

Mineralogy, structure and homology of ammonoid siphuncles

By

R. A. Hewitt and G. E. G. Westermann, Hamilton

With 14 figures and 1 table in the text

HEWITT, R. A. & WESTERMANN, G. E. G. (1983): Mineralogy, structure and homology of ammonoid siphuncles. — N. Jb. Geol. Paläont., Abh., 165: 378—396; Stuttgart.

Abstract: Connecting rings of Jurassic ammonoids, like proostraca of Mesozoic teuthids consist of francolite with a unit cell *a* dimension that varies significantly between samples. An outer isotropic francolite layer sometimes includes eucariote plant cells embedded in pseudomorphs after organic fibres suggesting formation after death. An inner primary francolite layer is birefringent in transverse section. The position of cameral membranes in *Nautilus* indicates that ectocochliate siphuncular tubes are a product of the inferior region of the septal secretory division and that ammonoid and nautiloid siphuncles are more closely homologous than has been supposed.

Key words: Cephalopoda (Teuthida), Jurassic, shell (proostracum, siphuncle), francolite, phosphate, inclusion, microorganisms, growth.

Zusammenfassung: Die Proostraken mesozoischer Teuthiden und die Siphonalhüllen jurassischer Ammoniten bestehen aus Frankolit, dessen Elementarzellen-Größe zwischen verschiedenen Proben signifikant variiert (Reichweite 9.30—9.35 Å). Die Siphonalhüllen bestehen (a) aus einer isotropen Frankolit-Außenschicht, in der manchmal 50—115 µm große, rundliche Eukarioten-Zellen in Pseudomorphosen nach organischen Fasern eingebettet sind und (b) aus einer primär frankolitischen Innenschicht mit Doppelbrechung in der Transversalebene. Ein Teil des Phosphats wurde also nach dem Tod durch Phosphat-Reduktion in der Nähe von verwesendem Körpergewebe oder von anoxischem Meeresboden gebildet; mineralogisch sind aber zwischen Proben aus aerobischer und anaerobischer Fazies keine Unterschiede zu erkennen. Die Anordnung der Kammermembranen in *Nautilus* weist darauf hin, daß die Siphonalhüllen von Ektocochleaten ein Erzeugnis der unteren Region des Septum-bildenden Mantels (septal secretory division) darstellen, und daß Ammoniten-Siphonalhüllen größere Homologien zu *Nautilus* aufweisen als bisher allgemein angenommen.

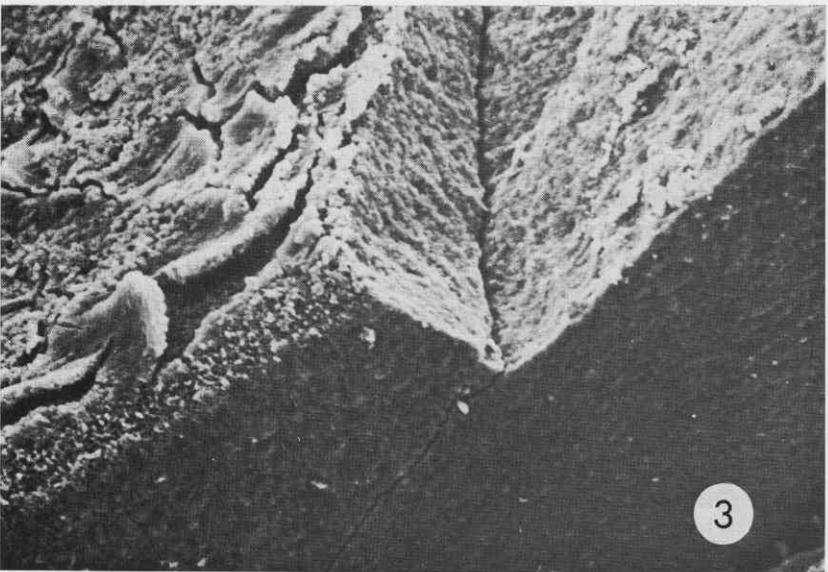
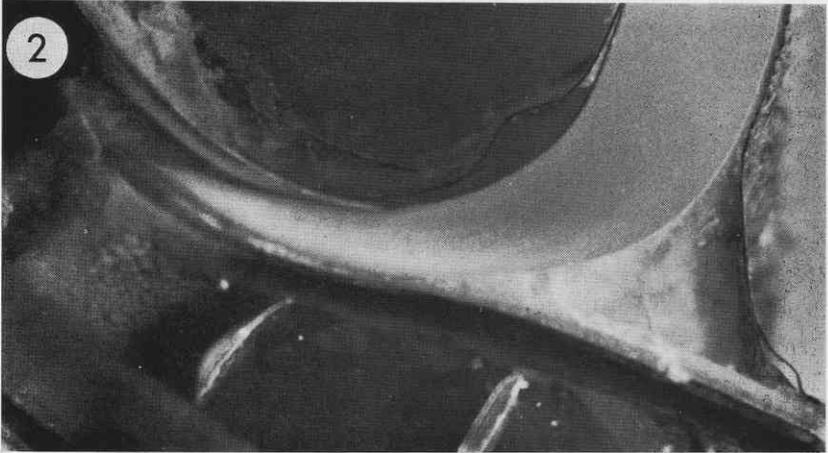
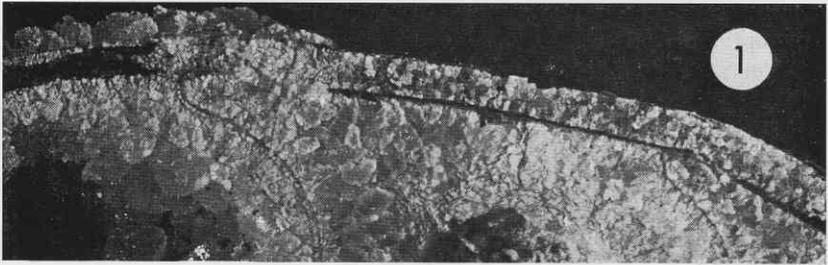
1. Introduction

The cylindrical ammonoid connecting rings and aragonite septal necks form a continuous siphuncular tube (Fig. 1), which enabled these originally aragonitic cephalopods to regulate their buoyancy like living *Nautilus*. In

nautiloids the connecting ring contains an inner uncalcified conchiolin (glycoprotein) "horny tube", surrounded by a porous ring of aragonite spicules and spherulites termed the "chalky tube" (HEWITT 1983, DENTON & GILPIN-BROWN 1966). Studies of freshly killed *Nautilus* embedded in resin have shown that these layers are both formed by the "inferior region" of the septal secretory division of mantle epithelia as defined by MUTVEI (1964). The cameral membranes cover the "semi-prismatic layer of the shell septum" and pass towards the invaginated body surrounding the growing margin of the connecting ring (Fig. 2). This indicates that there is no basic anatomical difference between *Nautilus* and ammonoids, except that the latter apparently lack a chalky tube and contain septal necks which bend the opposite way (prochoanitic) to the retrochoanitic necks of *Nautilus* (KULICKI 1979). Thus the homologies between the internal shell layers and structures of *Nautilus*, ammonoids and coleoids probably result from modifications of the cyclic changes within the inferior region of their septal division epithelia. This conclusion is at variance with discussions by BANDEL (1981). The present paper reviews the composition of the ammonite connecting ring. Its function is reviewed by WESTERMANN (1971 and 1982) and CHAMBERLAIN et al. (1981).

GRANDJEAN (1910) studied the phosphorus content and optics of 17 Mesozoic ammonites and one Carboniferous goniatite, which were found to have a connecting ring composed of calcium phosphate. ANDALIB (1972) showed that six Jurassic ammonite connecting rings from four lithologies are composed of the crystalline phosphate francolite (carbonate fluorapatite). In contrast, the connecting rings of a Campanian *Platylenticeras* from the Bearpaw shales of southern Alberta, with aragonitic shells preserved, consist of brown stained sparry calcite surrounded by a band of fungal hyphae or actinomycetes in white calcite spar (see below). Similarly the connecting rings of Jurassic phylloceratids are preserved as either phosphate or calcite (JOLY 1976); but described nautilid connecting rings are not phosphatic (see ANDALIB 1972, WESTERMANN 1982). An aragonitic *Haplophylloceras* from the Tithonian of Sula Island (J2034L) provided an example of a relatively unaltered francolite connecting ring (WESTERMANN, 1982). Diagenetic francolite in concretions and ammonite body chambers is known to have precipitated before early diagenetic pyrite cementation and sedimentary compaction (SEILACHER et al. 1976, p. 313; HEWITT 1981). Leaving aside the probable biogenic theory for ammonite francolite, which can be suggested by analogy with Recent *Lingula* (McCONNELL 1963), there are three models which could explain a localized phosphatisation of the connecting ring.

The first model assumes that the ammonite body tissues either decayed rapidly enough to reduce phosphate in the body chamber and siphuncle, or that they were surrounded by anoxic water. The chemical gradient through the connecting ring produced a phosphatic replacement zone along the inner deoxygenated edge, and a



Figs. 1—3 (Legend see p. 381)

zone of decay and oxidation within the camerae. The movement of oxygen from the camerae to the siphuncle caused a reverse gradient in the partial pressure of nitrogen, which acted together with residual osmotic forces to keep water out of the chambers. After the ammonite had decayed, the gradients reversed and any floating shells eventually sank to the sea floor, the increased hydrostatic pressure sometimes breaking the connecting rings in the chambers that remained gas-filled.

In the second model the camerae became deoxygenated by the decay of cameral membranes, while the tissues were either removed by predation, or decayed in an open oxygenated body chamber. The nitrogen tended to move out of the chamber and become rapidly replaced by water, while the partially decayed cameral membranes and outer layers of the siphuncle formed centres of phosphate or pyrite precipitation. In the case of an empty shell, the inner layers of the connecting ring should show evidence of decay and borings, resulting from contact with oxygenated sea water. The limited supply of organic matter in the camerae will limit the effectiveness of the model (see also MARSHALL 1981, p. 879).

The third model could involve in situ crystallisation from a phosphorous-rich organic molecule, such as the polysaccharide onupin found in polychaetes, or the recrystallisation of fine-grained apatite, such as the dahllite found in Recent vertebrate skeletons. This fibrous carbonate hydroxyapatite takes up fluorine from sea water and changes into granular francolite during diagenesis. Evidence for dahllite in the Recent cephalopod *Spirula* (ANDALIB 1972, p. 41–42) cannot be accepted, since the only convincing peak is more crystalline than aragonite and could be halite. The broad peaks displayed by the (21.1) reflection in belemnites (ANDALIB 1972, Fig. 6) may be dahllite, but the equivalent single peaks seen in *Belosepia* rostra and washed *Sepia* samples are indicative of francolite. Moreover, dahllites cannot be identified using the criteria of WATABE (1956) and ANDALIB (1972). Semi-quantitative E. D. A. X. analyses of chitinous *Nautilus* connecting rings (OBATA et al. 1969) and recent coleoid proostraca show no significant Ca and P enrichment. Curiously, Mesozoic coleoid proostraca are entirely composed of laminated francolite (HEWITT 1981).

2. Criteria used to interpret the francolite

2.1. Unit cell parameters

The hexagonal unit cell parameters of representative Mesozoic francolites from ammonites and teuthids are shown on Table 1. These values were calculated by the least squares program "cell" using CuK α radiation ($\lambda =$

Fig. 1. Saggital section of *Ludwigia* (J1597–19) after etching the sparry ferroan calcite with dilute acetic acid. Note the black francolite connecting rings and the septa delineated by acid-resistant brown membranes (x 2.9).

Fig. 2. Saggital thin section of a freshly killed *Nautilus pompilius* embedded in epoxy resin. Note the cameral membranes flanking both sides of the septum and the connection between these membranes and the connecting ring. The siphuncle has an internal diameter of 1.0 to 2.1 mm in this septal neck and the dark horny tube is interrupted by spherulitic white aragonite (x 26).

Fig. 3. Oblique view of a transverse hydrochloric acid etched section through a mid-chamber portion of a connecting ring shown on Fig. 1. Note the porous exfoliating outer margin and the fine grained massive inner margin of the francolite connecting ring (S.E.M. micrograph, x 850).

Table 1. Francolite unit cells and crystallinity in Mesozoic teuthids and Jurassic ammonoid connecting rings. Samples analysed by $\text{CuK}\alpha$ radiation (1.54178 Å), or recalculated from ANDALIB (1972) after converting his d values to $2\theta^\circ$ with the $\text{CuK}\alpha$ wavelength (samples marked with *). Material housed in the British Museum (BMNH) and McMaster University. D = dark grey, blue or black in reflected light, W = white or pale grey in reflect light, ? = peak height averaged between 2 and 4 times background noise, ?? = peak height less than 2 times background noise. The age of the samples is denoted by numbers representing stages and letters denoting zones and localities (see appendix). m. = median, l. = lateral field, hkl = number of peaks, n = number of grains, J85 = concretion in *Plesioteuthis* (muscular mantle excluding gladius).

Taxon and sample	Age & colour		Unit cell Å				Crystal size Å				S.E.M. n	
			<i>a</i>	1σ	<i>c</i>	1σ	hkl	X-ray <i>a</i>	<i>c</i>	mean		mean
<i>Psiloceras</i>												
1423*	1	D	9.355	0.005	6.893	0.005	16					
<i>Kossmatia</i>												
J1517-17	10	W	9.350	0.005	6.892	0.006	11	?491	?442	467	1034	151
<i>Sonnia</i> J1290	5a	D	9.341	0.003	6.905	0.003	15	276	221	394	778	196
<i>Sonnia</i> J1189	5b	W	9.339	0.005	6.893	0.005	10	?355	??461			
<i>Calliphylloceras</i>												
J1828	5c	D	9.338	0.013	6.896	0.013	4	??267				
<i>Macrocephalites</i>												
J2016E	7a	D	9.337	0.005	6.894	0.005	7	?316	??191			
Diagenetic J85	9a	W	9.335	0.003	6.907	0.003	14	216	292	306		
<i>Reineckia</i>												
J1780A	7b	W	9.335	0.011	6.892	0.011	6	?234	??244			
<i>Tusoteuthis</i>												
BMNH C.7990 m.	11	W	9.332	0.004	6.890	0.004	19					
? <i>Kelaeno</i>												
BMNH C.15441	7c	D	9.329	0.028	6.888	0.038	7					
<i>Trachyteuthis</i> J 284 m	9a	W	9.343	0.006	6.894	0.005	14	173	431	272		
<i>Trachyteuthis</i> J 283 m	9a	W	9324	0.004	6.900	0.004	17	377	331	346		
Perisphinctid												
ammonite*	9a	W	9.319	0.004	6.882	0.003	16	?275	??517			
<i>Ludwigia</i>												
J1597-18	4	D	9.319	0.011	6.888	0.016	7	?427	??220			
"White siphuncle*"	3	W	9.318	0.007	6.895	0.006	15					
"Blue siphuncle*"	3	D	9.315	0.006	6.894	0.006	13					
<i>Trachyteuthis</i>												
BMNH C.46843 l.	9b	D	9.311	0.006	6.885	0.007	19					
<i>Loligosepia</i>												
BMNH C.25278 l.	2	D	9.310	0.005	6.894	0.005	18					
<i>Ludwigia</i> J1597-19	4	D	9.301	0.004	6.896	0.003	13	279	?621	449	599	114

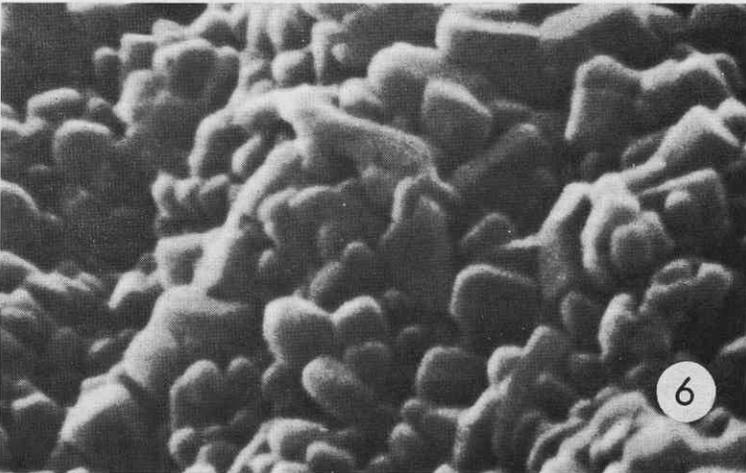
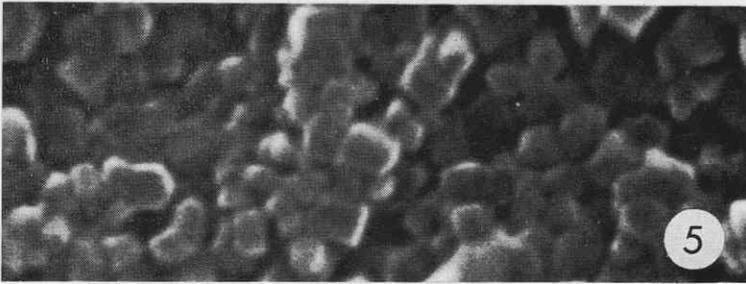
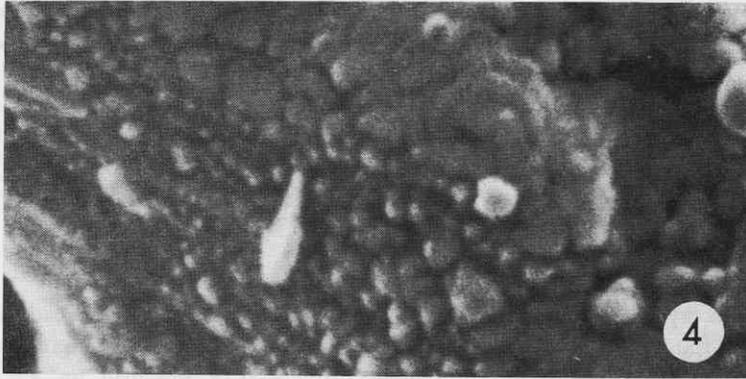


Fig. 4. Very fine grained francolite granules at the ventral outer margin of the connecting ring of *Haplophylloceras* (S.E.M. micrograph of fractured section, x 52,000).

Fig. 5. Typical francolite microstructure of the *Sonninia* connecting ring shown on Fig. 7 (S.E.M. micrograph of fractured acetic acid etched longitudinal section, x 52,000).

Fig. 6. Typical francolite microstructure of the *Kossmatia* connecting ring shown on Fig. 7 (S.E.M. micrograph of acetic acid etched longitudinal section near septal neck, x 52,000).

1.54178 Å) X-ray diffractometer traces. Quartz was used as an internal standard in all the new data. These results indicate that ammonite connecting rings have a similar range of unit cell parameters to Mesozoic teuthid proostraca. The francolite has an unusually high CO₂ and low water content (see McCLELLAN & LEHR 1969, McCONNELL 1970), but similar small unit cells are also found in diagenetic francolites (WHIPPO & MUROWCHICK 1969, MARSHALL & COOK 1981, samples of HEWITT 1981).

2.2. Crystallinity

The crystal size of the francolite was determined from peak broadening of the (00.2) and (30.0) reflections on X-ray diffractometer traces, and two axial measurements of grains sampled from a 0.19 μm grid on S.E.M. photographs taken at 52,500 to 52,000 times magnification. The profile of the (10.0) quartz peak was used as an indication of instrumental broadening and random errors in the generally low intensity francolite reflections. Following WARREN (1969), the crystal size along the a and c axes was calculated using the expressions:

$$B = \sqrt{B_M^2 - B_S^2} \text{ and } t = \frac{0.9}{B} \frac{1.54178}{\cos \theta}$$

Where;

- B = Extra breadth of the apatite peak relative to quartz peak (10.0).
 B_M = Width of apatite peak in degrees 2θ as radians at half height.
 B_S = Width of adjacent single CuKα quartz peak in degrees 2θ as radians.
 t = Crystal size normal to plane measured in Å.
 cos θ = Position of apatite peak on X-ray diffractometer trace.

The results shown on Table 1 show that each element of the granular aggregates observed in the S.E.M. (Figs. 3—7) is probably a single crystallographic unit. The data from *Trachyteuthis* (median field J283), *Ludwigia* (J1597-19) and *Sonninia* (J1290), suggest that the length of the c-axis is statistically equal to the a-axis. The mean axis calculated from all the larger X-ray diffraction peaks approximates to the mean grain size seen by S.E.M. (Table 1). The individual grains measured using the S.E.M. have an axial ratio that varies from 1:1 to 3:1, with a consistent mean of 1.5:1.0. They include 0.2 μm hexagonal tablets (a>c), elongate hexagonal prisms (0.3 μm c and 0.2 μm a) and numerous small subpolygonal grains (Figs. 4—6). The size frequency distribution of the maximum axis seen on these randomly orientated crystals (Fig. 7) is gaussian in *Sonninia* and lognormal in *Kossmatia*, *Haplophylloceras* and perhaps *Ludwigia*. The standard deviation of the mean is approximately constant after the log₁₀ transformation and is equal to half the mean in *Sonninia*. The mean is proportional to the degree of alteration of the aragonitic shell, but the large size variations occur within small areas of the S.E.M. micrographs. The estimated maximum porosity, deduced from the frequency of grain bound-

aries and apparent cavities on the grid, varies from 29% in *Sonninia* J1290 and 24% in *Haplophylloceras*, to 15% in the more crystalline and cubedral *Kosmatia* sample.

The small mean crystal size of connecting rings and teuthid proostraca sets them apart from typical francolite concretions (McClellan & Lehr 1967, p. 1378, Rooney & Kerr 1967, Marshall & Cook 1981), but the large standard deviation from the mean is inconsistent with a biogenic origin for their francolite fabric. Biogenic skeletal grains are more equidimensional and often show axial elongation and alignment.

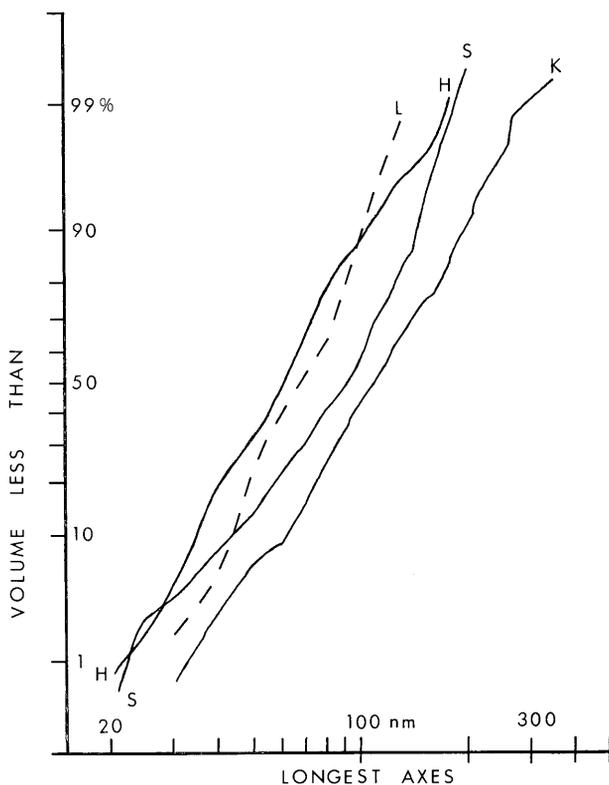
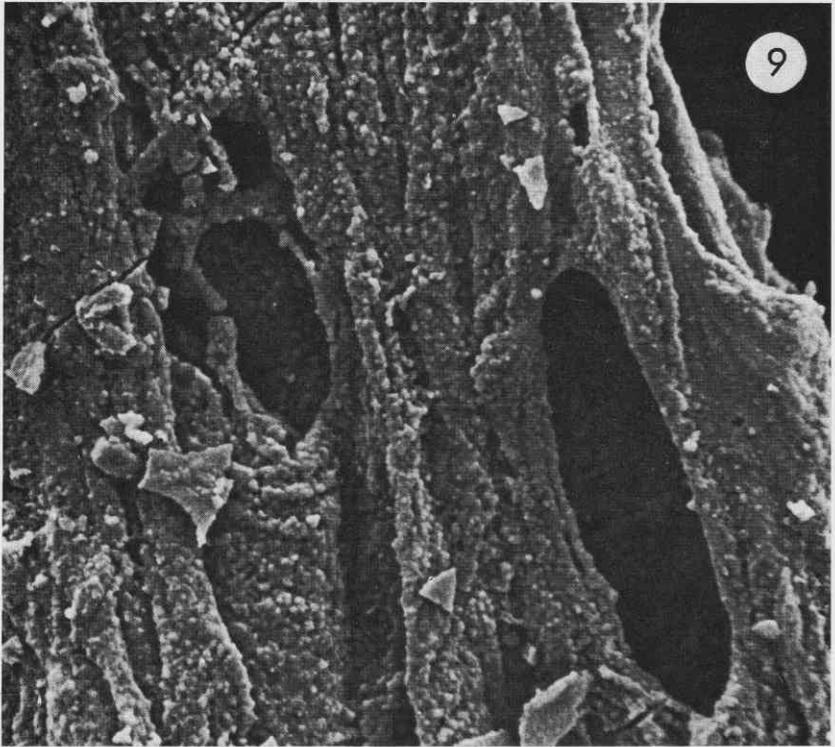
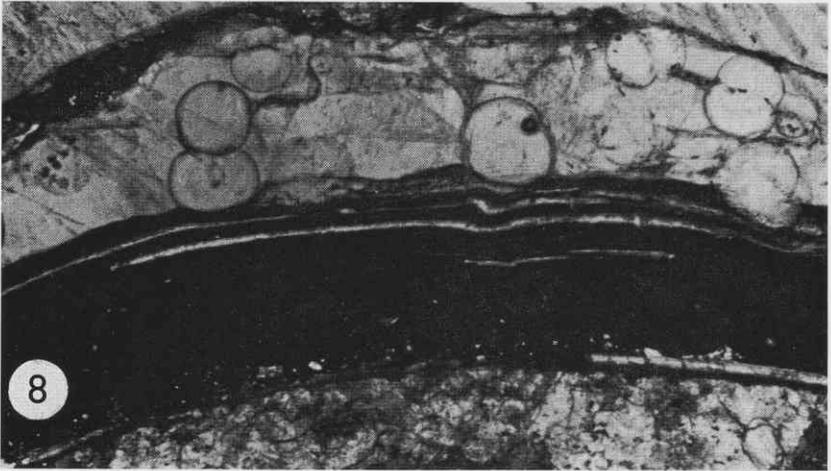


Fig. 7. Cumulative frequency distributions of francolite grains (maximum observed axes sampled on a grid) from Jurassic ammonite connecting rings (1 nm = 10 Å). The mean maximum and minimum observed axes are as follows: Isotropic *Haplophylloceras* J2034-L(H) = 659 and 424 Å, inner layer *Ludwigia* J1597-19(L) = 734 and 479 Å, inner layer *Sonninia* J1290(S) = 931 and 624 Å, *Kosmatia* J1517-17(K) = 1287 and 782 Å. Samples H and K show lognormal size distributions of grain volume.



Figs. 8—10 (Legend see p. 387)

2.3 Crystal orientation

Studies of *Ludwigia* (J1597-19) with an X-ray precession camera and Gandalfi camera, failed to show evidence of preferred crystallographic orientations. In contrast, transverse thin sections of the Bajocian connecting rings of *Ludwigia*, three *Somminia* (J1290, plus material of WESTERMANN 1971, Fig. 4) *Costileioceras* (J772) and *Emileia* (J1311 from Charahuilla, Argentina), all showed that half the thickness of the connecting ring displays an optical preferred orientation. This inner birefringent zone is typically composed of concentric length-fast bands and isotropic partings, which appear isotropic in longitudinal section. This indicates that the optic axes (c if uniaxial) of the francolite show a tendency to be aligned parallel to the lamination in a plane normal to the axis of the siphuncle. The outer homogeneous and exfoliated layer of the connecting ring is entirely isotropic and generally extends to the lumen on the ventral side.

According to the criterion of BENGTON (1976), these length-fast birefringent francolite sheets are primary biogenic structures; but inarticulate brachiopods contain biogenic francolites with a length-slow lamination. This criterion does, however, separate ammonite connecting rings and *Trachyteuthis* from the radial fibres in length-slow, diagenetic francolite crusts. Inner radial phosphate crystallites ($0.08 \times 3 \mu\text{m}$) seen in transverse sections of aragonitic *Haplophylloceras* correspond to 2–5 μm thick length-slow diagenetic layers seen on both margins of the connecting ring in a transverse thin section. The interior is equally divided into laminated outer isotropic and poorly laminated inner length-fast layers with a total thickness of 37 μm (internal diameter of inner layer is 0.55 mm). The ventral arc of the connecting ring is entirely isotropic and contains 1 μm laminae of granular and fine acicular francolite with a random orientation (Fig. 7H). The outer ventral margin is composed of very fine francolite granules set in more amorphous phosphatic material (Fig. 4). This arc of the connecting ring overlapped a longitudinal ridge overlying the inner prismatic layer of the shell wall. The ridge consisted of a central porous rod of longitudinally aligned aragonite fibres, surrounded by several layers of radial aragonite prisms, that now continue as isotropic francolite laminae on the dorsal crest of the ridge. The most dorsal of these layers is entirely free of ara-

Fig. 8. Transverse thin section of the *Somminia* J1290 connecting ring (crossed nicols) with an internal diameter of 4.0 mm, showing evidence of microbial cell division near the outer exfoliated margin ($\times 100$).

Fig. 9. Surface of the outer membrane shown on Fig. 8 after etching with dilute acetic acid to remove the calcite spar. The longitudinally aligned fibres are composed of crystalline calcium phosphate (S.E.M. micrograph, $\times 800$).

Fig. 10. Enlargement of the middle of Fig. 9 showing the phosphate granules (S.E.M. micrograph, $\times 3150$).

gonite and passes into a brown cameral membrane coating the ventral margin of the chamber (Fig. 14).

2.4. Microstructure of connecting rings in calcite ammonites

Scanning electron microscopy and E.D.A.X. analysis was used to study the structures seen in the exfoliating connecting rings of *Sonninia* (J1290) and *Ludwigia* (J1597-18 and 19). The *Sonninia* came from the Upper Weberg Member of east-central Oregon, representing a thick shallow water clastic sequence, while the *Ludwigia* came from limonitic oolites in the Inferior Oolite of Dorset (see appendix). The *Sonninia* contained bituminous sparry calcite with numerous twin lamellae (Fig. 8), while the *Ludwigia* is filled with unstrained white spar and carbonate sediment (Fig. 1). Sediment-filled *Ludwigia* camerae (J1679 from Chapel Quarry) contain undistorted connecting ring fragments showing the same textures as the in situ rings in spar filled camerae.

The outer layer of the distorted *Sonninia* connecting ring (Figs. 8–10), consists of many longitudinal 0.9–2.0 μm diameter “organic” fibres, which surround 30 μm diameter longitudinal pores. Similar, but transversely orientated pores are delineated by the silicified 0.3–0.6 μm diameter transverse fibrils within the septal neck of Cretaceous *Damesites* (OBATA et al. 1980). The *Sonninia* fibres and surrounding granular membranes are composed of calcium phosphate, which is unusual in showing traces of Al, Fe and Zn, that were probably concentrated in organic material that became phosphatised. These fibres are associated with 10 μm diameter subspherical crystals, that contain some Si, Al and K as well as calcium phosphate.

Towards the middle of the *Sonninia* connecting ring there are spherical bodies with a translucent wall (5 μm), that have a typical diameter of 70–115 μm and appear to be eucaryotic plant cells dividing by fission (J. J. MILLER personal communication 1982). They are filled with either quartz (chert) or sparry calcite, and have well defined margins that are often shared with adjacent spherules (Fig. 8). Some Ca, Al, Zn, Fe and relatively rare phosphorous is present in the silicified margin. The surrounding matrix is composed of granular francolite with randomly orientated fibrils (μm diameter) within each concentric sheet. The similarly orientated chitin fibres in the *Nautilus* horny tube have a diameter of only 0.015 μm and are grouped into 0.1 μm diameter bundles (GREGOIRE 1973, Figs. 20–21). Transverse preferred orientations of these *Nautilus* fibres are apparently confined to the junction between the horny tube and the septal neck (GREGOIRE 1973, p. 306) as in *Damesites* (OBATA et al. 1980); but there is some additional evidence for a transverse alignment of fibres in both these genera (GREGOIRE 1973, OBATA et al. 1980). The inner birefringent layer of the 4.3 mm diameter (internal) *Sonninia* connecting ring has a thickness

of 80–90 μm , compared to a thickness of 120 μm for the unexfoliated parts of the fibrous isotropic layer. This transverse alignment of the optic axes is not reflected in the shell microstructure.

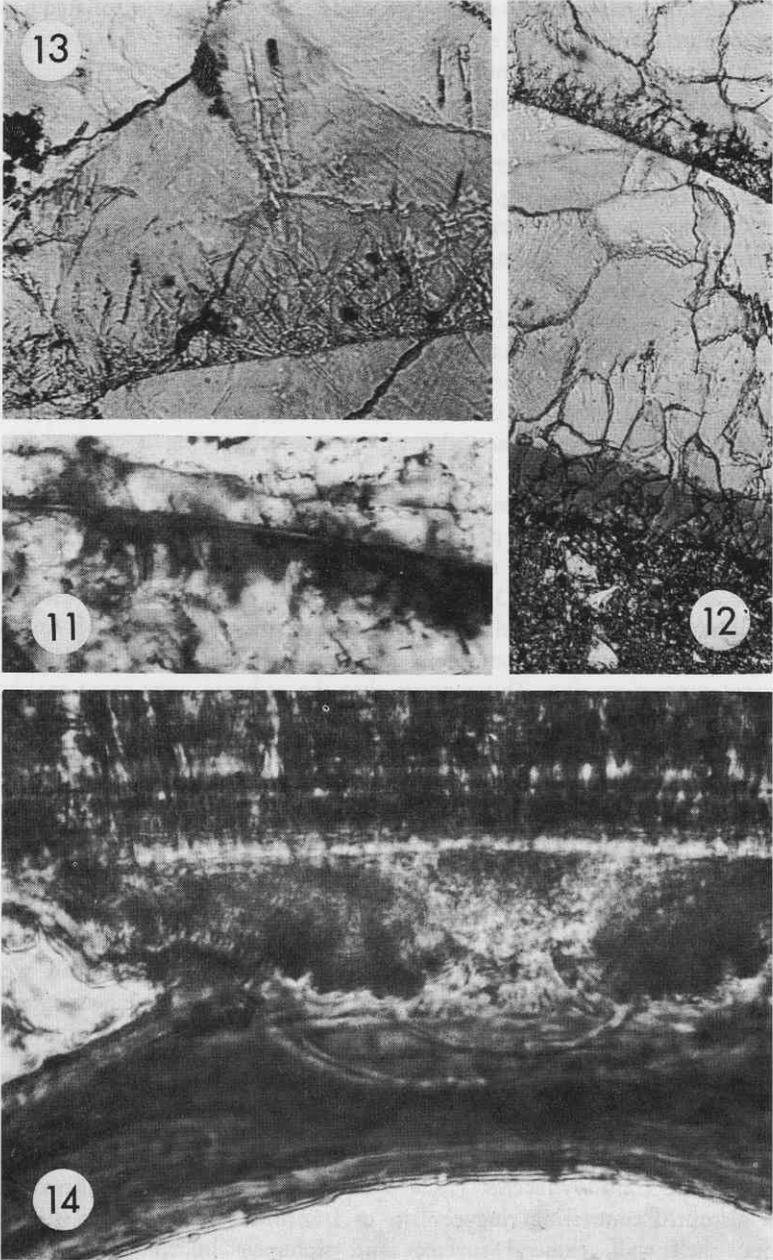
The *Ludwigia* connecting rings show a similar sequence of layers, but the outer exfoliating sheets consists of islands of porous francolite grains (0.2 μm), separated by finer grained francolite sheets showing evidence of electron beam damage (Fig. 3). These Cl-rich layers differ from the inner parts of the connecting ring in having a higher Ca/P counts ratio under constant E.D.A.X. operating conditions. Thin sections cut at an internal siphuncle diameter of 1.21 mm show an inner birefringent layer (55 μm) surrounded by isotropic exfoliating sheets and cameral membranes (25 μm when complete), that contain a few 40 μm diameter spheres filled with calcite. The cameral membranes coating all the cameral surfaces (Fig. 1), consist of brown prismatic carbonates with a high Al content and no phosphorus. The phosphatic inner edge of the connecting ring is covered by a thin film of calcite.

Other *Ludwigia* specimens and the *Emileia* show that both the inner and outer whorls can have a poorly phosphatised connecting ring. The disrupted connecting rings in the sediment of the last whorl (J1679) contain numerous interconnected 30 μm diameter spherical structures. Elongate problematica were observed attached to the ventral shell wall of *Emileia* (Fig. 11), in a chamber containing an undecayed and 15 μm thick unen-crustured connecting ring. This suggests that the camerae were more enriched in oxygen or organic nutrients than the siphuncle lumen.

2.5. Deformation of ammonite siphuncles

The *Macrocephalites* J2016E showed some connecting ring segments that were invaginated within the transverse plane and abruptly twisted along the longitudinal axis. The adjacent alternate segments show the normal cylindrical morphology. The lateral margins of the rings in *Sonminia* J1290 were flattened and folded parallel to their longitudinal axis, and were evidently once flexible in compression. Many phylloceratid connecting rings show pear-shaped cross sections suspended from a ventral ridge of altered aragonite (JOLY 1976).

Each connecting ring thins out and terminates over the septal neck, where the prismatic brown carbonate "cameral membranes" of *Ludwigia* come in contact with the lumen of the siphuncle (Fig. 1). The septa and ventral ridge of the *Calliphylloceras* J1828 were replaced by a clay mineral, but the disrupted connecting ring consists of francolite. Similarly the silicified septa, shell wall, cameral surfaces and siphuncle lumen of *Kossmatia*, contain unbroken francolite connecting rings (60 μm thick at 2.1 mm internal diameter). The general absence of a siphuncle near the ammonite body chamber (TRUEMAN 1920, WESTERMANN 1971) and in 1982, KULICKI 1979)



Figs. 11—14 (Legend see p. 391)

is often due to mechanical disruption into the chamber; but as noted above, it can also be related to infestation with chitinoclastic eucaryotes.

The francolite textures of *Haplophylloceras* are in close proximity to well preserved nacreous and prismatic aragonite of the septal neck and shell wall (Figs. 4 and 14). In contrast, the aragonitic Cretaceous *Platylenticeras* (501 and K191) show a thin recrystallised brown calcite connecting ring (100 μm in thickness at an internal diameter of 4.9 mm), surrounded by white spar containing an exfoliated membrane with narrow branching filaments (Figs. 12—13). Their morphology suggests that either an actinomycete (bacteria) or a fungus with narrow hyphae grew into the water filled camerae (J. J. MILLER personal communication 1982). A few patches of brown isotropic phosphate were observed within the exfoliated chitinous layers of the septal neck and pyrite occurs in the adjacent lumen. A section cut near the septal neck shows a 15—25 μm thick prismatic layer (presumably aragonite) between the brown calcite and the ventro-lateral filaments, which resembles the prismatic layer described by BIRKELUND & HANSEN (1974, Pl. 4, Fig. 7) in Cretaceous *Saghalinites*.

3. Discussion

When the evidence for intracameral exfoliation and decay of the outer margin of the ammonite connecting ring is considered in conjunction with the variable phosphatisation of cameral membranes (ERBEN & REID 1971, BAYER 1975 and above) and the general phosphatic composition of the inner layers of the connecting ring, one can conclude that the external decay model (1) is preferable to the cameral decay model (2) outlined above. The phosphatisation of teuthids and some ammonite connecting rings could result from burial in anoxic environments. Phosphatisation of ammonoid, as opposed to nautilid, connecting rings is ascribed to the decay of tissues within their long, tubular and possibly operculate body chambers. We tentatively interpret the length-fast phosphate laminae as an original feature of the *Trachyteuthis gladius* (both fields) and ammonoid connecting ring. This conclusion obviously complicates the discussion of diagenesis.

Fig. 11. Transverse thin section showing cameral surface of *Emeleia* J1311-2 adjacent to a 370 μm diameter connecting ring. Note elongate microorganisms (x 370).

Fig. 12. Transverse thin section through brown calcite replaced connecting ring and outer exfoliated layer of filaments in *Platylenticeras* (x 96).

Fig. 13. Enlargement of Fig. 12 showing filaments (x 244).

Fig. 14. Transverse thin section through the ventral connecting ring and aragonite ridge of *Haplophylloceras* embedded in epoxy resin (x 590).

Recent *Nautilus* shows a layer of 'semi-prismatic' aragonite, that is embedded between one or more glycoprotein membranes on the adapical side of the chamber, and extends for some distance into the septal neck (Fig. 2). This layer acts as a rigid porous wick which can rapidly transport liquid from the septal surface to the adjacent chalky tube, where it presumably passes through the entire length of the underlying horny tube (see CHAMBERLAIN et al. 1981). It must, however, be noted that it penetrates a variable distance into the septal neck, where it loses the porous texture and is isolated from the siphuncular epithelium by a layer of opaque and spherulitic aragonite that is relatively impermeable to stained solutions. This observation conflicts with those of BANDEL & BOLETZKY (1979) and BANDEL (1981).

Jurassic ammonites siphuncles are often preserved as partially disrupted and uncompacted francolite connecting rings, supported by originally aragonitic septal necks that do not appear to contain a particularly porous 'semi-prismatic' layer. The cameral membranes line the entire chamber of both *Nautilus* and ammonites, forming connections between the 'semi-prismatic layer' on the septum and the growing tip of the siphuncle. These membranes also cover the surface of a 'semi-prismatic' ridge joining the originally uncalcified ventral arc of the connecting ring to the adjacent shell wall (Fig. 14). The porous aragonite layers in the ridge passed dorsally into an originally chitinous fold, that was overlapped by successive chitinous layers of the connecting ring. This variation in septal and siphuncular microstructures was regulated through changes in the inferior region of the septal division of mantle epithelia. The chambers were presumably pumped dry via their cameral membranes, the longitudinally aligned ventral aragonite prisms and dorsolateral chitin fibres covering the connecting ring, rather than through the septal neck. The evolution of the intracameral walls and membranes of the *Sepia* cuttlebone should be envisaged as an extension of this 'semi-prismatic layer plus cameral membrane' phase of the ecto-cochliate cameral growth cycle.

The tentative interpretation of the ammonoid connecting ring as an originally chitinous tube that was stiffened internally with phosphate crystals could have the following functional significance. The outer chitinous layer increased the ultimate tensile strength of the expanded outer edge of tube, while the inner phosphatic layer resisted buckling and compressional stresses due to shearing by the invaginated body tissues. In at least some ammonoids the ventral side of the connecting ring was externally stiffened by an aragonite ridge or outer prismatic layer and there was no need for an internal ventral stiffening with phosphate. Similarly in *Nautilus* the horny tube is supported externally by the aragonitic chalky layer and long retrochoantic septal necks. The small size and largely random orientation of the observed francolite crystals would have made them less prone to tensile fracturing than aragonite crystals, while their high porosity

(20—30 %) would have permitted the camerae to be pumped dry along the whole axis of the connecting ring.

These interpretations could fall victim to further advances in our knowledge of connecting rings. The implication that the nautiloid chalky tube is not homologous to the partially analogous outer horny tube of ammonoids, could be disproved by a demonstration that the invaginated epithelia around the growing tip of the *Nautilus* connecting ring is the site of all the mitosis required for the growth and differentiation of the septal neck and horny tube. The inner and outer surfaces of their connecting rings could be the product of two different epithelia. The francolite fabric observed in ammonoids is produced by organic and inorganic mechanisms of phosphate precipitation which need to be clarified. It would therefore be unwise to make dogmatic statements about the porosity and other physical properties of the inner layer of the ammonoid connecting ring. It is, however, unlikely to have had a greater ultimate tensile strength than a *Nautilus* horny tube of equal radius and wall thickness. Phosphate would therefore tend to reduce the calculated maximum depth range of ammonoids (see WESTERMANN 1971, WESTERMANN 1982) by a small constant factor.

Acknowledgements

We wish to thank D. L. THOMPSON for assistance with the X-ray diffraction, discussions on line broadening and for reading the manuscript. I. HASSAN and Dr. H. D. GRUNDY put samples through X-ray cameras. Prof. E. J. DENTON C.B.E. suggested the role of partial gas pressures during postmortem drifting. Drs. J. J. MILLER, D. R. KOBLUK and M. J. RISK commented on the microflora. The PSEM 501 electron microscope was operated in McMaster University Medical Centre by M. MOORE. Dr. M. K. HOWARTH (British Museum, Natural History provided teuthid material.

Appendix

List of successive Jurassic stages and samples shown on Table 1.

- 1) The Württemberg "*Psiloceras* Limestone" of ANDALIB (1972, p. 38), within the Hettangian Planorbis Zone. The ammonite is largely composed of white calcite spar and may represent a deoxygenated facies.
- 2) Lateral field of *Loligosepia* (HEWITT 1981, Fig. 2B) in a dark calcite concretion from the Lias of Lyme Regis, Dorset. Evidence presented by JELETZKY (1965, p. 42) and HALLAM (1975, p. 34—37) strongly suggests that it came from a deoxygenated bituminous shale facies of Lower Sinemurian age.
- 3) Siphuncles of either *Harpoceras* or *Dactylioceras* from the Lower Toarcian Posidonienschiefer of Germany (ANDALIB 1972, p. 34). They were deposited in a largely anaerobic bituminous shale environment (HALLAM 1975, p. 37).
- 4) Acetic acid residue of two *Ludwigia* from the oolitic ironstones of Horn Park Quarry in Dorset. This was an Aalenian oxygenated substrate containing benthos.
- 5a) Acetic acid residue of *Sonnia* (*Euhoplaceras*) from the Upper Weberg Member of Colpit's Gully, in the Snowshoe Formation (Bajocian *Discites* Subzone) of Oregon. The chambers are filled with dark bituminous calcite. The surrounding

sandy limestones were probably deposited within an inshore oxygenated facies (IMLAY 1973).

5b) Acetic acid residue of *Sonninia (Papilliceras)*, from the red limestones of Bed 6a at Manflas, Atacama, Chile (Bajocian *Sauzei* Zone), containing articulated bivalves and brachiopods.

5c) Acetic acid residue of broken siphuncle in *Calliphylloceras* sp. of Bajocian age (*Humphriesianum* Zone). It came from a coarse-grained volcanogenic sandstone in the lower Yakoun Formation of South Balch Island, British Columbia (HALL & WESTERMANN 1980, p. 61). The aragonite shell is replaced by black chamosite or pennanite.

7a) Siphuncle from *Macrocephalites apertus* SPATH found in basal Callovian calcareous shales on the Sula Islands, Indonesia. This is an ammonite-rich facies with carbonate concretions, but some benthos is reported by SATO et al. (1978, p. 12).

7b) Acetic acid residue of *Reineckeia* from the slowly deposited, micritic limestone of Rouillé, near Pointiers (Callovian *Michalskii* Subzone of France). The ammonite contained limonitic ooliths and the horizon is reported to contain benthos (CARIOU 1981, Fig. 10).

7c) Small ? *Kelaeno gladius* from the bituminous (?Lower) Oxford Clay of Peterborough, England. It probably represents a rather deoxygenated Middle Callovian environment, but does contain benthos (DUFF 1975).

9a) Median field of *Trachyteuthis* and a perisphinctid siphuncle (ANDALIB 1972, Table 1 column 1), from the anaerobic Solnhofen Limestone facies (VAN STRAATEN 1971) of Bavaria (Lower Tithonian Hybonotum/Gravesia Zone, equivalent to the basal middle Kimmeridgian of English writers). Most of the macrofossils in the Solnhofen Limestone consist of francolite. The mantle of *Plesiotenthis* (J85) is diagenetic francolite.

9b) Lateral field of a *Trachyteuthis* from the Kimmeridge Clay of Speeton, Yorkshire. COPE (1974) implies that the bituminous clay sample probably came from the lower Pectinatus Zone, which is equivalent to the top of the Lower Tithonian; but a slightly older Tithonian age cannot be discounted. The *Trachyteuthis* in the Kimmeridge Clay of Dorset (probably the same age if they originate in the Blackstone), were deposited in a deoxygenated bituminous shale facies (TYSON et al. 1979).

10) Acetic acid etched *Kossmatia bifurcata* AGUILERA, showing black chert replacement of aragonite and a francolite connecting ring surrounded by chert. It came from the Upper Tithonian limestones and shales of the El Verde Member, La Caja Formation in San Luis Potosi, Mexico. Ammonites from this member sometimes show epifaunal encrustation (VERMA & WESTERMANN 1973, p. 143), but the undisturbed lamination and pelagic fauna found in the shales could be indicative of a deoxygenated environment.

11) Median rachis of *Tusoteuthis* from the Niobrara chalk of Kansas. This Cretaceous sample was probably deposited in a rather deoxygenated environment (ARTHUR et al. 1981 and personal communication).

Literature

- ANDALIB, F. (1972): Mineralogy and preservation of siphuncles in Jurassic cephalopods. — N. Jb. Geol. Paläont., Abh., 140: 33—48.
- ARTHUR, M. A., SCHOLLE, P. A., POLLASTRO, R. M., BARKER, C. E. & CLAYPOOL, G. E. (1981): Geochemical and sedimentological indicators of depositional environments in the Niobrara Formation (Upper Cretaceous), Colorado and Kansas. — Abstracts with Programs, 13: 398—399.

- BANDEL, K. (1981): The structure and formation of the siphuncular tube of *Quenstedoceras* compared with that of *Nautilus* (Cephalopoda). — N. Jb. Geol. Paläont., Abh., **161**: 153—171.
- BANDEL, K. & BOLETZKY, S. VON (1979): A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. — The Veliger, **21**: 313—354.
- BAYER, U. (1975): Organische Tapeten im Ammoniten-Phragmokon und ihr Einfluß auf die Fossilisation. — N. Jb. Geol. Paläont., Mh., **1975** (1): 12—25.
- BENGTSON, S. (1976): The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. — Lethaia, **9**: 185—206.
- BIRKELUND, T. & HANSEN, H. J. (1974): Shell ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their taxonomic implications. — Det. Kongelige Danske Videnskabernes Selskab Biol. Skr., **20** (6): 1—34, 16 pls.
- CARIOU, E. (1981): L'étage Callovien dans le centre-ouest de la France. Première Partie Stratigraphie et Paleogeographie. — U.E.R. Sciences Fondamentales et Appliquées, **325**: 1—37, 32 Figs., 2 Pls.
- CHAMBERLAIN, J. A., MOORE, W. A. & PILLSBURY, S. W. (1981): Flow properties and rupture strength of *Nautilus* siphuncular tube. — Abstracts with Programs, **13**: 425.
- COPE, J. C. W. (1974): New information on the Kimmeridge Clay of Yorkshire. — Proc. Geol. Ass. London, **85**: 211—221.
- DENTON, E. J. & GILPIN-BROWN, J. B. (1966): On the buoyancy of the Pearly *Nautilus*. — J. mar. biol. Ass. U.K., **46**: 723—759.
- DUFF, K. L. (1975): Palaeoecology of a bituminous shale, the Lower Oxford Clay of central England. — Palaeontology, **18**: 443—482.
- ERBEN, H. & REID, R. E. H. (1971): Ultrastructure of shell, origin of conellae and siphuncular membranes of an ammonite. — Biomineralisation, **3**: 22—31.
- GRANDJEAN, F. (1910): Le siphon des ammonites et des belemnites. — Soc. geol. France, Bull., **4**, 10: 496—519.
- GREGOIRE, C. (1973): On the submicroscopic structure of the organic components of the siphon in the *Nautilus* shell. — Arch. Physiologie Biochemie, **81**: 299—316, 1—14 pls.
- HALL, R. L. & WESTERMANN, G. E. G. (1980): Lower Bajocian (Jurassic) cephalopod faunas from western Canada and proposed assemblages zones for the Bajocian of North America. — Palaeontographica Americana, **9**, 52: 1—93.
- HALLAM, A. (1975): Jurassic environments. Cambridge University Press, Cambridge, 269 pp.
- HEWITT, R. A. (1981): Microstructural contrasts between some sedimentary francolites. — J. geol. Soc. London, **137**: 661—667.
- (1983): On the connecting rings of *Pseudorthocerataceae* (Carboniferous Cephalopoda). — J. Moll. Studies, **49** (in press).
- IMLAY, R. W. (1973): Middle Jurassic (Bajocian) ammonites from Eastern Oregon. — Geol. Survey Prof. Pap., **756**: 1—100, 1—47 pls.
- JELETZKY, J. A. (1966): Comparative morphology, phylogeny and classification of fossil Coleoidea. — Univ. Kansas Paleont. Contrib. Mollusca, Art. **7**: 1—162.
- JOLY, B. (1976): Les Phylloceratidae Malgaches au Jurassique. Generalites sur la Phylloceratidae et quelques Juraphyllitidae. — Docum. Lab. Géol. Fac. Sci. Lyon, **67**: 1—471.
- KULICKI, C. (1979): The ammonite shell: its structure, development and biological significance. — Palaeontologia Polonica, **39**: 97—142, pls. 24—48.

- MARSHALL, J. D. (1981): Zoned calcites in Jurassic ammonite chambers: trace elements, isotopes and neomorphic origin. — *Sedimentology*, **28**: 867—887.
- MARSHALL, J. F. & COOK, P. J. (1981): Petrology of iron- and phosphorus-rich nodules from the E. Australian continental shelf. — *J. Geol. Soc. London*, **137**: 765—771.
- McCLELLAN, G. H. & LEHR, J. R. (1969): Crystal chemical investigations of natural apatites. — *Am. Miner.*, **54**: 1374—1391.
- McCONNELL, D. (1963): Inorganic constituents in the shell of the living brachiopod *Lingula*. — *Bull. Geol. Soc. Am.*, **74**: 363—364.
- (1970): Crystal chemistry of bone material: hydrated carbonates apatites. — *Amer. Miner.*, **55**: 1659—1669.
- MUTVEI, H. (1964): On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. — *Arkiv för Zoologi*, **16**: 221—278, 22 pls.
- OBATA, I., TANABE, K. & FUKUDA, Y. (1980): The ammonite siphuncular wall: Its microstructure and functional significance. — *Bull. Nat. Sci. Mus. (Tokyo)*, Ser. C (Geol.), **6**: 59—72, 3 pls.
- ROONEY, T. P. & KERR, P. F. (1967): Mineralogic nature and origin of phosphorite, Beaufort County, North Carolina. — *Bull. Geol. Soc. Amer.*, **78**: 731—748.
- SATO, T., WESTERMANN, G. E. G., SKWARKO, S. K. & HASIBUAN, F. (1978): Jurassic biostratigraphy of the Sula Islands, Indonesia. — *Bull. Geol. Surv. Indonesia*, **4**: 1—28.
- SEILACHER, A., ANDALIB, F., DIETL, G. & GOCHT, H. (1976): Preservation history of compressed Jurassic ammonites from Southern Germany. — *N. Jb. Geol. Paläont., Abh.*, **152**: 307—356.
- TRUEMAN, A. E. (1920): The ammonite siphuncle. — *Geol. Mag.*, **57**: 26—32.
- TYSON, R. V., WILSON, R. C. L. & DOWNIE, C. (1979): A stratified water column environmental model for the type Kimmeridge Clay. — *Nature*, **277**: 377—380.
- VAN STRAATEN, L. M. J. U. (1971): Origin of the Solnhofen Limestone. — *Geol. Mijnb.*, **50**: 3—8.
- VERMA, H. M. & WESTERMANN, G. E. G. (1973): The Tithonian (Jurassic) ammonite fauna and stratigraphy of Sierra Catorce, San Luis Potosi, Mexico. — *Bull. Am. Paleont.*, **63**: 107—320.
- WARREN, B. E. (1969): X-ray diffraction. Addison-Wesley, Reading Mass., 381 pp.
- WATABE, N. (1956): Dahllite identified as a constituent of prodissoconch I of *Pinctada martensii* (DUNKER). — *Science*, **124**: 630.
- WESTERMANN, G. E. G. (1971): Form, structure and function of shell and siphuncle in coiled Mesozoic ammonoids. — *Life Science Contributions, Royal Ontario Museum*, **78**: 1—39.
- (1982): The connecting rings of *Nautilus* and Mesozoic ammonoids: implications for ammonoid bathymetry. — *Lethaia*, **15**: 373—383.
- WHIPPO, R. E. & MUROWCHICK, B. L. (1967): The crystal chemistry of sedimentary apatites. — *Trans. Am. Inst. Mining Metal. Engrs.*, **238**: 257—263.

Bei der Tübinger Schriftleitung eingegangen am 25. März 1982.

Anschrift der Verfasser:

Dr. R. A. HEWITT, Dr. G. E. G. WESTERMANN, Department of Geology, McMaster University, 1280 Main Street West, Hamilton, Ontario, Canada, 28S 4M1.