range of −190° to 300°C, can be used with internal electrical heating to temperatures around 1500°C. With transient heating techniques much higher peak temperatures could be reached satisfactorily.

F. P. BUNDY
General Electric Research Laboratory, Schenectady, New York

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29 October 1964

Paleozoic Mollusk: Hyolithes

Abstract: *An unusually well-preserved Ordovician fossil from Czechoslovakia shows that the enigmatic paired structures once thought to be outgrowths of the operculum of* Hyolithes *are really independent structures lying between the operculum and the aperture of the shell. The find seems to provide conclusive proof of the morphologic uniqueness of hyolithids.*

A recent textbook on paleoecology (*1*) summarizes conclusions of a paper on *Hyolithes* as follows: "Yochelson (1961) reexamined the Middle Cambrian fossil *Hyolithes carinatus* from the Burgess shale of British Columbia. Walcott had interpreted two structures at the apertural end of this shell as support for the fins like those of modern pteropods. Yochelson showed, however, that the structures in question were attached to the operculum and must have functioned as props to hold the operculum open during feeding. Thence he deduced that that animal could not have moved very much or the props would not have functioned. Yochelson therefore concluded that *Hyolithes* was virtually a sedentary benthonic organism, not planktonic as had formerly been supposed." The presumption regarding "outgrowths of the operculum" and their function was only one of the lines of evidence suggesting a benthonic habitat; other points were the large sizes and thick shells of some hyolithid specimens, the curved ventral surface, the anterior ventral shelf-like extension of the aperture in many genera, and the presence of a calcified operculum. The Burgess specimens are preserved essentially as two-dimensional compressions. Although the conclusion quoted seems to be mainly correct, the discovery of a remarkably preserved specimen shows that Yochelson's morphologic interpretation (*2*) was in error.

A latex cast of the external impression of a hyolithid from the Late Ordovician (Caradocian) Chlustina beds from Prague, Czechoslovakia, is portrayed in Fig. 1. The operculum which covers the lower end of the tubelike shell shows concentric growth lamellae and is curved to cover the rounded anterior shelflike extension; the outer edge of this ventral surface may be seen at the lower left, just below the operculum. Only the anterior part of the tubelike shell is preserved; growth lines are prominent and closely spaced on the dorsum.

To the left, between the operculum and the main part of the shell, is the structure which Yochelson designated a prop. This structure is evidently not an outgrowth from the side of the operculum, but is a third hard part, physically independent of both operculum and tube; the inner tip of this structure was probably attached to the inner surface of the operculum by ligaments or muscles. Earlier observations indicate that such structures are paired. In this specimen the critical part of the other side of the aperture is not preserved; a reconstruction is shown in Fig. 2. The length and curvature of the paired support is reconstructed partly from Middle Cambrian specimens figured by Yochelson (Fig. 3), but mainly from unbroken isolated structures which almost certainly belong to the Czechoslovakian species.

To the best of our knowledge, the illustrated specimen is the only one which unequivocally demonstrates the relation of these paired structures to the other two hard parts. One specimen in the Naturhistoriska Riksmuseet of Sweden shows the cross section of a structure between the operculum and shell (*3*). Although the isolated structures are not uncommon as fossils in the Cambrian, associations of the three types of hard parts are exceedingly rare. To the few occurrences noted by Yochelson, Marek (*4*) added several listings from the Paleozoic

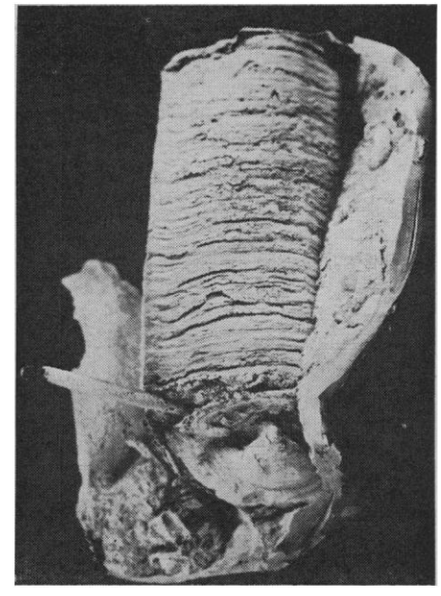

Fig. 1. Latex replica of an external mold of *Hyolithes striatulus* (Barrande), 1847; approximately × 3. Specimen in the collections of the Geological Institute, Czechoslovak Academy of Sciences, Prague.

strata of Czechoslovakia; although rare, occurrences of the structures are widely distributed geologically and geographically.

Among other characteristic features of the hyolithid operculum are elongate paired depressions on the interior of the operculum. Marek (*4*) surmised that these depressions, commonly reflected as bulges on the exterior of the operculum, accommodated the interior ends of the supports, but he was not able to prove this point conclusively before the collection of the illustrated specimen. Despite paucity of direct evidence, there is now sufficient indirect evidence to conclude that the paired structures are characteristic of the entire group.

The assumption that the exterior bulges of the operculum essentially reflect the tips of the paired structures aids reinterpretation of their function. First, it is apparent that these struc-

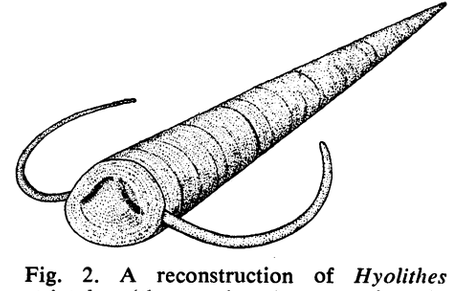

Fig. 2. A reconstruction of *Hyolithes striatulus* (the specimen); approximately natural size.

tures could not be withdrawn fully, if at all, within the shell; this lack of protection is the strongest single argument against the structures being covered by principal soft parts of the animal and used for the primary functions of feeding or respiration. Second, the hypothesis that they simply performed a mechanical propping function must be abandoned. Marek's conclusion (*4*) that they may have served to "pole" the shell slowly across the bottom seems to be the most reasonable explanation.

Fisher (*5*) indicated that the majority of hyolithoids (Hyolithina of his classification) were benthonic, and suggested that the supports served as "stiff leading edges for 'wings' which enabled the animal to move across the bottom like modern skates and rays." His interpretation of the paired structure was that they and the supported fleshy, frill-like, soft parts could be withdrawn into the shell. However, he reconstructed *Pterygotheca* Novak, 1891, the type of the Pterygothecidae, as a swimming form. Unfortunately this and other specimens studied by Novak were destroyed in Prague during World War II. Specimens of at least three species of hyolithids from the type-locality for *Pterygotheca* are overgrown by bryozoans (*3*). It seems more likely that the "swimming frill" characteristic of this genus is simply an overgrowth by a bryozoan colony. The apparent structure of *Pterygotheca* which makes it strikingly different from other hyolithids is thus subject to an alternative interpretation, and if this morphologic interpretation is accepted there is no reason to believe that the ecology of *Pterygotheca* was different from that of *Hyolithes*.

The operculum in another family, the Orthothecidae, is similar to that of hyolithids but does not show paired furrows, and there is no evidence that supports were present in this group. The shell lacks the anterior shelf of the hyolithids but is otherwise similar. Traditionally the two groups have been judged to be closely related. The ecology of the orthothecids is less well known than that of the hyolithids; they were probably benthonic, but not all species can be so assigned with assurance. As the shell is bilaterally symmetrical, Fisher's (*5*) reconstruction of *Circotheca* Syssoiev, 1958, and *Lentitheca* Syssoiev, 1958, living vertically with the aperture up and the shell tip implanted in the mud seems to us to be implausible.

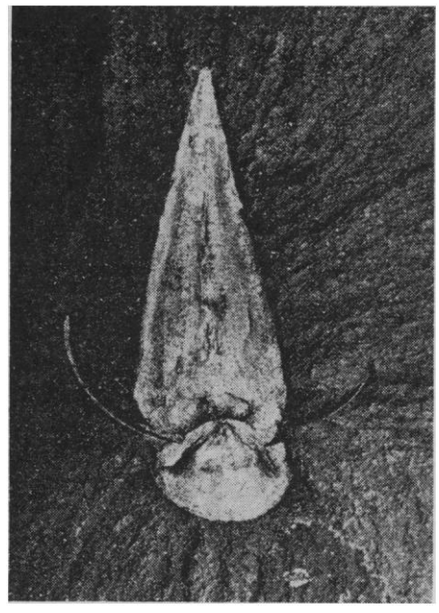

Fig. 3. A specimen of *Hyolithes carinatus* Matthew showing the operculum, paired supports, and shell; the various hard parts are slightly displaced by compression; approximately × 3. From the Middle Cambrian Burgess shale member of the Stephen formation, on the west slope of the ridge between Mount Field and Wapta Pass, 1.6 km northeast of Burgess Pass, above Field, British Columbia, Canada.

Like their ecology, the systematic position of the hyolithids and orthothecids has long been a puzzle. Although they have been placed in various phyla by earlier workers, their general morphology and shell structure are judged to be molluscan (*6*). Recently these animals were included within the class concept of the Coniconchia Lyashenko, 1955, tentatively referred to the Mollusca (*7*). Later they were placed in the Calyptoptomatida Fisher, 1962, which was judged to be an extinct class of Mollusca (*5*). Although we consider this proposal superior to the Coniconchia concept, the class Calyptoptomatida (*8*) still seems to us to be a heterogeneous assemblage; for example, the suborder Matthevina within this class seems to be a totally unrelated molluscan form (*10*). Several other genera included in Calyptoptomatida cannot be assigned to the mollusks without considerable question.

We therefore suggest that the hyolithids and orthothecids be placed in the molluscan class Hyolitha (*9*). The term Calyptoptomatida may be used for members of the class other than hyolithids and orthothecids. As we envision the Hyolitha, following Marek (*4*), it includes essentially all genera listed by Fisher (*5*) within the families Orthothecidae, Hyolithidae, and Pterygothecidae; the individual genera are now under study (*3*). The class Hyolitha may be informally defined as operculate mollusks with an elongate tapering shell, commonly septate in the apical portion. The hyolithids, which constitute the bulk of specimens and the majority of species and genera, are also characterized by a semicircular expansion of the ventral edge of the aperture and by elongate paired structures between the operculum and the aperture.

Regardless of how the enigmatic paired structures are interpreted, they are unique among the mollusks. Even if these structures, which dramatically focus attention on certain of these organisms, were unknown, the morphology of the shell and operculum of *Hyolithes* and its allies—creatures that flourished during the early Paleozoic and became extinct only at the close of that era—is so distinct that these animals deserve to be ranked as a class. If this interpretation of another class is generally accepted, some modification in present-day concepts of the evolution of the phylum will be required.

LADISLAV MAREK
Geological Institute, Academy of Sciences, Prague, Czechoslovakia
ELLIS L. YOCHELSON
U.S. Geological Survey, Washington, D.C.

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8. Despite the close publication dates of the works of Fisher, Yochelson, and Marek, their works on hyolithids were entirely independent at least until late in 1960. The class Calyptoptomatida was proposed by Fisher (*5*).
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