TAXONOMY AND PALEOBIOLOGY OF SOME MIDDLE CAMBRIAN *SCENELLA* (CNIDARIA) AND HYOLITHIDS (MOLLUSCA) FROM WESTERN NORTH AMERICA[1]

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Abstract—Selected hydrozoans and hyoliths from Utah, Idaho, and British Columbia are described or reevaluated as part of a project to document better Middle Cambrian biotic diversity in western North America. Following Yochelson and Gil Cid (1984), specimens of *Scenella* Billings are considered to be chondrophorine pneumatophores rather than shells of either monoplacophorans or gastropods. An emended generic diagnosis is the first to be based on an assignment of *Scenella* to the Chondrophorina. Additional specimens of *S. amii* (Matthew) are described from the Burgess shale of British Columbia. A new species, *S. radians,* is described from Utah. The holotype of *Crania? columbiana* Walcott probably is neither an inarticulate brachiopod nor, contrary to previous reassignment, a *Scenella.*

The new hyolithid genus *Haplophrentis* includes *H. reesei,* new and type species, and *H. carinatus* (Matthew), which is reassigned from *Hyolithes* Eichwald. Incomplete alimentary tracts in three specimens of *H. reesei* are the first soft parts to be described from representatives of the order Hyolithida. Another specimen of *H. reesei* is the first to show helens incompletely retracted within the conch. The helens were probably not attached to the operculum, and their function may have been to support soft respiratory or feeding organs as well as to provide balance. *Hyolithes cecrops* Walcott is suppressed as a subjective junior synonym of *Haplophrentis carinatus.* New specimens of *Hyolithes comptus* Howell and *Hyolithes idahoensis* Resser are provisionally retained in '*Hyolithes*' because of inadequate information about generic characters.

MEDUSOID CNIDARIANS and hyolith mollusks are uncommon in most Cambrian biotas of North America. Selected representatives of these groups from Utah, Idaho, and British Columbia are here described or reevaluated. This is part of a continuing project to document better Middle Cambrian biotic diversity in western North America. The emphasis is on biotas from Utah that have a low potential for preservation. Related recent studies include those by Willoughby and Robison (1979), Robison and Richards (1981), Conway Morris and Robison (1982, 1986, 1988), Briggs and Robison (1984), Robison (1984b, 1985, 1986, 1987), Sprinkle (1985), and Ubaghs and Robison (1985, 1988). New specimens are described from the Spence Shale of northern Utah and southern Idaho and from the Chisholm Formation of west-central Utah. For comparison, selected specimens are described from the Cathedral, Eldon, and Stephen formations of British Columbia.

Few Cambrian cnidarians have been described (Scrutton, 1979; Willoughby and Robison, 1979; Stanley, 1986). Although this is partly due to a low potential for preservation, recent studies (e.g., Yochelson and Stanley, 1981; Stanley, 1982, 1986; Yochelson, Stürmer, and Stanley, 1983; Yochelson, 1984b; Yochelson and Gil Cid, 1984; Stanley and Yancey, 1986) indicate that the pneumatophores of some chondrophorine hydrozoans were firm structures and had a better potential for preservation than previously thought. Some of these pneumatophores were misidentified in earlier literature. Such specimens from the lower Stephen Formation of British Columbia have been assigned to *Scenella amii* (Matthew, 1902). A few specimens of similar age from the Chisholm and Spence formations of Utah are assigned here to the new species *S. radians*.

A new hyolithid genus, *Haplophrentis,* is based on *H. reesei* n. sp. from the Spence Shale. Another species, *H. carinatus* (Matthew, 1899), is present in the Cathedral and Stephen formations of British Columbia. New specimens of two other species, *'Hyolithes' comptus* Howell, 1946, and *'Hyolithes' idahoensis* Resser, 1938a, are described from the Spence Shale.

The Burgess shale is famous for its rich soft-bodied fauna. It has been suggested, however, that the fauna is unusual for the Middle Cambrian in preservation only, not in general

taxonomic content (e.g., Conway Morris, 1981, 1986; Conway Morris and Robison, 1982, 1986, 1988; Robison, 1986). The presence of the same chondrophorine and hyolith genera in the Burgess shale of British Columbia and formations of about the same age in Utah supports that suggestion. Mounting evidence indicates that the biota of the Burgess shale is representative of Middle Cambrian open-shelf environments of North America.

Localities.—Topographic names mentioned from the Wellsville Mountains, Utah, are shown on the Brigham City topographic quadrangle map (U.S. Geological Survey, 1955, 7.5-minute series). All U.S. National Museum of Natural History (USNM) localities cited in this paper, except 37m, are among those described by Walcott (1912b:160–291). USNM locality 37m in northern Idaho was described by Resser (1938a:4). The following localities are identified by numbers from the research files of R. A. Robison:

432. Mudshale talus from about 45 m above the base of the Spence Shale in Antimony Canyon, near locality 781, Wellsville Mountains, Box Elder County, Utah.

781. Dark noncalcareous mudshale, about 4 m below the top of the Spence Shale on the south side of Antimony Canyon; NW sec. 31, T. 10 N., R. 1 W.; Wellsville Mountains, Box Elder County, Utah.

853. Limestone bed 21.3 m above the base of the Chisholm Formation on the east side of the Drum Mountains; NE SE NW sec. 22, T. 15 S., R. 10 W.; Millard County, Utah (Drum Mts. Well topographic quadrangle map, U.S. Geological Survey, 1971, 7.5-minute series).

Repositories.—All described specimens are deposited in either The University of Kansas Museum of Invertebrate Paleontology (KUMIP), Lawrence, the U.S. National Museum of Natural History (USNM), Washington, D.C., or the Royal Ontario Museum (ROM), Toronto.

Terminology.—Most of the morphological terms used for the hydrozoans follow Hyman (1940), Yochelson, Stürmer, and Stanley (1983), Yochelson and Gil Cid (1984), and Oliver (1984). *Anterior* and *posterior* slopes of a pneumatophore are arbitrarily defined as the

shorter and longer slopes, respectively, along the axis of bilateral symmetry, but no implication of function is intended. Terms used for the hyoliths are mostly from Pojeta (1987).

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PALEOBIOLOGY AND TAPHONOMY OF *SCENELLA*

Scenella Billings, 1872, includes small cap-shaped fossils that were previously identified as mollusk shells but are now considered by some authors (Yochelson, 1984b; Yochelson and Gil Cid, 1984; Stanley, 1986) to be internal floats, or pneumatophores, of chondrophorine hydrozoans. New specimens of *Scenella* from western North America provide additional information that supports their identification as pneumatophores and reassignment of the genus as a chondrophorine hydrozoan.

Scenella amii (Matthew, 1902) is widely distributed but generally rare in the lower Stephen Formation of British Columbia. Some bedding surfaces from the Burgess shale locality, however, are covered by numerous pneumatophores (e.g., ROM 25875, 45317, 45319-45322). One dense aggregation (ROM 45319) includes at least 82 specimens in an area of about 30 square centimeters. Some of these drape over one another indicating that, although firm, they were easily deformed (see Fig. 3,*3a,b*).

Scenella radians n. sp. is rare in the Chisholm and Spence formations of Utah. Specimens in limestone of the Chisholm Formation probably retain near-normal relief (see Fig. 4,*2,3*), but those from the Spence Shale are compressed (see Fig. 4,*1,4,5*). All specimens from the Chisholm have been infilled with calcite, whereas those

from the Spence seem to be altered organic films. One specimen from the Spence (see Fig. 4,*4*) has been partially exfoliated near the margin, but it has not broken away cleanly. The film remaining on the steinkern has an irregular surface like that described for chondrophorines and different from that of mollusks (Yochelson, 1984b:149).

Cracks or tears are evident in most specimens of *Scenella radians* from the Spence Shale. Tattered and folded margins (e.g., Fig. 4,*5*, left) indicate damage prior to compaction. No specimen of either *S. radians* or *S. amii* shows chipped and healed margins that are characteristic of mollusk shells (Yochelson, 1984b).

Scenella amii is common in turbidites of the Stephen Formation, and most specimens are oriented with their apices up (Walcott, 1912a:153; Piper, 1972:173). Of the specimens we studied, which are all from talus, more than 90 percent are oriented with apices in the same direction on each bedding surface. An apex-up orientation of mollusk shells is most stable under experimentally produced turbidity currents (Middleton, 1967), and the same may be true of firm cnidarian pneumatophores.

Specimens of *Scenella amii* are usually preserved with the margins somewhat flattened and the apices erect (see Fig. 3,*3a*). The apical region is slightly thicker than the marginal portions in a specimen figured in cross-sectional view by Piper (1972:fig. 4A). The margins of some specimens were probably torn prior to burial, but small cracks around the margins of other specimens may be due to rupturing during dorsoventral compression in shale.

The local aggregation of specimens of *Scenella amii* in the Stephen Formation is not unusual for a medusoid cnidarian. Similar clusters of Paleozoic medusoids on single bedding surfaces have been described by such authors as Huckriede (1967), Pickerill (1982), and Stanley and Yancey (1986). Some concentrations of chondrophorines may represent the remains of flotillas that sank into quiet water following a surface kill (Stanley and Yancey, 1986). Mass strandings of medusoids by onshore winds along modern beaches have also been reported (e.g., Hyman, 1940; Linke, 1956; and Stanley, 1986) and may account for the preservation of large numbers of specimens in some sandstone deposits (Pickerill, 1982). In the Stephen For-

mation, sedimentological evidence of bottom currents (Piper, 1972), the preservation of torn and overlapping specimens, and the mostly convex-up orientation together suggest that the specimens of *Scenella* were concentrated and buried by turbidity currents.

Soft parts probably were not attached to the examined specimens of *Scenella* from Utah and British Columbia at the time of their burial. This is suggested by the fact that comparable soft parts are preserved in a variety of associated fossils from both areas and because cnidarian soft parts have been described from other Paleozoic lagerstätten (e.g., Rauff, 1939; Moore and Harrington, 1956; Foster, 1979; Yochelson, Stürmer, and Stanley, 1983; Oliver, 1984). Upon death of the organism, the chondrophorine pneumatophore tends to separate quickly from surrounding tissue (Yochelson, Stanley, and Stürmer, 1983; Stanley, 1986), which may explain the absence of soft parts in specimens of *Scenella*.

FUNCTIONAL MORPHOLOGY OF HYOLITHID HELENS

Hyolithids from Utah and British Columbia provide new information about the functional morphology of the helens. These paired structures have been variously regarded as appendages, fins, props, oars, and poles, as well as supports for brachia, fins, gills, or the operculum. They are unique to the order Hyolithida and have been the subject of considerable discussion and speculation. Helens are rarely preserved in close association with opercula and conchs, except in such lagerstätten as those of the Spence and Stephen formations.

More than 23 specimens of *Haplophrentis carinatus* (Matthew, 1899) with associated conch, operculum, and helens are known from the Burgess shale. Of these, 11 were figured by Yochelson (1961, pl. 33, figs. 5, 7, 9–12; pl. 34, figs. 3, 5, 6, 8, 9; some being refigured by Marek and Yochelson, 1964, fig. 3; Runnegar and others, 1975, fig. 1; Runnegar, 1980, fig. 1; and Pojeta, 1987, fig. 15.4.I). Eight are in collections of the Royal Ontario Museum (ROM 38610, 45285–45289, 45309, 45312) and other unreferred specimens are in the U.S. National Museum of Natural History. Where substantial postmortem movement of the helens is not obvious, the proximal and more rounded

tips of the helens lie near the apex of the operculum, and usually beneath it. The proximal tips are not consistently positioned from specimen to specimen, and commonly the helens are not symmetrically positioned in single specimens (see Fig. 7,*3*). This may show the original position of the helens relative to the soft parts, the effects of compression, or both. The helens usually curve posteriorly and away from the aperture. One specimen (ROM 45309) has the helens extended anteriorly, but their proximal tips do not lie under the apex of the operculum, which indicates that they were moved from their original positions. Usually, short axes of the helens are slightly inclined toward the conch. Because of a slightly twisted structure, they incline distally into the matrix (see Yochelson, 1961:156; Runnegar, 1980:22). Muscle scars have not been observed on the helens, and none shows soft parts. All known helens from the Burgess shale are on surfaces with at least one operculum and one conch, although isolated helens have been reported from other localities (e.g., Walcott, 1890a, b; Marek, 1963; Yochelson, 1974; Marek and Yochelson, 1976). Eight specimens having opercula articulated to conchs lack visible helens (e.g., Fig. 7,*4,* left).

Single specimens of *'Hyolithes' idahoensis* Resser, 1938a, and *'Hyolithes' comptus* Howell, 1946, have helens preserved in association with an articulated conch and operculum. In both specimens, the helens incline into bedding and their distal tips point toward the apex of the conch. Little of the helens is exposed on the specimen of *'H'. comptus* because they are preserved at a high angle to bedding (see Fig. 8).

Twenty-eight specimens of *Haplophrentis reesei* n. g. and n. sp. from the Spence Shale have an associated operculum and conch. Of these, 13 also have visible helens. All but three show arrangements similar to those of most *H. carinatus*. Soft parts are not preserved about the helens of any specimen even though the conchs of some (KUMIP 204340, 204383, 204384) show remains of gut traces. Two specimens (see Figs. 5,*3,5,* 6,*1,6*) are unusual in having helens that curve anteriorly away from the aperture, rather than posteriorly (see Yochelson, 1961). Two previously figured specimens of *H. reesei* (Gunther and Gunther, 1981, pl. 64, figs. A, B; as reassigned here) also have helens extending

anteriorly. As in the more common orientation, the proximal tips of the helens lie under the apical region of the operculum. These different orientations may indicate that hyolithids were capable of some rotation of the helens and that the helens were not fixed in a posteriorly directed position. Such possibilities are supported by the single described specimen of a hyolithid having hard parts arranged in an uncrushed life association (Marek and Yochelson, 1964, fig. 1; Marek, 1967, pl. 5, fig. 5), in which the right helen is extended in a predominantly lateral direction.

One exceptional specimen of *Haplophrentis reesei* (Fig. 1,*1,* left) has both helens incompletely retracted into the conch. This provides the first evidence that hyolithid helens were retractable. The ends of the helens are obscured by the dorsum of the conch at one end and by the operculum, which lies slightly forward of the conch, at the other end. Because helens taper in width both proximally and distally (Fig. 1,*2*; also Yochelson, 1974, figs. 1a,b,e) and because growth lines are not evident on the helens, it is difficult to determine which end of each helen is beneath the operculum and which is inside the conch. The helens left no impression on the conch during compression, possibly because of their thinness. Nevertheless, the proximal ends of the helens must be inside the conch, otherwise the animal would have had to virtually vacate the conch if it were first to insert the distal ends of the long helens into the conch. Multiple muscle scars inside various hyolithid conchs (Marek, 1963:67, 68, figs. 14, 15; 1967:78, 81, 95, figs. 15, 19, 31) indicate that the hyolithid body was well anchored to the inside of the conch.

Hypothetical stages in protrusion of the helens from the conch are diagrammed in Figure 2. Based on the discussion above, it is reasoned that the proximal ends are within the conch of KUMIP 204343 (Fig. 2,*2*). When fully retracted, the helens probably lay above the pedal mass, near the internal surface of the dorsal conch (Fig. 2,*1a,b*). In the most parsimonious method of protrusion, the ventral edge of the operculum would rotate upward and away from the ligula, permitting the pedal mass to extend onto the shelflike structure. Simultaneously, the helens, which were probably borne on or attached to soft tissue, would first have glided forward out of the conch (Fig. 2,*2*), then

rotated (Fig. 2,*3*) into a position with the proximal ends beneath the operculum and the distal ends pointing posteriorly (Fig. 2,*4a,b*).
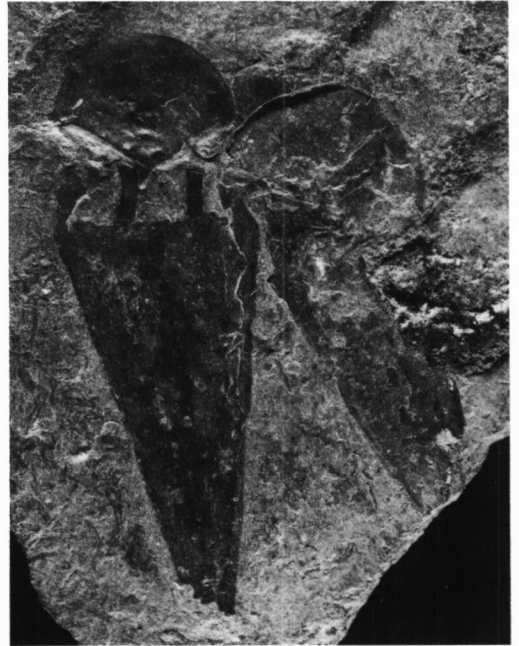
1

2

Fig. 1. *Haplophrentis reesei* n. g. and n. sp. from the Spence Shale, locality 781, Utah; all in dorsal view.——*1*. Specimen (left) having helens incompletely retracted into conch, associated with specimen (right) possibly having helens completely retracted into conch and filaments of the cyanobacterium *Marpolia spissa* Walcott (lower left); KUMIP 204343, ×2.——*2*. Helen showing tapering in both proximal (left) and distal (right) directions; coated with MgO; small articulate brachiopod near posterior edge of helen, probably a fortuitous association; KUMIP 204352, ×4.
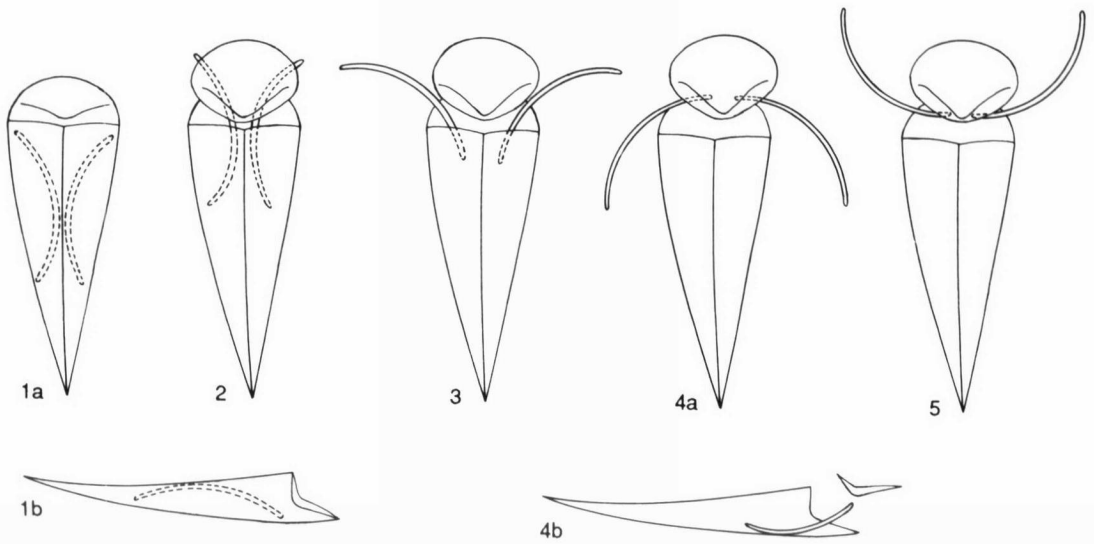
Fig. 2. Hypothetical movement of helens and operculum during protrusion of helens from conch; *1a, 2-4a,* and *5* are dorsal views, *1b* and *4b* are lateral views. Helens are dashed where concealed by other shell.——*1a, b.* Helens fully retracted in conch, lying against or close to slopes of dorsum; proximal ends are toward the apex; operculum is fully closed.——*2.* Operculum opens and helens move forward (compare Fig. 1,*1* left).——*3.* Helens extend further and begin to pivot laterally at proximal ends.——*4a, b.* Helens are fully extended with distal ends pointing posteriorly (compare Fig. 5,*1*).——*5.* Helens are fully extended with distal ends pointing anteriorly, which may be a postmortem configuration (compare Fig. 5,*3*).

Hyolithids also may have been capable of vertical rotation of the helens through about 180° so that they pointed anteriorly (Fig. 2,*5*), but such preservation may be the result of post-mortem deformation.

It has been suggested that the helens propped up a hinged operculum, keeping the aperture open, after a push by the body swung the operculum up and away from the ventral apertural edge of the shell (Yochelson, 1961). These bladed appendages, however, were probably too thin to have provided much support in the soft muds that formed the Spence and Stephen formations. Moreover, the extended pedal mass alone was probably sufficient to support the operculum and maintain an open aperture, as in modern gastropods. Based on evidence discussed above, the helens seem more likely to have been retractable supports for fleshy organs that were protruded for respiration or feeding, or both, an hypothesis originally proposed in somewhat different form by

Sysoev (1959b; see also Fisher, 1962, fig. 63). A respiratory function for soft tissue attached to the helens would have been advantageous to hyolithids living on poorly oxygenated muds and may explain the presence of specimens with helens extended in some dark shales of the Spence and Stephen formations. It may also help explain an abundance of hyolithids in some dark shales of late Paleozoic age (see Malinky, Mapes, and Broadhead, 1986) that were deposited under low-oxygen conditions. Some specimens with articulated opercula and conchs, but without visible helens (Fig. 1,*1,* right), may have their helens retracted within the conch. Most Paleozoic specimens, however, probably lack helens because of the low potential for preservation.

The helens, together with their inferred soft tissues, may also have had a balancing or stabilizing function as suggested by Howell and Stubblefield (1950:12), Yochelson (1961:158; 1974:722), and Pojeta (1987:442) but were

probably too thin and fragile to have had a significant locomotive function as suggested by Walcott (1911:121; 1913:48), Fisher (1962: W121), Marek (1963:63), and Pojeta (1987: 442).

HYOLITHID SOFT PARTS

Two specimens of *Haplophrentis reesei* show incomplete gut traces and one shows an incomplete gut filling. This is the first report of preserved soft parts from the order Hyolithida, but gut fillings are known from specimens assigned to the Orthothecida (Thoral, 1935; Runnegar and others, 1975). Parting surfaces pass longitudinally through the gut leaving traces on both the part and counterpart of at least two of the specimens.

A portion of alimentary tract having minor relief is preserved on the internal mold of KUMIP 204340 (see Figs. 5,*1*, 6,*4*). In this specimen, shell is present only at the apical end, along parts of the lateral margins, on the operculum, and on the helens. A small, slightly sinuous length of gut is indicated by a reflective film and is exposed along the dorsomedial surface of the mold, just to the right of center. By analogy with the alimentary tract of orthothecids, it is probably a dorsal rectum. In places the reflective film is broken away, revealing a gut filling that is similar to the matrix. This accords with the suggestion that hyolithids were deposit feeders (Yochelson, 1961, 1984a; Marek and Yochelson, 1976).

Incomplete gut traces in two specimens are indicated only by reflective strips on parts and counterparts. KUMIP 204383 (see Figs. 5,*5*, 6,*1*) has two disjunct gut remnants in the internal mold, just beneath the dorsum, which are best seen on the counterpart. This trace, probably a rectum, is slightly sinuous and narrower in the anterior remnant than in the posterior remnant. In KUMIP 204384 (see Figs. 5,*6a,b*, 6,*3*), the gut trace lies primarily left of center and is much wider than in the other two specimens. It is unclear whether this represents a rectum that is more compressed than in the other two specimens or whether some of the ventral intestine is also preserved.

SYSTEMATIC PALEONTOLOGY

Phylum CNIDARIA
Class HYDROZOA
Order HYDROIDA
Suborder CHONDROPHORINA
Family uncertain

SCENELLA Billings, 1872

Type species.—*Scenella reticulata* Billings, 1872, p. 479; by monotypy.

Emended diagnosis.—Chondrophorine pneumatophore having low, conical form. Apex eccentric, anterior from midpoint. Basal outline smooth and elliptical. Pneumatocysts concentrically arranged, numerous, closely packed; width increasing slightly away from apex and rate of increase is greater posteriorly than anteriorly. Radial ribs fine, numerous, closely spaced. Intersections of ribs and pneumatocyst walls may form reticulate pattern. Evidence of sail lacking.

Remarks.—The history of classification of *Scenella* has been well summarized by Yochelson and Gil Cid (1984:337–339). Recent morphological analyses (Yochelson, 1984b; Yochelson and Gil Cid, 1984) indicate that many fossils referred to *Scenella,* including those of the type species, are pneumatophores (internal floats) of chondrophorine cnidarians. Criteria for distinguishing superficially similar chondrophorine and molluscan fossils have been listed by Yochelson (1984b) and Stanley (1986). The total morphology of specimens described here from Utah and British Columbia is most consonant with that of chondrophorines.

Scenella was first classified as a patellinid gastropod and then as a monoplacophoran (e.g., Knight, 1952; Knight and Yochelson, 1960; Runnegar and Jell, 1976). Some authors (e.g., Berg-Madsen and Peel, 1986; Geyer, 1986) have continued to regard *Scenella* as a mollusk. In support of the monoplacophoran assignment, Rasetti (1954, pl. 12, figs. 5–8) illustrated as *Scenella* sp. internal molds of four conical shells having serially paired muscle scars. They are from limestone beds in British Columbia that Rasetti (1954:61) assigned to the Mt. Whyte Formation and that Fritz (1969: 1159) reassigned to the lower Cathedral Formation. Runnegar and Pojeta (1974:312, fig. 2)

and Runnegar (1987:299, fig. 14.22B) used Rasetti's specimens, retained in *Scenella,* as the basis for reconstruction of primitive monoplacophoran soft parts. Yochelson (1978:180), Yochelson and Stanley (1981:329), and Yochelson and Gil Cid (1984:337) have argued that those specimens do not belong to *Scenella* and are in need of a new generic name. Applying the criteria listed by Yochelson (1984b), we agree with Runnegar and Pojeta that Rasetti's specimens are mollusks, but we also agree with Yochelson, Stanley, and Gil Cid that they do not belong to *Scenella.*

Shaw (1962:329) erected *Protoconchoides* as a subgenus of *Scenella* to include "small conical untorted gastropods with subcentral to central apices" and those that lack "the torsion of the apex toward the anterior end." With reassignment of *Scenella* to the Cnidaria, the foundation for Shaw's subgenus is virtually eliminated. Curvature of the apex in any species of *Scenella* is minor at most, and that character seems to have little or no taxonomic value, especially above the species level.

Features of *Scenella* that seem to have taxonomic significance at the species level include apical and slope morphology, position of the apex, pattern as well as distinctness of pneumatocysts and radial ribs, presence or absence of lobation, length:width ratio, and relative size. Some of these characters are quite variable within collections, partly owing to taphonomic factors. The length:width ratio and the position of the apex may vary according to the original orientation of the specimen in the matrix and the amount of compression. The distinctness of pneumatocyst walls and radial-rib walls varies from specimen to specimen but tends to be greater in compressed specimens (compare Fig. 4,*1* and 4,*3a*). The steepness of the anterior and posterior slopes is related to eccentricity of the apex and may change with postmortem events. Compressed specimens commonly show differentially inflated pneumatocysts that impart concentric wrinkles to the pneumatophore (see Figs. 3,*1,* 4,*1*). Such wrinkles are not considered to have taxonomic value.

Stanley (1986) recognized 13 genera of fossil and recent chondrophorines. Of these, only *Scenella, Chondroplon* Wade, 1971, *Ovatoscutum* Glaessner and Wade, 1966, and *Palaelophacmaea*

Donaldson, 1962, have bilaterally symmetrical pneumatophores. *Chondroplon,* of late Precambrian age, is characterized by two equal lobes separated by a furrow and has no evidence of a sail. *Ovatoscutum,* also of late Precambrian age, is oval in outline, has wide pneumatocysts, has a prominent medial ridge on the anterior slope and two diffuse ridges that diverge from the apex on the posterior slope, and lacks evidence of a sail. The systematic position of *Chondroplon, Ovatoscutum,* and other Ediacaran organisms has recently been opened to new interpretation, but only preliminary discussions have been published (e.g., Seilacher, 1984; Seilacher in Gould, 1985:243–244). Herein we continue to regard *Chondroplon* and *Ovatoscutum* as cnidarians. *Palaelophacmaea,* which ranges from the Ordovician to Cretaceous, has wide pneumatocysts, has a distinct central ridge on the posterior slope, and lacks evidence of a sail.

Under the category *incertae sedis,* Geyer (1986:96–97) recently erected *Marocella* for some patelliform fossils of Cambrian age that closely resemble *Scenella. Marocella* differs from *Scenella* by having wider, fewer, and better defined structures that we interpret to be pneumatocysts of chondrophorine type. At least three species of *Marocella, M. mira* Geyer, 1986, *M. tichkaensis* Geyer, 1986, and *M. morenensis* (Yochelson and Gil Cid, 1984), show insertions of pneumatocysts at scattered points on the pneumatophore. Some insertions continue for only short distances before pinching out, whereas others appear to continue for more than one whorl (Geyer, 1986, pl. 6, figs. 82, 83). Such insertions have not been described in *Scenella,* but their apparent absence may be due to inadequate preservation of finer structures. Growth lines are not inserted in this manner by mollusks (E. L. Yochelson, 1988, personal communication). Therefore, insertion patterns are another feature that may be useful in distinguishing some chondrophorine pneumatophores from molluscan shells. One species of *Marocella, M. morenensis,* also shows possible lobation in large specimens (Yochelson and Gil Cid, 1984), a feature not observed in any species of *Scenella.*

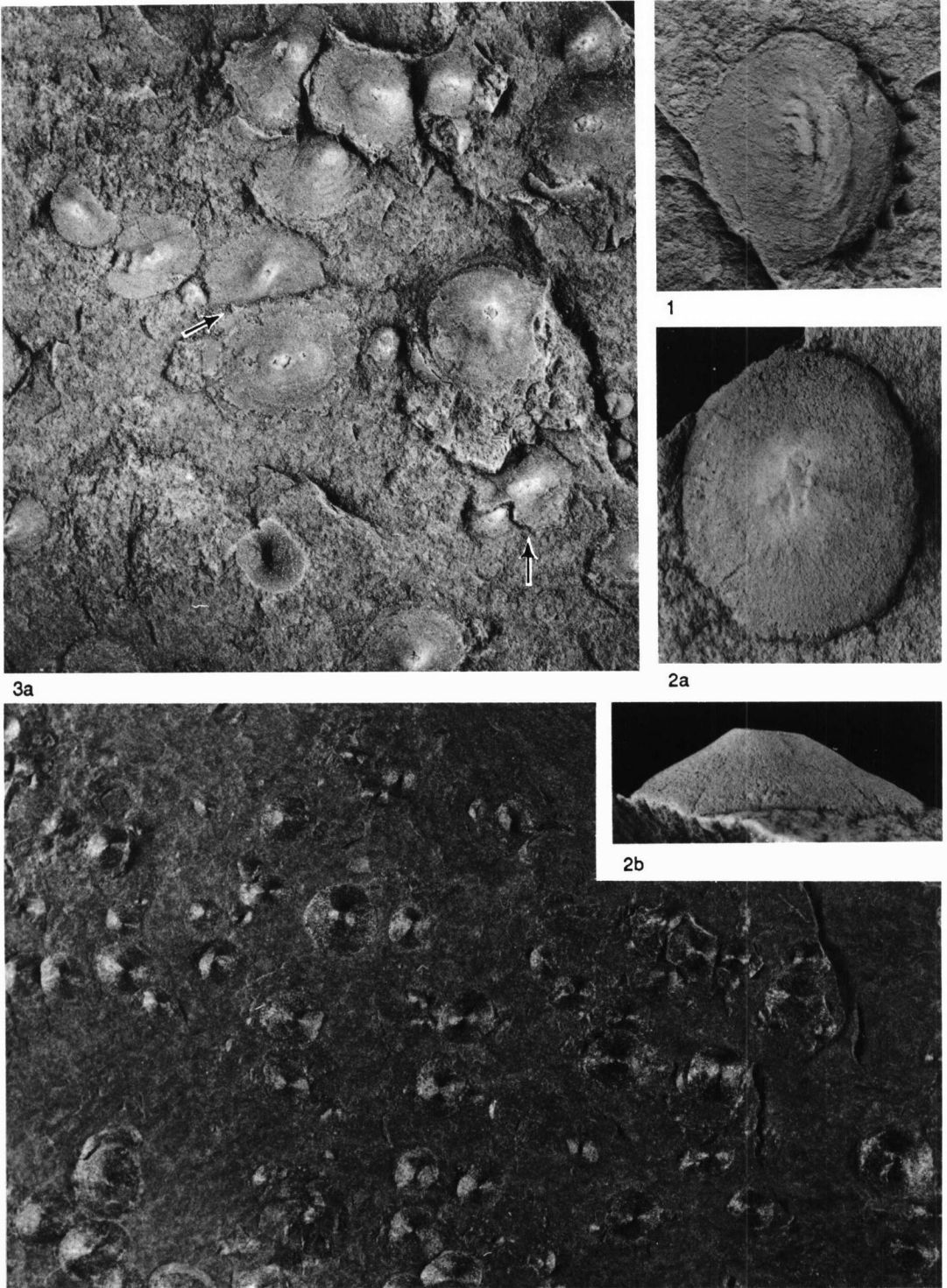Fossils referable to *Scenella,* as emended, range in age from Early Cambrian to Middle

3a

3b

1

2a

2b

Fig. 3. *Scenella amii* (Matthew) from the Stephen Formation of British Columbia; all coated with MgO, except *3b*.——*1.* Dorsal view of holotype pneumatophore from USNM locality 14s, ROM 8048, ×4.5.——*2.* Pneumatophore, USNM 96483a; *a,* dorsal view, and *b,* lateral view; both ×5.0.——*3.* Bedding surface with many pneumatophores from USNM locality 35k, ROM 45322; *a,* draped specimens (arrows), ×3.0; *b,* larger area, ×1.5.

Ordovician (Yochelson, 1984b). Representative specimens have been described from Asia, Europe, and North America.

SCENELLA AMII (Matthew, 1902)

Figure 3

Metoptoma amii MATTHEW, 1902, p. 111, pl. 1, fig. 12.
Scenella varians Walcott WALCOTT, 1908, pl. 1, fig. 6; 1912a, p. 153.
Scenella amii (Matthew) RESSER, 1938b, p. 19.
Scenella sp. ind. WHITTINGTON, 1985, fig. 4.17.

Holotype.—ROM 8048 (Fig. 3,*1*).
New material.—More than 500 specimens.
Emended diagnosis.—*Scenella* having blunt, subcentral apex. Length about 1.05 to 1.35 times width, ranging up to 10 mm. Pneumatocyst walls subtle. Radial ribs very weak, less distinct than pneumatocyst walls. Evidence of apical pore and marginal lobation lacking.
Remarks.—The holotype of *Scenella amii* (Fig. 3,*1*) is badly weathered, rendering characterization difficult. Staff members of the Royal Ontario Museum, however, have collected numerous and better preserved topotypes (e.g., Fig. 3,*3*), which we used in emendation of the species diagnosis.
Walcott (1908, pl. 1, fig. 6) figured a specimen from the Stephen Formation of British Columbia that he identified as *Scenella varians,* a species that he had previously described (Walcott, 1886:127, pl. 12, figs. 2, 2a) from Lower Cambrian rocks of Vermont. Walcott's figured specimen (Fig. 3,*2a,b*) from British Columbia is one of nine bearing USNM catalog number 96483, and all are clearly referable to *S. amii.* Compared to the types of *S. varians,* Walcott's specimens from British Columbia are much larger, less circular in outline, and have less distinct radial ribs.
Occurrence.—All specimens are from the Stephen Formation of early Middle Cambrian age on Mt. Stephen (USNM locality 14s) and near Mt. Field (USNM locality 35k), British Columbia. Locality 14s has produced the *Ogygopsis klotzi* faunule of Rasetti (1951:103–104). Locality 35k is C. D. Walcott's celebrated Burgess quarry with a slightly younger *Pagetia bootes* faunule of Rasetti (1951:103–104). Agnostoid trilobites from locality 35k also are represent-

ative of the *Ptychagnostus praecurrens* Interval-zone of Robison (1984a:5).

SCENELLA RADIANS new species

Figure 4,*1–5*

Etymology.—From Latin *radius,* referring to the strong radial ribs of some specimens.
Holotype.—KUMIP 204350 (Fig. 4,*1*).
Additional material.—Twelve specimens.
Diagnosis.—*Scenella* having blunt apex, positioned 0.2 to 0.4 times sagittal length from anterior margin. Length about 1.0 to 1.3 times width, ranging up to 15 mm. Pneumatocyst walls weak. Radial ribs strong to weak, more distinct than pneumatocyst walls. Evidence of apical pore and marginal lobation lacking.
Remarks.—The pneumatophore of *Scenella radians* is most similar to that of *S. hermitensis* Resser, 1945 (p. 192, pl. 19, figs. 11–14), from the Muav Limestone of Arizona. Both have a narrowly elliptical outline and radial ribs that are more distinct than the pneumatocyst walls. They differ, however, because *S. radians* has more numerous and stronger pneumatocyst walls, and its apex is more anterior. In profile, *S. radians* seems to be lower and more broadly conical than *S. hermitensis,* but this may be the result of compression.
Occurrence.—Eight specimens, including the holotype, are in collection 781 from the Spence Shale of the Wellsville Mountains and five are in collection 853 from the Chisholm Formation of the Drum Mountains. All are from the *Glossopleura* Assemblage-zone (Robison, 1976).

Phylum unknown

Genus undetermined

Figure 4,*6*

The poorly preserved holotype of *Crania? columbiana* Walcott, 1889 (Fig. 4,*6*), was originally described as an inarticulate brachiopod. It was collected from the Eldon Formation on Mt. Stephen, above Field, British Columbia. Subsequently, Resser (1938b:19) concluded that the specimen is not a brachiopod, and without giving morphological reasons he reassigned it to *Scenella.* We have examined the specimen, which appears to be an internal mold. Its maximum preserved diameter is 2.3 mm. Although radial ribs are well developed, it lacks
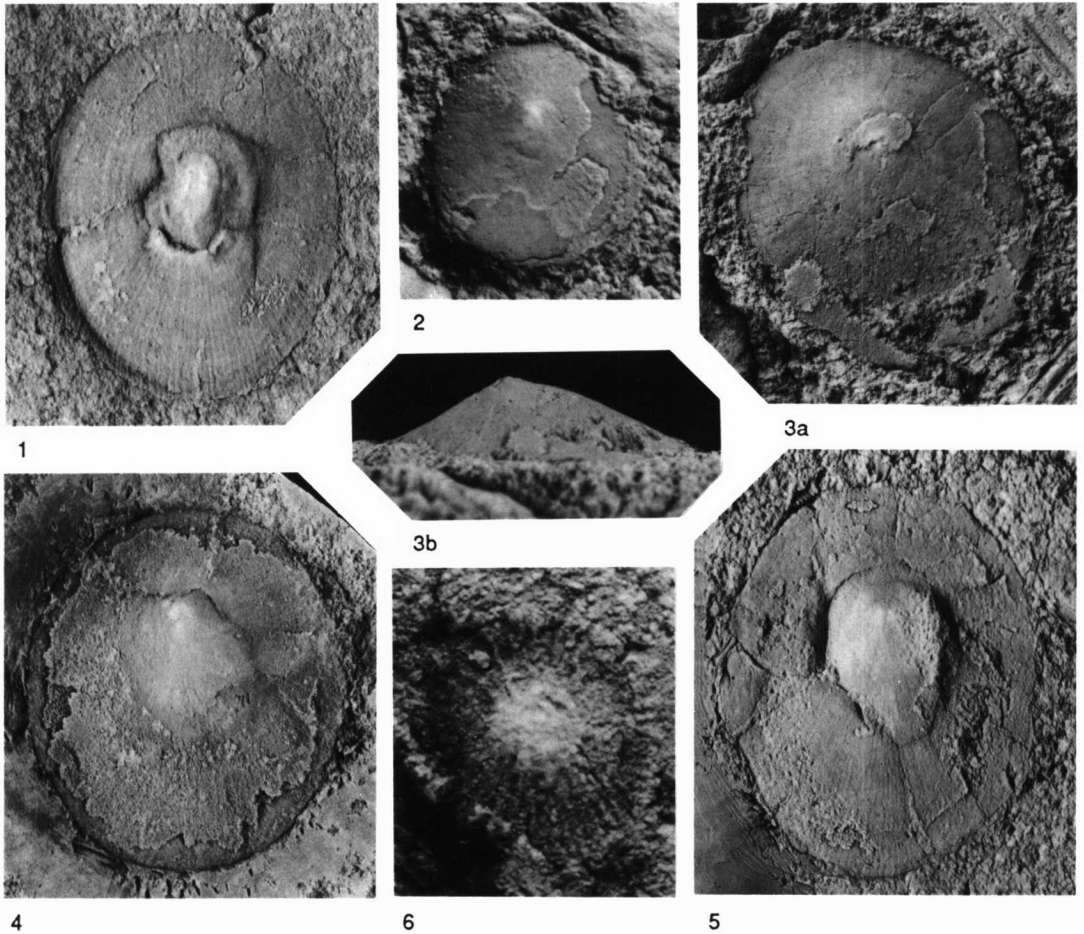
Fig. 4. *Scenella radians* n. sp. from Utah (*1-5*), and specimen unassigned to genus from British Columbia (*6*); all coated with MgO.——*1.* Holotype pneumatophore in shale, Spence Shale, locality 781; KUMIP 204350, ×6.0.——*2.* Small pneumatophore in limestone, Chisholm Formation, locality 853, KUMIP 204349, ×6.0.——*3.* Pneumatophore in limestone, Chisholm Formation, locality 853, KUMIP 204348; *a,* dorsal view, and *b,* lateral view; both ×4.0.——*4.* Partly exfoliated pneumatophore in shale, Spence Shale, locality 781, KUMIP 204347, ×4.5.——*5.* Large pneumatophore having tattered left margin and preserved in shale, Spence Shale, locality 781, KUMIP 204351, ×3.5.——*6.* Holotype of *Crania? columbiana* Walcott from the Eldon Formation, USNM 58307, ×16.

evidence of pneumatocysts. Symmetry, if originally present, is indeterminate because of poor preservation. A. J. Rowell (1987, personal communication) has examined the specimen and doubts that it is a brachiopod. We doubt that it belongs to *Scenella,* but we defer further judgment about its taxonomic assignment.

Phylum MOLLUSCA
Class HYOLITHA
Order HYOLITHIDA

Family HYOLITHIDAE Nicholson

Remarks.—The emended family diagnosis of Malinky (1988:219–220) is followed here.

The definition of *Hyolithes* was recently revised (Malinky, 1988; see also Malinky, Mapes, and Broadhead, 1986; Malinky, Linsley, and Yochelson, 1987) and only the type species, *H. acutus* Eichwald, 1840, from the Ordovician of Estonia was retained without question in the genus. Most species that have been assigned to

Hyolithes should be reassigned to other genera upon reassessment. One such species, *H. carinatus* Matthew, 1899, from the Stephen Formation is here reassigned to the new genus *Haplophrentis*. Two species from the Spence Shale, *Hyolithes comptus* Howell, 1946, and *H. idahoensis* Resser, 1938a, although seemingly distinctive, are provisionally designated as '*Hyolithes*' because available specimens are not well enough preserved to determine their generic affinities.

Opinions have differed as to whether hyoliths should be assigned to a class within the Mollusca (e.g., Marek, 1963; Marek and Yochelson, 1964, 1976) or a separate phylum (e.g., Runnegar and others, 1975; Runnegar, 1980; Pojeta, 1987). Although we favor a molluscan assignment, our purpose is not to evaluate these viewpoints but to document new material at the genus and species level.

HAPLOPHRENTIS new genus

Etymology.—From Greek *haplos*, single or simple, and *phrento*, wall; alluding to the single internal dorsal septum.

Type species.—*Haplophrentis reesei* n. sp.

Diagnosis.—Hyolithid with weak, longitudinal, dorsomedial septum in conch. Lateral longitudinal sulci singly paired on dorsum and venter.

Description.—Conch with single septum along inner dorsomedial surface, formed by thickening where slopes meet. Dorsum subangular, slopes subtly convex. Apical end slightly turned dorsally and laterally, usually to right. Lateral margins angular. Lateral longitudinal sulci singly paired on dorsum and venter, extending along entire length of shell. Venter slightly inflated. Ligula short, narrowly rounded. Apertural rim not flared. Aperture probably orthogonal. Growth lines fine, better developed on venter than dorsum.

Operculum questionably platyclaviculate; outline ovate, broad; apex bluntly pointed. Conical shield large, subtriangular; lateral sides nearly straight; ventral side broadly rounded. Cardinal shield broad, cardinal processes large. Growth lines and rugae present on shields, absent on rooflets.

Helens very thin, arcuate with slight vertical twist, tapering proximally and distally. Length along curve about 0.45 times maximum conch length, width about 0.06 times length. Growth lines fine, equally developed on both sides.

Remarks.—*Haplophrentis* resembles *Hyolithes* Eichwald, 1840 (*sensu* Malinky, 1988), and *Linevitus* Sysoev, 1959a, in having lateral longitudinal sulci. It differs from all described hyolithids, however, in having both an inner dorsomedial septum and longitudinal sulci on the dorsum and venter. The conch of *Haplophrentis* further differs from that of *Hyolithes* by having a higher dorsum. The operculum of *Hyolithes* is not known. *Haplophrentis* further differs from *Linevitus* by having only a single pair of ventrolateral sulci. *Haplophrentis* resembles *Elegantilites* Marek, 1967, in having large cardinal processes but differs by having a more broadly rounded dorsum and an internal septum.

Only two species are referred to *Haplophrentis*. These are *H. reesei* n. sp. and *Hyolithes carinatus* Matthew.

HAPLOPHRENTIS REESEI new species

Figures 1, 5, 6

Hyolithes cecrops Walcott RESSER 1939, p. 7, pl. 1, figs. 36–38; pl. 5, fig. 9; GUNTHER and GUNTHER, 1981, pl. 64, figs. A–C.

Hyolithes sp. YOCHELSON, 1961, pl. 33, fig. 1.

Haplophrentis reesei Babcock and Robison CONWAY MORRIS and ROBISON, 1988, fig. 27.

Etymology.—Named for Philip E. Reese, who collected the specimens with preserved soft parts.

Holotype.—KUMIP 204339 (Figs. 5,2, 6,5).

Additional material.—Twenty-eight conchs with associated opercula, 33 separate conchs, and 6 separate opercula.

Diagnosis.—Growth lines on conch fine, closely spaced; transverse on dorsum, highly arched on venter. Initial apical angle 15° to 18°, expanding to 22° to 30°. Apical angle of conical shield 95° to 110°. Rugae on conical shield subtle and comarginal.

Remarks.—*Haplophrentis reesei* ranges up to about 45 mm in length and differs from other hyolithids by its internal longitudinal septum, subangular dorsum, lateral sulci, large cardinal processes, fine growth lines, and lack of coarse rugae. Such specimens have previously been assigned to *Hyolithes cecrops* Walcott, 1917
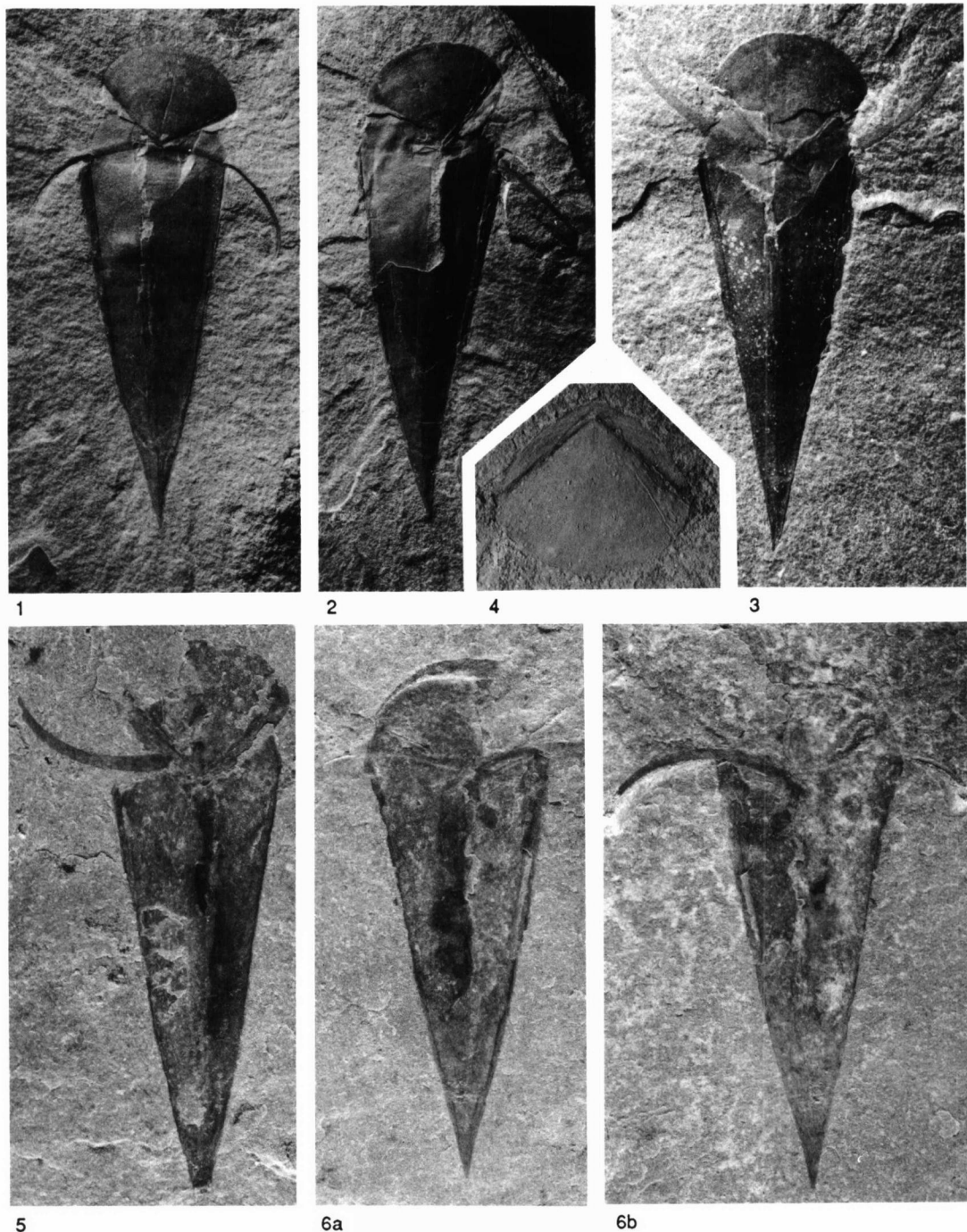
Fig. 5. *Haplophrentis reesei* n. g. and n. sp. from the Spence Shale, locality 781, Utah.——*1*. Specimen in dorsal view with dorsal shell mostly exfoliated, showing gut filling (compare Fig. 6,*4*), KUMIP 204340, ×2.0.——*2*. Holotype in dorsal view (compare Fig. 6,*5*), KUMIP 204339, ×1.5.——*3*. Small specimen in dorsal view with helens extended anteriorly and downward away from aperture (compare Fig. 6,*6*), KUMIP 204341, ×3.0.——*4*. Operculum, coated with MgO, external view, KUMIP 204342, ×3.0.——*5*. Counterpart of specimen exposing inside of dorsum and gut trace (compare Fig. 6,*1*), KUMIP 204383, ×2.0.——*6*. Specimen showing gut trace, KUMIP 204384; *a*, counterpart, inside of dorsum (compare Fig. 6,*3*), and *b*, internal mold; both ×2.0.

(Resser, 1939, p. 7, pl. 1, figs. 36–38; Gunther and Gunther, 1981, pl. 64, figs. A–C), but we reassign these to *H. reesei.* We also consider *H.*

cecrops to be a junior synonym of *Haplophrentis carinatus* (see below).

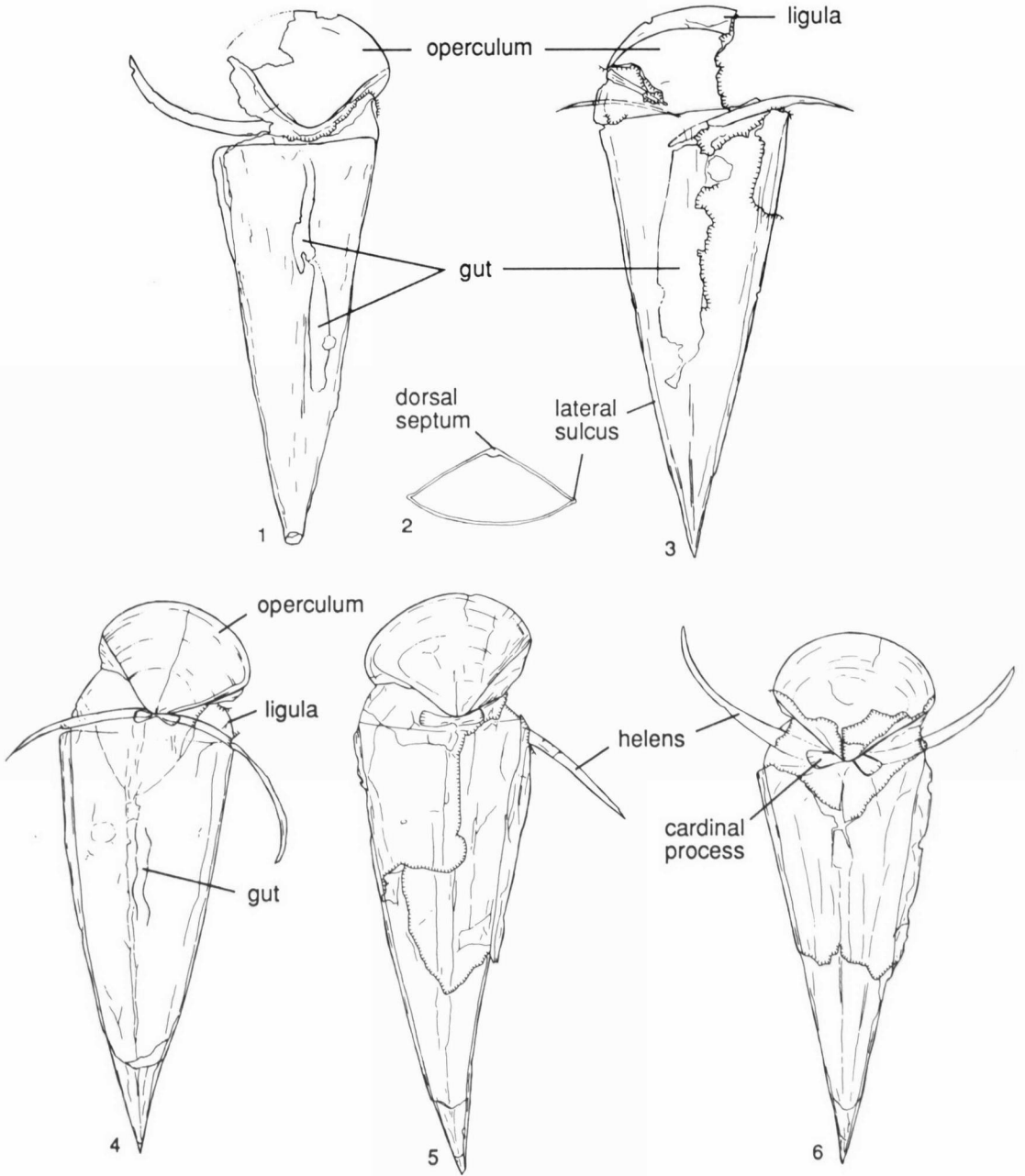*Occurrence.*—Most new specimens of *Haplo-*

Fig. 6. Explanatory drawings of *Haplophrentis reesei* n. g. and n. sp.——*1.* KUMIP 204383 (compare Fig. 5,*5*).——*2.* Reconstruction of conch in transverse section.——*3.* KUMIP 204384 (compare Fig. 5,*6a*).——*4.* KUMIP 204340 (compare Fig. 5,*1*).——*5.* Holotype, KUMIP 204339 (compare Fig. 5,*2*).——*6.* KUMIP 204341 (compare Fig. 5,*3*).

phrentis reesei are from the Spence Shale at localities 432, 781, and unnumbered localities in Hansen Canyon and Miners Hollow, all in the Wellsville Mountains, Utah. Two new conchs that are questionably assigned to *H. reesei* are from the type locality (USNM 55c) of the Spence Shale in southern Idaho. Specimens assigned by Resser (1939) to *Hyolithes cecrops* are from the Spence Shale of northern Utah (USNM localities 54l and 55e) and southern Idaho (USNM locality 55c). Most, if not all, of the new specimens are from the upper half of the Spence Shale, and all are from the *Glossopleura* Assemblage-zone.

HAPLOPHRENTIS CARINATUS
(Matthew, 1899)

Figure 7

Hyolithes carinatus MATTHEW, 1899, p. 42–43, pl. 1, figs. 5a–5b; 1901, p. 102; WALCOTT, 1911, p. 121, pl. 19, fig. 7; 1913, p. 48, pl. 6, fig. 8; SINCLAIR, 1946, p. 74; YOCHELSON (in part), 1961, p. 153–155, pl. 33, figs. 2, 3, 5–7, 9–12 (not fig. 8); pl. 34, figs. 1–9; FISHER, 1962, fig. 60,*1*; MAREK and YOCHELSON, 1964, fig. 3; YOCHELSON, 1974, p. 719; COLLINS and RUDKIN, 1981, pl. 2, fig. 6; WHITTINGTON, 1985, fig. 4.18.
Hyolithes costatus MATTHEW, 1901, p. 107, figs. 3a, b [see Sinclair, 1946:75].
Hyolithes cecrops WALCOTT, 1917, p. 27–28, pl. 5, figs. 3, 3a–c; SINCLAIR, 1946, p. 74; NORFORD, 1962, pl. 2, fig. 12.
Hyolith RUNNEGAR and others, 1975, fig. 1B.
Hyolithes sp. CONWAY MORRIS and WHITTINGTON, 1979, p. 131; CONWAY MORRIS and WHITTINGTON, 1985, fig. 22.
Hyolithid CONWAY MORRIS, 1977, pl. 11, fig. 3; RUNNEGAR, 1980, fig. 1; POJETA, 1987, fig. 15.4.I.
Hyolithes? cecrops Walcott MALINKY, 1988, p. 227, figs. 3.4, 3.9.

Lectotype.—Matthew (1899) erected *Hyolithes carinatus* on five syntypes from the Stephen Formation of Mt. Stephen, British Columbia. All are extensively weathered. Three of these are conchs showing the ventral surface and two are incomplete opercula. We here select the best preserved syntype conch, ROM 8463a (Fig. 7,*1*; also Matthew, 1899, fig. 5a), as lectotype.

New material.—Eighteen conchs with associated opercula, 27 separate conchs, 11 separate opercula, and approximately 70 separate conchs preserved in stringers (e.g., Fig. 7,*6,8*).

Emended diagnosis.—Growth lines on conch fine, closely spaced; transverse on dorsum, highly arched on venter; faint longitudinal grooves on dorsum intersecting with growth lines may produce cancellate appearance. Initial angle 24° to 32°, expanding to 24° to 35°. Apical angle of conical shield 100° to 137°. Rugae on conical shield strong and comarginal.

Remarks.—Our study of more than a hundred hyolithids from the Cathedral and Stephen formations has indicated the presence of only one distinguishable species. Although the lectotype (Fig. 7,*1*) and paralectotypes (ROM 8463) of *Hyolithes carinatus* are poorly preserved, enough characters are present to indicate that these specimens are conspecific with other, better preserved hyolithids that we examined from the Stephen Formation. From comparison of the types, we further consider *Hyolithes cecrops* Walcott to be a junior synonym of *H. carinatus,* and we reassign *H. carinatus* to *Haplophrentis* because of the presence of an internal dorsomedial septum (Fig. 7,*4*).

Haplophrentis carinatus differs from *H. reesei* by its wider conch (on average), the presence of faint longitudinal grooves on the dorsum, and the presence of stronger rugae on the operculum. Conch length in *H. carinatus* ranges up to 40 mm but is usually less than 25 mm. The postapical conch expansion in *H. carinatus* is between 24° and 35°, whereas it ranges from only 22° to 30° in *H. reesei*. Also, the difference in angle of apical and later conch expansion is greater in *H. carinatus,* as is the average apical angle of the the conical shield of the operculum. Although some of this variation may be due to compression, the two species can still be rather easily distinguished.

At least two animals of the Burgess shale preyed or scavenged on *Haplophrentis carinatus.* Shells of this hyolithid are the most common recognizable component of gut contents in the priapulid worm *Ottoia prolifica* Walcott (Conway Morris, 1977, 1979; Conway Morris and Whittington, 1979, 1985) and are also found, rarely, in the gut of the arthropod *Sydneyia inexpectans* Walcott (Bruton, 1981, fig. 94; Conway Morris and Whittington, 1985, fig. 11). *Ottoia* was a slow infaunal worm and the presence of hyolithids in its gut supports the interpretation of hyolithids as being virtually sedentary
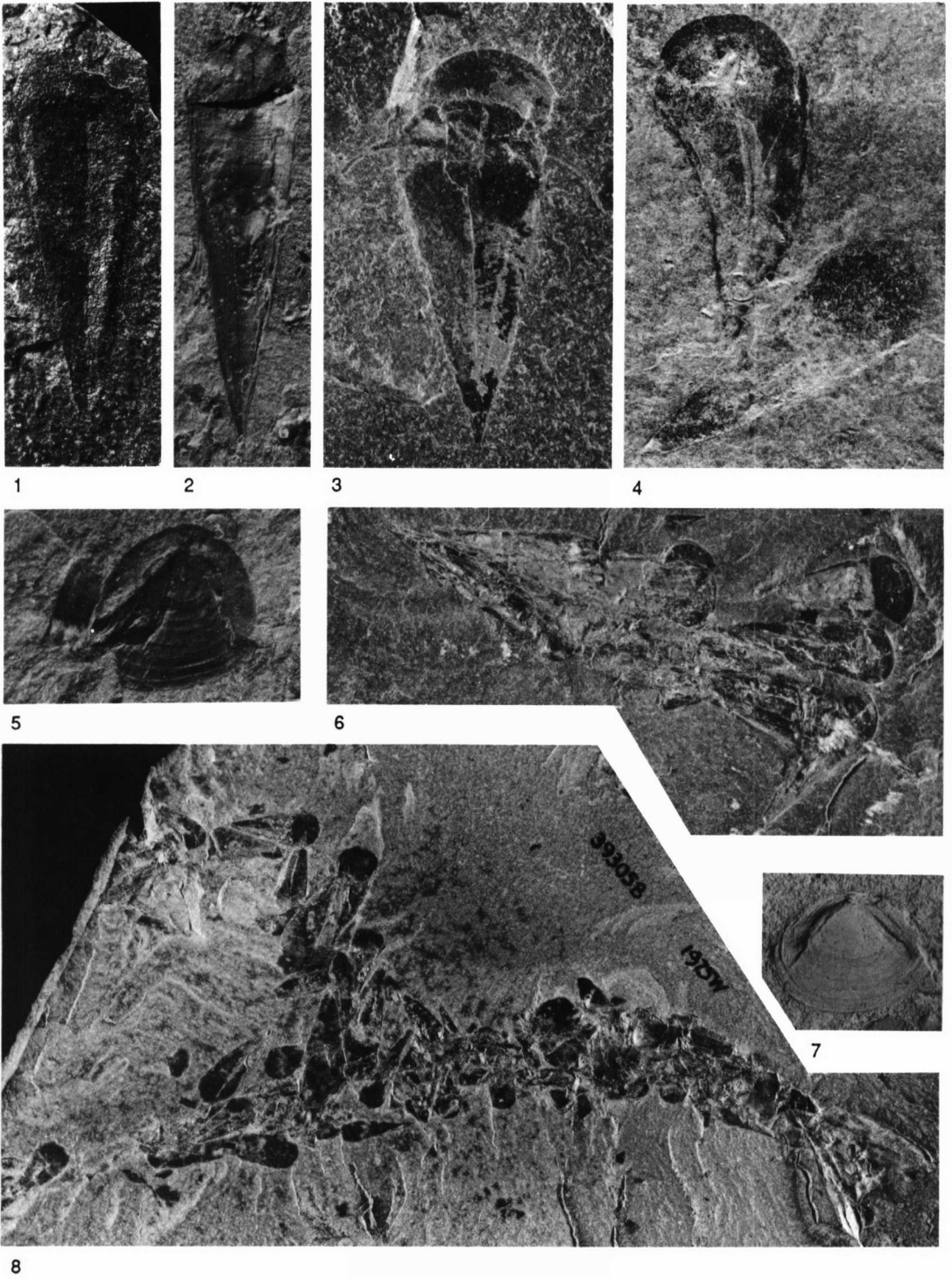
1   2   3   4

5   6

7

8

Fig. 7. (Explanation on facing page.)

benthic animals (Yochelson, 1961, 1984a; Marek and Yochelson, 1976; Marek and Galle, 1976).

Two or three dense, elongate, shell accumulations of *Haplophrentis carinatus* (Fig. 7,6,8) are not associated with recognizable predators or scavengers. In each, the apices of most conchs point in the same direction, a pattern previously noted for hyolithids that fell prey to the priapulid *Ottoia* (Conway Morris, 1977). On one bedding surface, more than 60 hyolithids, 1 articulate brachiopod, and 2 large quartz grains are arranged in either one or two stringers (Fig. 7,8). Some of the hyolithids are covered by a black, probably organic, film. These accumulations may represent either coprolites (Conway Morris, 1979:337) or gut contents of predators or scavengers whose bodies are not preserved. If the lagerstätten of the Burgess shale were deposited by turbidity currents (Piper, 1972; Conway Morris, 1986), most fecal remains probably disintegrated prior to burial and the hyolithid accumulations more likely represent gut contents. If only one animal is represented by the stringer in Figure 7,8, it must have been longer than 20 cm.

Occurrence.—*Haplophrentis carinatus* is rare to common in the Cathedral and Stephen formations of British Columbia. Most of the specimens we studied are from USNM localities 14s and 35k. The species ranges from the *Albertella* Zone to the *Ptychagnostus praecurrens* Zone.

?Family HYOLITHIDAE Nicholson

'HYOLITHES' COMPTUS Howell, 1946

Figure 8

Hyolithes ornatellus RESSER, 1939, p. 7, pl. 1, figs. 30–32 [name preoccupied by *H. ornatellus* HOLM, 1893, p. 64, pl. 1, figs. 37–40].
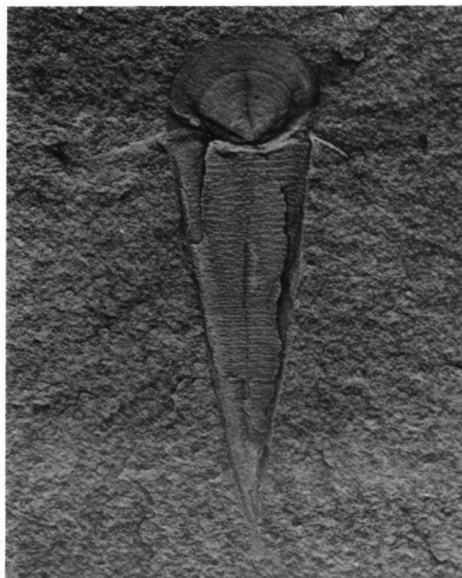*Hyolithes comptus* HOWELL, 1946, p. 71 [replace-

Fig. 8. '*Hyolithes*' *comptus* Howell from the Spence Shale, locality 781, Utah; associated conch, operculum, and helens in dorsal view; short axes of helens are at a high angle to the bedding surface; KUMIP 204344, ×4.0. Specimen is coated with MgO.

ment name for *H. ornatellus* Resser, *not* Holm]; SINCLAIR, 1946, p. 74.
Hyolithes? comptus Howell MALINKY, 1988, p. 227–228, fig. 3.10.

Lectotype.—Conch, USNM 96494a, from the type locality of the Spence Shale (USNM locality 55c); selected by Malinky (1988:228).

New material.—Two conchs with associated opercula and one separate conch.

Emended description.—Conch moderately wide with apical angle ranging from 20° to 26°. Apical end slightly turned to right. Dorsum probably subangular. Apertural margin of dor-

Fig. 7. *Haplophrentis carinatus* (Matthew) from the Cathedral (2) and Stephen (1, 3–8) formations, British Columbia.——1. Lectotype conch in ventral view; questionably USNM locality 14s, ROM 8463a, ×2.0.——2. Lectotype conch of *Hyolithes cecrops* Walcott in dorsal view; USNM locality 63j, USNM 63724a, ×1.5.——3. Small conch, dorsal view, with associated operculum and helens; USNM locality 35k, ROM 45288, ×4.0.——4. Two conchs; upper one with associated operculum is viewed from inside of dorsum and shows the septum and opercular features; USNM locality 35k, ROM 45291, ×4.0.——5. Operculum from the type collection of *Hyolithes cecrops* Walcott; USNM 63724b, ×3.0.——6. Aggregation of shells possibly representing gut contents or coprolite of unknown predator or scavenger; USNM locality 35k, ROM 45306, ×2.5.——7. Operculum, coated with MgO, exterior view; USNM locality 35k, ROM 45302, ×3.0.——8. One or, more likely, two aggregations probably representing gut contents or coprolites of unknown predator or scavenger; USNM locality 35k, ROM 39305B, ×1.2.

1a   **3**   **1b**   **2**
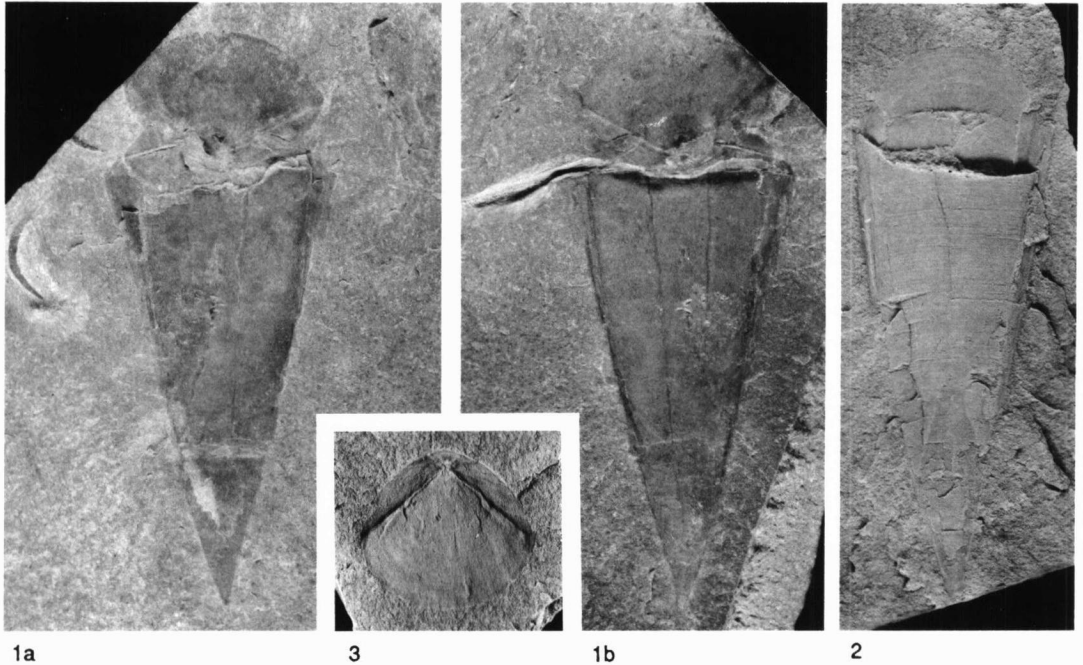
Fig. 9. *'Hyolithes' idahoensis* Resser from unnumbered localities in the middle part of the Spence Shale, Wellsville Mountains, Utah.——*1.* Conch with associated operculum and helens from Miners Hollow, dorsal view, KUMIP 204385; *a,* part; *b,* counterpart; both ×1.5.——*2.* Conch from Miners Hollow, dorsal view; coated with MgO; KUMIP 204345, ×1.5.——*3.* Operculum from Hansen Canyon, dorsal view; coated with MgO; KUMIP 204346, ×2.0.

sum slightly undulose, transverse. Ligula short, narrowly rounded. Growth lines coarse, closely spaced; may be discontinuous on dorsum of mature conch.

Operculum broadly ovate, apex blunt. Conical shield large and subtriangular; lateral sides nearly straight, ventral side strongly rounded; apical angle about 112°. Boundary between conical and cardinal shields sharp. Cardinal shield narrow (exsagittal). Cardinal processes not observed. Growth lines on conical shield coarse, comarginal.

Remarks. — *'Hyolithes' comptus* ranges up to 20 mm in length. It differs from other hyolithid species in the Spence Shale by the presence of coarse growth lines. Its conch was probably subtriangular in cross section, but because of compression of specimens, it is not possible to determine whether the slopes were concave or convex. Nothing is known of the interior surface of the operculum, and the apertural margin of the conch is incompletely known. Helens

are present on one specimen (Fig. 8), but they are not completely exposed.

Occurrence. —Specimens described by Resser (1939) are from the type locality (USNM 55c) of the Spence Shale, near Liberty, Idaho. Two new specimens are from locality 781 and one is from an unknown locality, all from the Spence Shale of the Wellsville Mountains, Utah. All are from the *Glossopleura* Assemblage-zone.

'HYOLITHES' IDAHOENSIS
Resser, 1938a
Figure 9

Hyolithes idahoensis RESSER, 1938a, p. 5, pl. 1, figs. 57, 58; SINCLAIR, 1946, p. 77.
Hyolithes sp. POJETA, 1987, figs. 15.5.A, 15.5.J.
Hyolithes? idahoensis Resser MALINKY, 1988, p. 228, figs. 3.7, 3.8.

Lectotype. —Operculum, USNM 95021, from the Rennie Shale (USNM locality 37m) of northern Idaho; selected by Malinky (1988: 228).

New material.—One conch with associated operculum and helens, 11 separate conchs, one separate operculum, and one questionably assigned conch with associated operculum.

Emended description.—Conch large, length ranging up to about 65 mm. Apical angle from 25° to 29°. Apical end usually straight, may turn slightly to right. Dorsum having nearly straight apertural margin and one pair of dorsolateral sinuses. Ligula relatively long, narrowly rounded. Growth lines coarse, closely spaced.

Operculum subcircular in outline. Conical shield large, subtriangular; lateral sides nearly straight, ventral side moderately rounded; apical angle 100° to 108°. Boundary between conical and cardinal shields sharp. Cardinal shield with wide rooflets. Cardinal processes not observed. Growth lines on conical shield comarginal. Rugae on conical shield relatively strong and comarginal.

Helens thin, strongly arcuate with slight vertical twist, tapering proximally and distally. Length along curve about 0.65 times maximum length of conch, width about 0.03 times length. Growth lines not observed.

Remarks.—The lectotype operculum of '*Hyolithes*' *idahoensis* (Malinky, 1988, fig. 3.8) is from the Rennie Shale of northern Idaho. It is 1.1 times wider than long and has wide rooflets, relatively strong rugae, and a conical shield with an apical angle of 100°. Features of the interior surface are not known. Associated conchs are characterized by an apical angle of about 26° and a broadly rounded dorsum with several weak longitudinal fractures. Malinky (1988:228) questioned whether or not the operculum and conchs assigned to *Hyolithes idahoensis* by Resser (1938a) were conspecific. A new specimen illustrated here (Fig. 9,*1a,b*) indicates that the association by Resser was correct.

Occurrence.—Specimens described by Resser (1938a) are from the Rennie Shale (USNM locality 37m) of northern Idaho. The new specimens are from the Spence Shale at its type locality (USNM 55c) in southern Idaho and from unnumbered localities in the middle part of the Spence Shale in the Wellsville Mountains, Utah. One specimen (conch and operculum) that is questionably assigned to the species is from locality 781. All specimens are from the *Glossopleura* Assemblage-zone.

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