

SKELETAL MICROSTRUCTURE OF HELENS, LATERAL SPINES OF HYOLITHIDS

by M. MARTÍ MUS* and J. BERGSTRÖM†

*Historical Geology and Palaeontology, Department of Earth Sciences, Uppsala University, Norbyvägen 22, S-752 36 Uppsala, Sweden; current address: Área de Palaeontología, Facultad de Ciencias, Universidad de Extremadura, E-06071 Badajoz, Spain; e-mail: martimus@unex.es

†Department of Palaeozoology, Swedish Museum of Natural History, PO Box 50007, S-104 05 Stockholm, Sweden; e-mail: jan.bergstrom@nrm.se

Typescript received 28 September 2005; accepted in revised form 9 October 2006

Abstract: In hyolithids the skeleton consists of four elements: a conch, an operculum and a pair of long, logarithmically curved ‘spines’ called helens. These last elements are rarely preserved, and have therefore remained poorly known and enigmatic. We have studied three-dimensionally preserved helens of the species ‘*Hyolithes lanceolatus*, from the Permian of New South Wales, Australia, and ‘*Hyolithes groenwalli*, from the Cambrian of Bornholm, Denmark. Helens were massive calcareous elements. Their original microstructure, herein reported for the first time, consisted of

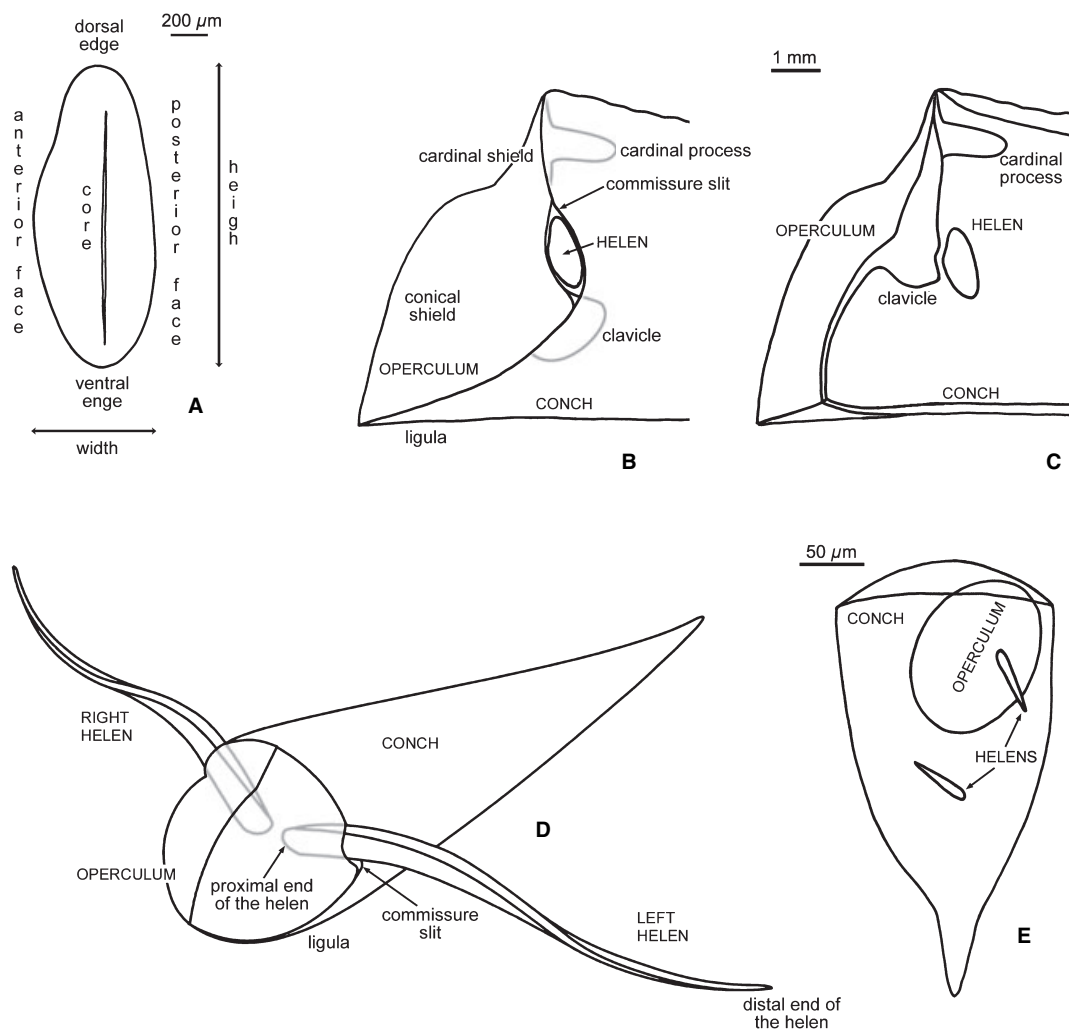
concentric lamellae surrounding a narrow elongated core, which may have been rich in organic matter. This concentric pattern resulted from the successive accretion of shell material at the proximal, internal portion of helens. This growth model is in accordance with helen morphology and with the presence of a characteristic surface sculpture of overlapping lamellae.

Key words: growth, helens, ‘*Hyolithes groenwalli*, ‘*Hyolithes lanceolatus*, hyolithids, shell microstructure.

HYOLITHS are a group of Palaeozoic metazoa with an external skeleton consisting of two main elements: a conical conch with a broad aperture and an operculum that closed it. They were important constituents of the earliest Cambrian faunas and although their stratigraphic range extends to the Permian they are only abundant in the Lower Palaeozoic. Hyoliths are divided into two morphologically distinct groups: the orthothecids and the hyolithids (Marek and Yochelson 1976). Orthothecids are a rather heterogeneous and relatively poorly known group showing considerable morphological diversity. Hyolithids are better characterized morphologically (Text-fig. 1) and constitute a coherent, probably monophyletic group. Their conch is dorsoventrally differentiated with the ventral margin of the aperture extending forwards to form a semicircular shelf called the ligula (Text-fig. 1B–D). The operculum is external, exactly fitting the margin of the aperture. It is divided into a flattened, dorsal portion (the cardinal shield) and an inflated, ventral part (the conical shield). The inner surface of the operculum (Text-fig. 1B–C) is morphologically complex, showing several types of inwardly protruding processes, particularly the radially arranged clavicles and the dorsally located cardinal processes (Marek 1963, 1967). Since the time of Walcott (1911) it has been widely known that hyolithids possessed a pair of long, curved ‘appendages’, later named helens by Runnegar *et al.* (1975). Disarticulated helens

had been described two decades earlier by the same author (Walcott 1890*a, b*) but he did not recognize them as elements of the hyolithid skeleton and erected the genus *Helenia* (hence the present name for these elements) for the then-enigmatic fossils. Helens are long, thin, tapering skeletal elements which, when the organism was living, curved ventrally following a logarithmic spiral (Runnegar 1980; Martí Mus and Bergström 2005; Text-fig. 1D). Helens were partially internal and extended outside the conch through a pair of slits present at the commissure between conch and operculum (Marek 1963, 1967; Martí Mus and Bergström 2005; Text-fig. 1B–D). The length of the internal portion of each helen is approximately half the width of the conch aperture (Martí Mus and Bergström 2005; Text-fig. 1D). A characteristic transverse ornamentation is present on the helen surface except for the proximal portion, which is smooth and has a rounded and convex termination. Height and width of helens (Text-fig. 1A, D) are at their maximum where ornamentation begins. From that point and towards the proximal end height decreases only very slightly while width seems to decrease rather abruptly. Both dimensions decrease gradually towards the distal end (Yochelson 1974; Butterfield and Nicholas 1996; Martí Mus and Bergström 2005; Text-fig. 1D).

Marek (1963) and Marek and Yochelson (1976) stressed that the operculum and helens were not merely



TEXT-FIG. 1. Schematic drawings illustrating different morphological features of hyolithids. A, cross-section of a helen. B, anterior portion of a hyolith showing relative position of operculum, conch and helen (sectioned at the commissure slit); conch drawn as if transparent to show position of clavicle and cardinal process inside the conch. C, same individual with left side sectioned. D, reconstruction of a hyolithid with its four skeletal elements articulated, operculum drawn as if transparent to show proximal portion of helens. E, line-drawing of juvenile individual with two small helens inside the conch, based on a specimen illustrated by Butterfield and Nicholas (1996, fig. 4.4). Drawings in A–C are based on *Hyolithes lanceolatus* (Morris, 1845) (specimens illustrated herein and in Runnegar *et al.* 1975, fig. 2a–b).

accessory elements accompanying the more robust (and more easily preserved) conch but essential constituents of the organism's skeleton, which in the living hyolithid consisted of four pieces (Text-fig. 1D). Knowledge of the operculum and helens is therefore important for systematics (Marek 1963) and essential for understanding the organization, functional morphology and phylogeny of the once living hyolithids. While the morphology, skeletal microstructure and mode of growth of conch and operculum are relatively well known, helens are considerably less well understood, and their shell microstructure and mode of growth have never been studied in detail. Here we present novel data on the original microstructure of hel-

ens and discuss their relevance to understanding helen growth.

PREVIOUS KNOWLEDGE OF SKELETAL MICROSTRUCTURE

Both conch and operculum grew by marginal accretion. Kouchinsky (2000) reviewed the history of research on hyolith skeletal microstructure and presented new evidence regarding the three-dimensional microstructure of the conch and operculum of Cambrian orthothecids. According to this evidence, orthothecid conchs have two

main layers: an outer one with longitudinally orientated bundles of fibres and an inner one with transversely orientated bundles. Previous reports of cross-lamellar microstructure in orthothecids and hyolithids (e.g. Runnegar *et al.* 1975) were reinterpreted as probably representing the same three-dimensional network of bundles (Kouchinsky 2000, pp. 77–78). According to Kouchinsky (2000) the operculum of orthothecids grew by deposition of lamellae (with radially orientated fibres) from the inner surface. These lamellae were responsible for the marginal growth of the operculum but also coated the whole inner surface. The microstructure of the hyolithid operculum has never been reported, but there is some evidence to suggest that it may not have been entirely massive, particularly at the clavicles (Marek 1963, 1976; Martí Mus and Bergström 2005). Because of the type of diagenetic alteration common in conchs and opercula and their originally fibrous microstructure (Kouchinsky 2000), the mineralogy of these elements is generally considered as primarily aragonitic.

Existing information on the mineralogical composition and microstructure of helens is scarce. Walcott (1890*a, b*) described the specimens of '*Helenia*' (see above) as collapsed hollow tubes but Yochelson (1974) redescribed them as solid blades and pointed out that 'Nothing in any of the material suggests that *Helenia* was a collapsed hollow tube ...' (Yochelson 1974, p. 719). According to Yochelson '*Helenia*' blades consisted of white sparry calcite, identical to that found in the co-occurring conchs and opercula of '*Hyolithes princeps*'. A similar account of helen mineralogy and microstructure was given by Poulsen (1967) in his description of disarticulated hyolithids from the Cambrian of Bornholm (Denmark). For Poulsen (1967, p. 26), the helens consisted 'of irregularly grained calcite of the type found in shells of molluscs in which primary aragonite has been replaced by calcite'. He remarked on the similarities between the helens and the co-occurring conchs of '*Hyolithes groenwalli*' and concluded that both skeletal elements were originally aragonitic. Interestingly, he agreed with Walcott (1890*a, b*) in describing helens as hollow tubes (with thick walls and a narrow central cavity; Poulsen 1967, p. 26, fig. 4; see below).

MATERIAL AND METHODS

Mineralized helens are uncommon in the fossil record (Walcott 1890*a, b*; Poulsen 1967; Yochelson 1974; Marek *et al.* 1997*a*); helens preserved as carbonaceous films are somewhat more abundant (e.g. Yochelson 1961; Babcock and Robison 1988; Butterfield and Nicholas 1996). The helens studied here are exceptional in being preserved as mineralized, relatively complete, three-dimensional elements and are ideal for microstructural and palaeobio-

logical studies. Because the material belongs to museum collections we tried to minimize specimen preparation. However, to study shell microstructure, two slabs (containing, respectively, specimens AM F20111 and MGUH 27821–6, the six MGUH specimens occurring together in the same slab) were slightly ground and polished on a single surface.

Energy-dispersive X-ray spectroscopy (EDS) and back-scattered electron (BSE) imaging on a scanning electron microscope (SEM) were used to identify the elemental composition of the fossils. The combination of these methods allows an *in situ* identification of elemental composition, providing an 'elemental map' of the fossil specimen. These methods have the benefit of being non-destructive and of providing images that are also informative for morphological studies. Specimens were coated by standard procedures to prevent charging.

When an electron beam is scanned across the surface of a specimen, different signals are emitted which yield different information; secondary electrons, backscattered electrons and X-rays are the signals most commonly detected in SEMs. Secondary electrons are responsible for the characteristic SEM images; in these, the contrast depends mainly on the three-dimensional morphology of the sample. When the image is formed using back-scattered electrons, the contrast depends mostly on the atomic number of the elements in the sample. The elements with higher atomic number appear brighter because they 'reflect' more primary (beam) electrons. The differences in tone are relative (can be modified using the brightness and contrast controls on the SEM) and cannot be used to determine elemental composition.

EDS is a chemical microanalysis technique that uses the X-rays emitted from the specimen (during bombardment by the electron beam) to characterize its elemental composition. EDS is used to determine the elements present in the sample and their relative abundance. A limitation of this technique is that minerals cannot be precisely identified. This is because it is complicated (and sometimes impossible) to obtain accurate quantitative chemical analyses and the technique provides no information of the crystalline structure of the sample. However, mineral 'families' (such as zeolites or calcium phosphates) can be identified with confidence, and this was considered sufficient for the purposes of this study. This chemical information considered in conjunction with the microstructural data enabled us to deduce whether the minerals present in the fossil shells are original (biogenic) or diagenetic. In the latter case, we could also infer (to a certain extent) the kind of transformations that the shell experienced during diagenesis and whether the original microstructure was likely to be preserved.

Institutional abbreviations. AM, Australian Museum, Sydney; MGUH, Geological Museum, Copenhagen.

SYSTEMATIC PALAEOLOGY

The specimens studied here were assigned to the genus *Hyalithes* by previous authors (Etheridge 1890; Poulsen 1967). *Hyalithes* is an old name that was generally used for all hyolithid species; this broad generic concept is now outdated and *Hyalithes* is in need of modern systematic revision (Malinky 1987, 2006), which is clearly beyond the scope of our paper. However, our results concern structural and functional aspects of the hyolithid skeleton (particularly the helens), and are not affected by the precise generic or specific assignment of the material.

'*Hyalithes*' *lanceolatus* (Morris, 1845)

Text-figures 2–4

Material. Specimen AM F20111 is a single articulated individual only labelled 'Permian. South Coast, New South Wales', Australia. The left side of it was ground and polished at the level indicated by Text-figure 2F–G (see also Text-fig. 1C).

Description

Conch and operculum. The different skeletal elements show the same black coloration and glossy appearance (Text-fig. 2). Externally, the conch has a marked transverse ornamentation consisting of ribs (Text-fig. 2E) that result from variation in shell thickness (Text-fig. 2C). Two layers of different microstructure can be seen in cross-section (Text-fig. 2C). Both layers vary in thickness but the inner layer is on average twice as thick as the outer; the contact between the layers is wavy. The inner layer shows a pattern of alternating dark and light, nearly vertical, stripes; the dark stripes are thinner than the light. Alternating stripes occur as well in the outer layer, although they are slightly wavy and appear more irregular; they are almost horizontal, dipping slightly towards the aperture. This type of microstructure was described from hyolithids of the same species and general geographical area by Runnegar *et al.* (1975). In cross-section, the microstructure resembles the characteristic molluscan crossed-lamellar fabric (Runnegar *et al.* 1975) but it may represent the distinct fibrous microstructure described by Kouchinsky (2000; see above) in orthothecid hyoliths.

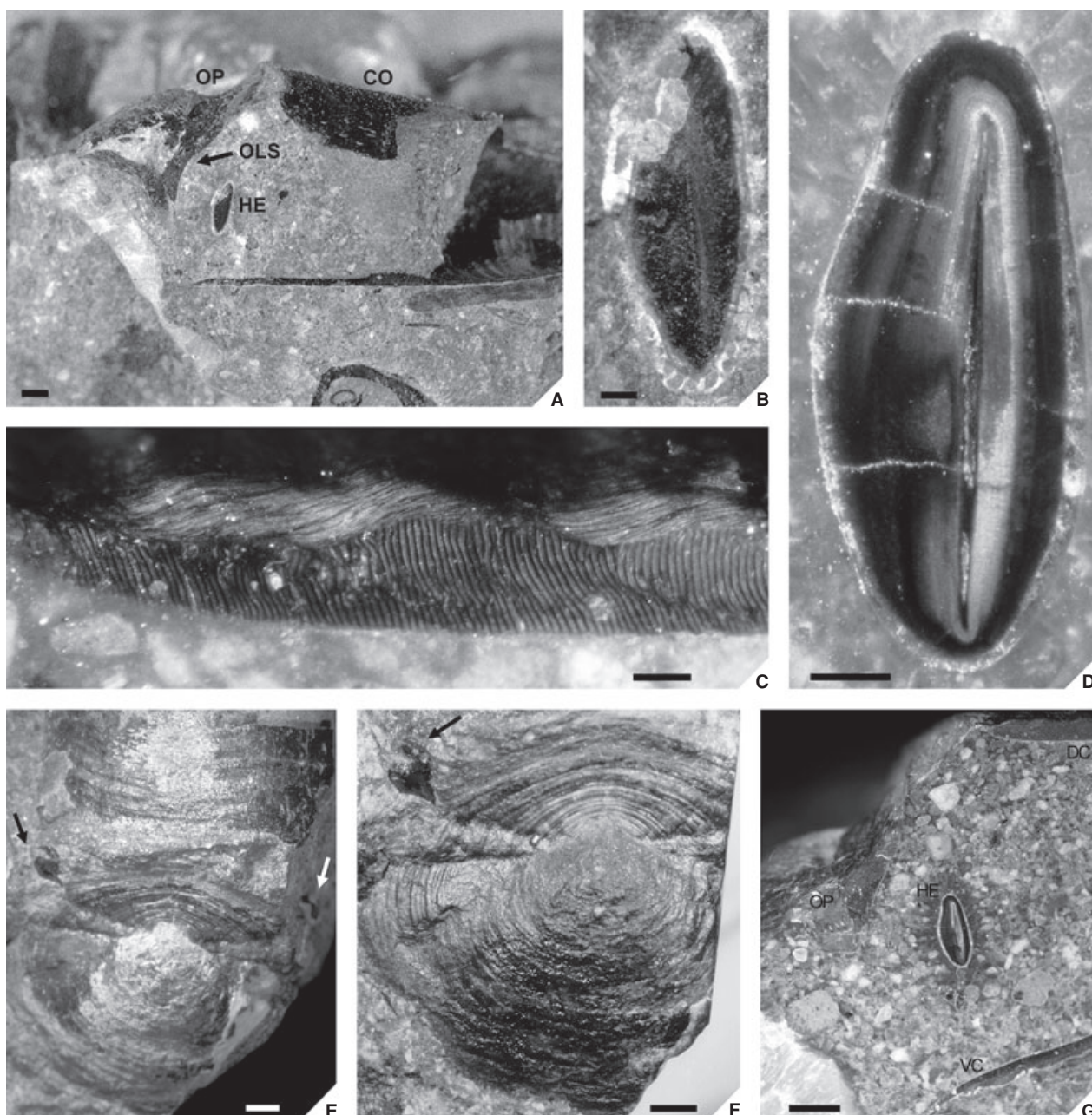
The mineral composition of the shell fragment consists of a phyllosilicate rich in Fe, Mg and Al, most likely chamosite (iron-rich chlorite) or berthierine. The phyllosilicate is probably an authigenic mineral that replaced the original mineral of the shell during early diagenesis. The retention of the (presumed) original microstructure of the conch suggests that the advancing phyllosilicate and the retreating original mineral remained in contact during the process (Folk 1965 restricted the term 'replacement' for this kind of fine-scale 'substitution', as opposed to a process

in which the dissolution of the original mineral significantly precedes precipitation of the advancing mineral; see also Maliva and Dickson 1992.) Although not a very common replacement, iron-rich chlorite has been reported in molluscan shells from sandstones rich in, or associated with, volcanic sediments (Haggart and Bustin 1999).

The ornamentation of the operculum consists of concentric ribs (Text-fig. 2E–F), being comparable with that of the conch. As seen in the polished section (Text-figs 2G, 3; see also Text-fig. 1C) the conical shield is thin and featureless. The cardinal shield (including the clavicle) is considerably thicker, the inner surface diverging markedly from the outer. Excluding the central portion of the clavicle (see below), this thicker part of the operculum has a lamellate structure (Text-fig. 3A–B). Lamellae appear continuous, extending from the dorsal margin of the operculum to the clavicle, and fading away ventrally. Each lamella corresponds to a single marginal increment (Text-fig. 3A–C). This microstructure indicates that growth took place by addition of lamellae on the inner surface of the operculum, as reported by Kouchinsky (2000) for orthothecids. The first (outermost) distinguishable lamella (grey in Text-fig. 3B) merges ventrally with the core of the clavicle (Text-fig. 3A–B). The whole coloured area represents a section through the margin of the operculum in an earlier ontogenetic stage. The row of 'cells' or partitions visible at the core of the clavicle (labelled 'CE' in Text-fig. 3B) resembles a feature of *Maxilites robustus* (Martí Mus and Bergström 2005; text-figs 9, 10A–B).

The chemical composition of the operculum consists of a mixture of the same phyllosilicate found in the conch, plus small amounts of calcium carbonate (Text-fig. 3D); the latter mineral occurs in patches with diffuse boundaries. As in the case of the conch, the phyllosilicate seems to have preserved the original microstructure and is therefore likely to constitute a diagenetic replacement (*sensu* Folk 1965). The mixed chemical composition may reflect a partial replacement with relict areas preserving the original mineralogy of the shell.

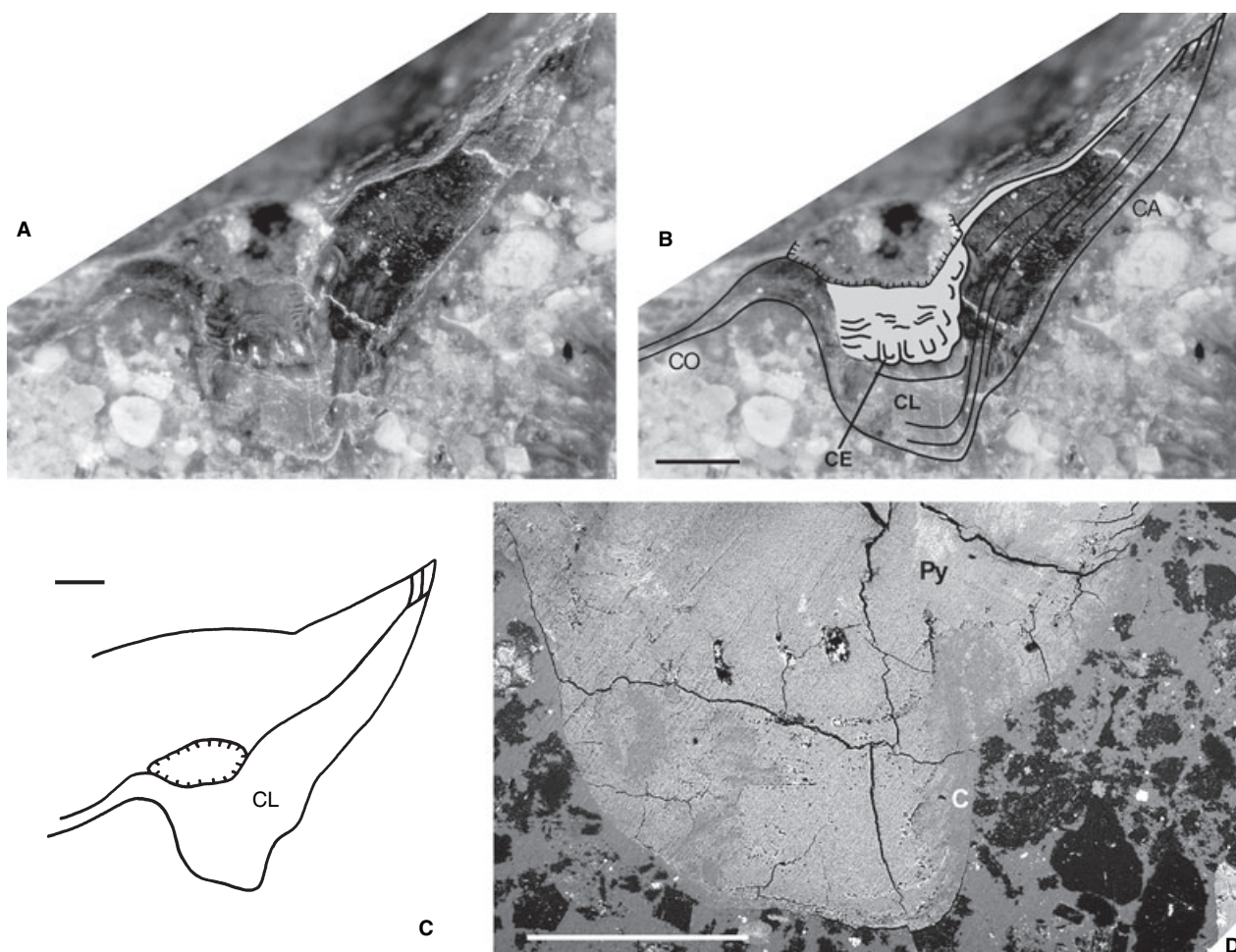
Helens. A fragment of each helen can be seen at right and left sides of the body, between conch and operculum, at a level broadly coinciding with the lateral sinuses (Text-fig. 2A, E–F). In the unprepared specimen the left helen was exposed in cross-section (Text-fig. 2A–B), its broadly elliptical outline partly obscured by crystal overgrowth. The surface of the section was slightly convex and wedge-like, with a central, dorsoventrally extended, raised rim. Sectioning of the specimen revealed the slightly sinuous outline of the anterior face of the helen (Text-fig. 2D). The dimensions of the cross-section (width, 0.67 mm; height, 1.60 mm) remained virtually unchanged throughout the ground portion. The proximal end of the helen was not reached, remaining unexposed inside the specimen. The sectioned helen shows a marked concentric pattern around a thin, elongated core (Text-figs 2D, 4). The position of the core nearly coincides with the dorsoventral axis of the helen but is slightly displaced posteriorly. The core is likely to correspond to the raised rim of the unprepared helen (compare Text-fig. 2B with 2D). Although the bulk of the helen is composed of the same phyllosilicate found in the conch and operculum, three other minerals occur, all disposed according to the concentric banding (Text-fig. 4).



TEXT-FIG. 2. *Hyolithes lanceolatus* (Morris, 1845), specimen AM F20111; Permian, New South Wales, Australia; articulated specimen with preserved shell. A, left lateral view of the entire specimen; left helen (HE) visible between conch and operculum; aperture to the left. B, close-up of left helen naturally exposed in cross-section; note wedge-like surface with a central raised rim. C, polished section of conch (close-up of fragment marked as 'DC' in G). D, polished section of left helen; note concentric pattern around elongated core (view after first polish). E, dorsal view of anterior portion of specimen; arrows point to the helens. F, anterodorsal view of specimen after polishing; arrow points to right helen. G, lateral view of specimen after polishing. Abbreviations: CO, conch; DC, dorsal part of the conch; HE, helen; OLS, opercular lateral sinus; OP, operculum; VC, ventral part of the conch. Scale bars represent 1 mm in A, E–G; 200 μm B–D.

The outermost layer, whitish under reflected light (Text-fig. 2D) and black in BSE images (Text-fig. 4), consists mostly of a Ca-zeolite (probably laumontite). The central area of the helen, including the core and the immediately surrounding layers, is

rich in calcium carbonate and calcium phosphate (Text-fig. 4A, D–E). These latter minerals grade into each other along the same concentric bands (Text-fig. 4B–C, E). Laumontite has been reported in shells from the same geographical area as the speci-



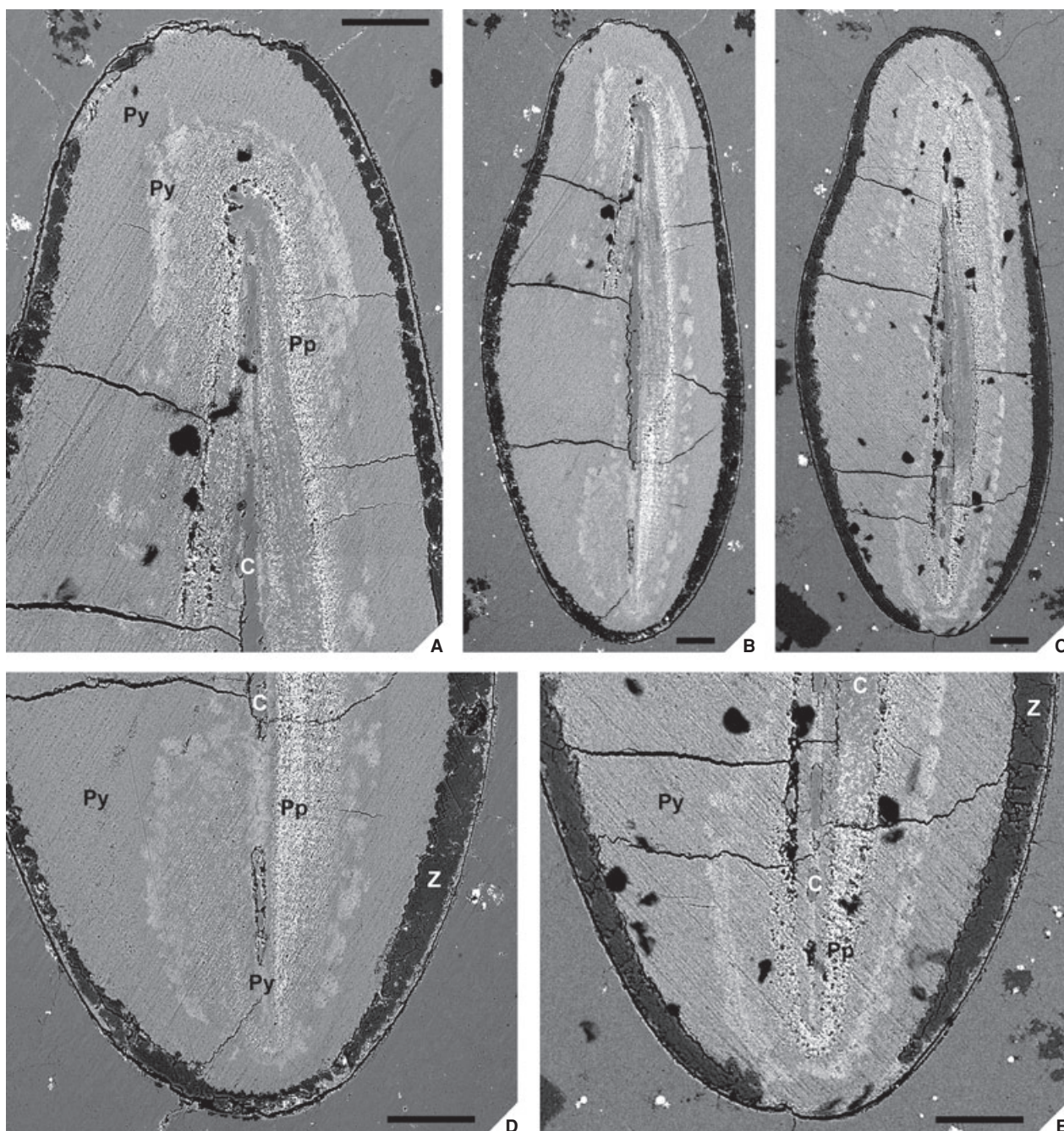
TEXT-FIG. 3. Operculum of '*Hyolithes lanceolatus* (Morris, 1845), AM F20111; Permian, New South Wales, Australia. A, lateral section of operculum showing shell microstructure. B, same image with superposed, interpretative drawing to highlight shell features; outermost layer of shell is light grey; hachured line outlines missing shell fragment. C, schematic drawing of sectioned operculum. D, BSE image of sectioned clavicle showing variations in chemical composition: phyllosilicate appears in different shades of light grey (which reflect small differences in elemental composition; lighter patches are relatively enriched in Fe), calcium carbonate is dark grey. Abbreviations: C, calcium carbonate; CA, cardinal shield; CE, aligned cells (see text); CL, clavicle; CO, conical shield; Py, phyllosilicate. Scale bars represent 0.5 mm.

men under discussion (Raam 1968; Wright *et al.* 1982). As with the chlorite-replaced shells mentioned above (Haggart and Bustin 1999), the zeolitized shells occur in volcanogenic sandstones. Waterhouse (1965) reported the presence of both chlorite and zeolite in bivalve shells from sediments in the Permian of New Zealand. In all these examples zeolite is likely to be an authigenic mineral, which precipitated during early diagenesis. As suggested in the case of the operculum, the calcium carbonate areas could constitute regions that escaped phyllosilicate replacement. Although the concentric pattern is intensified where mineralogical composition changes, it is also apparent in portions of the helen composed exclusively of phyllosilicate (compare Text-fig. 2D with 4B). As in the cases of conch and operculum it is likely that the phyllosilicate replaced the primary mineral of the helen, preserving an originally concentric microstructure (see above).

'Hyolithes' groenwalli Poulsen, 1967

Text-figures 5–7

Material. Poulsen (1967) erected the species *Hyolithes groenwalli* on the basis of a few disarticulated specimens found in close association with a fair number of '... appendages of the type frequently referred to as *Helenia* ...' (Poulsen 1967, p. 24). Here we restudy some of the original material that he described as well as newly exposed specimens in the same pieces of limestone. The material was collected from the lower part of the Lower Cambrian 'Green Shales', Læså Formation, at an unknown locality along the Grødby stream, Bornholm, Denmark (Poulsen 1967; V. Berg-Madsen, pers. comm. 2001). Figured specimens: MGUH 10558a, b are two overlapping helens illustrated by Poulsen (1967, pl. 5, fig. 3); MGUH 10558c shows a naturally

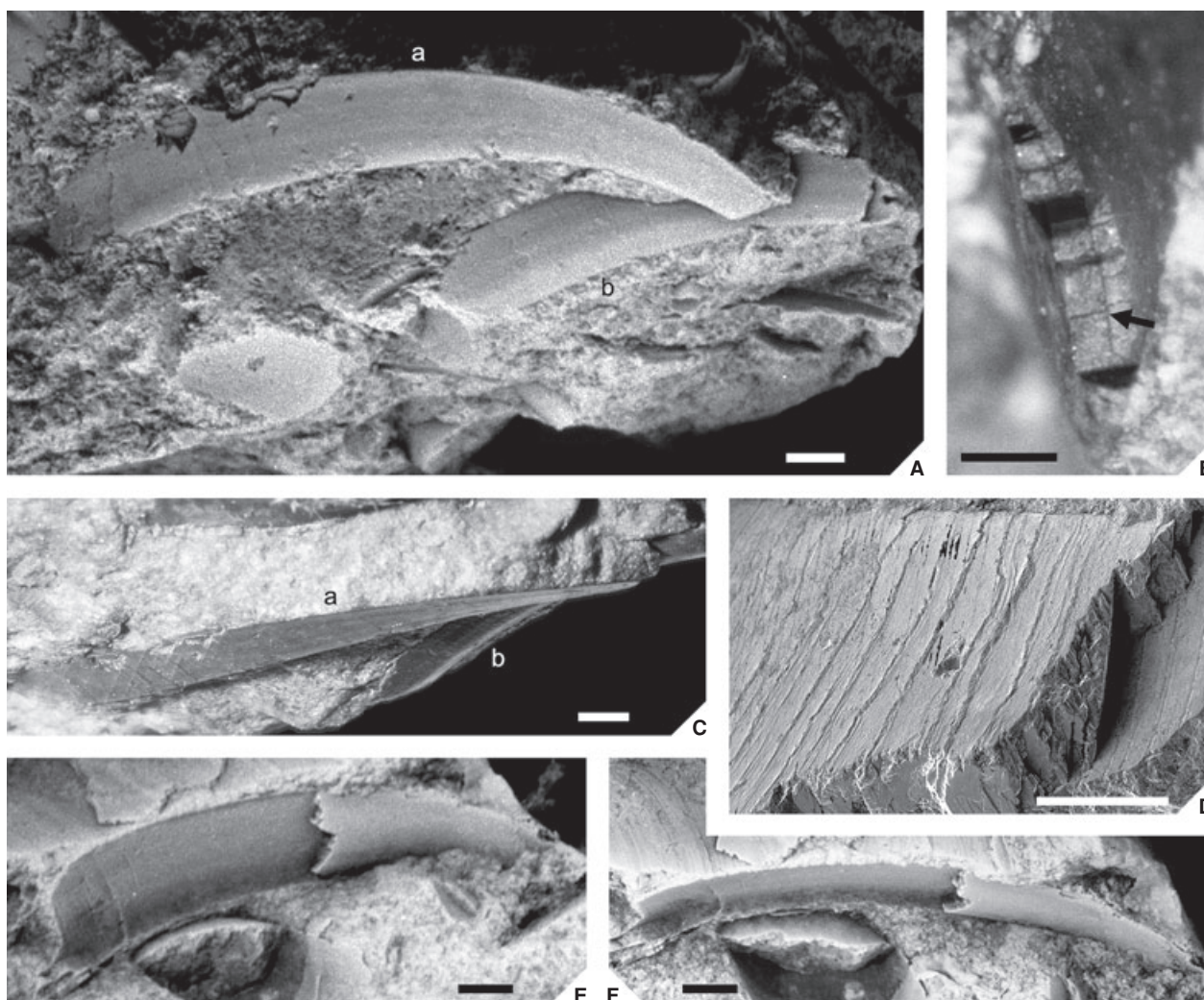


TEXT-FIG. 4. Left helen of '*Hyolithes lanceolatus* (Morris 1845), AM F20111; Permian, New South Wales, Australia. BSE images of sectioned left helen showing variations in chemical composition: phyllosilicate appears in different shades of light grey (which reflect small differences in elemental composition; lighter patches are relatively enriched in Fe), zeolite is black, calcium carbonate is dark grey and phosphate is white; black, irregular spots are artefacts resulting from contamination; note concentric layering around elongate core. A–B, D, view after first polish; C, E, view after second polish. A, close-up of dorsal edge. B–C, overview of helen in cross-section. D–E, close-up of ventral edge. For abbreviations see Text-figure 3 and Pp, phosphate; Z, zeolite. Scale bars represent 100 μm .

exposed cross-section; MGUH 27827 is a helen fragment with a pronounced surface sculpture; six other specimens, MGUH 27821–6, are sectioned helens that were exposed after grinding and polishing a limestone piece.

Description

Helens. The helens of this species are relatively high and narrow. Although there is considerable variation in the precise outline of the cross-section, it is consistently lanceolate, being more pointed



TEXT-FIG. 5. Helens of *Hyolithes groenwalli* Poulsen, 1967; Lower Cambrian, lower part of the 'Green Shales', Læså Formation, Bornholm, Denmark. A, C, specimens MGUH 10558a, b. A, a left helen (specimen a) in anterior view overlapping a right helen (specimen b) in posterior view; note logarithmic curvature. C, dorsolateral view of same specimens; note helicoid twist in specimen a. B, E–F, specimen MGUH 10558c, a right helen with naturally exposed cross-section; dorsal edge of the helen at the top of the image. B, close-up of cross-section; arrow points to helen core; posterior face exposed to the right of the image. E, entire specimen in posterior view; note logarithmic curvature of the helen. F, dorsal view; note posteriorly directed bending. D, SEM image of specimen MGUH 27827. Scale bars represent 1 mm in A, C, E–F; 0.5 mm in B, D.

at one of the edges (Text-figs 5B, 6B, E–F, 7). Specimen MGUH 10558c, a relatively large fragment of a right helen with a naturally exposed cross-section, shows that the pointed edge is dorsal

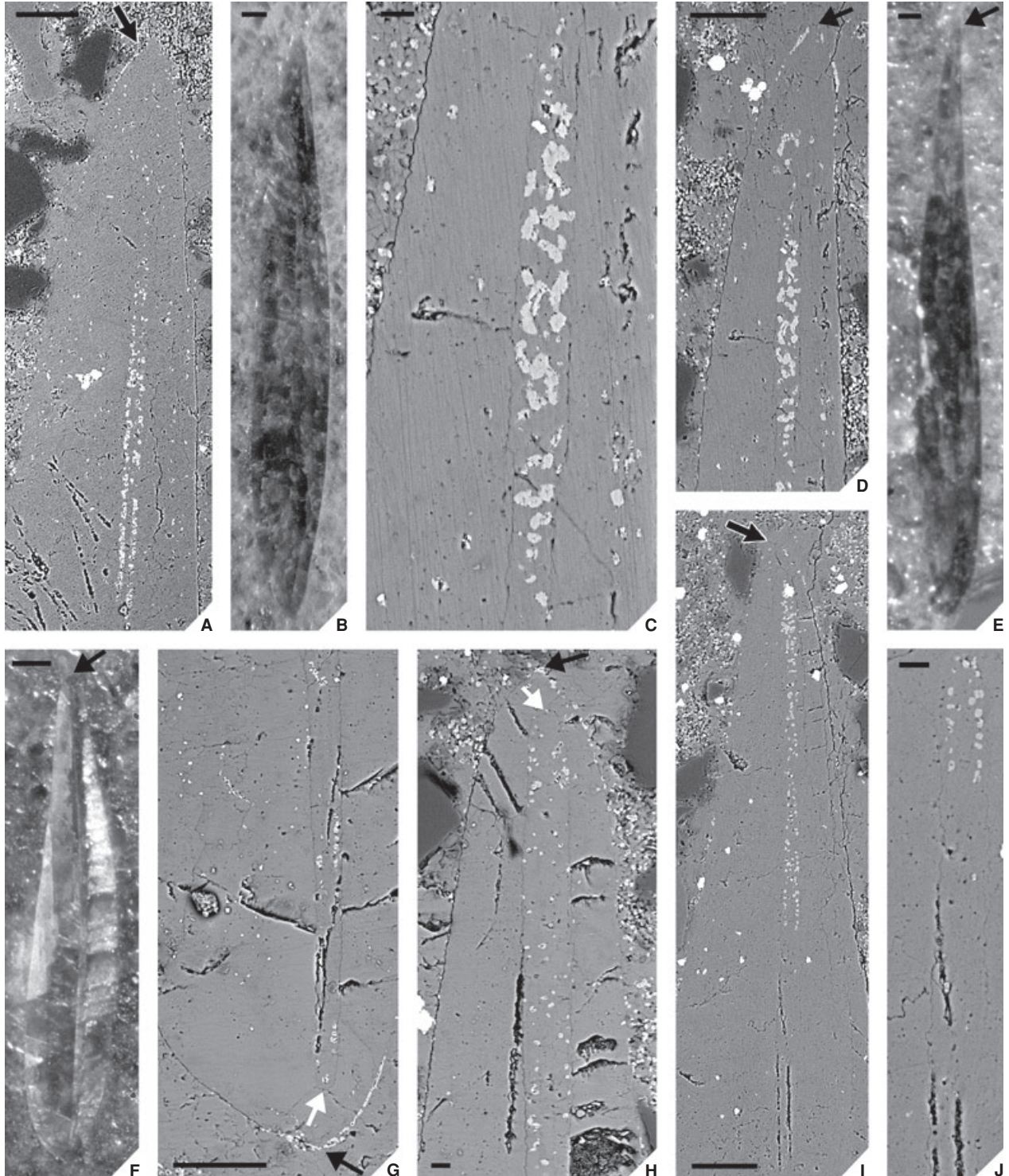
(Text-fig. 5B, E–F). The helens curve logarithmically (Text-fig. 5A, E). Some specimens show a concomitant helicoidal twist (Text-fig. 5C) while others bend anteroposteriorly, apparently

TEXT-FIG. 6. Sectioned helens of *Hyolithes groenwalli* Poulsen, 1967; Lower Cambrian, lower part of the 'Green Shales', Læså Formation, Bornholm, Denmark. A, C–D, G–J are BSE images: light grey indicates phosphatic composition; calcium carbonate is represented by a darker grey. B, E–F are reflected light images. A–B, specimen MGUH 27822. A, dorsal portion of the helen; note phosphate particles arranged in two parallel lines. B, overview of the specimen. C–E, specimen MGUH 27821. C, close-up of central core; note the narrow gap demarcating the core and the phosphate particles randomly distributed within the core. D, overview of dorsal portion of the helen, including the area enlarged in C. E, entire specimen. F–H, specimen MGUH 27824. F, overview. G, enlargement of ventral portion. H, enlargement of dorsal portion; note the gap demarcating the core and the phosphate particles within the core. I–J, specimen MGUH 27826. I, dorsal portion of the helen; note how the two rows of phosphate particles continue ventrally as grooves. J, close-up of I. Scale bars represent 50 μm in A, D, G, I; 100 μm in B, E–F; 10 μm in C, H, J.

without twisting (Text-fig. 5F); in both cases the result is that the logarithmic spiral does not lie in a flat plane and that the distal end of the helen is displaced backwards and upwards (Martí Mus and Bergström 2005). A few specimens show the characteristic surface sculpture of helens (Text-fig. 5D).

The outline of the helens is often demarcated by a gap that separates the skeletal element from the rock (Text-fig. 6A, C–D,

G–I). The helens are massive (Text-figs 5–6); some specimens show a microstructure consisting of large crystals (Text-figs 5B, D, 6F–G) regularly shaped and orientated. This microstructure is independent of the surface sculpture (Text-fig. 5D) suggesting that it is a diagenetic feature, probably resulting from the neomorphic transformation of skeletal aragonite to calcite (see Poulsen 1967, p. 26; quoted above). Although there are no obvious



traces of the original microstructure of helens, many specimens show a differentiated core (Text-figs 5B, 6A, C–D, F–J) consistently shaped and positioned, and similar to that present in the helen of '*H. lanceolatus*. In some specimens the core is visible in both reflected light and BSE images (Text-fig. 6F–H), while in others it is only seen in BSE images (Text-fig. 6A, C–D). As in the case of '*H. lanceolatus*, the core of '*H. groenwalli* is elongated and slightly displaced to one face (Text-figs 5B, 6A, C–D, F–J); specimen MGUH 10558c indicates that the displacement is also towards the posterior face (Text-fig. 5B, E–F). The core of '*H. groenwalli* extends also dorsoventrally without actually reaching the edges of the helen. The presence of this core in the two species (which have markedly different preservational modes) strongly suggests that it represents an original feature of helens.

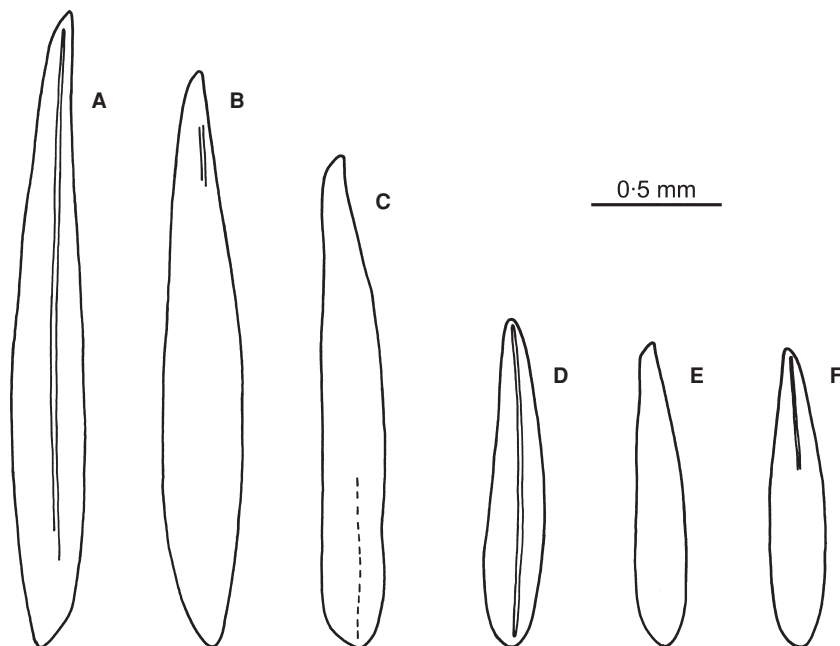
At present, the core consists of a mixture of calcium carbonate and calcium phosphate (Text-fig. 6A, C–D, G–J). Calcium phosphate occurs in the form of micrometre-sized, individual particles. Similar particles can be found also elsewhere in the helen but there is a clear concentration of them along the core. Calcium phosphate also occurs in the sediment, often lining the outer surface of helens (Text-fig. 6G) and the inner and outer surfaces of co-occurring conchs. Calcium phosphate particles can be randomly disposed within the core (Text-fig. 6C–D, H) or aligned along two parallel lines (Text-fig. 6A, I–J). There is evidence indicating that the core was originally 'delimited' within the helen: (1) in one specimen the rows of calcium phosphate continue ventrally as grooves (Text-fig. 6I–J); (2) in two specimens the whole perimeter of the core is clearly demarcated by a narrow gap (Text-fig. 6C, G–H); and (3) large crystals are interrupted at core boundaries (Text-figs 5B, 6F).

Finally, it is likely that the core just described, which is seen in natural cross-section as a dark band (Text-fig. 5B), was the feature identified by Poulsen (1967, p. 26, fig. 4) as a central narrow cavity (see above).

HELEN MICROSTRUCTURE AND GROWTH

Yochelson (1974), and later Runnegar *et al.* (1975) and Marek *et al.* (1997b), proposed a model of accretionary growth for helens. In this model, shell material was accreted at the base of the helen (i.e. at its proximal, unornamented portion), which was encased in a 'mantle fold' (Yochelson 1974). As new material was accreted, the helen was pushed outwards, growing in length. The helen grew periodically and the transverse 'ornament' represented growth lines, marking the successive positions of the outer edge of the mantle. Alternatively, Butterfield and Nicholas (1996) proposed that helens formed in a single event and were successively replaced during growth.

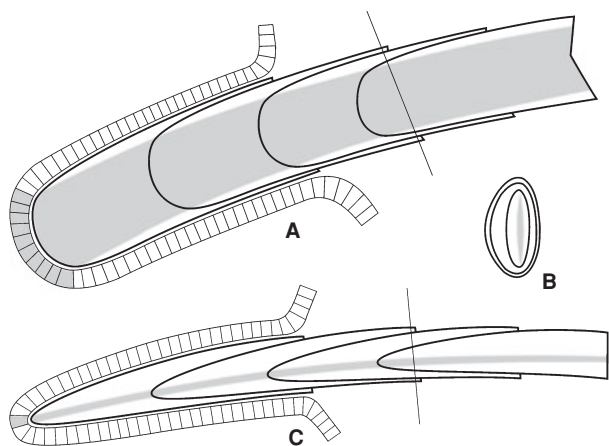
The curvature of helens follows a logarithmic spiral (see above) and, in the organic world, logarithmic spirals are found almost exclusively in skeletal elements that grow by terminal accretion and retain unmodified previous ontogenetic stages (Thompson 1942). Therefore, the shape of the helens is not only compatible with but also indicative of accretionary growth. The fact that a helen is a tapering element, gradually decreasing in all dimensions towards its distal end, also points to accretionary growth. According to Butterfield and Nicholas (1996), the presence of a longitudinal fabric in the organic framework of helens argues against accretionary growth. However, a comparable fabric (radial in this case) occurs in the operculum (Butterfield and Nicholas 1996, fig. 4.2), which clearly grew by accretion. In fact, the set of helens of different sizes figured by Butterfield and Nicholas (1996,



TEXT-FIG. 7. Schematic drawings illustrating the outline of the cross-section and the core in a number of helens of '*Hyolithes* *groenwalli* Poulsen, 1967. A, specimen MGUH 27821. B, MGUH 27822. C, MGUH 27823. D, MGUH 27824. E, MGUH 27825. F, MGUH 27826. Anterior to the left in A–B, D and F; in C and E the orientation is uncertain because no obvious core could be detected.

fig. 4) can be viewed as a growth series and illustrate particularly well both logarithmic and accretionary growth.

The evidence presented herein shows that helens were massive, mineralized spines with a microstructure consisting of concentric lamellae around an elongate core. This microstructure supports the model of accretionary growth elaborated by previous authors (Yochelson 1974; Runnegar *et al.* 1975; Marek *et al.* 1997b) and provides new insights into the details of the growth mechanism. As mentioned above, the growing portion of a helen was its unornamented part (its base), which must have been contained in an invaginated mineralizing epithelium. Within this mineralizing pocket the helen grew progressively in length and width. The cells situated deepest in the mineralizing pocket (grey in Text-figs 8A, C) secreted the proximal end of the helen, which would eventually become the core (once the growth in width was completed). Note that both the core and the proximal end are morphologically identical: narrow and high (Text-fig. 1A, D; this parallelism further supports the hypothesis that the core was originally massive because the proximal end is massive). As the helen was pushed outwards through the mineralizing pocket, successive cells were depositing calcium carbonate on its surface making it grow in width (Text-fig. 8A, C). This successive accretion of shell material on the helen surface produced the concentric lamination around the core (Text-fig. 8B).



TEXT-FIG. 8. Sections through the proximal portion of a hypothetical helen illustrating its inferred mode of growth (see text for explanation). The base of the helen is surrounded by a mineralizing epithelium, which forms a pocket that encloses it. The core and the cells responsible for its secretion are indicated in grey. A, longitudinal, dorsoventral, section of the helen; dorsal to the top of the image, base of the helen to the left. B, cross-section of the helen at the level indicated by the line in A and C; anterior to the left. C, longitudinal, anteroposterior section of the helen; anterior towards the top of the image; base of the helen to the left. All images to the same scale.

This model of helen growth bears similarities to that of polyplacophoran spines (Haas 1981), although the latter elements seem to have a simpler structure. It also shares relevant similarities to the mode of growth of the belemnite rostrum (Bandel *et al.* 1984; Sælen 1989, and references therein). Like the base of the helen, the belemnite rostrum is surrounded by soft tissue and grows by periodic accretion of shell material over its surface. In cross-section, the rostrum shows a conspicuous concentric pattern and a core (the apical line), which forms by the accretion of successive apices as the rostrum grows. The apical line usually stands out as a distinct feature; this 'distinctness' is interpreted to reflect an original difference in microstructure between the apical line and the rest of the rostrum (Bandel *et al.* 1984; Sælen 1989). Bandel *et al.* (1984) suggested that the first material to be secreted at the apex was organic, therefore serving as a base for further mineral deposition and giving the apical line its distinct appearance and susceptibility to diagenesis. The core of helens, which also stands out as a distinct feature within the helen mass, would be equivalent to the belemnite's apical line, representing a continuous internal layer resulting from successively accreted proximal ends. Characteristics of the core in '*H. groenwalli*', particularly the preferential phosphatization and its behaviour as a crystal boundary, suggests that it was organic-rich. The association between organic matter and diagenetic calcium phosphate is generally accepted and there is evidence suggesting that crystal boundaries in neomorphically replaced shells may be determined by the presence of organic-rich layers (Sandberg and Hudson 1983; Maliva *et al.* 2000, and references therein). An important function of skeletal organic matter is to act as a template for mineral growth; it is therefore likely that the first material to be secreted was particularly rich in organic matter. Helens may have had an external organic layer equivalent to the molluscan periostracum but, according to their mode of growth, this 'periostracum' must have been the last material to be secreted (Marek *et al.* 1997b) and could not have had a role in the mineralization process itself.

Marek (1976) and Dzik (1978) presented evidence regarding the earliest stages of hyolithid development. The embryonic skeleton consists of a conch with circular cross-section and no ligula, and a hemispherical operculum; there seem to be no lateral slits or helens present at this early stage. Once past the embryonic stage, the ligula starts to develop gradually, but it is unclear when helens begin to grow or to extend outside the conch. The newborn hyolithid was probably planktic (Marek 1976; Dzik 1978), whereas some of its mature features, particularly the ligula and the helens, have been interpreted as adaptations to a benthic mode of life (Marek 1976; Marek *et al.* 1997b; Martí Mus and Bergström 2005). Marek (1976)

speculated that because helens acted principally as stabilizers on the sea floor their development would be coupled with the process of settling. Butterfield and Nicholas (1996, fig. 4.4) illustrated a small 'post-larval' individual with two identical, spicule-looking helens inside the conch (see Text-fig. 1E). This finding led them to consider helens as fully retractable. In the same specimen, a rounded structure near the aperture was tentatively identified by Butterfield and Nicholas (1996) as the operculum. The perimeter of this putative operculum is identical to that of the conch aperture, therefore supporting such identification. In this specimen the entire length of each helen is less than half the width of the aperture (because the conch is flattened the original width of the aperture is better inferred from the operculum). However, the length of the internal portion of 'mature' helens is half the width of the aperture (Martí Mus and Bergström 2005; Text-fig. 1D). Therefore, we believe the position of the helens in this specimen has nothing to do with retraction. Instead, the specimen may capture the moment when helens start to develop inside the conch as small spicules completely embedded in soft tissue. With its developing ligula and helens the individual in question may have been about to settle.

Acknowledgements. We thank the Australian Museum, Sydney, and the Geological Museum, Copenhagen, for loan of the material and for allowing preparation of the specimens. V. Berg-Madsen provided access to the Bornholm material. U. Stuesson helped with the interpretation of the EDS results and with technical matters. H. Mutvei is acknowledged for scientific discussions and practical assistance. We are also grateful to A. Kouchinsky, J. Stone, Ø. Hammer and G. Budd for stimulating discussions. We thank two anonymous reviewers for constructive criticism and E. N. K. Clarkson and D. J. Batten for editorial assistance. This work was funded by Uppsala University, the Syskonen Almén's Fund (The Royal Swedish Academy of Sciences), and by NFR through a grant to M. Moczyłowska (G-AA/GU 09939-319).

REFERENCES

BABCOCK, L. E. and ROBISON, R. A. 1988. Taxonomy and paleobiology of some Middle Cambrian *Scenella* (Cnidaria) and hyolithids (Mollusca) from western North America. *University of Kansas, Paleontological Contributions, Paper*, **121**, 1–22.

BANDEL, K., ENGESER, T. and REITNER, J. 1984. Die embryonalentwicklung von *Hibolites* (Belemnitida, Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **167**, 275–303.

BUTTERFIELD, N. J. and NICHOLAS, C. J. 1996. Burgess shale-type preservation of both non-mineralizing and 'shelly' Cambrian organisms from the Mackenzie Mountains, north-western Canada. *Journal of Palaeontology*, **70**, 893–899.

DZIK, J. 1978. Larval development of hyolithids. *Lethaia*, **11**, 293–299.

ETHERIDGE, R. Jr 1890. On the further structure of *Conularia inornata*, Dana, and *Hyolithes lanceolatus*, Morris, sp. (= *Theca lanceolata*, Morris). *Proceedings of the Linnean Society of New South Wales*, **4**, 751–756, pl. 20.

FOLK, R. L. 1965. Some aspects of recrystallization in ancient limestones. 14–48. In PRAY, L. C. and MURRAY, R. C. (eds). *Dolomitization and limestone diagenesis: a symposium*. Society of Economic Paleontologists and Mineralogists, Special Publication, **13**, 180 pp.

HAAS, W. 1981. Evolution of calcareous hard parts in primitive molluscs. *Malacologia*, **21**, 403–418.

HAGGART, J. W. and BUSTIN, R. M. 1999. Selective replacement of mollusk shell by chorite, Lower Cretaceous Longarm Formation, Queen Charlotte Islands, British Columbia. *Canadian Journal of Earth Sciences*, **36**, 333–338.

KOUCHINSKY, A. V. 2000. Skeletal microstructures of hyoliths from the Early Cambrian of Siberia. *Alcheringa*, **24**, 65–81.

MALINKY, J. M. 1987. Taxonomic revision of lower and middle Paleozoic Orthothecida (Hyolitha) from North America and China. *Journal of Paleontology*, **61**, 942–959.

— 2006. Revision of Hyolitha from the Ordovician of Estonia. *Paläontologische Zeitschrift*, **80**, 88–106.

MALIVA, R. G. and DICKSON, J. A. D. 1992. The mechanism of skeletal aragonite neomorphism: evidence from neomorphosed mollusks from the upper Purbeck Formation (Late Jurassic–Early Cretaceous), southern England. *Sedimentary Geology*, **76**, 221–232.

— MISSIMER, T. M. and DICKSON, J. A. D. 2000. Skeletal aragonite neomorphism in Plio-Pleistocene sandy limestones and sandstones, Hollywood, Florida, USA. *Sedimentary Geology*, **136**, 147–154.

MAREK, L. 1963. New knowledge on the morphology of *Hyolithes*. *Sborník Geologických Věd, Paleontologie*, **1**, 53–73, pls 1–4.

— 1967. The class Hyolitha in the Caradoc of Bohemia. *Sborník Geologických Věd, Paleontologie*, **9**, 51–113, pls 1–10.

— 1976. On the ontogeny in Hyolithida. *Časopis Pro Mineralogii a Geologii*, **21**, 277–283.

— and YOCHELSON, E. L. 1976. Aspects of the biology of Hyolitha (Mollusca). *Lethaia*, **9**, 65–82.

— MALINKY, J. M. and GEYER, G. 1997a. Middle Cambrian fossils from Tizi n'Tichka, the High Atlas, Morocco. Part 2. Hyolitha. *Journal of Paleontology*, **71**, 638–656.

— PARSLEY, R. L. and GALLE, A. 1997b. Functional morphology of hyoliths based on flume studies. *Věstník Českého Geologického Ústavu*, **72**, 351–358.

MARTÍ MUS, M. and BERGSTRÖM, J. 2005. The morphology of hyolithids and its functional implications. *Palaentologia*, **48**, 1139–1167.

MORRIS, J. 1845. Description of fossils. 270–291. In STRZELCKI, P. E. DE. *Physical description of New South Wales and Van Diemen's Land*. Longman, Brown, Green and Longmans, London, 462 pp.

POULSEN, C. 1967. Fossils from the Lower Cambrian of Bornholm. *Kongelige Danske Videnskabernes Selskab, Matematisk-Fysiske Meddelelser*, **36**, 1–48, pls 1–9.

- RAAM, A. 1968. Petrology and diagenesis of Broughton Sandstone (Permian), Kiama district, New South Wales. *Journal of Sedimentary Petrology*, **38**, 319–331.
- RUNNEGAR, B. 1980. Hyolitha: status of the phylum. *Lethaia*, **13**, 21–25.
- POJETA, J., MORRIS, N. J., TAYLOR, J. D., TAYLOR, M. E. and McCCLUNG, G. 1975. Biology of the Hyolitha. *Lethaia*, **8**, 181–191.
- SÆLEN, G. 1989. Diagenesis and construction of the belemnite rostrum. *Palaeontology*, **32**, 765–798.
- SANDBERG, P. A. and HUDSON, J. D. 1983. Aragonite relic preservation in Jurassic calcite-replaced bivalves. *Sedimentology*, **30**, 879–892.
- THOMPSON, d'A. W. 1942. *On growth and form*. Second edition. Cambridge University Press, Cambridge, 1116 pp.
- WALCOTT, C. D. 1890a. Descriptive notes of new genera and species from the Lower Cambrian or *Olenellus* Zone of North America. *Proceedings of the United States National Museum*, **12**, 33–46.
- 1890b. The fauna of the Lower Cambrian *Olenellus* Zone. *US Geological Survey, 10th Annual Report*, 509–760.
- 1911. Cambrian geology and paleontology II: Middle Cambrian annelids. *Smithsonian Miscellaneous Collections*, **57**, 109–145.
- WATERHOUSE, J. B. 1965. Palaeotaxodont bivalves from the Permian of New Zealand. *Palaeontology*, **7**, 630–655, pls 96–98.
- WRIGHT, J. A., POWIS, G. D. and CARR, P. F. 1982. Zeolitised Permian fossils from the southern Sydney Basin, New South Wales, Australia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **6**, 367–374.
- YOCHELSON, E. L. 1961. The operculum and mode of life of Hyolithes. *Journal of Paleontology*, **35**, 152–161, pls 33–34.
- 1974. Redescription of the Early Cambrian *Helenia bella* Walcott, an appendage of *Hyolithes*. *Journal of Research of the United States Geological Survey*, **2**, 717–722.