



A COMPLETE RECONSTRUCTION OF THE HYOLITHID SKELETON

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ABSTRACT—Hyolithids are a group of Paleozoic lophotrochozoans with a four-pieced skeleton consisting of a conch, an operculum, and a pair of lateral ‘spines’ named helens. Both the conch and operculum are relatively well known and, to a certain extent, have modern analogues in other lophotrochozoan groups. The helens, on the other hand, are less well known and do not have clear modern analogues. This has hindered the knowledge of the complete morphology of the hyolithid skeleton, as well as other aspects of hyolithid biology, such as the organization of soft parts, and their ability to move. The material studied herein, consisting of disarticulated skeletal elements from the Silurian of Gotland, Sweden, illustrates a complete developmental sequence of a hyolithid species and includes the first complete, three-dimensionally preserved helens. Our material confirms that helens were massive skeletal elements, whose growth started proximally with the deposition of a central, coherent lamella. Further shell accretion took place around this lamella, but followed a particular accretion pattern probably constrained by the presence of marginal muscle attachment sites on the proximal-most portion of the helens. These muscle attachment sites were ideally located to allow a wide range of movements for the helens, suggesting that hyolithids may have been relatively mobile organisms.

INTRODUCTION

HYOLITHS ARE a group of extinct, shelled lophotrochozoans which began to diversify in the earliest Cambrian and were important constituents of the early Paleozoic benthos. Hyoliths are divided into two morphologically distinct groups: the orthothecids and the hyolithids.

Orthothecids have a conical conch of varied cross-section and a retractable operculum, but show considerable morphological diversity and are relatively poorly known. Hyolithids constitute a more homogeneous group, characterized by a skeleton consisting of four elements: a conical conch (with an oval or subtriangular cross section), a complex, external operculum that closed the conch aperture, and two lateral ‘spines’ named helens. The helens are the least known elements of the hyolithid skeleton, partly because of their relative fragility and rarity as fossils, and lack obvious analogues among living metazoans. Therefore they appear as relatively puzzling elements both from the morphological and the functional points of view. It is known that helens are long, flattened, curved spines which were partly internal and extended outside the conch through a pair of lateral gaps at the conch-operculum commissure (Marek, 1963; Marek and Yochelson, 1964). They tend to have a more or less oval cross section with a bulging anterior face, although in some species the section is flattened on both sides (Martí Mus and Bergström, 2005, 2007). It is also well documented that the most proximal portion of helens had a rounded, blunt margin (Butterfield and Nicholas, 1996, fig. 4), and lacked growth lines, although they occur throughout the rest of the helens’ length (Yochelson, 1974; Butterfield and Nicholas, 1996; Martí Mus and Bergström, 2005). Complete helens are best known from specimens preserved as carbonaceous films (e.g., Yochelson, 1961; Butterfield and Nicholas, 1996), whereas three-dimensionally preserved specimens are generally fragmentary or poorly exposed (e.g., Yochelson, 1974; Martí Mus and Bergström, 2005, 2007). However, despite the exceptional preservation of some of the carbonaceous films, all the three-dimensional information is lost in these specimens. Therefore, one of the least known aspects of the helens morphology is their

detailed three-dimensional morphology, particularly that of their proximal, internal portion. This includes the lack of information regarding muscle attachment areas on the helens, which contrasts with the diverse and abundant muscle scars recorded in the conch and operculum of different hyolithid species (Martí Mus and Bergström, 2005, and references therein). This lack of information limits our understanding of how helens grew and articulated with the other skeletal elements and, ultimately, how they functioned in the living animal.

The material presented herein, consisting of disarticulated skeletal elements, illustrates a complete developmental sequence of a single hyolithid species, and includes the first complete, three-dimensionally preserved helens. Therefore, in this work we will particularly focus on the description of the helens and the biological implications of the newly described features.

MATERIAL AND PRESERVATION

This study is based on material from three localities (Nyan 2, Linde 3, and Källdar 3) from the late Silurian (Ludlow) Hemse Group, southern Gotland, Sweden. The material from locality Nyan 2 (samples G72-13LJ, G93-950LJ, and G93-954LJ), situated in a coastal outcrop east of Lau Church, belongs to the upper part of the När Formation, at levels from 0.5 to 1 m below the contact between the När and Eke formations, within the Ludfordian *Polygnathoides siluricus* Zone (Jeppsson, 2005; Jeppsson et al., 2006). The material from Linde 3 (sample G89-797LJ) and Källdar 3 (sample G89-798LJ), both localities situated close to the Linde Church, belongs to the Gorstian Hemse Marl Northwest Part, within the *Ozarkodina excavata* n. ssp. A Zone.

All studied hyoliths are disarticulated, represented by loose conchs, opercula and helens. Most skeletal elements appear to belong to a single hyolithid species, however samples G72-13LJ, G93-950LJ, and G93-954LJ (all from locality Nyan 2) contain opercula belonging to a second hyolithid species. These opercula occur only in the largest fractions of the filtered residue (containing specimens measuring several mm) and

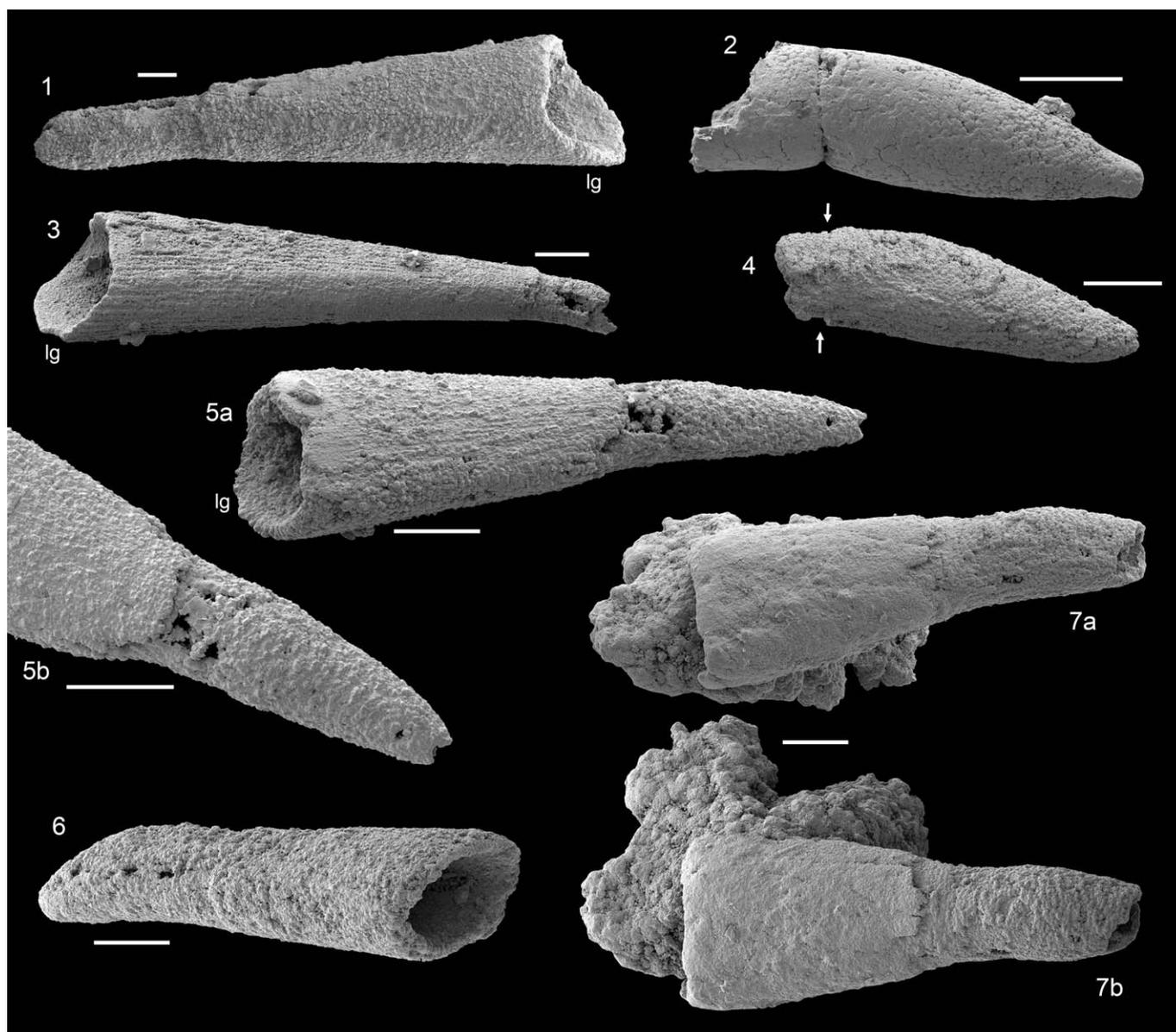


FIGURE 1—Hyolithid protoconchs, sample G89-797LJ, locality Linde 3, upper Silurian, Gotland (Sweden). 1, 3, relatively large conchs with well developed ligula and general adult morphology, protoconchs are also preserved: 1, specimen in lateral view, aperture to the right, SMNH Mo 167725; 3, specimen in lateral view, aperture to the left, the end of the protoconch is broken, SMNH Mo 167727; 2, internal mold, specimen in lateral view, aperture (not preserved) to the left, a discontinuity marks the boundary between protoconch and rest of the conch, SMNH Mo 167726; 4, complete protoconch in lateral view, arrows point to a poorly preserved constriction, aperture (not preserved) to the left, SMNH Mo 167728; 5, SMNH Mo 167729; 5a, general view of specimen, conch with incipient adult features, note short ligula and flattened cross-section, specimen in antero-lateral view, aperture to the left; 5b, close up of protoconch, dorsal view, aperture (not seen) to the left; 6, 7, specimens showing intermediate developmental stage with flattened cross-section and no ligula: 6, specimen in antero-lateral view, aperture to the right, SMNH Mo 167730; 7, SMNH Mo 167731; 7a, specimen in dorso-lateral view, aperture to the left; 7b, specimen in dorsal view, aperture to the left. All scale bars are 100 μ m. Abbreviation: lg=ligula.

represent the largest opercula present. Although the opercula of both species are similar, suggesting they belong to closely related species, their inner surfaces are readily distinguishable. We were unable to find conchs matching the second operculum, however hyolithid conchs are generally more similar to each other than opercula and there is a possibility that they went unrecognized; also, some of the largest conchs (which may have fitted the second type of operculum) are too fragmentary for evaluation. Regarding the helens, we were also unable to recognize more than one morphotype. Although we are confident that most of the illustrated specimens belong to a single species (the most abundant one) there is a possibility,

particularly in the case of the helens, that they represent a mixed assemblage. However since the present work focuses on particular aspects of hyolithid functional morphology, it is of no relevance whether the different skeletal elements belong to a single species or represent two morphologically similar ones.

The fossils are diagenetically altered skeletal elements, now consisting of a mixture of pyrite and iron oxide-hydroxides (the proportion of the different minerals being relatively variable between specimens). The different skeletal elements show the same chemical composition. Only one internal mold (Fig. 1.2), also of the same composition, was found among the hyolithid material. It is likely that the skeletal elements (originally of

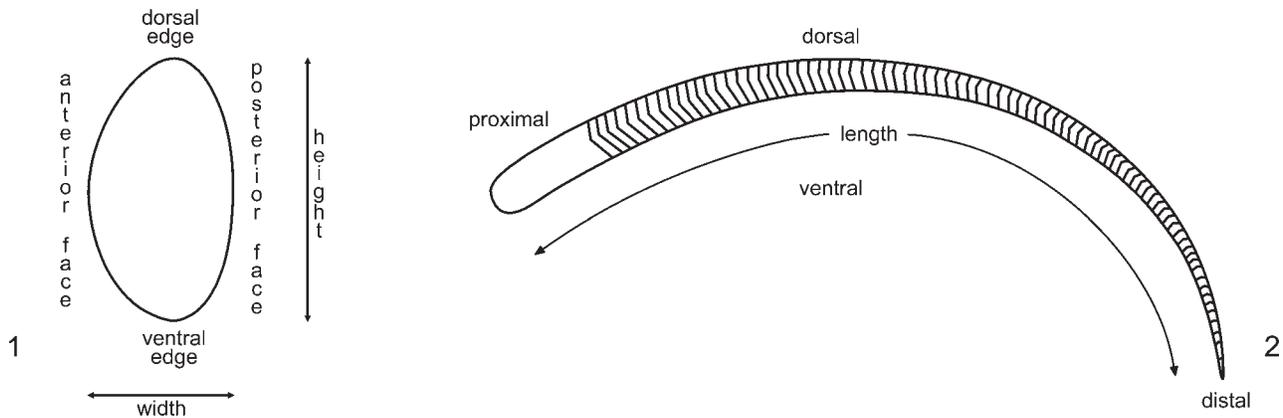


FIGURE 2—General morphology and terminology of helens. 1, helen cross-section based on *Gompholites striatulus* (Barrande, 1847); 2, plan view based on a complete helen illustrated by Butterfield and Nicholas (1996, fig. 4). Drawings modified from Martí Mus and Bergström (2005).

calcium carbonate composition) were first pyritized during diagenesis, and subsequently oxidized to various degrees. Although the fossils appear generally well preserved, delicate surface details and shell microstructure are not preserved.

Figured material is housed in the Swedish Museum of Natural History, Stockholm, Sweden (SMNH), with the prefix Mo (mollusks).

METHODS AND TERMINOLOGY

Samples were treated with buffered and diluted (10%) acetic acid, as described by Jeppsson et al. (1999), at Lund University Microfossil Laboratory. Illustrated specimens were gold-coated and photographed using a Scanning Electron Microscope (SEM). Energy dispersive X-ray spectroscopy (EDS) was used to analyze the elemental composition of selected fossils. SEM imaging and EDS were carried out at “Servicio de análisis y caracterización de sólidos y superficies de la Universidad de Extremadura”, using a Hitachi FE-SEM S-4800 equipped with a Bruker XFlash 5010 X-ray detector.

To describe hyolithid morphology we follow the standard terminology, developed in a series of papers by Marek (1963, 1967), and Martí Mus and Bergström (2005). Some important terms are defined in the text and marked on the illustrations. Figure 2 summarizes the terminology used for the helens.

NOTE ON SYSTEMATICS

The taxonomy of hyoliths has relied primarily upon features of the conch, as the conch is the most commonly preserved skeletal element. Sysoev (1958, 1976) provided lists of features, utilizing mainly the conch, by which genera and species could be distinguished. In contrast, the taxonomic schemes of Marek (1963, 1967) emphasized the operculum, and indeed the opercula exhibit a wide range of variation between taxa whereas the associated conchs are far less dissimilar to each other. However, Marek’s scheme is of only limited usefulness owing to the overall scarcity of opercula, and even in those cases when an operculum is available, a well-preserved interior surface is required in order to observe taxonomically important features.

Silurian hyoliths are relatively rare worldwide, since the group declines in the middle Paleozoic. However, a modern taxonomic treatment of the published Silurian species is lacking, most relevant publications being more than a century old. Most Silurian species are based on poorly preserved specimens (usually only conchs), and most genus names are outdated and bear little meaning in modern systematics. A systematic study of the hyolithid described herein (which would require, at least to a

certain extent, a revision of previously reported species), is therefore beyond the scope of this paper. Recently, several articles have been published revising the systematics of Cambrian and Ordovician Swedish hyoliths (Berg-Madsen and Malinky, 1999; Malinky and Berg-Madsen, 1999; Malinky, 2002; Malinky et al., 2009), while Silurian hyoliths are still awaiting revision. Holm’s (1893) classical monograph remains the latest detailed study of Silurian Swedish hyoliths. Holm (1893) recorded ‘*Hyolithus*’ *expansus* Holm, 1893, *H. lanceola* Holm, 1893, and *H. peracutus* (probably an orthothecid) Holm, 1893, from the Silurian of Sweden (all from localities in Gotland). As illustrated by Holm (1893), these species are known only from their conchs and none is well preserved, making comparisons with our material difficult. The conch of *H. lanceola* is similar to our specimens, but the cross-section has a more triangular outline, particularly the venter is considerably flatter. Opercula have been described for only two species of Silurian hyoliths (Moberg and Grönwall, 1909; Marek, 1967). Our material (Fig. 3.1a, 3.3) resembles externally the operculum of ‘*Hyolithus*’ *scanicus* Moberg and Grönwall, 1909, from the Silurian of Scania, southern Sweden, in terms of outline and especially the fold on the conical shield. Moberg and Grönwall’s (1909, pl. 3, fig. 3) material preserves the external morphology quite well, but the interior surface is unknown. The co-occurring conchs (Moberg and Grönwall, 1909, pl. 3, figs. 1, 2, 4) are generally similar to our material, but have a considerably flatter ventral side. The only other known Silurian hyolithid opercula (Marek, 1975, pl. 2) belongs to the species *Paolites obivius* (Barrande, 1867), from the Czech Republic, and is polyclavicate (having multiple clavicles rather than being monoclavicate with only a single pair), clearly distinguishing it from our material.

THE HYOLITHID LARVAL SKELETON

The earliest ontogenetic stage of the hyolithid skeleton is known for a number of species. The initial part of the conch (often named protoconch) has been frequently illustrated (e.g., Marek, 1976; Dzik, 1978; Bengtson, 1990; Butterfield and Nicholas, 1996), whereas the corresponding part of the operculum (protooperculum) is less well known (e.g., Dzik, 1978). Most protoconchs are fusiform with a pointed end, although globose protoconchs have also been reported (Dzik, 1978). A more or less conspicuous constriction separates the protoconch from the rest of the conch, and their length ranges from ~65 μm (e.g., Butterfield and Nicholas, 1996) to ~400 μm (e.g., Bengtson, 1990). Fusiform protoconchs usually show

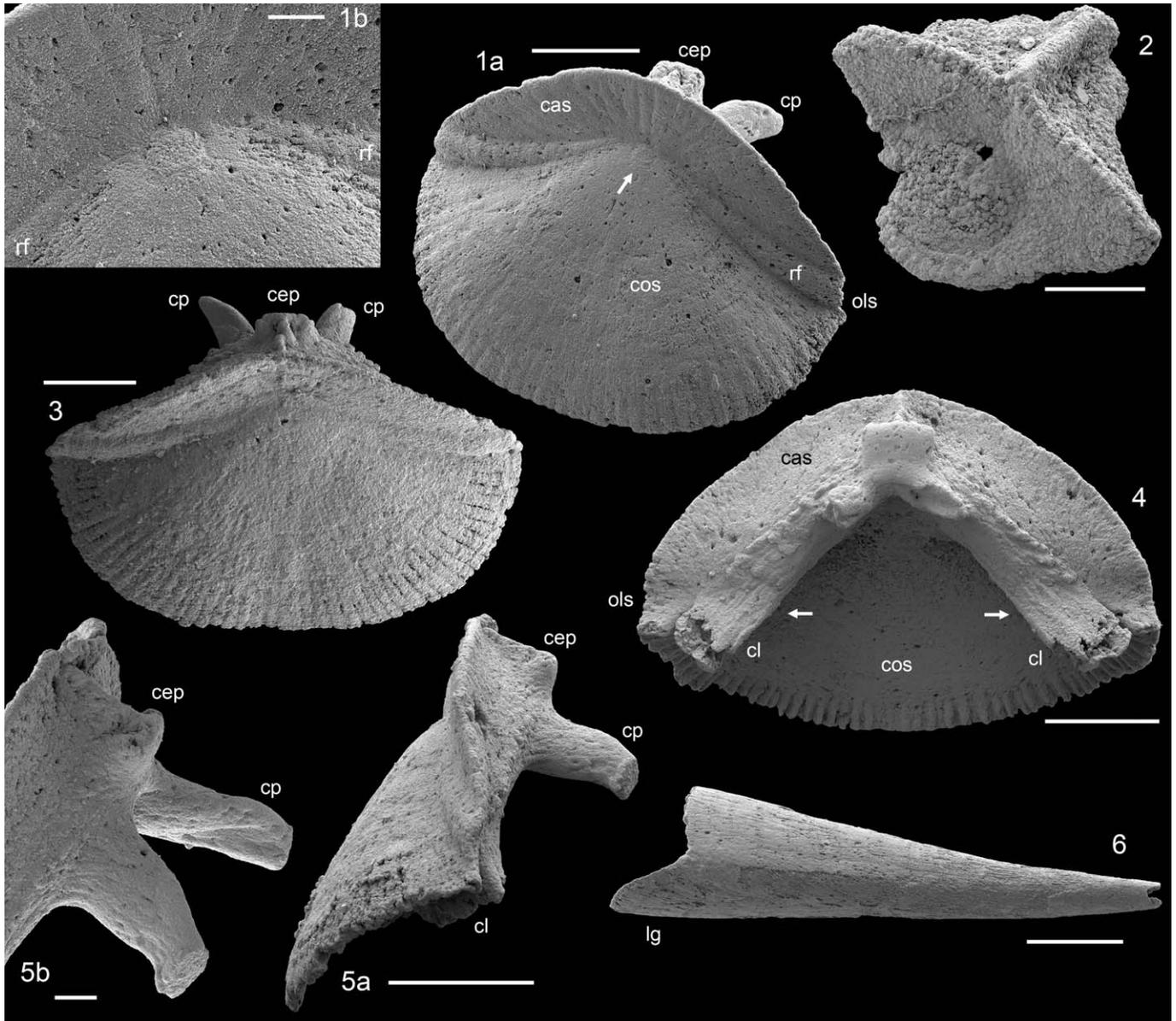


FIGURE 3—Hyolithid conch and opercula, upper Silurian, Gotland (Sweden). 1, 3–5, sample G72-13LJ, locality Nyan 2: 1, SMNH Mo 167732; 1a, external surface of operculum in antero-lateral view, some prominent internal features are visible, note preserved protooperculum (arrowed); 1b, close up protooperculum; 3, external surface of operculum in dorsal view, some prominent internal features are also visible, SMNH Mo 167734; 4, internal surface of operculum, arrows point to fold that accommodated helens, SMNH Mo 167735; 5, SMNH Mo 167736; 5a, operculum in lateral view; 5b, close up of cardinal and central processes; 2, 6, sample G89-797LJ, locality Linde 3: 2, operculum fragment showing protooperculum; 6, conch in lateral view, aperture to the left, SMNH Mo 167737. Scale bars are 100 μm for 1b, 2, 5b, and 0.5 mm for 1a, 3, 4, 5a, 6. Abbreviations: cas=cardinal shield; cep=central process; cos=conical shield; cl=clavicle; cp=cardinal process; lg=ligula; ols=operculum lateral sinus; rf=rooflets.

some degree of dorso-ventral inclination which tends to follow (although sometimes is more pronounced than) the general curvature of the conch. Although Marek (1976) pointed out that the direction of curvature of the protoconch may vary between different specimens of the same species, most illustrated specimens seem to follow the above pattern. Faint growth lines can often be distinguished in the fusiform protoconchs (Dzik, 1978; Bengtson, 1990).

Although the preservation is coarse, small conchs preserving the earliest ontogenetic stage are common in some of the studied samples (Fig. 1). Most of the features of these protoconchs are in accordance with those previously observed in other hyolithids. They are fusiform, with inflated sides, a rounded

cross-section, a pointed end and a constriction that separates them from the rest of the conch. This constriction is particularly well seen in the only internal mold recovered (Fig. 1.2), where it appears as a narrow and well-defined discontinuity. The length of the most complete protoconchs ranges between ~ 300 and $400 \mu\text{m}$, and the diameter of the aperture between ~ 100 and $150 \mu\text{m}$. The length-aperture ratio ranges between 2.5 and 3.2. The curvature of the protoconch has two components; first, the protoconch itself is usually gently curved (Fig. 1.5a, 1.6, 1.7a), and second, the conch and protoconch usually meet at a slight angle (Fig. 1.2, 1.3). A peculiar feature of these specimens is that, although the adult conch is almost straight (or curves slightly dorsally; Fig. 3.6), the protoconch is often slightly

ventrally inclined and therefore does not follow the general curvature of the adult conch (Fig. 1.2, 1.3, 1.5a, 1.6, 1.7a).

Apart from recording the earliest developmental stage of the conch, the present material also documents the next phase of early hyolithid development. After the protoconch, the conch went through an 'intermediate' growth stage with a flattened elliptical cross section and apparently no ligula, the aperture being straight and perpendicular to the conch length (Fig. 1.6, 1.7a, 1.7b). This intermediate stage reaches a length similar to that of the protoconch and does not terminate in any abrupt change or constriction but transforms gradually, slowly acquiring adult features. Specimens with a short ligula and retaining a flattened cross-section (Fig. 1.5a) illustrate this gradual transformation into adult morphology.

Several opercula show a small protooperculum (Fig. 3.1a, 3.1b, 3.2), a rounded, slightly convex cap located centrally and at the margin between the conical and the cardinal shields. Its diameter ranges from ~80 to 135 μm ., being similar to the size range observed for the aperture of the larval conch. The adult operculum developed radiating from the protooperculum (Fig. 3.1a, 3.1b). The rooflets (furrows that formed as a result of the accretion of the operculum lateral sinus; the lateral sinus is the fold at the margin of the operculum that allowed the exit of the helens) converge towards, but do not reach the margins of the protooperculum (Fig. 3.1a, 3.1b). Instead, they developed a little later, once the operculum had approximately doubled in size, and had started to show the adult differentiation in cardinal and conical shields (Fig. 3.1a). This is compatible with previous observations suggesting that the helens (and therefore the related opercular structures such as the lateral sinus and rooflets) are the latest skeletal elements to develop and that they do not extend outside the conch until the ligula (and therefore the fold of the operculum) is fully developed (Martí Mus and Bergström, 2007, and references therein). The smallest helen recovered in this study (Figs. 4.1, 5.1a, 5.1b), is significantly larger than these early conchs and opercula, and therefore likely belonged to a specimen with a fully developed adult morphology.

The constriction that marks the end of the protoconch (a shallow groove in the case of the operculum) is the only clear discontinuity registered in the hyolithid skeleton during early ontogeny. This type of discontinuity is often interpreted as recording hatching; however, this interpretation is not clear in this case, particularly because of the presence of growth lines in several fusiform protoconchs, at least in their distal portions (as mentioned above delicate surface details such as growth lines are generally not preserved in our material, but are visible in other illustrated specimens; e.g., Dzik, 1978; Bengtson, 1990). An alternative possibility is that the end of the protoconch marks the beginning of 'metamorphosis' (defined loosely as the process of acquisition of adult characters). But metamorphosis must have been a gradual, protracted process, as suggested by the presence of a long transitional stage between the protoconch and the fully adult shell and the lack of a discontinuity marking the beginning of the adult morphology. Helens may have started to develop during this protracted metamorphosis. This would imply an early hatching and a long larval period (until completed metamorphosis) for the hyolithids with fusiform protoconchs. Our interpretation of hyolithid development is similar to the one proposed by Dzik (1978), particularly considering that concepts like metamorphosis or larva haven't been unambiguously defined. Dzik (1978), comparing hyolithid development with that of gastropods, suggested an early hatching for those hyolithids with fusiform protoconchs. They would hatch as free-living trochophores and transform into veligers which would gradually acquire adult features. The

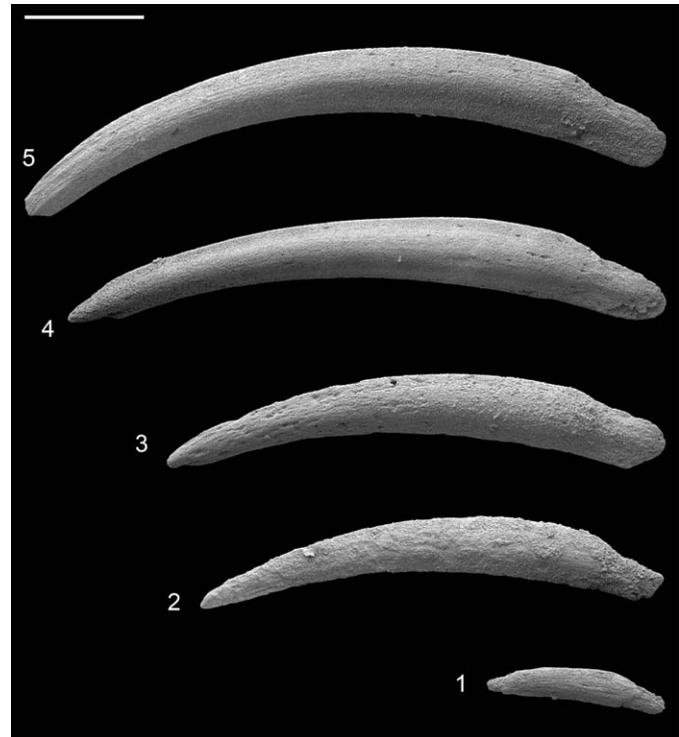


FIGURE 4—Growth series of the helen. All helens oriented in anterior view, with dorsal edge upwards and proximal margin to the right. 1, 2, sample G89-797LJ, locality Linde 3: 1, smallest helen recovered, right helen, SMNH Mo 167738; 2, right helen, SMNH Mo 167739; 3, left helen (flipped in image for comparison), G72-13LJ, locality Nyan 2, SMNH Mo 167740; 4, left helen (flipped in image for comparison), 93-950LJ, locality Nyan 2, SMNH Mo 167741; 5, right helen, G89-798LJ, locality Källdar 3, SMNH Mo 167742. Scale bar=0.5 mm.

larval period would terminate in a metamorphosis involving no major morphological changes. The constriction at the end of the protoconch would reflect the transformation from one larval type to another while adult characters would be acquired gradually, the process leaving no major discontinuities recorded on the shell.

The basic developmental pattern proposed herein is not unlike that observed in some recent lophotrochozoans, particularly annelids and molluscs.

ADULT SKELETON

Conch and operculum.—Both the conch and operculum of the species illustrated herein have a relatively standard hyolithid morphology. The conch has a well-developed, almost hemispherical (although slightly flattened anteriorly) ligula (Figs. 3.6, 6.2b, 6.2c, 6.3a), and an approximately oval cross section (Fig. 6.2a) with a flattened ventral side and an inflated dorsum. In lateral view, the dorsal margin of the aperture is convex (Figs. 3.6, 6.3a), receding both at the level of the lateral sinus (the margin of the conch which recedes to allow the exit of the helens; Fig. 6.3a, 6.3b) and at the highest point of the dorsum (Figs. 3.6, 6.2c, 6.3a). In lateral view the conch is almost straight or curves slightly dorsally (Fig. 3.6).

The morphology of the operculum also conforms to that which characterizes the group as a whole. The operculum is folded, consisting of a relatively flat cardinal shield, which fits the dorsum of the conch, and an inflated conical shield that fits the ligula (Figs. 3.1a, 3.3, 3.4, 6.3a). At the level where the conical and cardinal shields meet there is a symmetrical pair of furrows, the rooflets (discussed above; Figs. 3.1a, 3.3, 6.3a). The internal



FIGURE 5—Proximal portion of helens. 1, sample G89-797LJ, locality Linde 3, right helen, smallest helen recovered, SMNH Mo 167738; 1a, overview of complete specimen; 1b, close up of proximal portion; 2, 4, 5, 7, sample G72-13LJ, locality Nyan 2; 2, left helen, dorsal view, anterior face to the right, SMNH Mo 167743; 4, left helen, anterior view, dorsal edge to the right, SMNH Mo 167761; 5, left helen, anterior view, dorsal edge upwards, SMNH Mo 167744; 7, left helen, anterior view, dorsal edge upwards, SMNH Mo 167746; 3, 6, sample G93-950LJ, locality Nyan 2; 3, left helen, anterior view, dorsal edge upwards, SMNH Mo 167741; 3a, overview of complete specimen; 3b, 3c, close ups of proximal portion, arrow points to possible growth line; 6, right helen, anterior view, dorsal edge upwards, SMNH Mo 167745. All scale bars=100 μ m.

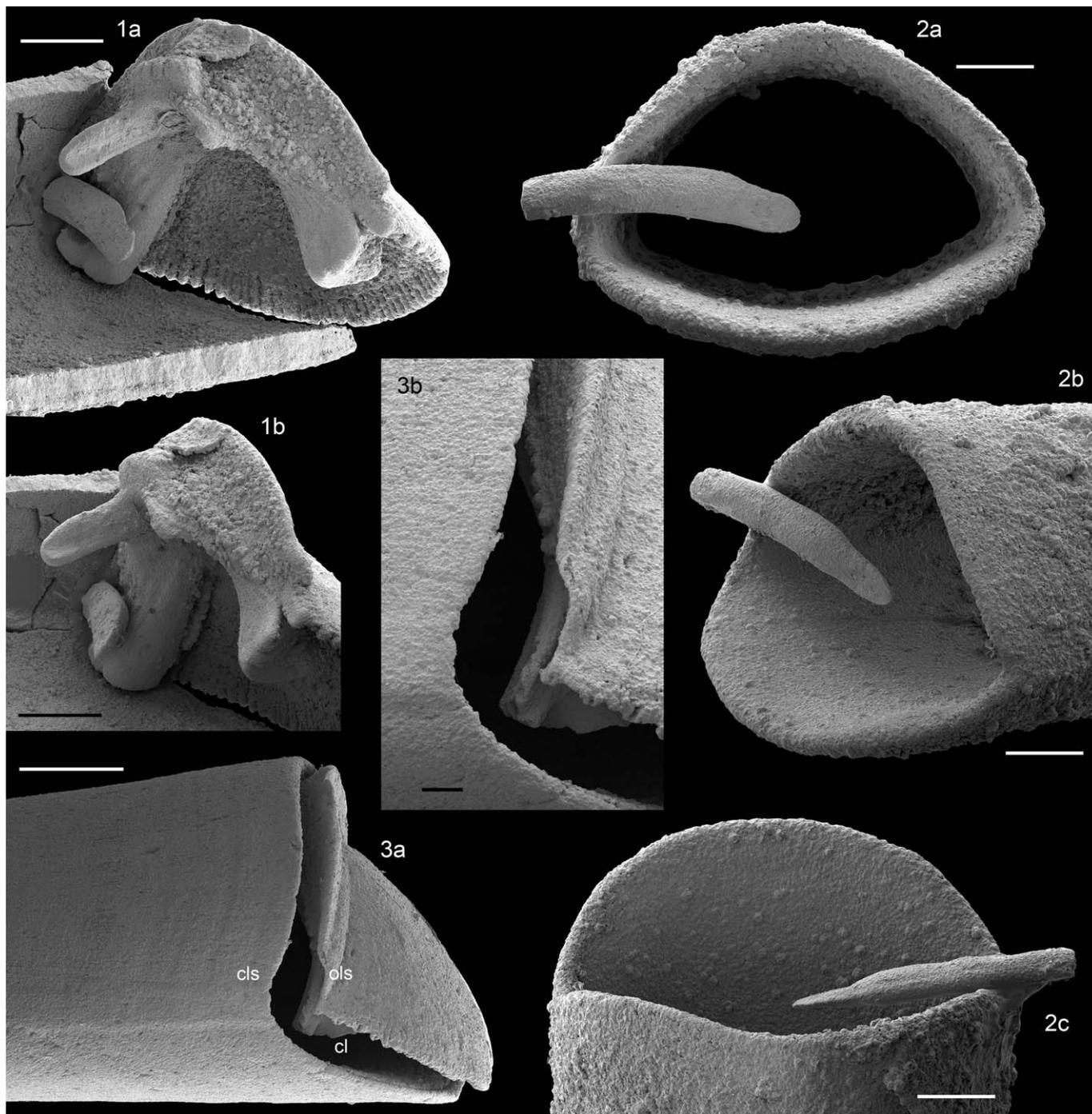


FIGURE 6—Composite specimens, reconstructed from loose skeletal elements to illustrate different aspects of hyolithid life position. 1, internal view of articulated conch (sample G93-954LJ, locality Nyan 2, SMNH Mo 167747), operculum (sample G93-954LJ, locality Nyan 2, SMNH Mo 167748) and left helen (SMNH Mo 167749); 2, conch (sample G93-954LJ, locality Nyan 2, SMNH Mo 167750) and right helen (sample G93-950LJ, locality Nyan 2, SMNH Mo 167751) in life position; 2a, anterior view; 2b, antero-lateral view, aperture to the left; 2c, dorsal view, aperture upwards; 3, articulated conch (sample G93-954LJ, locality Nyan 2, SMNH Mo 167752) and operculum (sample G93-950LJ, locality Nyan 2, SMNH Mo 167753); 3a, general view of specimen, lateral view, aperture to the right; 3b, close up of lateral slit (the gap through which helens extend outside the conch), note how the small tubercles lining the margin of the clavicle disappear at the level of the lateral sinus. Scale bars are 0.5 mm for 1, 2, 3a, and 100 μm for 3b. Abbreviations: cl=clavicle; cls=conch lateral sinus; ols=operculum lateral sinus.

morphology of hyolithid opercula is highly variable, and therefore unique for each species. However the general features observed in the present material are relatively common among hyolithids. A pair of robust, diverging cardinal processes are particularly prominent, and overlain by a square, blunt central process (Figs.

3.1a, 3.3, 3.4, 3.5a, 3.5b, 6.1a, 6.1b). A single pair of clavicles develops at the fold between the cardinal and conical shields (Figs. 3.4, 3.5a, 6.1a, 6.1b, 6.3a, 6.3b). At the level of the lateral sinus both the cardinal shield and clavicles form a mild, horizontally oriented fold to accommodate the helens (Figs. 3.4,

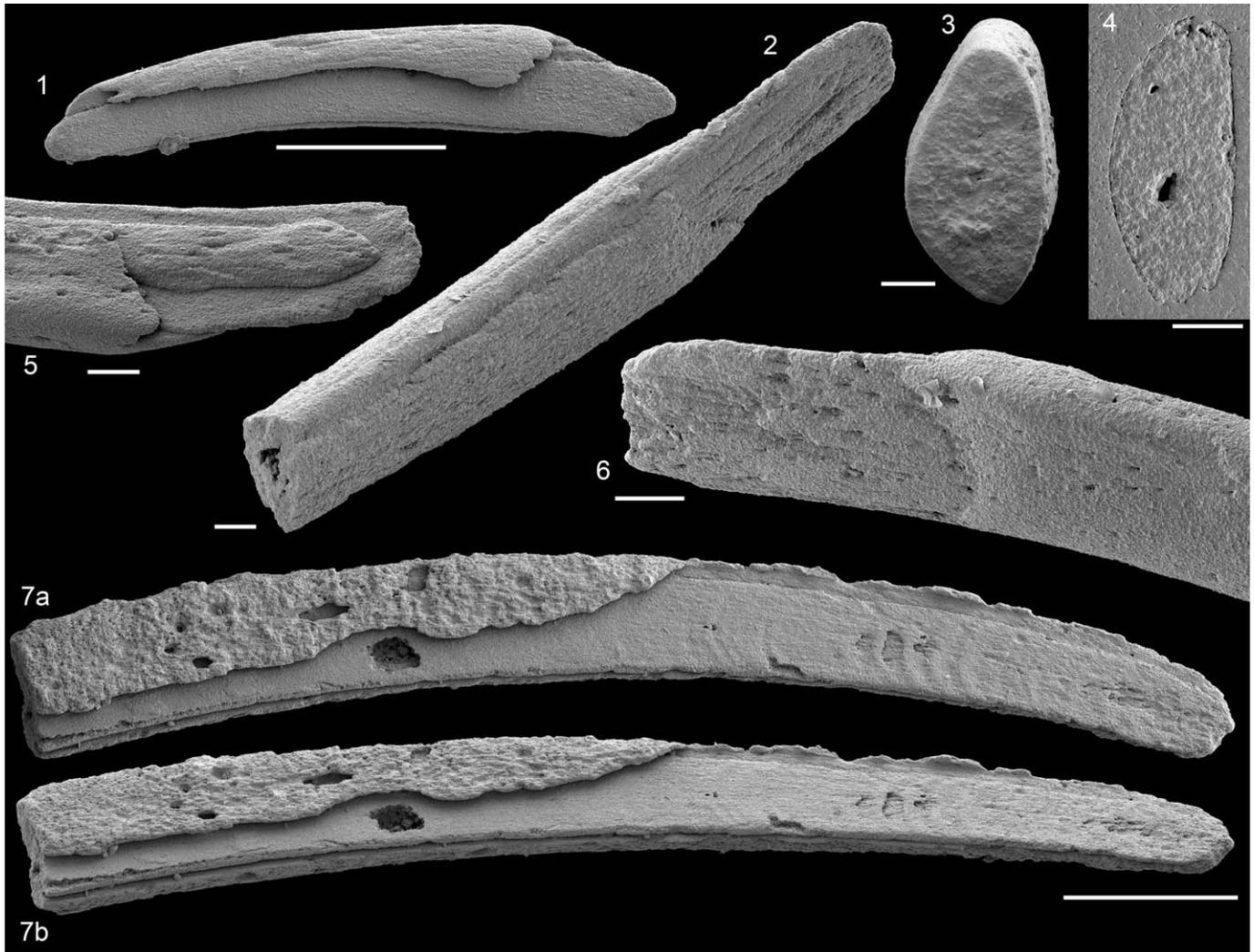


FIGURE 7—Different aspects of helen morphology and structure. 1, 2, 5, sample G72-13LJ, locality Nyan 2: 1, partly degraded helen showing concentric layering, SMNH Mo 167754; 2, proximal portion of helen in ventral-posterior view, right helen, SMNH Mo 167755; 5, partly degraded helen showing concentric layering, SMNH Mo 167758; 3, 4, cross-sections of helens, ventral edge downwards, anterior face to the left: 3, sample G93-954LJ, locality Nyan 2, SMNH Mo 167756; 4, G89-798LJ, locality Källdar 3, SMNH Mo 167757; 6, 7, sample G93-950LJ, locality Nyan 2: 6, proximal portion of helen in posterior view, right helen, dorsal edge upwards, SMNH Mo 167759; 7, partly degraded helen showing concentric layering and coherent central lamella, SMNH Mo 167760. Scale bars are 0.5 mm for 1, 7 and 100 μ m for 2–6.

3.5a, 6.1a, 6.1b, 6.3a, 6.3b). Lining the dorsal margin of the clavicles there is a row of small tubercles, which stops abruptly at the level of the above mentioned fold (Figs. 3.4, 6.3a, 6.3b).

As seems to be the case for many hyolithids, the commissure slit (the gap through which the helens exit the conch) slopes posteriorly (Fig. 6.3a, 6.3b), indicating that the helens were oriented with their dorsal edge tilting forwards when the conch was closed (Martí Mus and Bergström, 2005).

The smallest recovered conchs are those preserving the protoconch (illustrated in Fig. 1); the largest relatively complete ones measure \sim 12 mm. A few fragments of larger conchs occur in the samples but are too incomplete for identification. Small opercula are often fragmentary, but the smallest developmental stage of the operculum is recorded in a few specimens as discussed above (Fig. 3.1a, 3.1b, 3.2). The largest operculum belonging to the species described herein measures \sim 4.5 mm (as mentioned above, there are larger opercula of a second species) and must have belonged to a conch slightly larger than 12 mm.

Helens.—Complete and fragmentary helens of different sizes abound in the present material, many of them preserving the

fragile proximal end. The smallest complete helen recovered measures 0.7 mm in length (Figs. 4.1, 5.1a, 5.1b). The largest well-preserved, apparently complete helen measures \sim 4 mm in length, although there are more robust, fragmentary specimens that must have been considerably longer. As they grow in length, the helens develop a relatively open (of small constant angle) logarithmic spiral (Fig. 4). Also, the largest specimens are clearly, but gently, bent backwards. No obvious helicoidal twist can be observed in any of them. Most specimens appear to have a somewhat worn distal edge (Fig. 4); it is unclear if this feature is original or the result of sample processing. The cross section of the fully-grown helen approximates to an ellipse (Fig. 7.2–7.4), but has a marked antero-posterior differentiation with bulging anterior and flat posterior faces. The anterior face may be symmetrical or have the bulge slightly displaced ventrally. Also it may be evenly convex or slightly sinusoidal with a shallow recess above the central bulge (in one specimen recesses occur both above and below the central bulge; Fig. 5.5). The posterior face can be flat or slightly convex or concave.

The proximal portion of the helen is wedge-shaped, sharply increasing in width distally, and clearly represents the growing

portion of the helen (Fig. 5). Shell deposition seems to be completed a short distance from the proximal margin (at the end of zone 2; Fig. 8.2, 8.3), and the rest of the helen is a regular, curved blade that tapers gently in all dimensions towards the distal end (Fig. 4). The proximal margin is thin and rounded or subrectangular (with rounded corners) in plane view (Figs. 4, 5.1b, 5.3b–5.7b, 6.2a, 7.2, 7.6, 8.1). Starting at the margin, the helen grows in thickness and height rather steeply but not homogeneously. The increase in thickness occurs mostly on the anterior face, and the increase in height is more pronounced dorsally (Figs. 5, 6.2a–6.2c, 7.2, 7.6, 8). The growing portion of the helen can be divided in two zones, a proximal one (zone 1; Fig. 8.2, 8.3), where shell deposition is uneven (see below) and mostly restricted to the anterior face and a second zone (zone 2; Fig. 8.2, 8.3) where deposition appears more homogeneous and takes place all around the helen perimeter. Helen growth seems to have been completed by the end of zone 2 (Fig. 8.2, 8.3), where its perimeter is largest. An intriguing pattern of shell deposition can be observed in the first zone. Shell material is deposited evenly at the most anterior margin; however, soon afterwards, deposition becomes restricted to the central area of the anterior face, which results in the formation of two marginal embayments located roughly one above the other. The embayments are not entirely symmetrically situated since the ventral one is always slightly displaced distally. This pattern can be observed in all well-preserved helens, including the smallest specimens recovered (Figs. 5.1b, 5.3b–5.7b, 8.2, 8.3). On the posterior face, shell deposition is limited proximally, abruptly increasing at the beginning of zone 2 (Figs. 5.2, 7.2, 7.6, 8.3). Surface preservation is too coarse for details such as growth lines to have been preserved, however one of the best-preserved specimens shows one (or maybe two) faint transverse line which could represent a growth line (Fig. 5.3c). This line occurs a short distance after shell deposition is completed (Fig. 8). If this line represents the first growth line, and therefore marks the point at which the helen is extruded from soft tissue, then there is a short zone (zone 3; Fig. 8) where the helen is still encased in soft tissue but where no significant shell deposition occurs.

Shell microstructure details are lacking in our material, however many degraded specimens show the shell material arranged in concentric ‘layers’ (Fig. 7.1, 7.5, 7.7a, 7.7b). Some of these specimens illustrate a central, thin and ‘tall’ lamella that extends along the whole length of the helen and is surrounded by successive concentric layers (Fig. 7.7a, 7.7b). The central lamella is secreted at the most anterior margin (at zone 1a; Fig. 8) and remains a distinct, coherent layer throughout the helen blade. It is particularly apparent along zone 1 where it constitutes a base for subsequent shell accretion (Fig. 5.3b–5.7b, 8). Apart from this layering, helens appear as generally massive skeletal elements showing the same chemical composition as the co-occurring conchs and opercula.

HYOLITHID FUNCTIONAL MORPHOLOGY

Helen growth and articulation with the other skeletal elements.—Martí Mus and Bergström (2007) proposed a model of helen growth based on previous ideas (Yochelson, 1974; Runnegar et al., 1975; Marek et al., 1997) and novel observations of helen microstructure. The model was one of accretionary growth. Shell material was accreted at the proximal end (which was encased in soft tissue) while the helen was pushed outwards, thus growing in length (Yochelson, 1974; Runnegar et al., 1975; Marek et al., 1997). Martí Mus and Bergström (2007) particularly showed that the first shell material to be deposited formed a central, thin but ‘tall’ lamella, probably rich in organic matter, around which additional shell material was gradually accreted. This lamella was visible as a central core in a specimen with

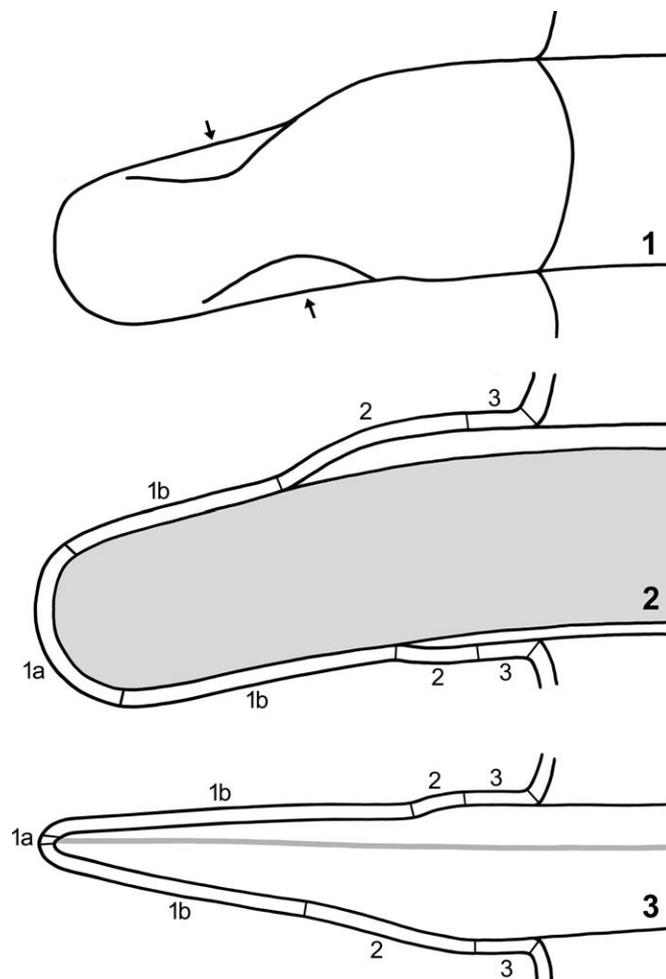


FIGURE 8—Schematic drawings of the proximal, growing portion of helens illustrating different aspects of the growth process. In all drawings the proximal margin is oriented to the left of the image. 1, anterior view showing external morphology, dorsal edge to the top of the image, arrows point to marginal embayments interpreted as muscle attachment sites, transversal line to the right indicates the margin of the encasing soft tissue (to the left the helen is encased in soft tissue, to the right it is naked and exposed to the external environment), limit of soft tissue is inferred from possible growth line in specimen illustrated in Figure 5.3; 2, longitudinal, dorsoventral, section of helen, with encasing mineralizing epithelium, dorsal to the top of the image; 3, longitudinal, anteroposterior section of helen, anterior face of the helen facing downwards. Numbers indicate distinct growth zones along the proximal portion of the helen. Central lamella is colored gray.

preserved shell microstructure (Martí Mus and Bergström, 2007, fig. 2D). The new data presented herein supports the above model in all its details and particularly illustrates the formation of the central lamella and its likely role as a template for further shell accretion.

The material presented herein provides additional information regarding some peculiarities of the growth process. In particular it suggests that shell deposition was constrained on the first portion of the growing part of the helen, in zone 1 (Fig. 8). While in zone 2 the shell accretion pattern conforms to the fully-grown (external) morphology of the helen, in zone 1 shell deposition follows a pattern which appears unrelated to the morphology of the fully-grown helen. Instead, it seems the result of avoiding shell deposition in two well-defined, consistently situated, semi-circular areas on the dorsal and ventral margins of the anterior-most part of the helen. While the reasons for this pattern are enigmatic, they seem unrelated to helen growth itself and may be

related to helen function instead. Because of this, and because it is consistent with previous knowledge of the helen's life position and functional morphology (Martí Mus and Bergström, 2005), we propose that these two areas could represent sites for muscle attachment. As muscle attachment sites they would be peculiar for interfering so markedly with shell growth, but they would be ideally situated to provide a good leverage and to articulate the helens to the other skeletal elements. Muscular attachments in shelled lophotrochozoans do not usually significantly interfere with shell growth, since they tend to occur in areas of the shell where growth is basically completed and restricted to the deposition of thin, internal shell layers. However, helens have a unique mode of growth and lack clear analogues among other organisms, which makes comparisons with other skeletal elements difficult. Both in the conch and operculum of hyolithids, muscle attachment sites occur at such distance from the margin so as not to interfere with marginal shell accretion (Martí Mus and Bergström, 2005). However, deposition of thin layers of shell, continually remodeling the inner surfaces of the conch and operculum, takes place in many hyolithid species and is responsible both for obliterating old abandoned attachment sites and for making possible the preservation of functional muscle attachment sites as slightly depressed areas where inner shell deposition is prevented. Muscle scars have not been observed in any of the conchs or opercula in the present material, perhaps because surface preservation is too coarse. The putative muscle attachment sites on the helens are therefore likely preserved precisely because they interfere with helen growth and are thus more conspicuous.

The discussion that follows is based on the present knowledge regarding the articulation, relative proportions, and life position of the different elements of the hyolithid skeleton, as well as on the evidence that suggests that all hyolithids shared a common muscular system (Martí Mus and Bergström, 2005). As illustrated in Figure 6.2a, the growing portion of the helen is proportionally short (representing less than a quarter of the conch width) and the portion of the helen encased in soft tissue (as indicated by the possible growth line at the end of zone 3; Fig. 8), seems to be accordingly short. Two other specimens have been illustrated in the literature (Butterfield and Nicholas, 1996, fig. 4.1, 6; Martí Mus and Bergström 2005, text-fig. 16A, 16C) where the proportions of the part of the helen that was attached to soft tissues could be inferred, since both the proximal margin and the beginning of the growth lines are preserved. In both, the proportions are similar to those of the specimen illustrated here (particularly the ratio between the length of the smooth portion of the helen and its height at the level where growth lines begin), suggesting that the part of the helen attached to soft tissue was generally short in hyolithids. However, most articulated specimens consistently show that each helen was inserted inside the conch so as to reach the middle plane (Martí Mus and Bergström, 2005, p. 1160) implying that a portion of the helen that was likely fully-grown and bore growth lines is consistently found inside the conch (Martí Mus and Bergström, 2005; illustrated this possible skeletal configuration in their text-fig. 19D based on observations of a single specimen, also illustrated in text-fig. 16A, 16C). This suggests that helens may have been partly retractable.

The location and morphology of the putative muscle attachment sites on the helens suggests that muscle fibers were attached marginally, holding the helens both ventrally and dorsally. Although the attachment sites are only apparent on the anterior face, muscle fibers could have attached also on the posterior face (grabbing the margins of the helens on both sides) but leave no trace because shell deposition is more restricted there. As it has been described for other hyolithid species and discussed above,

the helens must have fitted the closed conch with their dorsal margin tilted forwards. In this configuration the dorsal and ventral muscle attachment sites would have been oriented antero-dorsally and postero-ventrally, respectively. This suggests that the antero-dorsal muscles may have attached to the operculum and the postero-ventral ones to the conch. The muscle scars which occur on the conical shield of the operculum (Martí Mus and Bergström, 2005, text-figs. 19, 20), particularly the one located on its summit, were perhaps the best situated to hold the muscles which attached to the dorsal edge of the helen. The scars that occur laterally, and relatively deeply, on the conch could have held the muscles attaching to the ventral edge of the helens.

The articulated skeleton at work.—The marginal and proximal location of the putative muscle attachment sites is ideal to allow a wide (and independent) range of movements for the helens, which could act as oars, as stabilizers, and also orient the aperture to currents and lift the anterior part of the conch above the sea floor (Marek, 1963; Marek and Galle, 1976; Marek et al., 1997; Galle and Parsley, 2005). Regarding their action as oars, the characteristic shape of the helen cross section, with a convex anterior face and a flattened posterior one, could be relevant. During the backward stroke, the posterior, flat, face of the helens would 'push' the sediment backwards, allowing for maximum sediment displacement. During the forward stroke, on the other hand, the helen would approach the sediment with its convex surface, therefore meeting less resistance to the movement. However, this type of cross section is not universal among hyolithids, and some species have markedly flat, blade-like helens (Martí Mus and Bergström, 2005, 2007). Evidence suggesting that hyolithids were capable of actively orienting themselves to currents comes mostly from the presence of bryozoa and tabulate corals living as epibionts on hyolithid conchs (Marek and Galle, 1976; Marek et al, 1997; Galle and Parsley, 2005; Malinky, 2006). This evidence has also strengthened the view that hyolithids were filter (or suspension) feeders. Although the tabulate corals restricted their distribution to the dorsal and lateral sides of the helen conch, bryozoa grew as well on the ventral side of the conch (Galle and Parsley, 2005; Malinky, 2006). The bryozoa zooecia colonizing the ventral side of the hyolithids were smaller in size than those of the dorsal side, reflecting different living conditions. Based on the above evidence, Galle and Parsley (2005) have suggested that hyolithids could have used their helens to elevate the anterior part of the conch above the substrate, therefore creating a cryptic environment for the epibionts.

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