Mattheva, a Proposed New Class of Mollusks

GEOLOGICAL SURVEY PROFESSIONAL PAPER 523-B

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By ELLIS L. YOCHELSON

CONTRIBUTIONS TO PALEONTOLOGY

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A discussion of the biologic placement of the Late Cambrian fossil Matthevia

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CONTRIBUTIONS TO PALEONTOLOGY

MATTHEVA, A PROPOSED NEW CLASS OF MOLLUSKS

By ELLIS L. YOCHELSON

ABSTRACT

Basic features of the hard parts of *Matthevia* Walcott suggest that this fossil is a mollusk. *Matthevia variabilis* Walcott, first described from the Late Cambrian Hoyt Limestone Member of Theresa Dolomite near Saratoga Springs, N.Y., has been found widespread throughout the western conterminous United States in rocks of Trempealeau age. Walcott interpreted the preserved part of *Matthevia* as a conical shell. The genus is interpreted here as an animal having two hard parts, one anterior and one posterior. The presumed anterior piece is elongate and contains two conspicuous cavities; the presumed posterior piece is somewhat narrower and shorter but also contains two cavities. If this interpretation is correct, the hard parts differ markedly from those of other mollusks. It is proposed that *Matthevia* is the sole known representative of an extinct class here given the name Mattheva.

Pseudomatthevia of Dresbach age is judged to be closely related to *Hypseloconus* and is provisionally transferred to the Monoplacophora.

INTRODUCTION

Matthevia variabilis Walcott is an enigmatic Cambrian fossil. The original description of the genus and species (Walcott, 1885) is excellent; it emphasizes the unusual appearance of two cavities separated by a wide septum within an otherwise massive subconical shell. Walcott placed this genus along with 10 others under the Pteropoda, doing this with "considerable reservation," because "They form a group although representative, in a measure, of the recent Pteropoda, differ in other respects so much that it appears as though a division of the Gastropoda, equivalent to the Pteropoda, might be consistently made to receive them." The identical description, but with better illustrations, was republished the following year (Walcott, 1886) without any comment about the biological position of the genus except that it was a pteropod. Walcott (1912) reillustrated the types of *Matthevia* with no further comment on their systematic position; these illustrations are photographs, though his drawings of 1886 are almost as satisfactory.

Miller (1889, p. 392) briefly redefined *Matthevia* and placed it within the class Pteropoda. Currently most workers on Recent Gastropoda consistently place Pteropoda as a group of lower rank under the class Gastropoda. In regard to the Pteropoda as used by him, Miller (1889, p. 389) stated, "It may well be doubted whether or not any of the Palaeozoic fossils belong to this order." Other authors of the late 1800's expressed similar reservations as to the occurrence of true Pteropoda in Paleozoic strata. The Paleozoic "pteropods" were a heterogeneous assemblage; the principal feature common to the various genera was the absence of characters that would permit the genera to be placed readily into established classes and phyla.

In the classic textbook by Zittel under the suborder Pteropoda, family Hyolithidae, three genera are listed in addition to *Hyolithes* and its synonyms. These are *Pterotheca*, *Phragmotheca*, and *Matthevia*. Although there is no discussion, the implication is obvious that these three genera are all closely related and are all associated with *Hyolithes*. In every revision and foreign-language edition of this work, the generic name is rendered as *Matthewia*, a name which can only be treated as an invalid emendation or a typographical error.

Knight (1941, p. 20) declared: "*Matthevia* Walcott, 1885, a strange and incomprehensible shell, seems more likely to have belonged to some otherwise unknown class of the Mollusca or even to some unknown phylum than to the Gastropoda." Two major references on American fossils, Grabau and Shimer (1909) and Shimer and Shrock (1944), do not list *Matthevia*. Flower (1954, p. 31) suggested that this genus "is not closely similar to either the hyolithids, the tentaculitids, or the gastropods." Neither the French "Traité de Paléontologie" (Piveteau, 1952) nor the Russian handbook (Orlov, 1958) mention *Matthevia*, though some of the other Paleozoic "pteropods" are discussed and classified. Finally, Fisher (1962, p. W128) placed *Matthevia* as the sole genus within his new suborder Matthevina of his new molluscan class Calyptoptomatida.

ACKNOWLEDGMENTS

Critical comments of my colleagues over a period of 8 years have played an important part in shaping my

thoughts regarding the biologic and taxonomic placement of *Matthevia*. Though it is obvious that much yet remains to be learned about this genus, several associates have encouraged me to put my opinions on record so that others may confirm or refute them.

In particular, I am indebted to A. R. Palmer, U.S. Geological Survey, who first called my attention to this animal, and to J. F. McAllister, U.S. Geological Survey, who at my request collected large quantities of material in difficult terrain. V. E. Barnes, Bureau of Economic Geology, University of Texas, loaned additional specimens from his collections, as did W. L. Stokes, University of Utah, and Anthony Reso, Tenneco Oil Co., Houston, Tex.

OCCURRENCE AND DISTRIBUTION OF *MATTHEVIA*

Matthevia originally was described only from the type locality in the Hoyt Limestone quarry, 1 mile northwest of Saratoga Springs, N.Y. The matrix is a nearly black exceedingly fine grained limestone. Walcott (1885, p. 19) noted that this fossil is associated with *Collenia*. Fisher (1962a, p. W120) suggested that there may be a relationship between the large bodies of *Collenia*-forming "reefs" and the occurrence of *Matthevia*. He indicated that the form could have been a grazing animal, though he did not rule out the possibility that specimens observed in the Hoyt may be a lag deposit.

The Hoyt Limestone Member of the Theresa Dolomite is of Late Cambrian age and is considered to be a correlative of the lower part of the Trempealeau, the youngest of the three stages of the Upper Cambrian. The latest published comprehensive stratigraphic data on the New York Cambrian (Fisher, 1962b) indicate that the Hoyt Limestone is a local facies of limited areal extent and is an eastward-extending tongue of the Little Falls Dolomite. Flower (1964, p. 57) indicated the Hoyt as a facies of Whitehall Formation and reported "*Matthevia* in local concentrations" within the Fort Ann quadrangle in easternmost New York State.

Since the close of the Second World War, *Matthevia* has been found to be widespread in the western conterminous United States. The occurrences outside the type locality are all of silicified specimens and have provided a fairly large series for study. Specimens are available from the Wilberns Formation in Texas (Cloud and Barnes, 1948, p. 118), the Ajax Formation in Utah, the Desert Valley (Reso, 1963) and Nopah Formations in Nevada, and the Nopah Formation in California. The genus also was identified in the Upper Cambrian rocks of the Arbuckle Mountains of Oklahoma by the late Josiah Bridge (W. Ham, written commun., 1964) though apparently no specimens were obtained. All known occurrences are of Late Cambrian Trempealeau age. Locality details are given by Yochelson, McAllister, and Reso (1965). Representative specimens are also figured there.

All the known occurrences of *Matthevia* are in limestone or dolomite. In the Nevada-California occurrences, the dolomite contains fairly little silt, and the acid residues consist almost exclusively of fossil fragments. A. R. Palmer (oral commun., 1964) observed little silt in the Utah and Texas matrix. The arrangement of the fossils in partly dissolved blocks shows evidence of sorting. J. F. McAllister searched for algal structures associated with *Matthevia* in eastern California. He reported (written commun., 1963) that at one locality in the Nopah Formation he observed "cryptozoon-like structures in small masses a foot or two across and a few girvanella-like ovoids," and that "certain differences in textures and local accumulations seem to indicate some redistribution of carbonate debris."

SYSTEMATIC PALEONTOLOGY

Class MATTHEVA, new class

Description.—Mollusks having two massive calcareous plates, one anterior and one posterior.

Discussion.—The molluscan nature of *Matthevia* is highly probable but is difficult to demonstrate conclusively. Evidence of its basic molluscan character is the calcareous shell material of the type lot. The manner in which the shell exfoliates from the steinkern is precisely like that of other mollusks broken from limestone and unlike that of other shelled invertebrates. This feature is well shown in Walcott's drawings of the types. The shell when silicified is spongy in texture, also a characteristic of most mollusk shells. Although growth lines, bilateral symmetry, and a thick shell are not characters that are the exclusive property of mollusks, they are strongly suggestive of that phylum.

The subordinal name Matthevina was proposed by Fisher (1962a, p. W128) within the order Hyolithida Matthew, one of the orders in Fisher's class Calyptoptomatida. Marek and Yochelson (1964, p. 1675) specifically excluded this suborder in discussing the class Hyolitha. Although there are no applicable rules of nomenclature, there is considerable precedent for keeping class-rank names independent of ordinal-rank names. The class name given above is based on the stem of the typical genus with "a" added as a suffix; this scheme is identical with that used by Marek (1963) for the class name Hyolitha.

Should any ordinal subdivisions within the class be proposed in the future, Fisher's name Matthevina is available. For the present, there is no need to define any categories at this level.

Family MATTHEVIDAE Walcott, 1885

Description.—Hard parts consisting of two bilaterally symmetrical subpyramidal plates of calcareous material, one anterior and one posterior, each of which contains two cavities. Soft parts unknown in detail, but presumably including a distinct head and a fairly narrow foot.

Walcott (1885, p. 17–18) suggested that the peculiar form that he had named *Palaenigma* might be a connecting link between *Conularia* and *Matthevia*. It is now generally accepted that *Palaenigma* was based on the partial filling of a conulariid (Sinclair, 1944, p. 87); nothing seems to link that form to *Matthevia*.

Although the question of the systematic position of the conulariids is beyond the scope of this paper, it is of historical interest that many authors between 1850 and 1925 included these forms with the other Paleozoic "pteropods." Repeatedly, these same authors noted that this classification was simply a matter of convenience and did not necessarily represent any zoological affinity. Nothing about the conulariids provides any substance to the idea that they should be classified as mollusks, a practice common in at least the older textbooks.

Genus MATTHEVIA Walcott, 1885

Matthevia Walcott, 1885, p. 17, text figs.; Walcott, 1886, p. 224; Miller, 1889, p. 392; Walcott, 1912, p. 265; Fisher, 1962, p. W128.

Description.—Hard parts consisting of a larger anterior(?) plate, flattened on one side, presumed ventral, and a posterior(?) plate having less obvious flattening on one side.

Discussion.—As only one genus containing one species is known within the class, all descriptions above the specific level have been made brief intentionally. If other genera are assigned to this class, it will facilitate their placement without extensive revisions at every taxonomic level. The relatively detailed description of the species may incorporate features of higher rank.

Sketches of the two hard parts are shown in figures 1 and 2.

Matthevia variabilis Walcott, 1885

Plate 1, figures 1–45

Matthevia variabilis Walcott, 1885, p. 17, figs. 1–6 of p. 20; Walcott, 1886, p. 224–225, pl. 32, figs. 1–12; pl. 33, figs. 1, 1*a-f*; Miller, 1889, p. 392, fig. 647; Lesley, 1889, p. 381–382 (text figs. from Walcott, 1886); Walcott, 1912, p. 265, pl. 41; Fisher, 1962a, p. W128, text fig. 72, 1*a*–1*g*.

Description.—Anterior(?) plate bilaterally symmetrical, elongate. Sides diverge from anterior point at an angle near 25°; sides distinct, nearly vertical, turn abruptly into the base and only slightly less abruptly into the slightly rounded dorsum. Dorsal surface diverges from ventral surface at an angle near 40° and is only slightly arched in profile, the arching most apparent near the anterior. Juncture of sides and dorsum a little rounded, the dorsal surface only slightly curved in section. Ventral surface is flattened and is mainly in a horizontal plane, except curving downward slightly near anterior, and forms almost a right angle at juncture with sides. Posterior margin of dorsal surface has a wide U-shaped sinus, the depth of which is about one-fourth the total length of the plate. Posterior dorsal margins produced strongly outward and less strongly downward from center of dorsal sinus to vertical part of wall, the curvature of margin edge increasing toward this point. At juncture with sides, the lateral margins turn through an acute angle, which forms the most posterior area of the plate, and proceed straight inward and downward nearly to the base; at juncture with base, the margins turn slightly to form a long, straight, gradual slope extending toward the ventral surface about midway along the maximum length of the piece, the margin on the ventral surface joining in a shallow U-shaped sinus, the base of which is

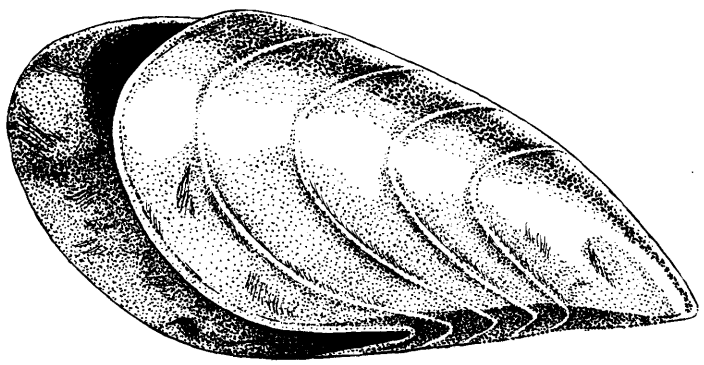

FIGURE 1.—Presumed anterior piece, approximately three times natural size.

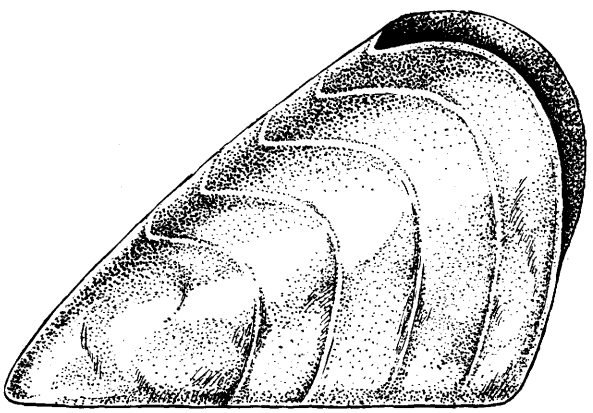

FIGURE 2.—Presumed posterior piece, approximately three times natural size.

about two-fifths of the distance between anterior and posterior of plate. Interior has two cavities: small dorsal cavity, about twice as wide as high, located just below the dorsal surface and separated by a fairly narrow septum from a lower cavity; lower cavity, subcircular in section, occupies nearly half the total height.

Posterior(?) plate bilaterally symmetrical and sides diverge from posterior at an angle near 15°; sides smoothly and slightly arched throughout their length. Maximum width of plate near an oblique plane at right angles to plane of symmetry bisecting the sides. Both dorsal and ventral surfaces rather well rounded and not clearly set off from the sides. Dorsal and ventral surfaces diverge at an angle near 30°. Anterior dorsal margin has a wide, shallow sinus, the depth of the sinus being less than one-sixth the length of the plate. Anterior lateral margins produced strongly outward and less strongly downward from center of dorsal sinus, on either side, to the rounded junction of dorsum and sides, for a total of about one-fifth the distance to the ventral surface. Margins turn to form an obtuse angle, slightly greater than a right angle, on either side of piece and proceed gently inward and strongly downward. Margins join at ventral surface with only a slight emargination. Interior has a small cavity wider than high, located just below the dorsal surface. Remainder of interior has smooth surfaces, elongate in dorsal-ventral plane but otherwise funnel shaped. Cavity mouth about one-fourth the distance from margin to posterior tip; cavity mouth subrectangular, the upper edge just along the midline and the lower edge slightly more than three-fourths of the total height below the smaller dorsal cavity.

Discussion.—The description is based on examination of several of Walcott's type specimens and his illustrations, supplemented by several dozen silicified specimens from California, several dozen from Nevada, more than a dozen from Texas, and about half a dozen from Utah. To avoid future nomenclatural problems, the original of Walcott's figure 6 of 1885 is here designated lectotype. The remaining specimens of the type lot, all catalogued under USNM 27548, are here designated as paralectotypes. Some of the type lot of specimens illustrated in 1886 and 1912 are missing; all the 1885 specimens may be available, but there is some uncertainty about matching them with the illustrations. Although there may be additional specimens collected by Walcott (the late Josiah Bridge, oral commun., 1952), they have not been found in the U.S. National Museum collection despite an intensive search for them and for the missing types.

I am taking the broadest view of individual variation and consider that all the available material belongs to a single species. This seems to be the most meaningful practical approach. Although I recognize the strong likelihood that specimens collected 2,000 miles apart would not belong to the same species, my present knowledge provides no way to distinguish between individual variation and interspecific variation.

Much material is available, but almost all specimens are worn or broken. This, coupled with the loss of some types and the lack of topotype material, has hampered any meaningful work on the specific level. Some differences have been noted. The specimens from Texas have relatively larger cavities than those from California; the Utah material may have more strongly curved ventral surfaces than specimens from other areas. These possible differences are illustrated here and in Yochelson, McAllister, and Reso (1965).

I do not propose to formalize these possible differences as they may well be the result of selective preservation of extreme examples of variation. The larger collections from California and Nevada show a fair amount of variability in the shapes of the two parts, though not enough to obscure the basic differences between the two forms. Statistical study of individual variation in the sizes of the two pieces in each population eventually might be a useful approach. If significant differences could be established, a series of subspecific names might be applied to the geographically separated populations; this approach would satisfy both zoological and nomenclatural considerations. However, until additional, better preserved material is available, I prefer to use only a single species name without any trinomial subdivisions.

RECONSTRUCTION OF *MATTHEVIA*

At each locality from which a fair number of specimens are available, the specimens fall into two general kinds. This observation was first made by Walcott, and it was reinforced when silicified material in quantity was first studied. Walcott's figures of 1886 (pl. 33) definitely show that two growth forms, a wide shell and a narrow shell, occur in the type lot. In addition to these two forms, Walcott (1885, 1886) described a specimen that is lozenge shaped in section and has an eccentric apex. Although he interpreted this specimen as an operculum, I disagree; the outline of the supposed operculum is discordant with that of other specimens he illustrated. Walcott did not note cavities in this supposed operculum. This particular specimen has the base broken away, and the shell is exfoliated only near the apex. From neither end of the specimen could he have had the opportunity to observe any internal cavities.

It is possible that this supposed operculum may not be congeneric with *Matthevia*. If it were a simple cap-shaped shell of the monoplacophoran type, it would not have contained the two cavities. Unfortunately, this particular specimen is missing and the question cannot be answered. The presumed operculum is not the only point of my disagreement with Walcott's pioneer work. The orientation he employed is even more fundamental.

Walcott illustrated *Matthevia* with the apex dorsal. Thus, in the wider form, there were two ventrally opening cavities separated by a wide septum or internal process. Neither of these cavities is particularly large. If the narrower piece is oriented in a similar position, with the apex dorsal, the septum is so large and both cavities are so small that they could have contained only a small fraction of the soft parts of the animal. For the narrower piece, at least, this orientation seems most unlikely, and it is illogical to expect that the two generally similar pieces would have had strikingly different orientations.

If one accepts the view that the hard parts of *Matthevia* consist of a single piece, then one must also accept the fact that at many localities two closely related species, or, more likely, two closely related genera lived near each other. Although this possibility cannot be ruled out, it seems unlikely to me. On the assumption that the cavities functioned to protect vital soft parts, one form had a distinct advantage over the other. It is difficult to see how this biological situation could have occurred. Even if the situation existed, the probability of its occurring on a continent-wide geographic range seems so improbable that the notion of two related genera is abandoned.

An alternative explanation is that the two forms reflect sexual differentiation. A prime difficulty with this interpretation is that among living mollusks sex-related conchological differences are the exception rather than the rule. It is unlikely that sexual differences would be pronounced in primitive forms. Recent cephalopods, particularly those with shells reduced or absent, show the most obvious sexual differentiation within the Mollusca; they are also generally considered the most advanced members of the phylum.

As additional occurrences of *Matthevia* were found, it became increasingly evident that these two pieces are best considered as parts of the same biological entity. Even though the two plates, or pieces, occur in different numbers at the various localities, this need not interfere with the theory. The pieces have slightly different shapes and weights because of the size of the cavities. These variations result in different hydrodynamic properties, and if some sorting or reworking of the hard pieces may have occurred, physical processes easily could account for the difference in relative abundance of the two kinds of pieces. Sorting of aptychi from cephalopod conchs and opercula from gastropod shells are well-known examples of this process.

My suggestion that *Matthevia* represents an animal having more than one hard part obviously is at considerable variance with the original generic concept. Rather than consider this animal as possessing a septum separating two cavities, I suggest that it grew calcareous "shells" with such geometry that each "shell" contained two holes. These holes were not "body cavities," but they did contain soft parts of some sort.

If one accepts the interpretation that *Matthevia* contained more than one plate, a number of interpretations can be made of the biologic significance of these plates. Until a specimen with several pieces intact has been collected, none of these possibilities can be entirely ignored, but some of the more unlikely reconstructions can be effectively discarded.

One must consider briefly the possibility that the specimens were part of an internal skeleton rather than an external shell. Growth lines, though admittedly not an invariable criterion, are strongly suggestive of external shells. Except for advanced cephalopods and gastropods in which the shell is reduced to a remnant, an internal shell is unknown in this phylum. It seems unlikely that an internal shell would be a primitive character. Evidence from other fields of zoology indicates that a true internal skeleton, at least in a primitive animal, seems to be the exclusive province of the Deuterostoma.

Once it is assumed that the shell pieces were external, there are several orientations into which they could be placed. Both hard parts have in common a plane of bilateral symmetry; any reconstruction involving the soft parts should also involve such symmetry. Thus, a reconstruction having one sort of plate on one side of the animal and another on the other side would violate this symmetry.

If these two plates were dorsal, with the apex upward as implied by Walcott (1885, 1886, 1912) and Fisher (1962), it would follow that to preserve bilateral symmetry one piece would be behind the other. It is difficult to imagine that the plates could have performed any sort of function in this position. Although these shell pieces may have been functionless, the large and growing volume of literature on functional morphology indicates that there are relatively few functionless structures in the animal kingdom. Structures having apparently neutral survival value do occur among animals, but evidence is increasing that the concept of nonadaptive evolution is of little importance. In my

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view, a plausible function seems inherent in any reconstruction of this extinct form.

Several other orientations are symmetrical but violate the concept of function. If one piece were dorsal and the other ventral, symmetry would be preserved, but it is difficult to conceive of soft parts that might fit between these two plates. If there were similar parts laterally and a different part on the anterior, posterior, or both, the hard parts would be arranged symmetrically and there would be bilateral symmetry of the soft parts. The resulting animal, however, is so unlikely that it need not be considered further.

Thus, largely through a process of elimination, one is left with a somewhat elongate animal having one hard plate anterior and a second plate posterior. This also seems most likely to be the correct orientation because it reflects the bilateral symmetry shown by the hard parts. If this orientation is correct, the apex is not dorsal but is either anterior or posterior. In addition, the ventral aperture of earlier illustrations is not ventral but opens centrally.

The choice remains as to which part is anterior and which is posterior. The differences between the two do not clearly resolve this particular question. The detailed description of the species is based on the supposed orientation outlined in the following discussion, but it is appropriate to remark that other paleontologists have suggested that the anterior and posterior designations should be reversed.

The plate taken to be anterior is more streamlined in that it is more elongate, wider, and lower than the second. Further, this plate is characterized by relatively larger cavities than the other. The width seems particularly critical as the margins are most likely to be broken. By nesting the narrower within the wider plate, the margin of each is partly protected. Were the margins of this piece anterior, there seems to me greater chance that they might have been broken during forward movement of the animal. The larger cavities might have provided more protection for anterior sense organs. Cephalization is a fundamental tendency within the mollusks and related phyla. This tendency was probably characteristic of even early members of the phylum.

Each hard piece contains only one plane of symmetry. If this is taken as a dorsal-ventral plane, then on the presumed anterior piece one surface is arched and the opposite surface is flattened and curved downward slightly toward the anterior apex. If the flattened side is oriented as ventral, the larger cavity is below the smaller one. The ventral side of the cavity is partly open because of the U-shaped sinus.

The orientation of the second, shorter, narrower, and higher plate is somewhat less obvious. It too is a flattened asymmetrical pyramid but without any clear distinction between dorsal and ventral surfaces, both being arched outward. If this piece is oriented with the longer surface as ventral, the small cavity is above the larger cavity, as in the wider piece. In this orientation, the lateral margins of this piece are slightly sinuate and thereby complement the lateral margins of the anterior piece which are lobate. This orientation of the two pieces is shown in figure 3*A*.

Reversing the anterior and posterior pieces as an alternative orientation has been tried by placing the two parts on a clay model of soft parts. As noted, the wider piece is open toward the anterior and the resultant reconstruction is not quite as streamlined as for the first orientation. This alternative, less satisfactory orientation is shown in figure 3*C*.

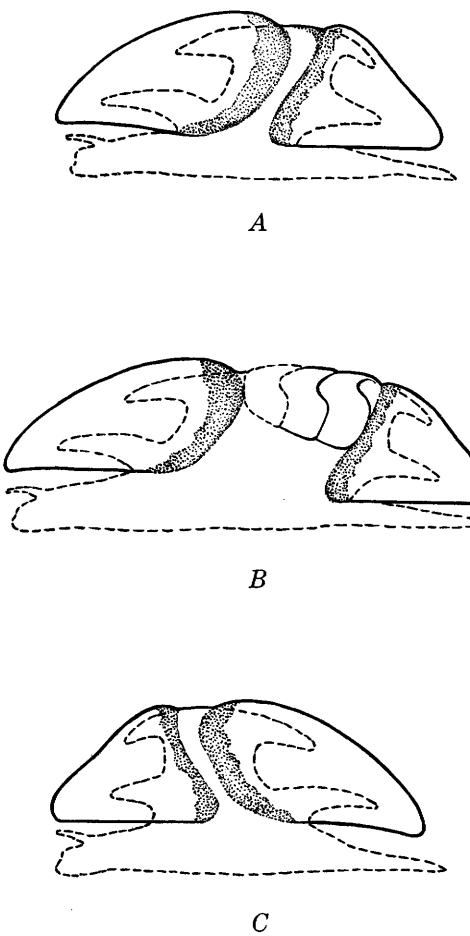

FIGURE 3.—Possible reconstruction of *Matthevia*. *A*, Preferred orientation of hard parts. *B*, Same orientation but with hypothetical intermediate plates. *C*, Alternative orientation of hard parts. Approximately life size.

One other possible structural element must be discussed. After study of one fragment found before 1958, I speculated that *Matthevia* may have been a multiplated animal having peculiar anterior and posterior plates and intermediate plates much like those of an amphineuran. Having obtained some additional material, I mentioned this possibility (Yochelson, 1963). Since that time, larger collections have been obtained from one locality that yielded presumed intermediate plates. After studying these larger collections, I am now convinced that the idea of intermediate plates, though appealing, is unlikely. The presumed intermediate plates are now interpreted as nothing more than selected worn fragments of the anterior plate. Almost all degrees of preservation occur, from pieces that show slight abrasion of the anterior slope with the cavities open at their anterior or posterior ends, to pieces that are badly worn.

Nevertheless, I cannot rule out the possibility that intermediate plates might occur. One plausible example of an intermediate is illustrated on plate 1, figures 15–17, so that the reader may judge the validity of this hypothesis. An alternative reconstruction, having intermediate plates in place, is shown in figure 3*B*. The sides of all possible intermediate plates observed are always much shorter than the anterior and posterior pieces and are reconstructed accordingly. The reconstruction might equally well have been done with the presumed posterior and anterior reversed, but there seems little to be gained in laboring this point. Additional speculation, that intermediate plates were not preserved because they were less heavily calcified or perhaps even chitinous during life, is considered very tenuous.

As I envision *Matthevia*, it was a moderately elongate animal. Presumably it crept about the sea bottom on its muscular foot; the foot, even if modified, is a common feature of mollusks. The narrowness of the plates implies that the body and foot were narrow. The streamlined shape of the hard parts would permit moderately rapid currents to flow over them without upsetting the animal's balance. The combination of narrow body and relatively high plates, as well as the absence of intermediate plates to provide flexibility, would limit ability to live in areas of strong current and wave activity and to cling to rocky surfaces. Despite its apparently poor adaptation, it is still easier to imagine *Matthevia* in the role of a clinger than as part of the vagrant benthos.

A head and probably a short neck extended outward from beneath the opening in the anterior plate. The mantle cavity may have been partly protected by the extended flanges on either side of the anterior plate. Water may have entered from below and been directed upward, a common pattern in mollusks. The dorsal gape between anterior and posterior pieces could well have resulted from fouled water inhibiting shell growth in this zone. The number, position, and kind of gills is speculative, as with nearly all fossil mollusks. If the gills were partly protected from sediment by being within the anterior flange, then there is some likelihood that this animal could have moved across a muddy bottom for at least short distances.

The upper cavity of the anterior plate and the two cavities of the posterior plate could have functioned as insertions for powerful muscles. It would certainly have taken a fairly strong series of muscles to move the posterior heavy piece forward, even when it rested on the foot. *Matthevia* probably was mobile though not motile. One may further speculate that, in the event of danger, the foot and body mass could have been contracted so that a maximum proportion of the soft parts would be covered by the hard parts. When the animal was fully or partly extended, there was probably a fringe of the mantle around the anterior and posterior margins to permit these pieces to continue gnomonic growth.

Speculation as to diet contributes little. Recent primitive gastropods are herbivorous, scraping vegetation with a radula. Other recent primitive mollusks, including some protobranch pelecypods and the monoplacophoran *Neopilina* Lemche (Lemche and Wingstrand, 1959, p. 63), are deposit feeders. Some recent amphineurans show both food preferences, and a few are omnivorous; in general, however, they are herbivores that rasp plants from rocky surfaces. There is no clear basis for suggesting either mode of nutrition for *Matthevia*. From the streamlined shape of the anterior part alone, it is tempting to consider *Matthevia* as mainly a deposit feeder plowing the bottom, rather than as a grazer. On the other hand, the occurrence of specimens near algal remains may be more than a coincidence. Perhaps *Matthevia* lived on algal colonies.

These ideas toward reconstruction of the soft parts cover only the more elementary anatomical requirements. Withal, *Matthevia* remains an enigmatic animal. In particular, the weight of the anterior and posterior plates must have been a serious problem. Perhaps the animal was oversupplied with calcium carbonate in its diet and these heavy plates were a method of removing this mineral from the body. Perhaps, alternatively, this weight was one method of solving the problems that arise if an elongate shelled animal moves from a quiet-water environment into a zone of somewhat higher energy.

The occurrence of sorted pieces near algal "reefs" in two areas suggests moderately active water in the ecological niche where *Matthevia* may have lived. In a sense, *Matthevia* may have been the ecological precursor of the Amphineura, but this attempt to populate a moderately high energy, shallow-water environment was of limited success. The experiment seemed almost doomed to fail when *Matthevia* was placed in competition with the Amphineura, mollusks more specialized for clinging to curved, rocky surfaces. In contrast to the flattened amphineuran body covered by the flexible multivalved shell, the relatively high, narrow, and heavy end pieces of *Matthevia* seem indeed a poor mechanism for maintaining balance against the pull of waves and currents.

MATTHEVIA AS THE REPRESENTATIVE OF A CLASS OF MOLLUSKS

Not only are there no rules of nomenclature to follow above the family level, but also there is little accepted zoological practice to guide one through problems at higher systematic levels. My proposal of a new class of mollusks, therefore, must carry some explanation.

The first point at issue is that of placement on the phylum level. Although it is theoretically possible for a fossil known only from its hard parts to be a representative of an extinct phylum, in actual practice few paleontologists have proposed new phyla. I do not consider such a course necessary here because the hard parts of *Matthevia* are molluscan, as I have defined this term (Yochelson, 1961, p. 164) for paleontological usage.

If one accepts Walcott's original description of this form as an essentially conical shell having two cavities separated by an interior septum, there is no place for it among the extant classes of mollusks. Its shape is distinct from the four classes of univalves. Without belaboring the point, the conchological differences between *Matthevia* and Gastropoda, Cephalopoda, and Scaphopoda are obvious. Although the Monoplacophora includes, in part, a heterogeneous assemblage, some of the less typical members are now better known through unpublished work and can be assigned elsewhere. Even if the class remains a heterogeneous one, it is beyond the limit of any reasonable taxonomic scheme to assign *Matthevia* to Monoplacophora. Although some fossil monoplacophorans approach *Matthevia* in the external shape, internal details are incompatible with the dual cavity arrangement of this genus. Comparison with the bivalved Pelecypoda is preposterous.

By a process of elimination, comparison with the Amphineura remains. If *Matthevia* is considered a univalve, the morphologic uniqueness of the genus is evident. It is only if *Matthevia* is considered to represent an animal with more than one hard part, that comparison with the Amphineura is necessary. Even then, differences are striking. Although amphineuran valves are differentiated at the anterior and posterior, they in no way resemble the hard pieces of *Matthevia.* Amphineuran valves commonly are wider and much lower, have a different shape, are relatively thin rather than massive, and, above all, lack the two cavities within the hard parts. The pocket in end valves of a few forms is hardly comparable. No morphologic feature, except the presence of more than one hard piece, can relate *Matthevia* to the Amphineura.

A more logical alternative is to consider *Matthevia* a representative of a distinct class. In the final analysis, probably the only zoologically valid criterion for a class is that it be distinct from all other classes in the phylum. Even with the limitation imposed by the absence of soft parts, *Matthevia* seems to fit that criterion.

PSEUDOMATTHEVIA

Pseudomatthevia was named because of an apparent superficial similarity to *Matthevia.* However, in the original description, Shaw (1956, p. 51) noted that the cone-shaped shell lacked the internal septum of *Matthevia* and was in no way related to that genus. The type species, *P. conica* Shaw, is known from four specimens from the upper Dresbach (*Aphelaspis* zone) Dry Creek Shale near Boulder, Wyo.

Shaw described this genus as operculate. Paratype A11204c was designated as the operculum. This specimen is a low conical steinkern, broken at the margin. As nearly as one can determine, the specimen was originally circular, the apex was central, and there was a crenulation in the shell about midway between the apex and the margin. Although the remaining specimens are described as slightly ovate, I would consider the two paratypes distinctly ovate and the holotype possibly so. Thus, the aperture does not have the same shape as that of the margin of the supposed operculum. In other features the original description is accurate.

I cannot accept this as an operculate mollusk. In my judgment, two genera have been confused. The "operculum" is not generically identifiable, though in some respects it resembles *Palaeacmaea* Hall and Whitfield, 1872. The holotype and two remaining paratypes of *Pseudomatthevia* are closely related to *Hypseloconus*, particularly the less strongly curved Lower Ordovician form illustrated by Knight and Yochelson (1958). For the time being, *Pseudomatthevia* is best treated as distinct from *Hypseloconus;* further study

of the highly variable *Hypseloconus* may lead to modification of this opinion.

A single specimen identified as *Pseudomatthevia*? species was described and figured by Shaw (1962, p. 319, pl. 49, figs. 6, 7) from the lower Dresbach (*Cedaria* zone) Hungerford Slate of Doll (1961), near Highgate Center, Vt. The illustrations of this specimen suggest a curved posterior(?) slope from which a major part of the apex has been broken away. Were this apparent curve projected to the presumed apex, the resulting form would be quite similar to species included within *Hypseloconus* Berkey. Accordingly, I suggest that the unnamed species be transferred to that genus.

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PLATE 1

FIGURE 1. Left side view of steinkern of posterior piece. USNM 146894; × 1½. From USNM loc. 37b, ½ mile east of village of Salem, Washington County, N.Y. Collected by C. D. Walcott, September 1893 (date is in error). (This specimen is in the same tray with others from loc. 76a. In view of the similarity between the specimen and others from the Hoyt Limestone Member of Theresa Dolomite (76a) as well as its similarity to Walcott's figure of 1889, I am inclined to believe that the wrong locality number was affixed.)

2–3. "Casts of the chamber of habitation and the inner chambers. The septa are seen at *S*, *S'*." From Walcott, 1886, pl. 33, figs. 1 and 1a. Fig. 1 is the original specimen of fig. 2; fig. 3 is probably the original of figs. 4 and 5. The figures are oriented as published by Walcott.

4–5. Anterior and left side views of steinkern of posterior piece. USNM 146895; × 2. From USNM loc. 76a; Railroad quarry, 1 mile north of Saratoga Springs, N.Y. Undoubtedly from the Hoyt Limestone Member of the Theresa Dolomite.

6–7. Dorsal and interior views of posterior piece. USNM 146896; × 2. From USGS loc. D–1057–CO, near head of Lucky Strike Canyon along ridge running eastward from south end of hill 6612; coordinates 516,000 ft. E. 570,300 ft. N., Charleston Park quadrangle, Nevada. Nopah Formation. Collected by R. J. Ross and L. A. Wilson, 1961.

8–11. Ventral, dorsal, interior, and right side views of posterior piece. USNM 146897; × 1½. From USGS loc. D–1057–CO.

12–14. "End, side and summit views of the most characteristic form, enlarged." From Walcott, 1886, pl. 32, figs. 1–3; oriented as published.

15–17. Dorsal, ventral, and anterior(?) views of worn fragment. USNM 146898; × 2. From USGS loc. 3818–CO, isolated hill, 5.5 miles in straight line N. 56° E. from Pyramid Peak, Ryan quadrangle, California. Nopah Formation. Collected by J. F. McAllister, 1962.

18. "Associated operculum, with portions of shell removed." From Walcott, 1886, pl. 32, fig. 4; oriented as published.

19–22. Dorsal, right side, interior, and ventral views of anterior piece. USNM 146899; × 1½. From USGS loc. D–1057–CO.

23–26. Left side, interior, ventral, and dorsal views of anterior piece. USNM 146900; × 2. From USGS loc. D–1057–CO.

27–29. "Summit, end, and side views of the conical variety, having a deeply sinuous margin." From Walcott, 1886, pl. 32, figs. 7–9; oriented as published.

30–32. Left side, interior, and right side views of posterior piece. USNM 146901; × 1½. From USGS loc. D–1057–CO.

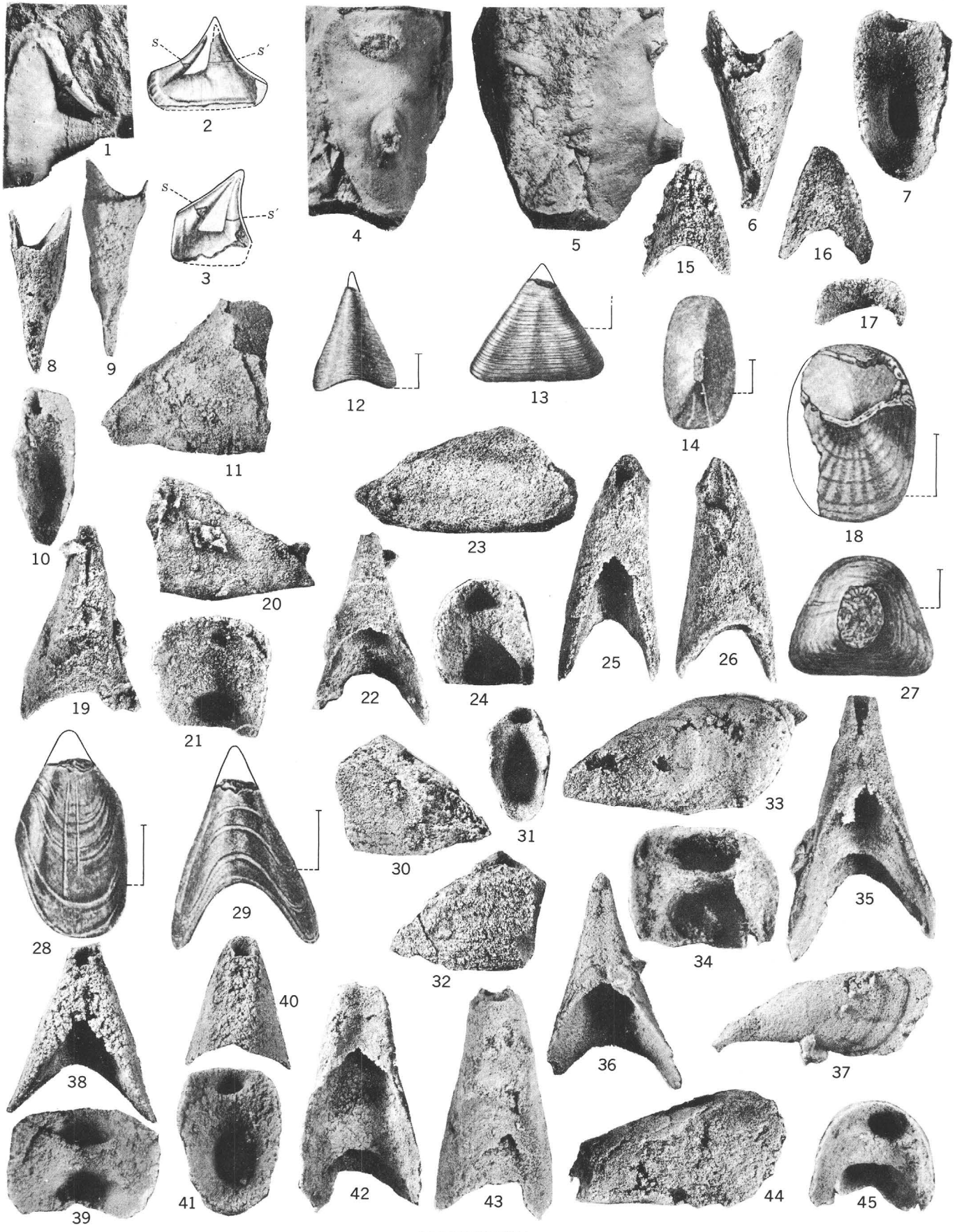
33–35. Left side, interior, and ventral views of anterior piece. USNM 145317; × 1½. From USGS loc. D–1057–CO. [One view of this specimen was illustrated by Yochelson, McAllister, and Reso (1965).]

36–37. Ventral and left side views of anterior piece; the dorsal surface is broken and the posterior half of the profile is thus not correct. USNM 145316; × 1½. From USGS loc. 2043–CO, Ajax Dolomite, from above the middle part; 50–75 feet of dark-gray dolomite that immediately underlies the Garden City Formation. Sec. 27, T. 1 S., R. 7 W., Timpie quadrangle, Tooele County, Utah. Collected by Dwight E. Arnold, 1955. [One view of this specimen was illustrated by Yochelson, McAllister, and Reso (1965).]

38–39. Ventral and interior view of anterior piece. USNM 145312; × 1½. From USGS loc. 1734–CO, dolomite facies of San Saba Member near top of Wilberns Formation. Along west side of a pasture road, 1 mile west of Blanco County line and 3,400 feet north of North Grape Creek, Gillespie County, Tex. Collected by L. H. Dixon and V. E. Barnes, 1947. [One view of this specimen was illustrated stereoscopically by Yochelson, McAllister, and Reso (1965).]

40–41. Dorsal and interior views of posterior piece. USNM 145313; × 1½. From USGS loc. 1734–CO. [One view of this specimen was illustrated stereoscopically by Yochelson, McAllister, and Reso (1965).]

42–45. Ventral, dorsal, left side, and interior views of anterior piece. USNM 146902; × 1½. From USGS loc. D–1057–CO.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