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DEVONIAN HYOLITHS IN SOUTH AFRICA, AND THEIR PALAEOENVIRONMENTAL SIGNIFICANCE.

by

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ABSTRACT

Hyoliths, an extinct group of molluscan or mollusc-like invertebrates that secreted elongate conical shells, are relatively uncommon and often overlooked members of Middle Palaeozoic marine fossil assemblages. They have been recorded from a number of widespread localities in the argillaceous Gydo and Voorstehoek Formations of the Bokkeveld Group. Most of the specimens are crushed or are without opercula and other taxonomically important features of the aperture and therefore must remain indeterminate. The hyoliths occur in bioturbated mudstones along with brachiopods, trilobites, bivalves, gastropods, crinoids, cephalopods and conulariids. This assemblage is interpreted as representing an inner shelf community that occupied quiet waters below wave base seaward of the prograding Bokkeveld deltas. Unlike many of the other elements of the shelf community, the epifaunal, deposit-feeding hyoliths are not found in the shallower water communities and can be taken as diagnostic of the offshore environments.

INTRODUCTION

Hyoliths were a group of marine invertebrate animals that occupied calcareous, probably aragonitic, bilaterally symmetrical elongate conical shells commonly 15 mm-30 mm long. They are present in pre-trilobite faunas of the USSR (Rozanov *et al.*, 1969) and were abundant during Cambrian and Ordovician times. They occur less commonly in younger Palaeozoic rocks, finally becoming extinct in the late Permian (Downie *et al.*, 1967).

The exact taxonomic position of these creatures has been the subject of debate for more than a century. Early workers included them among the pteropod gastropods along with such diverse forms as conulariids and tentaculitids. Others viewed them as cephalopods or operculate worm tubes (Fisher, 1962). More recently the tendency has been to regard them as an extinct class of molluscs (Downie *et al.*, 1975; Marek and Yochelson, 1964; 1976) or, alternatively, as a separate phylum of their own (Runnegar and Pojeta, 1974; Runnegar *et al.*, 1975). In a recently published text-book, the hyoliths are indeed treated as being sufficiently different from the molluscs to warrant their inclusion as a separate phylum that is thought to share a distant common ancestry with molluscs (Pojeta, 1987).

The South African specimens are not well enough preserved to add to this debate so this author takes the more conservative approach and regards hyoliths as an extinct class of molluscs that can be divided into two orders: Hyolithida Matthew, 1899 and Orthothecida Marek, 1966.

Morphologically the two orders are quite similar: both possess a bilaterally symmetrical exoskeleton consisting of a tapering conch with an aperture at the larger, anterior end, and an operculum that closes the aperture. The main difference between the orders is found in the form of the aperture and operculum, but in addition the hyolithids possess a pair of thin scimitar-shaped calcareous appendages, called helens, placed between the operculum and the conch (fig. 1a).

At the anterior end of the hyolithid conch is a shelf-like extension of the ventral surface, the ligula, so that the aperture is not in a single vertical plane but has a marked angulation. The operculum that fits over this aperture also has an angulation so that it extends to the anterior margin of the ligula. In contrast, the orthothecid conch lacks a ligula so that the aperture does lie in a single more-or-less vertical plane. The orthothecid operculum fits within the aperture rather than butting against the peristome as in hyolithids (fig. 1b). Aspects of the biology of hyoliths have been described and discussed by Runnegar *et al.* (1975) and Marek and Yochelson (1976).

They were almost certainly deposit-feeders as evidenced by the gut fillings preserved in a number of occurrences (see Pojeta, 1987). The general consensus is that they lived unattached epifaunally and were essentially sedentary although they may have been capable of very slow, inefficient locomotiom (Marek and Yochelson, 1976).

HYOLITHS IN SOUTH AFRICA

Hyoliths have been recorded from the Gydo Formation and the Voorstehoek Formation of the Bokkeveld Group

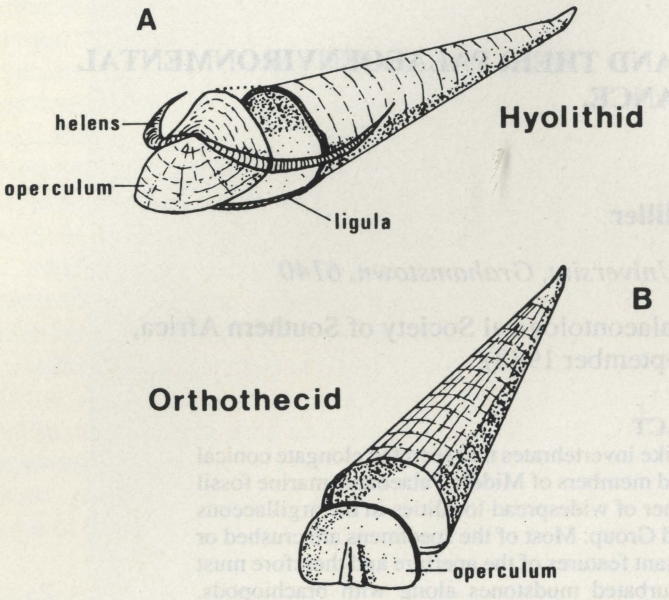


Figure 1. Diagrammatic reconstruction of (a) a hyolithid, and (b) an orthothecid, showing the main features of and principal differences between the two orders. (Based on Pojeta, 1987).

(Salter, 1856; Reed, 1925; Theron, 1972; Oosthuizen, 1984). Although often overlooked members of the fauna, they are now known from Clanwilliam and Ceres in the west, to the Kaba Valley in the Alexandria district in the east, where they are locally fairly common.

Salter (1856) provided the original description of *'Theca' subaequalis*. He also identified another specimen as a worm tube, *Serpulites sica*, but the woodcut illustration of this looks remarkably like a hyolith. Reed (1925) lists two species, *Hyolithes subaequalis* (Salter) and *Hyolithes d'orbignyi capensis* Reed; in addition to these Oosthuizen (1984) lists *Hyolithes schenki* Ulrich and *Orthotheca steinmanni* Knod as well as five further unnamed species of *Hyolithes* and one unnamed species of *Orthotheca*. It is doubtful whether there truly are as many as eight species of *Hyolithes* and two of *Orthotheca* in the Bokkeveld Group. Indeed, Reed (1925: 102) points out that *H. subaequalis* from South Africa and *H. schenki* from Bolivia are probably identical. *H. d'orbignyi capensis* is distinguished from the Bolivian form *H. d'orbignyi* Kozlowski on the basis that the longitudinal ornament, as seen on the only specimen, is not as strongly developed as the transverse ornament, as is the case with the South American species (Reed, 1925: 102).

Identification of imperfect specimens is extremely difficult especially when the diagnostic characters of the apertural region are not preserved. Without such characters assignment to either of the orders is virtually impossible. Malinky (1987: 944) states that only specimens with complete apertures, or having growth lines which follow the outline of the apertural morphology, permit confident distinction between hyolithids and orthothecids. For almost a century *Hyolithes* Eichwald 1840 and *Orthotheca* Novak 1886 were the only generic names given to hyoliths. The former was diagnosed as having a sub-triangular transverse cross-section, while the latter had circular or oval transverse outlines. Following the work of Syssoiev (1958), these generic concepts have been revised and it is now known that some orthothecids have subtriangular transverse shapes.

The specimens currently available to the author are, unfortunately, rather poorly preserved, most having been crushed to a greater or lesser degree. No opercula have been identified and the details of the apertures are obscure, hence the specimens must remain indeterminate.

PALAEOECOLOGY AND ENVIRONMENTAL SIGNIFICANCE

Notwithstanding the difficulties associated with their taxonomic assignment, the presence of hyoliths in a fauna can be of use to the stratigrapher. Hyoliths occur with other fossils that are taken to be indicative of normal marine salinity, such as brachiopods and trilobites, and by inference are thought, themselves, to indicate such conditions.

Within the marine environment hyoliths seem to have favoured rather quiet low energy conditions. Certainly the majority of post-Cambrian specimens have been recovered from shales (Marek and Yochelson, 1976: 68). Many Cambrian species are known from limestones while a few have come from sandstones. In the latter case the shells may have been entrained by storm-driven currents and deposited along with the coarsest fraction of the sedimentary load (Marek and Yochelson, 1976: 68). In general, therefore, it seems that hyoliths lived for the most part in rather quiet settings, probably below wave base, in which fine-grained sediment was deposited. This accords well with their interpretation as epifaunal deposit-feeders (Runnegar *et al.*, 1975; Marek and Yochelson, 1976). Malinky *et al.* (1987), in discussing the palaeoecology of *Hallotheca* (Hyolithida from the Middle Devonian of central New York), concluded that the fine silt in which the specimens were found suggested that the animals lived in moderately deep water, of the order of 15 - 30m deep. The abundant fauna accompanying *Hallotheca* suggested fairly well oxygenated conditions.

The South African specimens all come from the two lowest argillaceous formations of the Bokkeveld Group. At those localities from which they were taken, they were part of an abundant and diverse invertebrate fauna. In a recent analysis of the Bokkeveld fauna, Hiller and Theron (1988) recognise four benthic communities that occupied different sites within the deltaic setting in which the rocks were deposited. Hyoliths belonged to the shelf community that occupied the deeper quieter waters of the inner shelf in front of the deltas. This community, which lived on or within a relatively firm but muddy substrate, is the richest and most diverse of the four communities. It comprises, in addition to

hyoliths, brachiopods, trilobites, bivalves, gastropods, echinoderms, corals, bryozoans, conulariids and cephalopods.

Alhough this total assemblage is fairly distinctive and can be recognised as belonging to the shelf environment, many of the elements in the assemblage also occur in the shallower water communities, some of which are associated with fine-grained sediment. However, hyoliths have not been recorded from any shallower community and their presence in the fauna can be used to distinguish the shelf community. Malinky et al. (1986) have used the presence of hyoliths to interpret dark grey shales as being of offshore origin rather than lagoonal shoreline deposits.

SYSTEMATIC PALAEONTOLOGY
Class HYOLITHA Marek, 1963
Order HYOLITHIDA Incertae sedis
"Hyolithes"? subaequalis (Salter, 1856)
(Figure 2 A-C)

1856 *Theca subaequalis* Salter: 215, figs. 3,4.
1856 *Serpulites sica* Salter: 222, pl. 25, fig. 19.
?1893 *Hyolithes schenki* Ulrich: 37, pl. 3, fig, 9.
1904 *Hyolithes subaequalis* (Salter); Reed: 247.
?1908 *Hyolithes schenki* Ulrich; Knod: 517, pl. 23, fig. 7.
1908 *Hyolithes subaequalis* (Salter); Reed: 387,
1913 *Hyolithes subaequalis* (Salter); Clarke: 163, pl. 2, figs. 7,8.
1925 *Hyolithes subaequalis* (Salter); Reed: 102.

Type

The specimens described by Salter are reported by Reed (1925) to be in the British Museum (Natural History) but their existence has not been verified by the author.

Material

This description is based on material from the locality in the Voorstehoek Formation in the Kaba Valley near Alexandria, Eastern Cape. In all 50 specimens, preserved

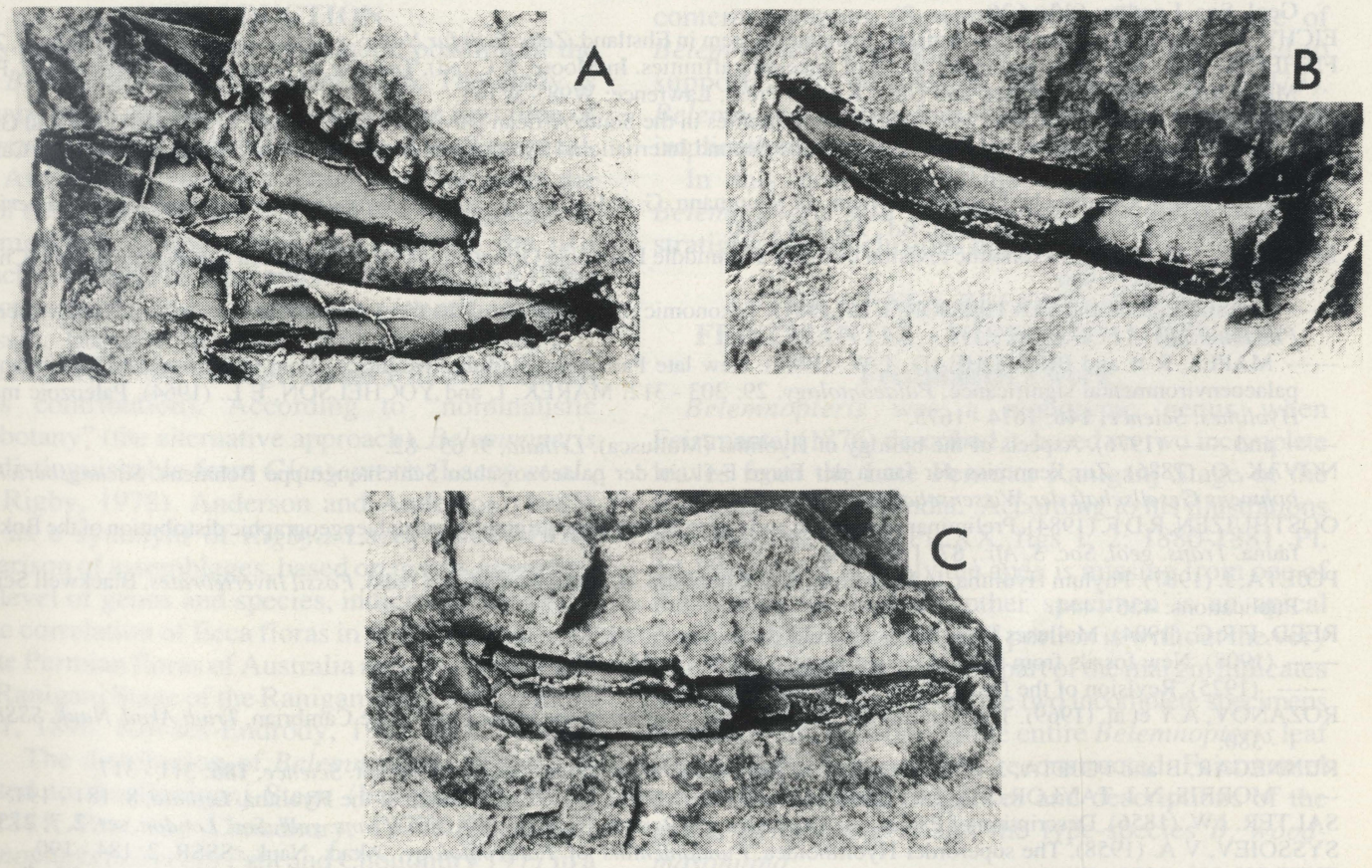


Figure. 2: A-C *"Hyolithes"? subaequalis* (Salter, 1856).
A lateral view of two broken conches. AM 4813, x4;
B lateral view of conch, AM 4814, x5;
C ventral view of a slightly crushed conch, AM4815, x5.;
Specimens are in the Albany Museum, Grahamstown.

as natural internal and external moulds, were used in the description. The specimens are housed in the Albany Museum, Grahamstown.

Description

Tapering conical shells up to 25mm long with maximum diameter up to 3,5 mm at anterior end and often gently curved towards dorsum. Transverse outline subcircular at posterior end, becoming ovoid to subtriangular anteriorly where venter is flat to gently concave and dorsum is broadly rounded. Complete aperture and operculum unknown. Very faint transverse growth lines are the only ornament observed.

DISCUSSION

Without a complete aperture or operculum it is impossible to assign the present specimens to either of the two hyolith orders. However, in his description of *H. subaequalis* from Brazil, Clarke (1913: 164) mentions that the "dorsal face projects at the stoma". Clarke seems to have used the terms dorsal and ventral the wrong way round in his description so that a projection of the ventral surface at the aperture may refer to the presence of a ligula. Unfortunately, Clarke's illustrations are of no help in determining whether the specimens are hyolithids or orthothecids.

Ulrich's (1893) description of *H. schenki* is of a shell very similar to *H. subaequalis* but he points out that the South African form seems to have more rounded lateral edges, a more convex venter and flatter dorsum than his Bolivian specimens. It may be that these differences can he accounted for by differences in preservation but without a modern re-description of the material it is not possible to substantiate Reed's (1925) contention that the two species are identical. Certainly *H. schenki* is a hyolithid. The growth lines on the specimens described by Ulrich (1893) indicate the presence of a ligula and further specimens described by Knod (1908) show a typical hyolithid operculum.

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