belosaepia* from the nearshore facies of London Clay Formation and the ‘Barton Beds’ display a relatively curved and laterally compressed rostrum, with rugose pits on their proximal margins, and often a blunt apex, seen in BMNH CC.393 and the specimen figured by de Blainville (1827) (named as *Beloptera sepioidea* in the text and plate caption correction in 1825, see de Blainville 1825–27: pp. 622, 663, pl. 11: 7).

### Genus *Ceratisepia* Meyer, 1989

Type species: *Ceratisepia elongata* Meyer, 1989, by monotypy.

#### *Ceratisepia vanknippenbergi* sp. n.

Figs 2A, D, 3A, C, E, 4A.

Holotype: NHMM 1997106 (*ex van Knippenberg* Collection, no. M459).

Type locality: ENCI-Maastricht BV quarry (Maastricht, the Netherlands).

Type horizon: the base of the late Maastrichtian Gronsveld Member (Maastricht Formation *sensu* Felder 1975).

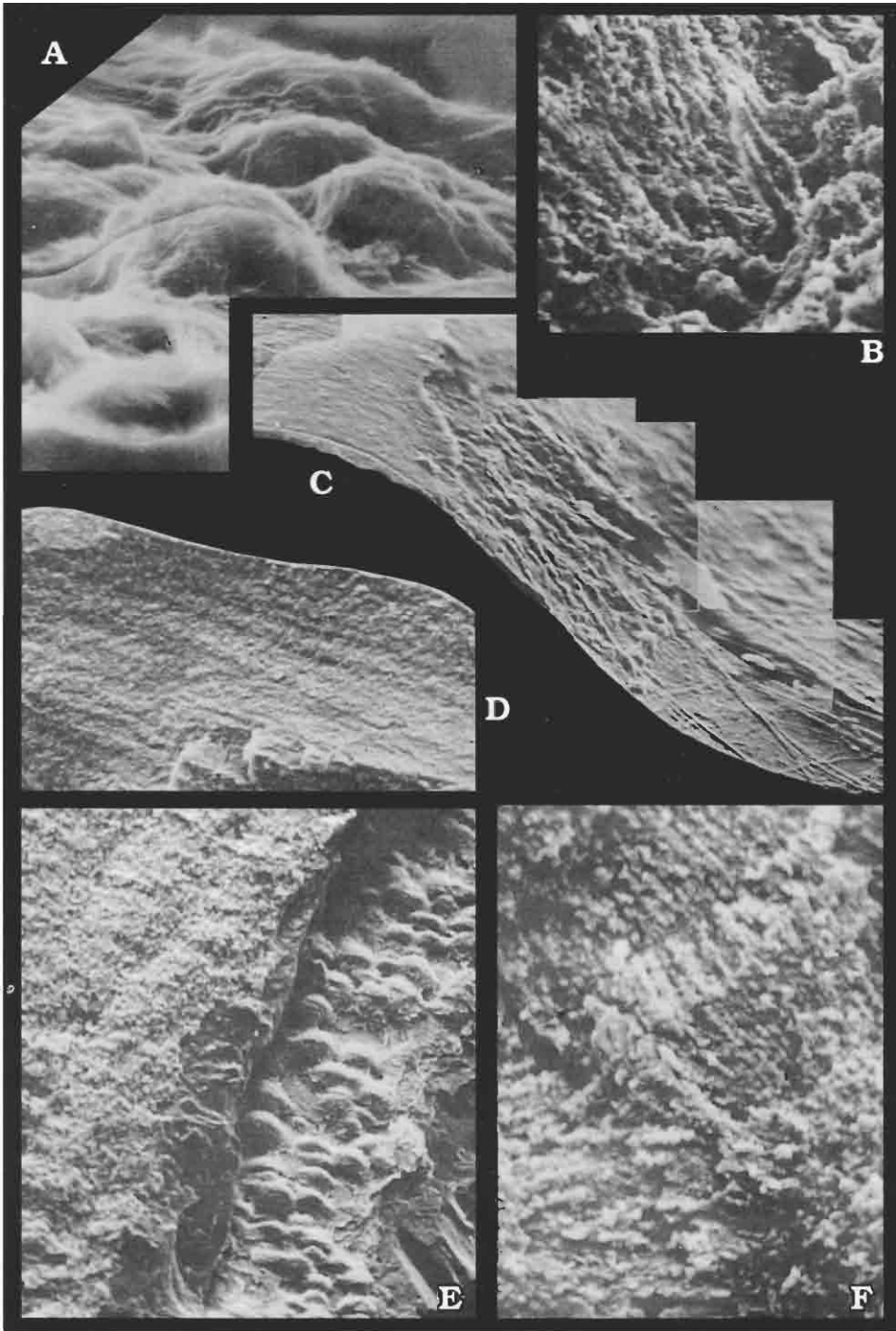
Derivation of name: Named after Paul H.M. van Knippenberg, who discovered the specimen and put it at our disposal.

**Diagnosis.** — A species of *Ceratisepia* the embryonic stage of which differs from that of the single previously known species in having a dorso-median keel.

**Material.** — The holotype is the only known specimen and has a total and probably complete length of 3.64 mm, and is preserved by silica cementation and replacement of an unbroken phragmocone.

**Description.** — The total length and other measurements (Table 1) were made on the fourteen major growth increments on the dorsal shield. Narrower and more irregular grooves are seen in the median ridge near the aperture and they correspond to minor growth increments of the dorsal shield that are too thin and closely spaced to be septal sutures (Fig. 3A). They are developed in major increments 8 to 11 and near the aperture, where they are clearly discordant to the septal suture. The first three major growth increments occur on the hemispherical apex of the conch defined by the constriction of the dorsal and lateral sides of the conch between major increments 3 and 5 with a diameter of 0.7 mm. The apex shows nearly circular growth ridges and an undulating topography (Fig. 3C). The initial calcification of the shell was delayed until increment 11 with a total length of 2.5 mm, as in *Sepia* (Bandel & von Boletzky 1979: p. 379). The radius of curvature of the dorsal profile of the shell remains constant at about 1.57 mm between increments 4 and 11, and then abruptly develops a spiral geometry with a whorl expansion rate (W) of 12 (Fig. 4A).

Fig. 6. Vampyromorph microstructures homeomorphic with those of *Sepia* shown on Fig. 5. **A.** Enlargement of domes within central layer 2 in **C**,  $\times 3229$ . **C.** Ramp through anterior, dorsal-up *Vampyroteuthis* layers 1–3,  $\times 233$ . **B, D–F.** Dorso-lateral views of Sinemurian *Loligosepia bucklandi* (Voltz, 1840) (BMNH 25278) showing francolite-replaced layers 1–2. **B.** Lateral view of pseudomorphed prismatic layer 1 with



maximum thickness of  $34\ \mu\text{m}$ ,  $\times 5650$ . **D**. Folded dorsal surface and chitinous laminae of layer 2,  $\times 2200$ . **E**. Dorsal view of spherulites within layer 1,  $\times 550$ . **F**. The same enlarged,  $\times 5500$ .

The boundary between growth increments 11 and 12 is a septal suture, with a tangential thickness of 30  $\mu\text{m}$ . It marks an increase in the width of the median ridge defined by radial folds on the dorsal shield. The spacing of the septal sutures may correspond to that of the major increments 6 to 12 (i.e. 0.40 mm when measured around the arc of the dorsal surface in the median plane) and it increased to 0.80 mm if increments 13 and 14 are dorsal surface ridges. The entire specimen is embryonic and the absence of the narrow septal sutures grown after the embryonic stage of *Belosaepia*, *Ceratisepia*, and *Sepia* is due to it having died during or just prior to hatching. The silica replacement of the chipped anterior margin preserved the following *Belosaepia* layers (Fig. 3E), also listed in the last section of the present paper:

- 1c. 9  $\mu\text{m}$  thick, planar dorsal prism sheet.
- 1b. 25  $\mu\text{m}$  thick, cavernous, dorsally radiating prisms.
- 1a-3. 50–60  $\mu\text{m}$  thick massive silica with smooth ventral surface overlying a parting.
- S. Prismatic to granular septum, 20–30  $\mu\text{m}$  thick.

The contact angle between the plane of septal suture and the median profile of the dorsal shield was found to be about  $42.5^\circ$  by direct measurement. The smaller contact angle between the curvature of the septum and the same section through the dorsal shield was calculated from the radius of curvature and found to be about  $18^\circ$ . This low angle is less than that of the sepiid illustrated by Squires (1988).

The height of the cap formed by the exposed and external concavity of the septum is about 3.4 mm (measured normal to the preserved apertural plane itself defined by the edge of the septal suture). This measurement implies that the uniform radius of curvature of the concave surface varies from about 2.17 mm in the plane of the septum width (2.33 mm) to a more speculative estimate of 2.62 mm in the plane of the septum length (2.58 mm) containing distortions due to the siphuncle. The implosion depth (Westermann 1973) of this septum with a likely thickness of 20  $\mu\text{m}$  and a tensile strength of at least 131 MPa would be about 200 m. There is no reason to assume that such a septum had or required intracameral support structures to resist the water pressures developed at the bottom of the 'chalk sea' in the southeast Netherlands.

The siphuncle is obscured by chert micronodules on the scanning electron micrographs showing the septum (Fig. 2A). The large and non-circular transverse section of the siphuncle is confirmed by the study of Danian *Ceratisepia* by Meyer (1993) and the Eocene sepiid described by Squires (1988). However, the latter specimens appear to have a more circular siphuncular tube, less oblique septa and a more depressed wall section than the much smaller specimen described here.

**Remarks.** — The holotype of *Ceratisepia vanknippenbergi* sp. n. differs from *Belosaepia* and *C. elongata* of the same small size in having a narrow median ridge resembling the more pitted dorsal furrow of *Naefia* Wetzel, 1930. This structure presumably represents a more continuous dorsal muscle attachment behind the head than the scar sometimes seen in *Belosaepia*. Another difference between embryonic *Ceratisepia* and *Belosaepia* is seen in Table 1. They both have a cap-like geometry, with straight septal sutures displaying a slight lateral lobe; but the embryonic *Belosaepia* have a more elongated aperture and the median profile is lower and less endogastrically coiled at the same width.

The morphological features used to separate *Sepia* from the Spirulida were only partly developed in this Maastrichtian representative of *Ceratisepia*. Meyer (1993)

proposed that the intracameral walls and related innovations of *Sepia* were not present until the late Eocene. It is difficult to imagine how this radical change in the mechanical functions of the shell could occur, except in uncalcified and flooded embryonic shells (i.e. not exposed to water pressure). The new find confirms that any such change had not taken place during the late Mesozoic. It is evident that less radical changes in shell morphology, such as increased size of the dorsal wall, siphuncle, obliquity and flatness of septa had taken place. A pelagic dispersal stage is probably represented by *Ceratisepia vanknippenbergi* sp. n. We are reasonably confident that it did not metamorphose into *Actinosepia*. The microstructure of that genus is so similar to *Trachyteuthis* that it must have had eight, not ten, arms (see below).

Accepting Obradovich's (1993) date of  $65.4 \pm 0.1$  Ma for the K/T boundary, Vonhof & Smit's (1996) calculations would imply an absolute age of c. 65.8 Ma for *C. vanknippenbergi*.

## Superorder Octobrachia Fioroni, 1981

### Order ?Vampyromorpha Pickford, 1936

#### Family Muensterellidae Roger in Piveteau, 1952

#### Genus *Pearceiteuthis* gen. n.

Type species: *Pearceiteuthis buyi* sp. n., by monotypy.

Derivation of name: combination of Joseph C. Pearce (1811–1847) and Greek for a squid.

**Diagnosis.** — Conus with about 20 dorsally expanding, asymmetric radial corrugations that are not confined to an anterior sector of a laterally compressed conus as in *Muensterella* Schevill, 1950 and the finer ribs of *Tusoteuthis* Logan, 1868. High and wide, ventrally constricted embryonic shell, resembling the more symmetrically placed apex of *Listroteuthis* Wagner, 1859. Little trace of the concentric ribbing seen on the similarly shaped *Listroteuthis* and *Celaenoteuthis* Naef, 1922. No sign of the anterior rachis characteristic of muensterellids.

**Distribution.** — *Kosmoceras phaeinum* Subzone of late Callovian Oxford Clay at 'Chippenham' (i.e. Christian Malford) and uncertain Callovian horizon within the Oxford Clay of Peterborough, England (Page & Doyle 1991).

#### *Pearceiteuthis buyi* sp. n.

Figs 7C, D, 8A, B.

*Sepia*? (two species of); Morris 1850: p. 316.

?*Kelaeno*; Hewitt *et al.* 1983: pp. 353, 357.

?*Kelaeno*; Hewitt & Westermann 1983: pp. 382, 394.

Derivation of name: named after William Buy, labouring man of Sutton Benger.

Holotype: BMNH 34468.

Type locality: 'Chippenham' (Christian Malford, Wiltshire, England).

Type horizon: Uppermost Peterborough Member, Oxford Clay Formation.

**Diagnosis.** — same as genus.

**Description.** — In addition to the holotype with a length of 35.6 mm, a breadth of 21.0 mm and an apically worn height of 4.1 mm (Fig. 7D), there is a similar large specimen from Peterborough (BMNH C.15441) and more than ten other Chippenham specimens. One of the latter (BMNH 21430) was partly destroyed for X-ray dif-

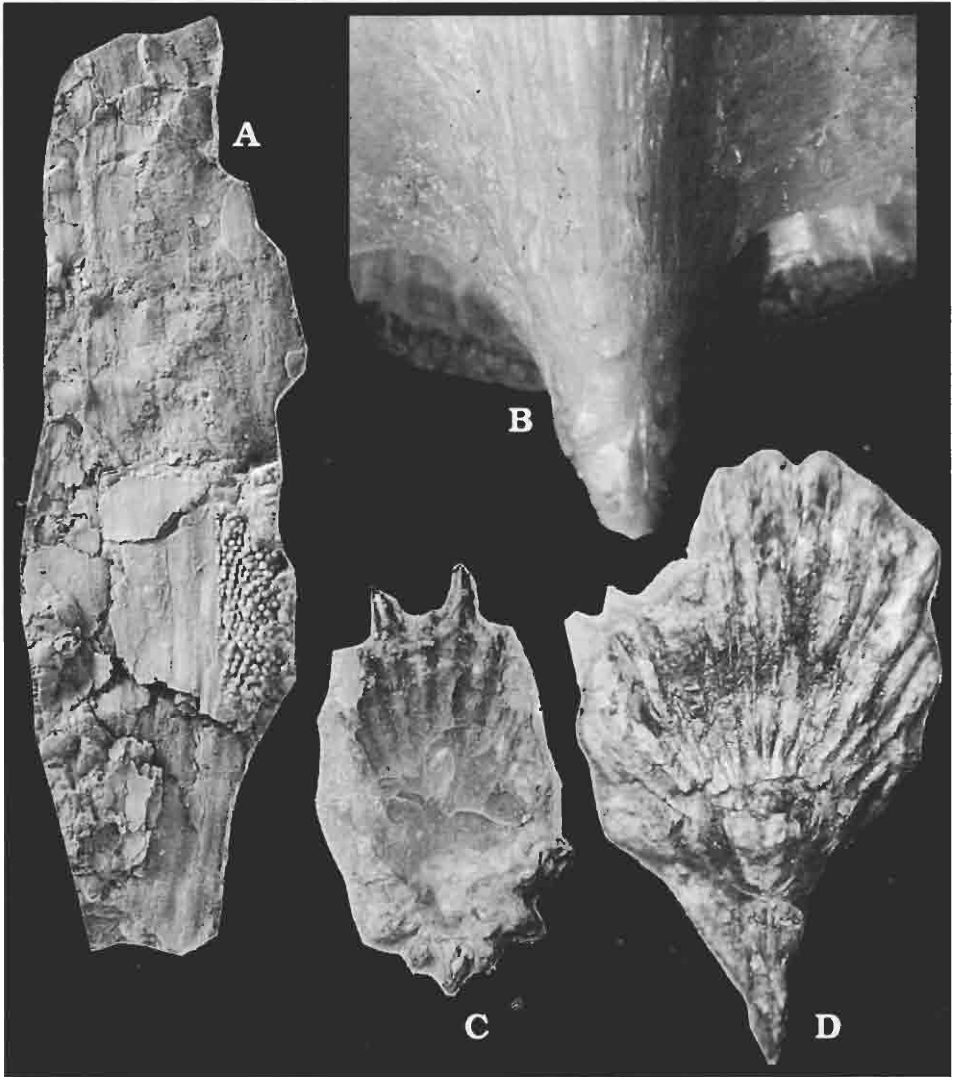


Fig. 7. Homeomorphy between Jurassic vampyromorphs (A, C, D) and Recent *Sepia officinalis* L. (B). A. Tithonian *Trachyteuthis* sp. (BMNH C.46843), dorsal view,  $\times 1$ . B. Dorsal view of unregistered *Sepia* showing rostrum within dried conus vane,  $\times 9$ . C, D. Ventral and dorsal views of late Callovian *Pearceiteuthis buyi* gen. et sp. n., BMNH 21430 and BMNH 34468 (holotype), respectively,  $\times 3.2$  and  $\times 2.4$ , respectively.

fraction and geochemical studies of sheets and 2.0 mm high dorsal spines with 35  $\mu\text{m}$  diameter hemispherical ornament (not BMNH C.15441 as reported by Hewitt *et al.* 1983). This specimen had a length of 18.7 mm, a breadth of 10.0 mm, a height exclusive of spines of 4 mm and an apical, embryonic concavity with a depth of 0.6 mm at a length of 1.2 mm and a breadth of perhaps 4 mm, bounded by a median ventral constriction.

The apex of specimen BMNH 21430 showed the following francolite-replaced layers:

1c. 6  $\mu\text{m}$  thick smooth coating on spines.

1b. 100  $\mu\text{m}$  thick layer locally developed into 2 mm long spines bearing hemispheres. Contains 100  $\mu\text{m}$  diameter holes cemented by phosphate granules.

1a. More fissile 210 to 440  $\mu\text{m}$  thick layer composed of smaller hemispherically shaped sheets (Fig. 8A, B), interbedded with thin prismatic sheets (Fig. 8A) and becoming increasingly folded into radial ribs dorsally.

2. 100 to 150  $\mu\text{m}$  layer grown at angle to the other layers at anterior aperture, and having smooth internal laminae.

3. 140 to 180  $\mu\text{m}$  thick, ventral unconformable coating of layer 2 including a 50  $\mu\text{m}$  thick sublayer (3b) composed of thick and thin chitinous couplets with a periodicity of 1.4  $\mu\text{m}$ .

**Remarks.** — These remains were given the informal, incorrect and now invalid (ICZN 1997) name *Kelaeno* von Münster by 19th century curators. The microstructure is similar to *Trachyteuthis* and *Actinosepia*, described below.

## Microstructural observations on other genera

This section of the paper compares and correlates the shell layers of the skeletons presented above with those of other coleoid genera. Numbers are used to denote the cycle of growth of the cells forming the ventro-anterior layers of the conothecal wall and adjacent septa (S). Letters a, b and c denote the calcification of protein-chitin sheets by the dorso-anterior shell sac. In a cuttlebone there is a thick equivalent of the ectocochliate periostracum (layer 1) that is termed the middle plate when it is subsequently calcified in a dorsal direction within one day. The microstructures of *Spirula* represent the outermost or rostral layer of *Sepia* (1c), the inner prismatic layer (3) and the lamello-fibrillar layer of belemnoid or *Sepia* septa (S2). The numbered units are equivalent to terms of Mutvei (1964) which refer to the cells of *Spirula*, not cell products.

### Superorder Decabrachia Boettger, 1952

#### Order Spirulida Stolley, 1919

#### Family Groenlandibelidae Jeletzky, 1966

#### *Naefia neogaeia* Wetzel, 1930

Fig. 3D.

Age: Cretaceous (Campanian).

The spirulids of Cretaceous age do not have a *Sepia* middle plate and ammonoid 'coating layer' as claimed by Doguzhaeva (1996). The growth increments slope ventrally and the 'coating layer' includes sheet nacreous microstructure and external growth escarpments formed by aligned, rather than dorsally radiating, prisms, as visible on the specimen of *Naefia neogaeia* Wetzel, 1930 from the Campanian (Fig. 3D). The section was measured on a 5.5 mm diameter conothecal wall on the ventral side where the nacreous layer develops from the inner rather granular half of the outer dorsal prismatic layer.

1. 4 to 6  $\mu\text{m}$  thick, outer aligned prismatic layer formed by anterior epimarginal cells. Develops transverse ridges.

2. 6  $\mu\text{m}$  thick layer of sheet nacre, with mean band thickness of 390 nm, formed by posterior epimarginal cells (Fig. 3D).

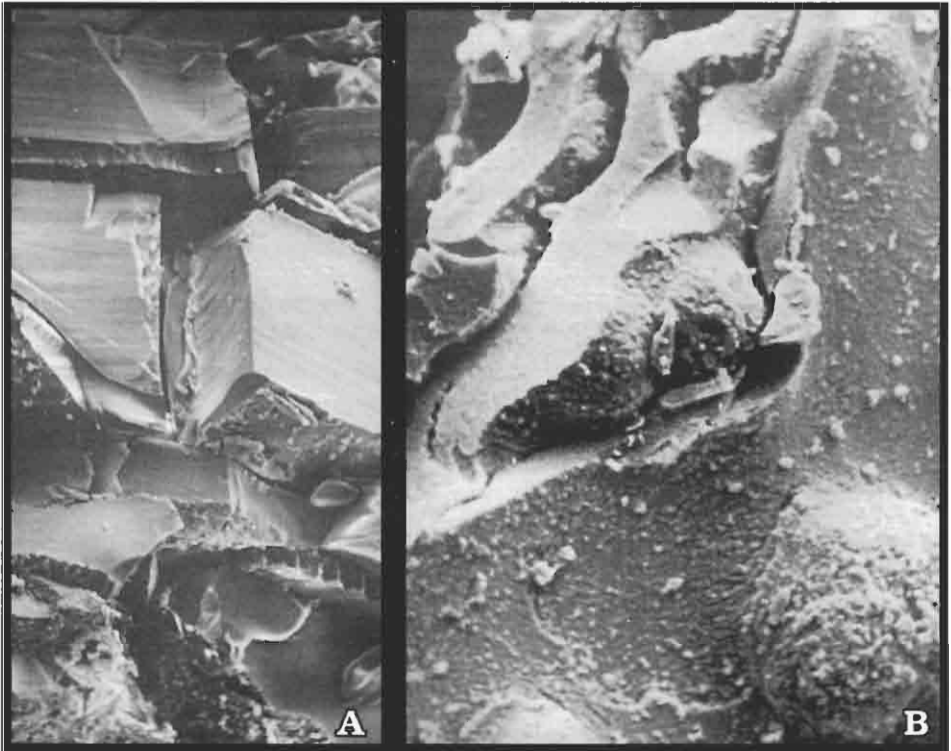


Fig. 8. Late Callovian muensterellid *Pearceiteuthis buyi* gen. et sp. n., from the Oxford Clay (BMNH 21430) showing francolite-replaced sheets in layer 1a. **A.** Chitinous but dome-shaped laminae separated by probable prismatic aragonite layers, with dorsal below,  $\times 570$ . **B.** Small domes presumably representing aragonitic nucleation sites, with dorsal on right,  $\times 2560$ .

3. 40  $\mu\text{m}$  thick layer of aligned prisms with hexagonal, 3  $\mu\text{m}$  outer cross sections, grown by so-called myo-adhesive cells.

S1-2. Gap representing cameral membrane overlain by lamello-fibrillar microstructure of septum. But the dorsal suture shows prisms extending for 12  $\mu\text{m}$  into 2  $\mu\text{m}$  thick sheets forming the mural part of the same septum.

S3. Ventral prismatic layer and wall or pillars on septa near siphuncle seen in other spirulids (Bandel & von Boletzky 1979; Doguzhaeva 1996).

## Order Sepiida von Zittel, 1895

### Family Sepiidae Keferstein, 1866

#### *Sepia officinalis* L.

Figs 2B, C, 5A, C, D, 7B.

Age: Recent.

**1b.** 17.4  $\mu\text{m}$  thick layer of spherulites consisting of 90 degree sectors grown in protein-chitin matrix in one day = middle plate.

**1a.** Longitudinally folded membranes sometimes folded transversely on a larger scale over future sutures.



2. 23  $\mu\text{m}$  thick, lamello-fibrillar layer developing 1.5  $\mu\text{m}$  thick bands defined by 300 nm continuous aragonite sheets when starved in experiments by Packard (1972: p. 281).

3. 12.4  $\mu\text{m}$  thick layer of aligned prisms. Elsewhere extends as longer prisms in blocks of granules forming mural ridge behind septal sutures.

S2. Parallel lamello-fibrillar layer of anterior septum with local maximum thickness of 3.4  $\mu\text{m}$ .

S3. Prismatic layer of septum with thickness of 4.5  $\mu\text{m}$ . Locally followed by longitudinal intracameral walls with a height of about 400  $\mu\text{m}$ .

## Superorder Octobrachia Fioroni, 1981

### Order Vampyromorpha Pickford, 1936

#### Family Vampyroteuthidae Thiele, 1915

##### *Vampyroteuthis infernalis* Chun, 1903

Fig. 6A, C.

Age: Recent.

Median anterior section about 50 mm from apex, after three years in preservatives, which may have decalcified layer 1a.

1c. 5  $\mu\text{m}$  thick layer with small longitudinal folds.

1b. 6  $\mu\text{m}$  thick layer of 8  $\mu\text{m}$  diameter, rough-looking hemispherical folds.

1a. Cores of 1b show porous triangular spaces.

2. 3  $\mu\text{m}$  thick layer of 180 nm thick chitinous bands, folded parallel to shell edge but generally planar.

3. 3  $\mu\text{m}$  thick, more homogeneous and more folded layer (particularly in lateral fields).

#### Family Loligosepiidae Regteren Altena, 1949

##### *Loligosepia bucklandi* (Voltz, 1840)

Fig. 6B, D–F.

Age: Jurassic (Sinemurian).

Large median field of BMNH 25278 from Sinemurian in which the cumulative thicknesses of the francolite replaced aragonitic and chitinous layers is enlarged by calcite sheet-cracks (not included below).

1c. 10  $\mu\text{m}$  thick layer of 20–40  $\mu\text{m}$  wide growth ridges with spherulitic subunits (Fig. 6E).

1b. 6  $\mu\text{m}$  high, longitudinally elongated domes, composed of francolite granules that pseudo-morph 360° sectors of spherulitic, 1  $\mu\text{m}$  diameter aragonite prisms on the basal membrane (1a). The prisms radiate through 180° in transverse sections but are not seen in longitudinal fractured sections.

1a. 11  $\mu\text{m}$  diameter cores of the same spherulites originally composed of 200–500 nm diameter prisms. They have been replaced by calcite but are preserved in cross section as dimples on the surrounding francolite-replaced protein sheet.

2. 21  $\mu\text{m}$  thick layer composed of about 15 regularly spaced bands that were deposited under a gently folded surface composed of a single surviving band. They resemble septal sutures of *Sepia* in their general morphology but seem more likely to have had the same uncalcified composition as ammonoid siphuncular tubes (Fig. 6D).

3. 230  $\mu\text{m}$  thick, more homogeneous laminations, with a smooth ventral surface covered with a fibrous ornamentation (i.e. en-echelon folds parallel to the edge with a wavelength of 1  $\mu\text{m}$ ).

#### Family Trachyteuthididae Naef, 1921

##### *Trachyteuthis* sp.

Figs 7A, 9A, B.

Age: Jurassic (Tithonian).

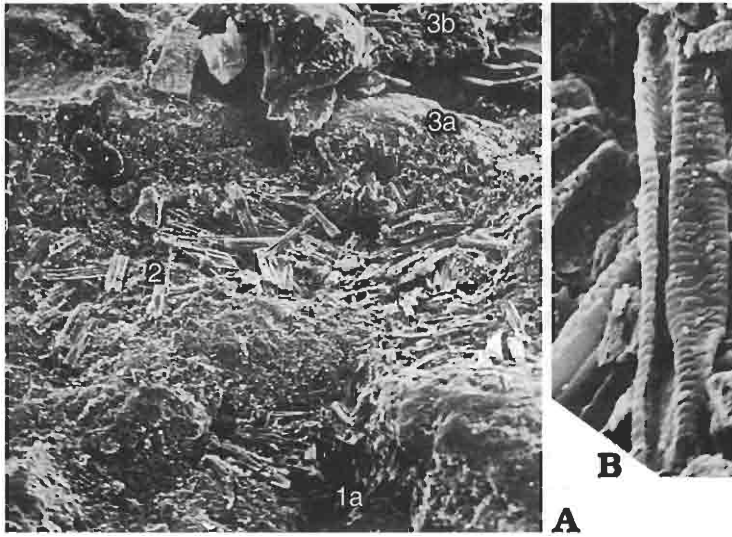


Fig. 9. Tithonian *Trachyteuthis* sp. (BMNH C.46844) split on base of hollow spherulites. **A.** Complete and untreated fractured section of ventral half of skeleton with layer 1a at base,  $\times 465$ . **B.** Further enlargement of layer 2 resembling the diatom *Thalassionema*,  $\times 3350$ .

In the 70 mm wide median field of Tithonian specimen BMNH C.46844, the majority of longitudinal lineations and compacted 15  $\mu\text{m}$  high walls and hollow pillars represent selective francolite replacement of the aragonite prism margins that once separated the planar sheets of layer 2 (Fig. 9A). Some diatoms and coccoliths are also present.

**1c.** 210  $\mu\text{m}$  to 500  $\mu\text{m}$  thick layer of transverse and hemispherically folded sheets.

**1b.** 200  $\mu\text{m}$  thick layer of hemispherically folded, more weathered-looking francolite sheets.

**1a.** Exfoliated accretionary surfaces probably composed of two 15  $\mu\text{m}$  thick layers, showing longitudinal lineations with a spacing of 2  $\mu\text{m}$  horizontal sheets and corrugated or tubular walls between these sheets. Form hollow cavities (Fig. 9A).

**2.** 220  $\mu\text{m}$  thick layer composed of relatively planar and ventrally grown, coarse sheets.

**3.** 310  $\mu\text{m}$  thick layer of less laminated, planar sheets (3a, 3b on Fig. 9A), with a ventral thickness of 30  $\mu\text{m}$ , forming only a dorso-median groove on the fully exposed ventral surface of BMNH 59540.

### *Actinosepia canadensis* Whiteaves, 1897

Age: Cretaceous (Maastrichtian).

Transverse thin section A-238 and horizontal dorsal section A-1408 from Fox Hills Formation (Maastrichtian), localities 9 and 34, Dewey County, South Dakota, loaned by K.M. Waage of Yale Peabody Museum (Waage 1965; Hewitt & Wignall 1988). The same layers seen in *Trachyteuthis* are described here as optical properties of 10  $\mu\text{m}$  thick sheets.

**1a–c.** 900  $\mu\text{m}$  thick, isotropic layer of dorsally grown sheets folded into 500  $\mu\text{m}$  diameter domes separated by opaque vertical sheets.

**?2.** Central accretionary surface with thin birefringent francolite sheets between the isotropic francolite.

**3.** 1000  $\mu\text{m}$  thick, planar, ventrally grown layer of birefringent francolite. The sheets of both *Actinosepia* and *Trachyteuthis* are normally length-fast with first-order birefringence colours.

## Discussion and conclusions

It is convenient to compare the three layers of all these skeletons with the three conothecal wall layers of ectocochliates, *Belemnotheutis* (Bandel & Kulicki 1988; Donovan & Crane 1992) and the ventral side of *Naefia neogaeia*, and it seems that Dauphin (1984, 1985) was correct in deriving *Belosaepia* and *Sepia* microstructures from diplobeliniid belemnites. These belemnites contain two clades that had separated from each other in the Cretaceous. One (*Conoteuthis*) is almost indistinguishable from the late Cretaceous Sepiida, and the other (*Diplobelus*) was the source of the Aptian Spirulida. This view is unpopular. For example, Engeser (1990: p. 163) claimed that the shell of all non-belemnoid coleoids, 'consists of the inner nacreous layer (septum), the inner prismatic layer and the outer organic layer [...] which stems from the basic pattern of the Cephalopoda.' In reality these coleoids resemble belemnoids in having a unique septum microstructure, termed the lamello-fibrillar microstructure, which is also present as a modified nacreous layer of their wall (layers 2 and S2). Doguzhaeva (1996: p. 704) made the correct inference that belemnoids have retained the original nacreous microstructure of layer 2 lost in most non-belemnoid coleoids.

Since the synapomorphy of a lamello-fibrillar microstructure was present in belemnoid septa, it could extend independently in the walls of Triassic–Jurassic vampyromorphs and Cretaceous spirulids. This was further explored in Hewitt's unpublished thesis (1975: p. 201): 'The shell of *Spirula* could have evolved into a cuttlebone by an acceleration of the shell growth cycles relative to the growth of the body chamber. The first cycle of shell growth would only form the organic part of the middle plate before the start of the second cycle. Thus the septa of *Spirula* became the *Sepia* inner plate and the *Spirula* siphuncle the *Sepia* septa and supporting walls.'

Similar conclusions were drawn by Bandel & von Boletzky (1979). The ventral side of the shell of the Aptian spirulid *Naefia kabanovi* Doguzhaeva, 1996 has the septal lamello-fibrillar layer (S2) fully covering layer 3 of the wall, and an adjacent *Sepia*-like prismatic layer (S3) covering the free part of the septum (Doguzhaeva 1996: fig. 2). This early spirulid could have developed into the later *Ceratisepia* by generating ventro-posterior cells to produce a rapid spiral expansion rate of the chambers and siphuncle. But another *Naefia* species (Fig. 3D) and *Sepia* (Fig. 5C) retain some nacre in wall layer 2. If Doguzhaeva *et al.* (1999) have correctly identified a spirulid among Carboniferous heteromorph ammonoids, then the *Sepia* clade could have developed from the spirulids by partial fusion of septa to form a laminated inner plate (layer 2). But how can they be so certain? Ambiguous microstructural evidence produces a long hiatus in fossil records of spirulids.

Doguzhaeva (1996) claimed that the 'outer plate' (layer 1b) of non-belemnoid coleoids was a conservative feature derived from a *Spirula*-like ancestor. Engeser (1990: p. 169) repeated the similar erroneous view that the Sepiida developed from the late Eocene spirulid *Vasseuria* with an entirely prismatic wall and oblique prismatic septal sutures. The time of separation of the *Sepia* and *Spirula* clades is now extended back into the Mesozoic, and beyond the acquisition of a spherulitic 'outer plate', axial curvature, large rostra and oblique septa by spirulids. A spherulitic calcification of the dorso-anterior margin of layer 1 appeared independently in pre-Jurassic octobrachs, late Cretaceous Sepiida and Eocene Spirulida. There is no microstructural reason why

the Coleoidea cannot remain as a monophyletic clade (see Pignatti & Mariotti 1995: p. 35). The similarity between the initial chambers of *Spirula*, *Groenlandibelus* and the more distantly related ammonoids can be ascribed to functional convergence during mesopelagic hatching.

In conclusion, separate origins of the Sepiida and Spirulida within Cretaceous diplobeliniid belemnites is still the most attractive hypothesis, until the case for pre-Aptian fossil records of spirulids becomes overwhelming.

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## **Mastrichtcka *Ceratisepia* oraz mezozoiczne homeomorfy mątw**

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### **Streszczenie**

Dokonano przeglądu potencjalnych mezozoicznych przodków mątw (rząd Sepiida von Zittel, 1859 *sensu stricto*; nadrzęd Decabrachia Boettger, 1952). Wyniki badań mikrostruktur szkieletów mezozoicznych homeomorfów mątw (*Pearceiteuthis* gen. n., *Loligosepia*, *Trachyteuthis*, *Actinosepia*) potwierdzają ich przynależność do nadrzędu Octobrachia Fioroni, 1981. Znalezisko embrionalnej muszli *Ceratisepia* w osadach górnego maastrichtu Holandii wskazuje, że Sepiida powstały przez kenozoikiem. Kredowe dziesięciornice z rzędu Spirulida Stolley, 1919 nie wykazują grzbietowo-przednich wektorów wzrostu muszli, które można obserwować u kenozoicznych spirul, mątw oraz ośmiornic. Hipoteza głosząca, że Sepiida oraz Spirulida wyodrębniły się niezależnie z kredowych diplobeliniidowych belemnitów jest wciąż najbardziej atrakcyjnym wyjaśnieniem pochodzenia obu tych grup. Opisano dwa nowe taksony: *Ceratisepia vanknippenbergi* sp. n. z górnego maastrichtu Holandii oraz *Pearceiteuthis buyi* gen. et sp. n. z keloweju Anglii.