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A RESTUDY OF THE LATE CAMBRIAN MOLLUSCAN FAUNA OF BERKEY (1898) FROM TAYLORS FALLS, MINNESOTA

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NOTE ON MEASUREMENTS USED IN THIS REPORT

Although the metric system is preferred in scientific writing, certain measurements are still routinely made in English customary units; for example, distances on land are measured in miles and depths in drill holes are measured in feet. Preference was given in this report to retaining the units in which measurements were made. To assist readers, conversion factors for some of the common units of measure are provided below.

English units to metric units:

To convert from	to	multiply by
inch	millimeter	25.40
inch	centimeter	2.450
foot	meter	0.3048
mile	kilometer	1.6093

Metric units to English units:

To convert from	to	multiply by
millimeter	inch	0.03937
centimeter	inch	0.3937
meter	foot	3.2808
kilometer	mile	0.6214

A RESTUDY OF THE LATE CAMBRIAN MOLLUSCAN FAUNA OF BERKEY (1898) FROM TAYLORS FALLS, MINNESOTA

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ABSTRACT

The molluscan fossils described and illustrated by C.P. Berkey from Upper Cambrian rocks at Taylors Falls, Minnesota, are redescribed and printed in this report. They comprise rare Gastropoda and relatively abundant and diverse Tergomya. The latter are supplemented by a few additional specimens collected decades ago. Palmer's reexamination of trilobite specimens collected by Berkey indicates an Elvinia age for the fauna.

We conclude that the species differentiated by Berkey (1898) are mostly well founded. Berkey's study was significant because it documented the diversity of Mollusca in nearshore sandstones of Cambrian age. To place this nineteenth century paper in context, included herein is a summary of the changing views on evolution of portions of molluscan classification and a survey of some of the older-named, early Paleozoic, North American bilaterally symmetrical univalve species.

INTRODUCTION

When C.P. Berkey was a geology graduate student at the University of Minnesota, he made a geologic map, interpreted the topography and glacial geology, and described the lithology of sedimentary and igneous rocks he encountered over a 60 square mile area. His doctorate, the first given by the University of Minnesota in geology, was granted in 1897. Berkey's thesis was published in three parts. The third part described fossils from a new locality that yielded an assemblage of Late Cambrian fossils, dominated by mollusks and including a number of species. "The marginal conglomerates have proved most fruitful, and recently a fauna has been discovered in these conglomerates which is unique. Several new species and a few rare types are included in it. ...Over a hundred specimens have been obtained..." (Berkey, 1898, p. 275). The fauna he described was from "Taylor's Falls." As shown on Figure 1, the town name is now rendered without the possessive, and the original spelling will only be used in an historical sense within quotations.

To show his competence in paleontology, Berkey described and illustrated the fossils, almost all of which he considered new. He provided descriptions of the species in keeping with the standards of his time and illustrated the fossils with line drawings of all species. For the Mollusca, Berkey used both a lateral view and an outline of the aperture. There was a certain degree of guesswork in producing the latter, but mostly they appear to be fairly accurate.

He also included photographs of a few specimens. Although Berkey's effort of producing photographs of fossils at that time is commendable, unfortunately they add little to the understanding of the taxa. His few general remarks in the text indicate a grasp of the literature, and he had a clear concept of the difference between individual variation and species differentiation. Insofar as there was a philosophical basis in his discussion, Berkey did consider that the various mollusk species that occurred together were a morphologic series leading from one to another within a genus and leading from one genus to another.

Berkey spent most of his career at Columbia University in New York City (Grout and Aldrich, 1965). At least some of his fossil collection was numbered and more formally labeled at the Geological Museum of Columbia University, an entity that no longer exists. Eventually, specimens were transferred to the American Museum of Natural History (AMNH), but by this time it was mainly the figured material that were rehoused and recatalogued, using the same numbers that had been assigned earlier, and even a few of the illustrated specimens were no longer present. Just when this last transfer was made is uncertain, but when Knight (1941) was investigating the type species of *Hypseloconus*, he viewed the specimens at Columbia University. Several labels with the collection indicate that the numbers were entered in the AMNH catalogue during October, 1977. Whether there were additional specimens of Berkey which were not transferred to the AMNH is not known, but it seems unlikely as the collection

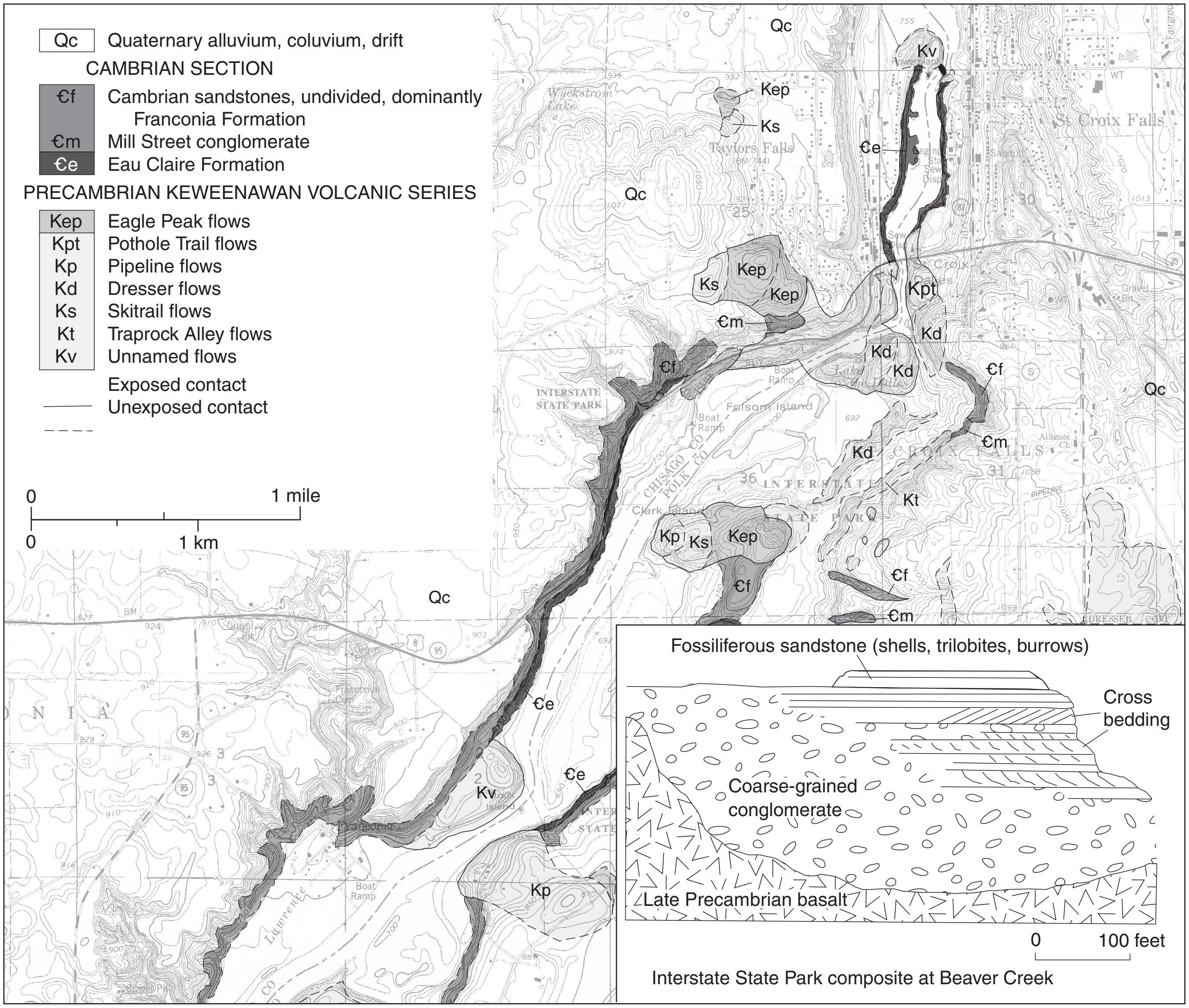


Figure 1. A portion of the geologic map of the St. Croix River valley area (Baker and others, 1989). The outcrop of the Mill Street conglomerate is 1 kilometer south of the "A" in "Taylors." Inset—an unpublished cross-section by R.H. Dott of the conglomerate and overlying Cambrian sandstone, with the center of the upper line of the diagram just below the location of another outcrop of the formation, approximately 2 kilometers southeast of the Mill Street outcrop collected by Berkey.

includes a few additional specimens that are not types or figured specimens.

STRATIGRAPHIC SETTING AND GEOLOGIC AGE

The conglomerate at Taylors Falls from which Berkey collected Late Cambrian mollusks is now referred to by the informal name "the Mill Street conglomerate," and is Elvinia zone (upper Steptoean; lower Franconian) in age (Fig. 2). Lithostratigraphically, it occupies a position in the lower part of the Ironton Sandstone, unconformably above the Galesville Sandstone and conformably below finer-grained sandstone and shale of the Franconia Formation. The conglomerate may be seen in the maintenance area of Interstate State Park that impinges on the southern boundary of Taylors Falls (Fig. 1). It is very coarse-grained, consisting of angular to well rounded basalt blocks as much as 2 feet in diameter surrounded by fine- to medium-

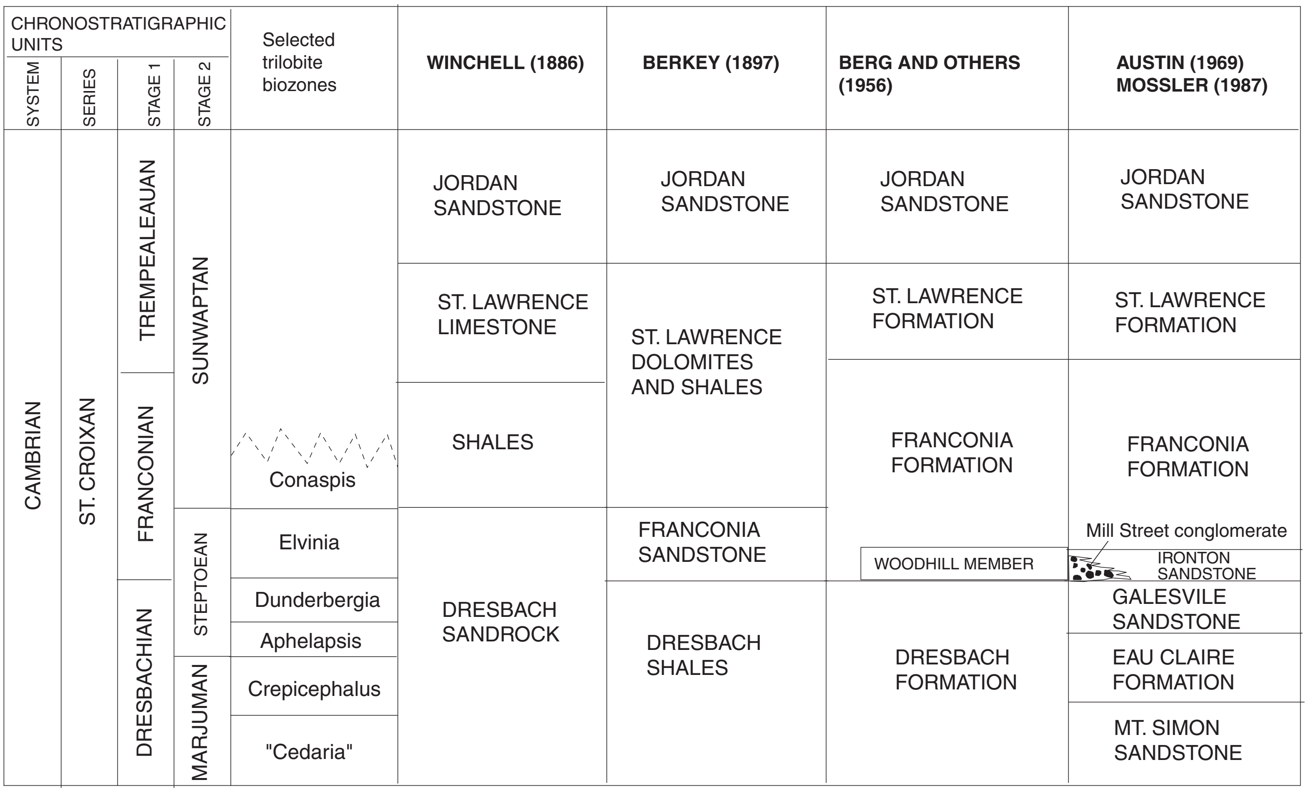


Figure 2. Upper Cambrian formation nomenclature as used by various authors.

grained, buff quartzose sandstone (Cavaleri and others, 1987, p. 37).

Although it was generally accepted early on that the fauna was "Upper Cambrian" in age (Berkey, 1898, p. 292), a review of the literature on the mollusk-bearing conglomerate at Taylors Falls reveals some confusion and inconsistencies with regard to its stratigraphic position and precise age within the Late Cambrian. Berkey's confusing description of the stratigraphic context of the locality is in part responsible and some of his comments form a good starting point for discussion of this matter. "The conglomerate at Taylor's Falls belongs stratigraphically to the lower part of the Franconia sandstone member of the Basal Sandstone series, and extends downward into the next underlying member, the Dresbach sandstone" (Berkey, 1897, p. 376; Fig. 2). A subsequent passage inconsistent with the preceding statement is "Fossils reported from the Dresbach at Taylor's Falls and St. Croix Falls are:..." (Berkey, 1898, p. 273). This phrase was preceded by a brief discussion of shales and followed by a list of four brachiopod species. He then mentioned his discovery of previously named forms and new species, stating that the sandstone which yielded these fossils was within the Dresbach, and from the standpoint of both abundance and preservation of fossils, this sandstone could be differentiated from the overlying "Franconia sandstone."

In his summary, Berkey (1898, p. 291) also mentioned the occurrence of the inarticulate brachiopod *Lingulepis pinniformis* Owen in the "Dresbach shales," and also at Taylors Falls. He noted that the species did not occur above the Dresbach, but did not describe it; Berkey (1898, pl. 21, Fig. 1) produced only a poor photograph of what were supposed by him to be two separate species. Walcott (1912a, p. 545-546) transferred Owen's species to *Linguella* (*Lingulepis*) *acuminata* (Conrad), though the occurrence at Taylors Falls was not considered by Walcott in his monograph. The inarticulate brachiopods are a further indication of the diversity at Berkey's locality, but specimens were not described and we will not discuss them further.

Berkey's comparison of the Taylors Falls collection to other areas also had implications as to the age of his mollusk collection, and included statements maintaining that his fossils were from the "Dresbach sandstone." "The remarkable group of fossils from Eikie's quarry [in some literature as Eikie], near Baraboo, Wisconsin, bears such a striking resemblance to the new forms from the Dresbach of Taylor's Falls that it seems appropriate to enumerate them here. Notwithstanding the difficulties of stratigraphy at Baraboo and the inclination of the Wisconsin geologists to place them much higher in the series of formations, it is at least clear that the two faunas are in all essential respects similar" (Berkey, 1898, p. 274). Berkey listed the fossils described by Whitfield in making his comparison, and it should be noted that Whitfield's study was virtually the only literature pertinent to his investigations.

In the decades after Berkey's work, formal Upper Cambrian stages were established for North America. They were based largely on upper Mississippi River valley strata and fossils. The Dresbach, Franconia, and Trempealeau formations of some workers were stratotypes for the Dresbachian, Franconian, and Trempealeauan stages (Fig. 2). Refined North American biozonation, especially for trilobites and conodonts, as well as improved stratigraphic concepts, resulted in the development of a nomenclature system in which lithostratigraphic units were clearly separate from chronostratigraphic units (for example Berg and others, 1956). In Minnesota today, the lithostratigraphic nomenclature follows Austin (1969) and Mossler (1987); the stage terminology proposed by Ludvigsen and Westrop (1985) of Marjuman, Steptoean, and Sunwaptan does not seem to be in general use. Despite advances in stratigraphy, the age of Berkey's Mill Street conglomerate collection continues to be a source of confusion; inconsistencies and uncertainties that originated with Berkey's original description were simply transferred to a new set of lithostratigraphic and chronostratigraphic units (for example Cavaleri and others, 1987).

In an effort to clarify the stratigraphic problems, we visited Baraboo and the Taylors Falls area, reviewed literature and maps published after Berkey's work, and re-evaluated the age of the associated fauna, particularly the trilobites. First of all, in one sense, Berkey's interpretation of the stratigraphic context of basalt boulder conglomerate at Taylors Falls is correct, in that it at least as lenticles occurs from what he referred to as the "Dresbach shales" up into his "Franconia sandstone." Clements Nelson (1951) reported that basalt conglomerate at lower elevations in the Taylors Falls area yields Crepicephalus zone (Dresbachian stage; upper Marjuman) trilobites, whereas higher elevation conglomerates yield Elvinia zone (lower Franconian stage; upper Steptoean) trilobites. Further studies of Franconia (upper Steptoean) stage trilobites in Minnesota (Bell and others, 1952) and Wisconsin (Berg, 1953, 1954) do not specifically discuss the Taylors Falls faunule, but Berg does state that at Taylors Falls "...a boulder conglomerate containing the *Elvinia* fauna rests on Precambrian diabase. This is the Mill Street conglomerate of Berkey (1897) and represents a shore phase of the Woodhill member [basal member of the Franconia Formation]" (Berg, 1954, p. 871-872). The Woodhill member is today's Ironton Sandstone. Thus the work of trilobite specialists such as Berg (1954) and Nelson (1951) indicated that Berkey's Mill Street conglomerate locality is Elvinia Zone in age. However, they did not provide enough information to know for certain that they identified Berkey's specific locality and collected trilobites from it. In a further effort to document the age of Berkey's Taylors Falls mollusk fauna, we located specimens of trilobites that he collected at the same site, and described as six species. At this stage of our knowledge, we would place greater emphasis on the trilobites for biostratigraphic purpose than in the less widely distributed mollusks. As a practical matter, far more is known of the distribution of Late Cambrian trilobites and more people have studied and collected these fossils than have been interested in the less common mollusks. The handful of trilobites collected and described by Berkey have been reexamined at our request, and in the appendix of this report, A.R. Palmer assigns them to the Elvinia zone. Accordingly, we are satisfied that the molluscan fossils from the Mill Street conglomerate, at Berkey's locality, are of earliest Franconian (upper Steptoean) age. In our usage of the Mill Street name therefore, in this report, we mean for it to apply to only the classic mollusk-bearing outcrop from which Berkey obtained the fossils described herein, as from Ironton Sandstone, and Elvinia zone age.

As for similar mollusks collected from outside of Minnesota, despite Berkey's suggestion of morphologic similarity to the Mill Street conglomerate, the southeastern Wisconsin mollusc collection at Eikie's quarry is substantially younger than that of Taylors Falls. We believe that we located the site of Eikie's quarry about seven miles from Baraboo, Wisconsin, and collected one fragmentary mollusk from the carbonate. We also searched, without success, the shoreline of the nearby "Baraboo Islands" for additional fossils. Dott (unpub. data, 2002) likewise found no fossils in the Baraboo area, though a few have been reported. We speculate that as a generalization, the carbonate environment was more amenable to life by providing a more uniform environment, whereas on a storm-influenced coast, the presence or absence of living forms would be more subject to chance. The Wisconsin geologists alluded to by Berkey were correct in placing Eikie's quarry as younger than his fossiliferous bed. In fact, the carbonate beds at Eikie's quarry have long been considered significantly younger and were near the middle of Ulrich's "Ozarkian" System (Byers, 2001). What was called the Mendota or Black Earth Dolomite is of Late Cambrian age and is near the base of the Trempealeauan (middle Sunwaptan; Wanenmacher and others, 1934) stage. The rocks at Eikie's quarry are now referred to as the Black Earth Member of the St. Lawrence Formation (Dalziel and Dott, 1970).

Another locality with similar mollusks in Montana is measurably older than the Mill Street fauna, and therefore it would appear that the range of the mollusk *Hypseloconus* is longer than that of the individual ranges of the various trilobites associated with it. A report of the mollusk *Hypseloconus elongatus* from an *Aphelaspis* zone assemblage in Montana included the following quote which may still be pertinent. "Ten specimens have been assigned to this species, [*Hypseloconus elongatus*] the genotype of *Hypseloconus*, even though the horizon is somewhat older than that of the Minnesota specimens which occur in the lower *Elvinia* zone assemblages" (Lochman and Hu, 1962, p. 440). Hypseloconus forms similar to those at Taylors Falls are therefore known from Late Dresbachian stage (early Steptoean) in Montana through early Trempealeauan (in Wisconsin) age strata.

AVAILABLE MATERIAL AND SIGNIFICANCE

As a result of what he termed extensive collecting—which may apply to more than the Taylors Falls locality—Berkey (1898, p. 275) reported "Over a hundred specimens have been obtained and the range of variability which they exhibit throws some light upon the classification of the early forms of gastropods." If this number refers to the mollusks, less than a quarter of the specimens mentioned are still available.

Ever since Webers located Berkey's collecting locality, he repeatedly visited the limited outcrop at Taylors Falls, Minnesota, but has found virtually no useful molluscan fossils. The site had been modified for a railroad grade, and abandoned. Although we cannot prove it, we suggest that this construction may have preceded Berkey's investigations and fortuitously left freshly broken fossiliferous sandstone for him to examine.

The fossil collections of the University of Minnesota contained about two dozen specimens from Taylors Falls. These were donated to the National Museum of Natural History. They include several fragmentary gastropods that serve to reinforce our interpretation, presented in the systematic section, of *Euomphalus strongi* variety *sinistrorsus* Berkey, and four other low, conical forms. In contrast to this paucity, about a dozen and a half specimens, mainly steinkerns of *Hypseloconus*, are included. There are also three specimens of a form that was not described by Berkey and will be considered as a supplement to the systematic paleontology. Whether any of these fossils were part of Berkey's original lot or were subsequently collected at Taylors Falls, Minnesota, is unknown, but we are inclined toward the former interpretation.

The collection of the University of Missouri—Rolla is reported to have several *Hypseloconus* from this locality (B.L. Stinchcomb, unpub. data, 2002). The only material from Taylors Falls that was available in the collection of the National Museum of Natural History (USNM) is a single specimen of *Hypseloconus* collected and illustrated from the locality by Stinchcomb (1980; USNM number 278642). The term "steinkern" refers to the preserved matrix that has filled in the interior of a shell. The terms "casts" and "molds" are interpreted in a variety of ways and the use of steinkern avoids this ambiguity. Most of Berkey's mollusk specimens are steinkerns, and only a few are external molds. No shell material is preserved, and the sandstone matrix is inferior to that of a limestone in preserving details of the exterior. Commonly, only an external mold shows growth lines and ornament, though with rare specimens some information on these features may be gleaned from a steinkern. On the other hand, the steinkern may show features such as muscle scars that cannot be observed when the shell is present. As a rule, steinkerns cannot be identified to the generic level and even assigning them to a family may be uncertain.

With limited material of indifferent quality, one may question whether the material warrants restudy. However, if one is interested in the early history of any group of fossils, study of Cambrian specimens is critical. To take a pragmatic approach, the remaining types are all one is likely to obtain from the locality and if there is to be a study they constitute all one is ever likely to have available; this is unfortunately true for many classic localities. As a practical matter of systematics, once a name is in the literature, it remains there in perpetuity. After more than a century, Berkey's species deserve to be reexamined to see where they fit in more recent classification and whether his specific names have a biological significance.

The outcrop collected by Berkey at Taylors Falls has produced one of the oldest and most diverse Late Cambrian molluscan faunas in the United States. Dake (1930, p. 89) collected fossils from the Ozark area near Sunlight, Missouri. Using Berkey's (1898) publication, Dake produced a faunal list containing six species and three varieties of *Hypseloconus* and three undetermined species of Tryblidium, though the material was not documented by description and illustration. Rocks are poorly exposed in the area, but these fossils were probably collected from the lower part of the Davis Formation, essentially the same age as the Minnesota locality (Stinchcomb, unpub. data, 2003). Stinchcomb (1975) described two new species of *Hypseloconus* from massive dolomites near the top of the underlying Bonneterre Formation. These outcrops in the Big River area of the Ozarks are dated as Dresbachian (Steptoean) stage and demonstrate that *Hypseloconus* ranges through the Late Cambrian; other publications document Early Ordovician occurrences of the genus in Missouri.

There are many reports of mollusks in Lower and Middle Cambrian rocks. Some may be authentic mollusks, others may be questioned, and still others may be incorrectly assigned. A monographic study of the Early and Middle Cambrian presumed mollusks could be enlightening, but it would be a formidable undertaking. In the interim, should such a study be undertaken, a restudy of Berkey's types may directly yield data pertinent to the evolution of the Mollusca and this in turn may indirectly help to clarify the confusion in the older part of the record.

PALEOECOLOGICAL SPECULATION

Little can be written concerning the paleoecology of these ancient mollusks. The current interpretation of the locality is that large blocks of Precambrian basalt forming the bulk of the Mill Street conglomerate fell from a sea cliff (Fig. 1, inset). Dott (1974) studied a comparable conglomerate around Baraboo, Wisconsin in detail, and considered the force of waves necessary to shape the individual boulders. For comparative purposes, he examined the Minnesota occurrence on two separate occasions. "The boulders smaller than about 3 feet diameter are pretty well rounded, indicating movement enough to abrade them thoroughly. The largest (up to 8 to 10 feet) are not very rounded, indicating that breaking (storm) waves were able to tumble and move the smaller sizes frequently enough to round them, but were not powerful enough to move the largest boulders very often, if at all" (R. Dott, unpub. data, 2002). Many of the boulders are reported to bear percussion marks.

A matrix of sandstone fills the area between the basalt boulders and it is this matrix that contained the fossils. The sand is relatively coarse-grained, and one small pebble has been noted within the filling of one sample (AMNH number 22274). The presence of the sand filling the space between the boulders carries with it an implication of nearshore and shallow water environments. During the interval when organisms were present, there is no evidence to support an interpretation of either unremitting vigorous wave activity beating at the foot of a cliff or a somewhat quieter habitat with sand drifting into the area by quieter water movement. The fact that many of the fossils do not appear to be broken immediately after death or abraded suggests that they were covered by sand during relatively quiet times; some individuals are complete, and the broken parts of others are equally well explained as a result of collecting. On present-day rocky shores, abundant organisms may be found in the lee side of some boulders.

The boulders in the rocky shore environment of the Mill Street conglomerate may have formed an excellent surface for attached inarticulate brachiopods. Apparently these fossils were originally very common at Berkey's original locality. Indeed, according to a few oral statements, so much collecting was done for Ward's Natural Science Establishment (a geologic materials supplier) that the outcrop was undercut. In several trips to the outcrop, the only specimen that we recovered was a single inarticulate brachiopod. Berkey mentioned the presence of brachiopods in his work, but their abundance was not considered. B.L. Stinchcomb (unpub. data, 2003) reported having seen specimens of inarticulate brachiopods attached to boulders in what is now the main terrace area of Interstate State Park, confirming the comment by Berkey (1898, p. 291) and later workers that such fossils occur at the locality. No brachiopods were seen in the Berkey collection at the AMNH.

Within the Late Cambrian Dresbachian (Steptoean) stage outcrops of the Bonneterre Formation in the Ozark Mountains of Missouri, tergomyans are associated with large digitate stromatolites. Locally, they are exceedingly abundant near the shores of buried hills, but seemingly absent further offshore. Based on sampling at several localities, Stinchcomb (1975) estimated that *Hypseloconus* and *Proplina* are present in numbers measured in the 100,000 range. Most occur between stromatolite "fingers," and Stinchcomb speculated that they lived in that macroenvironment "…possibly well below the upper surface of the reef," (Stinchcomb, 1975, p. 417) and were protected from severe wave action.

We suggest that the boulders of the conglomerate provided such a protected habitat, at least locally, in a quartz-sand beach habitat. The conical and limpet-like forms could safely move among the boulders, sheltered from any heavy wave action, if such were present. By comparison to present-day rocky marine shores, one may argue that although stromatolites did not develop in this environment, algal films could flourish on the boulders to provide a food supply for the mollusks.

If the former University of Minnesota material is treated as a single collection, it mirrors the Berkey types in having a preponderance of *Hypseloconus*, with all other forms sparse. That three specimens of a form not known to Berkey are included allows one to speculate that apart from *Hypseloconus*, the mollusks were extremely patchy in their distribution. In the reefal environments of the Ordovician and Silurian of Sweden, a few kinds of mollusks are abundant and most other forms are rare. The modern "golden cone" provides an analogy to such irregular distribution, as it was the rarest of shells, until one new habitat investigated unexpectedly produced dozens of specimens.

To delve into autecology, present-day gastropods have developed a "neck" as a result of a twisting or torsion of the soft parts. This allows for greater movement of the mouth and allows them to be efficient grazers, as anyone who has watched snails clean algal film from the sides of an aquarium can attest. Those marine gastropods that have a low, conical, bilaterally symmetrical shell, that is "limpets," retain torsion of the soft parts, but as viewed from the exterior are effectively bilaterally symmetrical and they show less flexibility of the mouth parts than more typical gastropods. Such limpets are characteristic of rocky shores, and locally, they are extremely efficient in scraping algal films from rocks.

These limpets are considered a closer functional model to the tergomyans, discussed below, than the typical gastropods; indeed for many decades, the fossil tergomyans were considered to be part of the patelliform, or less commonly, capuliform gastropods; as with "limpet," these are terms of morphology rather than systematics. The living limpet gastropods tend to move less than gastropods with the typical coiled shells and tend to be gregarious; the two shell forms are not mutually exclusive, but where gastropods are present, an equal admixture of the two shapes seldom occurs. If the comparison to limpets has any applicability at the Taylors Falls locality, the abundance of tergomyans and the paucity of gastropods may be interrelated.

A BRIEF ESSAY ON THE CLASSIFICATION OF EARLY PALEOZOIC MOLLUSCA, AND PARTICULARLY GASTROPODA, IN NORTH AMERICA OVER ELEVEN DECADES

Classification of organisms is an additive and ever expanding activity, but major changes in systematics occur at irregular intervals and new discoveries of critical forms are rarely made. Both living and fossil mollusks have been known and observed by humans for thousands of years. However, in the formal zoological sense, there were not even Mollusca in 1758 when Linnaeus laid down the first elements of the current classification of animals. It was not until nearly half a century later that Cuvier (1798) recognized the Mollusca as a major distinct entity.

The definition, classification, and functional boundaries of Cuvier's work differs in many respects from what is accepted today. The phylum has been restricted, and major forms originally included have been assigned to other phyla, but the diversity of major groups within the phylum has been expanded. As a parallel development, the concepts for understanding Mollusca that paleontologists and neontologists (those who study the Recent biota) employ do not always coincide. The definition of living mollusks as "…a soft body within a hard shell" encompasses this dichotomy (Yochelson, 1999b, p. 784).

This survey does not cover all the views expressed in the North American literature. As another exclusion, except in passing, it does not consider the views of neontologists. Additionally, except as it affected the principal events highlighted herein, most foreign literature has been excluded. For example, Yu Wen (1990) presented views on the early evolution of the Mollusca quite at variance to any of those discussed below.

In publishing parts of his thesis, it was not Berkey's aim from the fossils of one new locality to consider the early evolution of the Gastropoda in any detail, let alone the overall aspect of the phylum. Indeed, it is likely that some, or perhaps all, of the comments he made resulted from interaction with F.W. Sardeson, who taught at the University of Minnesota (Weiss, 2000). Nevertheless, Berkey (1898) published late in the nineteenth century and summarizing events in this field during the twentieth century and into the twenty-first century is worthwhile. A more rational reason is that these remarks may help to explain why all but two of Berkey's species of gastropods are no longer included within that class.

Mollusca in the late nineteenth and early twentieth centuries

We will start with a prescient comment, which was overlooked for half a century. "Indeed, when the almost incalculable length of time intervening between our days and the Silurian is considered, together with the similarity of recent limpet shells which are secreted by widely different animals, it is almost inconceivable that the Silurian form should have any closely allied recent representatives. The rhythmical manner in which the adductor scars of *Tryblidium* are arranged in pairs, clearly indicates a peculiar disposition of the organs which might, indeed, have paralleled in some particulars the organization of the *Chitons* of that ancient time" (Dall, 1893, p. 287).

The prime event in the study of Paleozoic Gastropoda during the last decade of the nineteenth century was publication by the Minnesota Geological Survey (then the Minnesota Natural History and Geological Survey) of "The Lower Silurian Gastropoda of Minnesota" (Ulrich and Scofield, 1897). As used, Lower Silurian referred to strata that would now be considered Ordovician. Further, despite the title, much of the material described and illustrated was from the Middle Ordovician of Kentucky. This work set new standards in detailed discussion and illustration. Ulrich could see the significance of details that escaped the observation of many of his contemporaries; he went on to become an outstanding paleontologist.

Little of the Ulrich and Scofield (1897) publication is devoted to theoretical matters, but the work considered the Gastropoda to include seven subclasses, the first three of which were Scaphopoda, Polyplacophora, and Pteropoda; the first two of these subclasses subsequently were raised to the status of class, albeit "minor" ones (Yochelson, 1999a). The four remaining subclasses were characteristic gastropods as the concept is used today. The first of these four was the provisional use of subclass Docoglossa, for bilaterally symmetrical shells that ranged from cone-shaped to coiled. The authors were quite clear is suggesting that *Patella* and *Bellerophon* were "primitive" members of the subclass. In the next section of the work, the Paleozoic limpet genera were discussed, and these are the genera that were later summarized by Berkey.

In regard to the Patellidae two comments are pertinent. "The Paleozoic shells which are usually placed in this family are an exceedingly difficult group. ... While we admit freely that it may not be possible to prove that the Paleozoic *Patellidae* are in all cases generically distinct from the living types of the family, we are nevertheless fully convinced that such is the case" (Ulrich and Scofield, 1897, p. 819-820). These comments, while not so insightful as those of Dall quoted above, point to the same conclusion, and almost certainly were developed independently; unfortunately neither Dall nor Ulrich pursued the concept further.

Evolution of the Gastropoda was never a primary concern of Berkey's, yet in exceedingly few sentences, he made several significant comments. "Nothing is known as to the real nature or internal structure of the earliest forms classed as gastropods, and in the absence of biologic evidence the only rational basis of classification is that of variation in form" (Berkey, 1898, p. 276).

This key point may be amplified. As with many of the major groups in the Linnaean hierarchy, definitions were originally based on study of living forms, and emphasis was placed on the soft parts. Thus, within the Mollusca, Gastropoda are conventionally defined as organisms that have undergone torsion, a specialized form of twisting of the soft parts resulting in the anus being above the head. If one depended on pure logic alone, there cannot be any fossil gastropods, for with none of the shells preserved in the fossil record can one conclusively demonstrate torsion; in the absence of soft parts to examine, torsion is an assumption.

A more fruitful approach in paleontology is to compare the hard parts of fossils with the hard parts of living gastropods. The morphologic similarities are so great that certainly from the Middle Ordovician onward, the probability that the forms that paleontologists identify as gastropods are correctly assigned approaches 100 percent. The Lower Ordovician rocks contain an even larger variety of shapes that are not close to living forms. Notwithstanding that the occurrence of some specimens closely comparable to those of living forms and similarity of preservation to those somewhat removed from present-day shapes makes the probability that gastropods occur in these rocks at least as high as 98 to 99 percent. It is with the fauna of the Late Cambrian where greater uncertainty should begin. When considering material from still older rocks, one ought to be cautious in recognizing fossils as representatives of extant classes of the Mollusca or even as members of that phylum.

Berkey made no claim that remarks on Gastropoda evolution were original with him, yet he ably summarized what may be deduced as the prevailing view. Based on what was known of the Cambrian fauna, he noted "1st, that the simple symmetrical cone was probably the earliest form of gastropod"

(Berkey, 1898, p. 276). He then listed four features of variation among this group: height, apertural shape, external ornament, and shell thickness. As a result of his considerations, he next proceeded to divide these conical forms into two genera based on the presumed inclination of the apical area and the more mature shell. The first, "…those anteriorly (acuminately) inclined…," he assigned to *Tryblidium*, and the second, "…those posteriorly (obtusely) inclined or recurved…," he placed in his new genus *Hypseloconus* (Berkey, 1898, p. 276). For this first group, Berkey named five new species of *Tryblidium* and transferred a Whitfield species from *Metoptoma* to this genus. Berkey named five new species of *Hypseloconus.* In his systematics, these two genera preceded description of two asymmetrically coiled forms, coinciding with the interpretation that simple, bilaterally symmetrical cones preceded typically coiled gastropods. Even on this point, there is still no consensus.

To continue, Berkey detected two steps in the variation of the conical fossil mollusks he had studied. "1st, a tendency to acuminate [to render sharp or keen] aperture followed by or accompanied by excentricity [sic] of apex," and "2nd, a tendency to a more irregular aperture usually more or less triangular or notched followed by or accompanied by more or less excentricity [sic] of apex" (Berkey, 1898, p. 276). By notched, we surmise that Berkey was referring to the apertural slit that characterizes pleurotomariacean gastropods.

Sardeson (1903) produced an evolutionary study of Cambrian gastropods in which the Taylors Falls fauna figured prominently. He included an ecological aspect in his views. "This is, I think, the aspect of the known earlier Cambrian molluscan faunas, that Hyolithes and other supposed pteropodous similar genera are common and widely distributed in the marine sediments, and gastropods, Scenella, and others are rare, local, and probably lived adjacent to land" (Sardeson, 1903, p. 474). Sardeson wrestled with the issues of torsion and asymmetric coiling of shells, and elaborated on the few sentences of Berkey. "The asymmetrical long conical shell is taken as the most primitive form among Cambrian gastropods, and the one from which short conical shells, on the one hand, and the spiral and coiled shells on the other have descended" (Sardeson, 1903, p. 491). This paper proves that some ideas portrayed as new approaches have a long ancestry.

The most popular textbook for decades was that of Zittel (1900), translated to English by Eastman, with the various classes and phylum updated by specialists. W.H. Dall was the author for most of the Mollusca and H.S. Pilsbury described the Gastropoda. This compendium recognized and discussed the commonly accepted five classes of mollusks in the following order: Pelecypoda, Scaphopoda, Amphineura, Gastropoda, and Cephalopoda. The only Paleozoic fossils, which eventually formed a new class half a century later, were ensconced within the typical gastropod arrangement. The only concession to strange forms was that an order Conularida, which included the hyoliths, was added to the opistobranch gastropods.

Grabau and Shimer (1909, 1910) identified six molluscan classes: Pelecypoda, Scaphopoda, Gastropoda, Conularida, Pteropoda, and Cephalopoda. The Conularida was a hodgepodge of Paleozoic fossils that included hyoliths; the Pteropoda alluded to recent, small, pelagic gastropods and listed only the Devonian genus *Styliolina.* This was presumably a compilation of index fossils, and accordingly, because of their rarity as fossils, the Amphineura/ Polyplacophora received no mention. It is perhaps of more historical interest in the context of this study that in the Grabau and Shimer (1909, 1910) textbook, the first genus within the Gastropoda was *Tryblidium*, in the context of species of that genus as they had been described by Berkey, and the third genus was his *Hypseloconus*.

The concept of Monoplacophora—to the mid-twentieth century

During the early 1930s, J. Brookes Knight began to critically examine the type species of Paleozoic gastropod genera (Knight, 1941) to clarify the distinctions among them. One ancillary comment of Knight's was to remove the hyoliths from the gastropods; conulariids and a few other forms were evicted by him from the Mollusca. Concurrently with Knight's investigations, Wilhelm Wenz (1938-1944) began work on a general classification of Gastropoda. "The novelties introduced by Wenz in 1938 into the classification of Gastropoda were not in the highest categories but at the familial level" (Knight, 1952, p. 2).

Bilaterally symmetrical, multiple, paired muscle scars were well known in some Paleozoic patelliform mollusk shells. These were especially well illustrated from Silurian strata in Gotland, Sweden in *Tryblidium* and *Pilina*, described by Lindström (1884), but occurrences in similar older forms were in the literature of the time. Such fossils were placed within the extant Patellacea, essentially those gastropods with low, conical shells. Patelliform, capuliform, and limpet are terms for shapes that have no systematic meaning; they are used interchangeably for a variety of recent and fossil shells that are bilaterally symmetrical.

Wenz wrote to Knight inquiring whether any coiled bilaterally symmetrical Paleozoic shells were known that showed paired muscle scars. By chance, one curved, not coiled, specimen of *Cyrtonella* had been found in the Devonian of Michigan that showed two pairs of scars. After the first volume of the Wenz (1939) treatise was produced, he published a significant short paper (Wenz, 1940). In it, Wenz outlined the concept of the Monoplacophora as a group of limpet shells that had not undergone torsion, a point documented from the presence of multiple pairs of muscle scars on the interior of the shell. Although the external shape was similar, the Monoplacophora were judged as fundamentally distinct from the Patellacea, which have a horseshoe-shaped muscle scar in the shell. Because the one curved Devonian age steinkern that showed multiple pairs of muscle scars was a bilaterally symmetrical shell, Wenz included all Bellerophontacea within the Monoplacophora.

Knight objected to this placement of the Bellerophontacea (Knight, 1941). The reason that the assignment of the Bellerophontacea has been, and continues to be, a source of argument is that there are no close models to this form of shell among the living gastropods. In a later work, Knight (1952) refined his arguments on placement of these coiled, bilaterally symmetrical shells. Yochelson (1967) suggested that most of the Bellerophontacea, as classically used, belonged within the Gastropoda, but a few curved or coiled forms might be monoplacophorans. As a generalization, paleontologists who study Paleozoic gastropods concur; paleontologists who study other classes of Paleozoic mollusks do not concur. Inasmuch as none of these bellerophontiform fossils occur in the Berkey collection, this particular subject need not be discussed further. Following the systematic description of Berkey's material, the subject is considered briefly.

The standard American paleontology textbook of the times was by Twenhofel and Shrock (1935). It used Amphineura, Pelecypoda, Gastropoda, Scaphopoda, and Cephalopoda, in that order, for the classes of the phylum, but gave no space in the pages devoted to the phylum to less typical Paleozoic fossils that earlier investigators had appended to the Mollusca. These authors did mention the concept developed by neontologists of a hypothetical ancestral mollusk.

The 1950s and the 1960s

Knight (1952) published a seminal paper outlining his concept of evolution of the early Gastropoda. His views on torsion or lack of torsion in some Cambrian forms were based on his interpretation of anterior and posterior in "cap-shaped" shells. This phrase was used for his interpretation of the shape of a "liberty cap" or the classical "Phrygian" cap. Unlike the "watch cap" of sailors, which fits snugly on the head, this form contains additional fabric and when placed on the head is thrown into folds. The prominent indentations seen in the outline superficially resemble the outline of the Cambrian *Helcionella*; when worn, the apex of the cap would be "posterior," again fitting Knight's interpretation. In partial contrast, the overall shape of the better known Silurian *Tryblidium* and *Pilina* was considered "spoon-shaped," that is having a form similar to the bowl of a spoon. Caps and spoons have a variety of shapes and neither term in precise. For example, *Proplina* is cap-shaped like a Santa Claus-type stocking cap; the shape Hypseloconus might be described as cap-shaped if one has in mind the conical form worn by storybook witches, with the apex bent back.

Knight accepted part of the Wenz concept of Monoplacophora in that early Paleozoic "limpets" had not undergone torsion. He judged that Monoplacophora first occurred in the Early Cambrian and formed the ancestral stock from which the Gastropoda were derived. Knight recognized the importance of torsion and followed the concept of the British biologist Garstang in considering this twisting of the soft parts as a feature of larval development. He considered it as a first step to be followed by a second step of coiling of the shell. Knight suggested that coiled shells, which were bilaterally symmetrical or nearly so, were the earliest gastropods, citing the occurrence of five Late Cambrian genera assigned to the Bellerophontacea (Knight, 1947b, 1948).

The next evolutionary step in his interpretation were shells coiled in three dimensions, and for these he discussed the concepts of dextral (right) and sinistral (left) coiling of gastropod shells, and he also made better known the concept of hyperstropic coiling. This mode of coiling is best summarized as ultradextral, with the spire extended downward rather than upward as in a dextral shell. He also suggested that a few Cambrian and Ordovician gastropods might have been hyperstropically coiled.

Knight devoted a separate section to the issue of the Early Cambrian *Pelagiella* Matthew and its allies that occur in the Early and Middle Cambrian and not only are coiled, but are asymmetrically coiled. Thus, this presented a problem, for in his view both primitive and advanced mollusks then occurred in rocks of the same age. He resolved this issue by stating: "I am not prepared to abandon the hypotheses as to the derivation of the main lines of gastropod descent until other hypotheses are presented that better explain the observed facts" (Knight, 1952, p. 42).

The prime conclusion of this work was to support the concept of Monoplacophora as a distinct entity, though without the Bellerophontacea. To emphasize this view, he proposed to reduce the number of classes of Mollusca from five to four. The Gastropoda were divided into two subclasses, those that had undergone torsion (Anisopleura or Gastropoda in the traditional sense) and those that had not undergone torsion (Isopleura). The Isopleura subclass contained three orders, the single-shelled Monoplacophora, the eight-shelled Polyplacophora, and the non-shelled Aplacophora.

Knight's publication received little attention, except for a brief discussion in one Austrian textbook.

Over the years, some authors have credited the term Monoplacophora to Wenz (1940), and others to Knight (1952). Ohdner (1960) recounted his visit to Wenz in 1937 and one must conclude that the proper citation is Wenz (1940), for the name was not taken from a manuscript by Ohdner, though if one is interested in the coining of the name it was contributed orally by Ohdner. The Ohdner (1960) paper was one of the few of that time to critically and favorably comment on Knight's basic conclusion.

At about the same time that Knight published, living monoplacophorans were dredged off Costa Rica (Lemche, 1972). When described as the new genus *Neopilina* Lemche (1957), the specimens were immediately accepted as representatives of Monoplacophora and considered by neontologists as another class of Mollusca. This new class created a ferment as to the interrelations of the various classes of Mollusca, which has not abated. In the *Treatise on Invertebrate Paleontology*, Yonge (1960, p. I12) may have been among the first of modern neontologists to suggest that the shell-less Aplacophora should be a separate class, distinct from the Polyplacophora. Knight and Yochelson (1960) accepted the Monoplacophora as a class, but in effect repeated most of the preliminary classification given by Knight in 1952, with the additions of Knight and Yochelson (1958). The concept of hyperstropic coiling as used by Knight (1952) was also accepted uncritically (Knight and others, 1960).

To Yochelson, the notion that a class of Mollusca could only be accepted if a living representative of it was discovered seemed unreasonable. This conservative approach was especially strange when considered in the light of the geologic record of Arthropoda and Echinodermata, which included several classes, all of whose representatives were extinct. He proceeded to propose several extinct classes of Mollusca, or participate with others in such activity. The aim was to clarify the concept of Gastropoda in the Paleozoic and more generally to provide a standard for removal of mollusk-like forms from the true Mollusca. One point pertinent to this discussion was establishment of Hyolitha as a distinct class apart from the Gastropoda. The Early Cambrian appearance of the Monoplacophora in the fossil record and the Late Cambrian appearance of the Gastropoda were implicitly accepted.

Horny (1963) published a major study of Monoplacophora from Bohemia. He followed this with a detailed study of muscle scars in a species of *Cyrtolites*, which also included a general summary of the Monoplacophora. In this summary, he divided the Monoplacophora into two groups; their rank was not specified, but presumably these names were for either orders or subclasses. The Tergomya were relatively low shells with a large number of multiple-paired muscles; *Proplina*, discussed below, was included in the Tergomya. The Cyclomya were more varied in shape, from simple cones to curved or even coiled shells, and generally had fewer pairs of muscles, or had the muscles fused into bands; *Hypseloconus*, discussed below, was included in the Cyclomya.

When the paleontological textbook by Moore and others (1952) appeared, it recognized only the five typical classes of mollusks. Amphineura and Scaphopoda received little mention before discussion of Gastropoda, Cephalopoda, and Pelecypoda. Like the paleontological textbooks cited earlier, it would appear that they were not particularly interested in relationships of the classes or more theoretical molluscan concepts.

The 1970s and the 1980s

The concept of extinct classes of Mollusca fell on fallow ground in the sense that Pojeta and others (1972) proposed the class Rostroconchia, ranging from Cambrian to Permian, with no known living representatives. This proposal laid part of the basis for a summary paper on early evolution of the Mollusca (Runnegar and Pojeta, 1974). Among the numerous points outlined, one notion was that "We conclude that the small, dextrally coiled Early Cambrian shells *Aldanella* and *Pelagiella* were the first gastropods..." (Runnegar and Pojeta, 1974, p. 314).

Quite apart from this activity, Yochelson and others (1973) described a new septate monoplacophoran, *Knightoconus*, from the Late

Cambrian of West Antarctica and suggested that it might be the progenitor of the Cephalopoda. Although there have been attempts to modify this hypothesis to include older genera, it appears to be firmly established in the literature. Still, Peel (1991, p. 171) has outlined three alternatives for the ancestral form that had been proposed in the literature and added a fourth suggestion of his own. As another development, the Hyolitha were removed from the Mollusca and classified as an extinct phylum by some authors (Runnegar and others, 1975), though still considered a member of the Mollusca by others (Marek and Yochelson, 1976). Runnegar (1980, 1983) repeated the claim of a separate phylum, dismissing the evidence of similar shell structure to that of undoubted Mollusca as less significant than the theoretical argument that the archetypical mollusk was presumed to have a dorsal shell and the hyolith shell could not be interpreted as dorsal.

The original publication of the Rostroconchia was supported by a major study of the group (Pojeta and Runnegar, 1976). Included within that work, the phylogeny of the Mollusca was considered in some detail. The several class proposals of Yochelson were dismissed and both the Gastropoda and Monoplacophora were judged to extend backward in time to at least the Early Cambrian, as well as other matters touched upon by Runnegar and Pojeta (1974) paper. So successful was the proposal of Rostroconchia and the dismissal of other extinct classes that a major zoological textbook (Russell-Hunter, 1979, p. 348) recognized eight classes within the Mollusca: Monoplacophora, Aplacophora, Polyplacophora, Scaphopoda, Rostroconchia, Gastropoda, Pelecypoda, and Cephalopoda, discussed in that order.

A response supporting the concept of a number of extinct classes of Mollusca and a later origin of the Gastropoda (Yochelson, 1978) received little attention. Yochelson (1979) also published a more detailed discussion of the issue. Included in this, he considered the concept of "Pteropoda" as it had been used in connection with Paleozoic fossil gastropods and emphasized its incorrect usage. He also proposed that a variety of fossils be removed from the Mollusca. Like Yochelson's paper of the previous year, it received little attention or comment.

During this time interval, an earlier concept of application of Cope's law to the fossil record of invertebrates began to be emphasized. Allegedly, one reason for a poor geologic record of Cambrian mollusks was that the average size of specimens in the phylum was tiny. The size of "cyrtonellid and tryblidiid monoplacophorans" and "bellerophontid monoplacophorans" along with other mollusks, when plotted on a logarithmic time scale, approximates a straight line (Runnegar and Jell, 1976, Fig. 5). Unfortunately, in connection with the plot no data are given as to the number of specimens examined, nor the names of species or genera included in each group, and though the gastropods are mentioned in the figure caption, they were not included on the diagram. In particular, Runnegar (1983) emphasized size increase through time and indicated that a dramatic increase in the average size of Mollusca occurred during the Early Ordovician period.

Average size within a class, let alone a phylum, is a difficult concept to grasp, but for gastropods the living neritaceans seem to be a likely candidate for the title of average size. If this is granted, the above generalization of small average size is quite wrong for the Late Cambrian period. Both the Taylors Falls fauna and the Heritage Range Peak fauna from West Antarctica (Webers and others, 1992) contain mainly specimens that fall within the average size range suggested above.

As an aside, there are at least three possible reasons for the apparent small size of earlier Cambrian mollusks. First, and most speculative, little is known of the their paleoecology. Some groups characterized by a small size may have inhabited an ecological niche unlike that of the later Mollusca in which small size was critical. Second, much depends on the definition of Mollusca one chooses to use when dealing with early Paleozoic fossils; if Hyolitha are assigned the rank of an extinct class rather than an extinct phylum, the generalization is wrong, for large hyoliths occur in the Early Cambrian period. Likewise, some of the tiny Early Cambrian forms assigned to the Mollusca may belong to other phyla. Third, and perhaps most significant, much of the study during the last few decades of Early Cambrian faunas has been based on phosphatic residues, and to a lesser extent on silicified residues. The process of acid etching of limestone to obtain such fossils is strongly biased in favor of obtaining small individuals. Dzik observed specimens of the Early Cambrian (Tommotian) *Bemella* on an outcrop that reached 25 millimeters in length. "This is hardly different from sizes typical for Ordovician molluscs. The supposed small size of the earliest molluscs is thus a preservational artifact" (Dzik, 1991, p. 52).

Runnegar (1982, 1983) further indicated a comparable dramatic increase in systematic diversity on both the specific and generic levels following the close of the Cambrian period, parallel to the purported size increase. The diversity shown among the limited number of specimens from Taylors Falls and the diversity in the larger collection from West Antarctica, combined with that of the Late Cambrian Bonneterre Formation of Missouri (Stinchcomb, 1975), would argue that this generalization is greatly overdrawn. Also, just as acid etching to obtain phosphatic residues tends to emphasize small size, it tends to produce steinkerns. Regardless of how carefully steinkerns are studied, they cannot produce data on the external shape and ornament of mollusks, and the amount of diversity that might otherwise be observed is accordingly reduced.

As one more issue, which again must be treated as an aside, *Pelagiella* reappeared as a subject of discussion. Linsley (1977, p. 203-204) remarked "As Knight (1952) suggests they are quite ungastropod-like in their general shape, but he could not verbalize the nature of these differences. I believe that the major differences lie in the fact that the elongation of the aperture is quite different, essentially at right angles to that of modern gastropods and the position of angulations and re-entrants varies considerably from those of other gastropods." In contrast, Runnegar (1981, 1983) interpreted *Pelagiella* as "...one of several asymmetrically coiled monoplacophorans which had undergone only a few degrees of torsion" (Runnegar, 1983, p. 127). It is fair to state that this was a fundamental expansion in the concept of that class, in both ignoring bilateral symmetry and proposing some degree of torsion of the soft parts. The Early Cambrian *Aldanella* Vostokova also entered into arguments, being variously interpreted as an anistrophic coiled monoplacophoran, as a gastropod, or as a coiled tube of a worm.

As a different approach to the classification of these early coiled forms, building on the "laws" of Linsley (1977), Linsley and Kier (1984) proposed the extinct class Paragastropoda. In essence, they suggested that the apparently left-handed (sinistral) coiled shells of the early and middle Paleozoic could be interpreted as not having undergone torsion and therefore the specimens were not Gastropoda. *Pelagiella* and several Late Cambrian–Early Ordovician genera were particularly emphasized. Curiously enough, *Scaevogyra,* one of the two gastropods described by Berkey, was not mentioned, though the related *Matherella* was. *Pelagiella* and questionably *Aldanella* were assigned to the proposed class, along with a variety of younger genera.

Quite apart from the fossils, enough literature in favor of a change in rank had developed that the present-day, shell-less Aplacophora were generally accepted as having the status of another separate molluscan class (Scheltema, 1978). As a next step, some neontologists (Salvini-Plawen, 1980) divided the Aplacophora into two classes. The Aplacophora contain few genera, and if nothing else, this further high-level splitting demonstrates that a class definition is based on the degree of morphologic differentiation from other classes and not on the number of included genera. Whether this class(es) was originally shell-less, or has lost an external shell through time remains to be resolved.

The textbook market expanded further with that of Tasch (1973). This compendium mentioned the existence of Aplacophora without a fossil record, but concentrated on seven molluscan classes. In order of presentation they were Monoplacophora, Polyplacophora, Scaphopoda, Gastropoda, Bivalvia, Cephalopoda, and Hyolitha. That text was followed by the major compilation edited by Boardman and others (1987). The overall presentation was more strongly paleobiological than biostratigraphic. Interrelationships between eight classes of Mollusca were considered and the Hyolitha were presented as a separate phylum. This should come as no surprise inasmuch as the text on the Mollusca was compiled mainly by Pojeta and it closely followed the arguments of Pojeta and Runnegar (1976). *Pelagiella* was reconstructed in this textbook as a partially torted asymmetrical monoplacophoran.

This interval also saw a fundamental change in approach among paleontological textbooks, and it was a harbinger of different views of the discipline. Raup and Stanley (1971) developed a process/problem approach with little regard to systematics. Nevertheless, *Neopilina*, the living monoplacophoran, gained both a mention and a photograph.

The last decade of the twentieth century and the start of the twenty-first century

Although much of the century had seen a gradual transfer of a few genera out of the Gastropoda of the nineteenth century, and even out of the Mollusca, new techniques and new collecting areas have resulted in workers adding forms that stretch the limits of the phylum. The trend toward detailed study of tiny steinkerns has been mentioned, and the great diversity noted in a small collection of worm tubes from one locality (Bockelie and Yochelson, 1979) has been reinterpreted, using material from a number of localities, to demonstrate the morphologic diversity of gastropods (Dzik, 1994). Another trend has been the assumption that Cambrian multiparted individuals may have been mollusks. A prime example is the Middle Cambrian *Wiwaxia* Walcott, interpreted by one paleontologist as a mollusk and another as an annelid worm.

Setting aside the trend toward inclusion of organisms that may or may not be mollusks, Peel (1991) contributed a new view to the study of Cambrian univalves in two aspects. First, he suggested that the concept of the class Monoplacophora had grown unwieldy. "The complex relationships within the morass of early untorted molluscs are obscured by this embracive use of a Class Monoplacophora and the term becomes too generalized for satisfactory employment in phylogeny" (Peel, 1991, p. 159). He therefore restricted "Monoplacophora" to one of the two subdivisions proposed by Horny (1965) and raised his term Tergomya to class rank as a replacement name. This class consists of those fossils that in general have a multiple number of bilaterally paired muscle scars. In connection with a study of Ordovician mollusks from Morocco, Horny (1997, p. 43) used Tergomya as a class heading.

Peel's second initiative was to propose a new extinct class, the Helcionelloidea for the "cap-shaped" Early and Middle Cambrian genera discussed by Knight (1952) as ancestral to the Gastropoda, plus several additional taxa named after 1952. Gubanov (2000) supported the view that the Helcionelloidea are important as untorted mollusks; Parkhaev (2001) supported the view that the Helcionelloidea are members of the Gastropoda. A more recent systematic paper uses Helcionelloidea as a class (Landing and others, 2002). There is no description of hyoliths in this paper, but they are listed as a distinct phylum and illustrated as "...non-molluscan small shelly fossils" (Landing and others, 2002, p. 293).

That same paper described Early Cambrian specimens of *Pelagiella* and placed them within the Gastropoda; there is no discussion of the concept of Paragastropoda. Consideration of these developments is beyond the scope of this work, except to remark that after a half of century of debate, the issues of what is a member of the early fossil class Gastropoda and what is a class within Mollusca remain to be resolved to the satisfaction of most paleontologists.

The redescription of the Late Precambrian *Kimberella* Glasessner (Fedonkin and Waggoner, 1997) as a non-shelled, mollusk-like organism has yet to have any impact on theoretical discussions of gastropod-tergomya relations. Despite the lack of a fossil record, the Aplacophora have assumed ever greater importance as representatives of a theoretical spiculose primitive stage, which in the views of some workers, preceded the development of a shelled molluscan stage.

To cite one current example of divergent views between paleontologists and neontologists, Sutton and others (2001a, p. 461) described a vermiform Silurian fossil, reconstructed from serial grinding, as "a plated aplacophoran." The exceptionally well-preserved features of soft and hard parts are described in detail. "This combination of molluscan characters is not found in extant taxa, but the most parsimonious placement of the new genus, in both of the two competing models of molluscan phylogeny, is as an aplacophoran sister group to the caudofoveates" (Sutton and others, 2001a, p. 463). Response was forthcoming from two neontologists, who specialize in the study of Aplacophora, suggesting assignment of the fossil within the Annelida. "As many polychaete families have highly plastic morphology, the characteristics of *Acaenoplax* fit well within this frame" (Steiner and Salvini-Plawen, 2001, p. 602). In reply, the authors continued to support interpretation of this fossil as a mollusk. "Although *Acaenoplax* displays a mosaic of molluscan characters that does not accord with any single modern group, this does not necessarily eliminate it from the phylum as a whole" (Sutton and others, 2001b, p. 602). This brings us back to the issue of what features characterize fossils assigned to the phylum Mollusca.

We will not offer any suggestion on this controversy. On one hand we are intrigued, but on the other hand, it seems most likely that as new techniques are developed, more atypical fossils are going to be found and the problem of where to place them will recur repeatedly. *Acaenoplax* is a capsule of the issue of whether one extends the limits of a known taxon, or whether one establishes limits on older taxa and proposes new ones. The former process may mask interesting developments at the higher levels of classification, whereas the latter process may clarify them. In determining to use the more restricted Tergomya rather than the expanded Monoplacophora, it is our view that a small, well-defined group, along side of miscellaneous fossils having no immediately obvious placement at the moment in higher classification, is preferable to a larger encompassing unwieldy group.

As regards new techniques, the shell structure of mollusks developed a considerable body of literature over the years, but the study of shells replaced by phosphate is still relatively new. A major investigation of such shell structure, interpreted mainly from the surface of steinkerns, has been published, encompassing a number of presumed Early Cambrian Mollusca (Kouchinsky, 2000a). A needle-like sclerite stage in one genus is presented to support an interpreted evolutionary link between coeloscleritophorans and "monoplacophorans." Kouchinsky (2000a) supported the view of earlier investigators that hollow sclerites are homologous to shell prisms in monoplacophorans. We note that the interior of the small specimen illustrated to show the sclerites does not appear to be like that of any non-disputed mollusk and this brings one back again to the basic questions of what is a monoplacophoran, and even what is a mollusk.

Additional data have recently been published on the phosphatized shell of Early Cambrian hyoliths (Kouchinsky, 2000b). Whether the hyoliths are in the phylum Mollusca or not, a critical point is that the material studied be correctly identified. It is likely that many of the genera assigned to the orthothecid hyoliths, particularly in the Cambrian period, are representatives of other phyla and any study of their shell structure should be approached with extreme caution.

Thus the "circothecid" shell structure may be different because the external shape of circothecids is convergent to the hyoliths, rather than a true representative of that group. Fortunately, at least some of the specimens described in detail by Kouchinsky (2000a) are more reliably assigned to the Allothecidae within the undoubted orthothecid hyoliths and accordingly, the data may be useful.

Another caution should be noted, however. The study of phosphatized shell structures is relatively new and is confined mainly to Early Cambrian specimens. It would be helpful to have studies of post-Cambrian phosphatized specimens of authentic molluscan specimens for comparison. Casual observations of many silicified specimens over decades indicates that in some occurrences, what appears to be original shell structure is replaced, but in other occurrences, extremely peculiar microstructure is present.

The argument in part for placing the Hyolitha as an extinct phylum seems to be that although cross-lamellar structure is present, it is not closely comparable to the cross-lamellar structure of extant mollusks. This is not to cast doubt on any of the findings of the author, but rather a plea for more information to allow one to make more informed comparisons and evaluate differences. At all levels, systematics is based on evaluating similarities and differences. One may ask, for example if one compares only the cross-lamellar structure of Gastropoda, Pelecypoda, and Hyolitha would the differences be significant enough to support the view that three phyla are represented. If one added Cephalopoda to this comparison, the result might be to make that class a separate phylum.

More recently, "hyolithid-type microstructure" has been reported (Feng and others, 2001) in another Early Cambrian fossil, virtually identical to that reported by Kouchinsky (2000a). The specimen is atypical of any of the described genera placed within the Hyoliths. If this microfossil is included within the Hyolitha, then the concept of the morphologic diversity with that class/phylum may be readily extended to include all the extinct bilaterally symmetrical bellerophontiform mollusks, and by extension of some of the definitions, all of the Monoplacophora. Inasmuch as the name Hyolitha has priority over Monoplacophora, this would present either an insoluble problem or a circle for future systematists to pursue.

In summary, the molluscan class now called Tergomya is firmly established in the literature. Except for occurrences of Pleistocene and recent specimens, it is a class whose members occur in the early and mid-Paleozoic.

Recognition of this class opened the door for suggestions of various extinct groups of mollusks to be raised to class rank, including a variety of plated forms that may not be related to the Polyplacophora. Currently two such extinct classes, Rostroconchia and Helcionelloidea, appear to be generally recognized; although the proposal of others has been challenged, they deserve further thought. The Hyolitha seem to be excluded from the Mollusca, though again a clear definition based on hard part morphology, which differentiates them from the Mollusca, remains to be presented.

That the issue of extinct classes is now more or less static is supported by the fact that a mumpsimusly-oriented view of multiple extinct classes (Yochelson, 2000) did not generate interest. The issue of when the oldest Monoplacophora and Gastropoda appear in the fossil record remains open, as does the question of whether they both appeared at the same time. Our view is that the reports of elements of both classes in the Early Cambrian are subject to different interpretation and our adoption of Tergomya is based on the interpretation of a first-known appearance—to date—in the Late Cambrian.

In the final analysis, the arbiters of "taste" in high-level classification are those who compile textbooks, for these influence the next generation of workers. The latest text in the English language (Clarkson, 1998, p. 200-201) recognizes seven classes of Mollusca. In order of discussion these are Monoplacophora, Polyplacophora (Amphineura), Scaphopoda, Bivalvia (Lamellibranchiata or Pelecypoda), Rostroconchia, Gastropoda, and Cephalopoda. The author indicated that this was a conservative classification and left the door open for additions.

It is too early to judge any North American textbooks from the current century, but increasingly, the trend of the profession seems to be away from systematically oriented investigations and toward process or problem oriented matters. From this trend one may infer that it is likely that phylogeny of the Mollusca will not be a "hot" topic. Early Paleozoic adaptive radiation of the Echinodermata and Arthropoda may be highlighted as examples of this phenomenon, but it is reasonable to assume that the Mollusca will not, for the current classification shows little of such diversity. One may surmise that because the Mollusca have so few hard parts, differences among various forms are more subtle and lead to a variety of interpretations, so that no consensus is yet possible.

MUSCLE SCARS AND ORIENTATION OF SPECIMENS

From the foregoing comments, it should be clear that muscle scars in mollusks have played a major role in reinterpretation of the phylogeny of the Mollusca. During the late 1950s, after the discovery of *Neopilina*, the idea that the "magic number" of eight pairs of muscle scars in fossil monoplacophorans and eight plates of polyplacophorans became briefly popular. Fortunately, this notion was never published, for as the patterns of several genera were studied it became apparent that the number of pairs of muscle scars in tergomyans varied to some degree among genera, even to the point where the individual pairs were fused.

In a similar vein, for a brief period, lower and middle Paleozoic limpet-shaped shells were judged to be monoplacophorans and externally similar upper Paleozoic shells were judged to be patellacean gastropods. The description by Horny (1963) of Silurian shells with a patellacean muscle pattern ended that notion. Patellaceans are now known from rocks as old as Middle Ordovician (Yochelson, 1988). Steinkerns that preserve muscle scars are the exception in the fossil record, rather than the rule. One must assume that some species that are similar in shape on the exterior to those which have muscle scars are correctly assigned to that genus. To date, there does not seem to be any confusion in the literature between early Paleozoic Tergomya and early representatives of the patellacean gastropods, but one must be careful. There is no definitive method of determining whether a well-preserved conical or curved shell of the type considered herein and known only from the exterior is a tergomya or a gastropod. Fortunately for this inquiry, so far as we know, no claims of Patellacea in Cambrian rocks have been made in the last half-century.

To some unknown degree, the thickness of the molluscan shell is related to the preservation of muscle scars. In a thick-shelled form, muscles may be shallowly or deeply impressed in the shell. In a thin-shelled form, they cannot be deeply impressed. Thus, the absence of muscle scars does not automatically remove a genus from the Tergomya. Berkey emphasized that *Hypseloconus* had a thin shell, an observation we can confirm from several localities and preservation in limestone, as well as sandstone.

In extremely well preserved steinkerns of tergomyans, several different shapes of paired muscle scars can be observed. Those near the apex tend to be more complex and there may be some agreement that these were associated with the radula (Starabogatov, 1970; Yu Wen and Yochelson, 1999), and if so, this would tend to fix the position of the mouth to that area. Even without such an interpretation, it seems to be generally assumed that the more complex of the paired muscle scars are at the anterior of the fossil. Most of the known tergomyans are relatively broad with relatively low shells having an aperture that is oval and wider at one end, and with the apex near or at one end of the shell. Thus, the apex of *Proplina* may be anterior and the animal moved with the apex forward. In this interpretation the smaller end of the oval aperture is anterior and the larger end is posterior.

In *Hypseloconus* and its allies, the bilaterally symmetrical shell is compressed to a greater or lesser degree, conical, relatively high, and there may be a very slight curvature of the cone. In even the most strongly curved of the hypseloconids, the apex of the shell does not extend outside the plane of the aperture, and depending on the degree of curvature, the apical position is better described as more subcentral than at one end of the shell. The anterior and posterior slopes are differentiated, but there is no obvious indication of orientation.

Like *Proplina*, the apertural opening of *Hypseloconus* may be generalized as egg-shaped with one end of the oval smaller than the other, and in some forms the shell above the narrow end of the oval is moderately sharp rather than rounded. If this narrow end of *Hypseloconus* is oriented as in *Proplina*, that is as the anterior, the curvature of these cones is the reverse of that of *Proplina*, as Berkey pointed out with his use of acuminate and obtuse orientation.

This may be a profound difference and the distinction is not readily resolved. One answer to the apparent difference in curvature is that *Proplina* had not undergone torsion, whereas *Hypseloconus* had.

That this is a simplistic interpretation is provided by a juvenile shell of *Knightoconus* in which the direction of curvature changes during growth (Webers and Yochelson, 1989).

The issue of muscle scars in *Hypseloconus* has been a source of argument. "Several of these specimens have a well-defined slightly depressed area extending completely or almost completely round the cast [steinkern] usually about one-fourth to one-third the distance from the base to apex. The persistence in occurrence and position of this band strongly supports the view that it represents the position of muscle scars of this genus. On several casts there is a circle of slightly raised areas lying in this position on the cone. On only a few casts are these well preserved but in all cases the marks are the same in form and position and number. It is therefore added as a character of the genus,—that the muscle attachments form a circle of six pairs of scars considerably above the aperture and parallel to it" (Berkey, 1898, p. 283).

In contrast, when Knight (1941) studied the type lot, he was positive that no discrete scars were present on the specimens he examined. During the late 1950s, Yochelson examined the hypseloconids in the U.S. National Museum collections and did not observe any paired muscle scars. A subsequent comment reopened this issue. "Moreover, despite assertions to the contrary by Knight (1941) and Yochelson and others (1973), many specimens of the type species of *Hypseloconus* have a ring of discrete muscle scars (Berkey, 1897) [sic] like those found in some early cephalopods" (Runnegar, 1983, p. 130). This is a confusing statement because no specimens were illustrated or cited to support this assertion.

Enough steinkerns of *Hypseloconus*, especially in the Early Ordovician forms, show elements of a ring-shaped bulge, which is positioned significantly closer to the aperture than to the apex, that a plausible interpretation is of a continuous or nearly continuous depression in the shell. We know of no data that would support the interpretation that this bulge is divided into discrete muscle scars. We suggest, like Berkey, that it may represent a series of muscles that have been fused, or far less likely, the attachment of the pallial line within the shell.

Comparing the overall forms of *Proplina* and *Hypseloconus*, it is evident that a foot in the former would include relatively more of the main body mass and be relatively much larger than the same anatomical feature in *Hypseloconus*. To this should be added the obvious point that a relatively low, broad shape provides less resistance to water and therefore should be more stable than a high, nearly conical shell. Also, *Hypseloconus* may have fused discrete paired muscles into a ring to provide greater control of the unwieldy shell by the soft part. This again leads us to the view that the Taylors Falls locality may have represented a quiet water habitat. Even moderate wave action might have reached the lee of boulders and disturbed these possibly less stable conical forms.

It should be apparent that interpretation of muscle scars involves a great deal of speculative discussion. Knight (1947a) emphasized that muscle scars demonstrated support for interpreting a genus of bellerophontacean as a gastropod. A later examination of some of the same specimens by Runnegar (1981) was used to interpret these fossils as belonging to the Monoplacophora.

Along the same lines, considerable time has been spent by authorities arguing whether one end of these limpet shells was anterior or posterior, and whether the soft parts within the curved and coiled forms were arranged as a result of endogastric or exogastric coiling. At least as much effort has gone into arguments as to whether various genera had or had not undergone torsion, and investigations of the same form may lead two different investigators to diametrically opposite views. In our descriptions of the tergomyans, we have used the terms concave or convex surface, or alternatively longer and shorter surface so as to avoid any arguments on anterior or posterior orientation. Such terms are fine for developing theoretical considerations, but if used in description they tend to prejudice any discussion before it starts.

To move to another subject, Berkey (1898, p. 276) noted four kinds of variation in the mollusks he studied. "a. Variation in hight [sic];. b. Variation of aperture in shape between the circle and symmetrical ellipse;. c. Variation in striation, growth lines and radial striae being at most only specific characters and subject to obliteration in the process of fossilization;. d. Variation in thickness of shell." For almost all molluscan species, Berkey had line drawings to show a lateral view and an outline of the apertural margin. We do not judge that all his apertural outlines were precise, for some of his species are based on incomplete material and required a fair degree of guesswork in reconstruction. Despite that caution, Berkey was ahead of his time in documenting the shapes of apertures and considering apertural shape as a prime character. He was also fully aware of the importance of measurements and provided length, width, and apical angle within many of his descriptions. We have confirmed that these data are accurate and have not repeated the information.

THE CLASS GASTROPODA

As noted, there is disagreement over the morphologic limits of a variety of shelled fossils in the Lower and Middle Cambrian rocks. Much of the study of these early fossils is based on steinkerns and these provide limited information. Although some have been assigned to the Gastropoda, we remain skeptical that such an assignment is correct. In addition, not all coiled forms are automatically gastropods. We lack proof, but in our interpretation of the class, the oldest Gastropoda do not occur before the Late Cambrian, and perhaps not in the oldest third of that subdivision. Others would argue that they first occur as fossils at or near the base of the Cambrian period. Until more convincing evidence is presented to support torsion in Early and/or Middle Cambrian shells, we hold strongly to our opinion, but we recognize that this issue may never be resolved, without an incredible event of preservation showing the soft parts within these shells. The issue of torsion in these older fossils may remain a "yes it is," "no it isn't," argument, rather than a scientific discussion.

Even within the Late Cambrian period, there is need for caution in assigning fossils to Gastropoda. For the last half century, one of the driving considerations in classification has been that gastropods having an apertural slit were the earliest forms. Knight (1952) discussed four genera of Bellerophontacea that were assumed to have an apertural sinus or an apertural slit. The living pleurotomariaceans have two gills, and the slit in the shell aperture serves primarily to channel exhalant water away from the animal. Because all other marine gastropods have a single gill, the pleurotomariaceans are therefore "primitive." In Knight's view, bilateral symmetry of shells preceded asymmetry. It is critical to restudy the stratigraphic occurrence and morphology of the Cambrian "Bellerophontacea" to determine if one or more of these genera are older, younger, or coeval with the Taylors Falls fauna.

The best preserved Late Cambrian molluscan fauna collected to date is from the late Dresbachian stage in the Heritage Range, Ellsworth Mountains, West Antarctica (Webers and others, 1992). It is also the most diverse such fauna of that age known to date. None of the species included in the Gastropoda show any evidence of a slit or even a slight sinus within the aperture. In addition, all the forms interpreted as gastropods are coiled sinistrally. These two points are enigmatic, but they deserve consideration.

The issue of the placement of the asymmetrically coiled *Pelagiella* and its allies is equally critical to an appraisal of whether the Gastropoda began in the Early or Late Cambrian period. The subject cannot be pursued here, but again deserves careful study. We are inclined to the view that the concept of Paragastropoda, asymmetrically coiled non-torted forms, may be appropriate for *Pelagiella* despite its emphasis on unknown soft parts. We are convinced in part because of the small size of Early and Middle Cambrian specimens, but we find it less convincing when applied to Late Cambrian and younger species.

Future investigators should be aware that in older North American literature, *Pelagiella* has been used in two different ways, and our opinion on Paragastropoda applies only to the Early Cambrian and early Middle Cambrian taxa. Comparison of Late Cambrian coiled species that have been referred to as *Pelagiella*, such as the large forms as represented by *P. paucivoluta* (Calvin; see Yochelson and Nuelle, 1985) and smaller forms, such as *P. bridgei* Lochman, to the Late Cambrian bellerophontiform genera described by Knight could result in removal of some species of "*Pelagiella*" from that genus and may resolve at least a small part of this particular problem. On the basis of three specimens that were not in Berkey's collection, we have discussed this issue in more detail in the systematics section.

THE CLASS TERGOMYA

In Moore (1960), relatively few genera of class Monoplacophora were reported from the Cambrian–Early Ordovician interval and we will review their status. *Scenella* Billings was questionably assigned to the class. The type species of *Scenella* is Early Cambrian (see Knight, 1941). Specimens similar to the type have been interpreted as possible cnidarians (Yochelson and Gil Cid, 1984) and others have maintained that the genus belongs in the Mollusca (Landing and Narbonne, 1992). In large part, *Scenella* was placed in the monoplacophorans because of the presence of possible muscle scars on specimens from the Middle Cambrian Burgess Shale (Rasetti, 1954). What is pertinent is that the Burgess Shale species is not congeneric with *Scenella* in our current understanding of the morphologic limits of the genus, and thus, the reported musculature is not useful to the assignment of the genus. When reexamining that Middle Cambrian mollusk, future investigators might give some consideration to the *Microdiction* model of fossils wherein separate hard parts are scattered along the sides of a soft-bodied animal. *Palaeacmaea*, as noted, has been removed from the Mollusca and may be a cnidarian (Webers and Yochelson, 1999).

Proplina Kobayashi assumes more importance with the transfer of some of Berkey's *Tryblidium* species to it. The Early Ordovician *Bipulvina* Yochelson remains essentially unchanged since its proposal, with no published material added to the concept; Stinchcomb (1986, p. 206) recognized a *Proplina-Bipulvina* zone in the Lower Ordovician rocks of Missouri. In contrast to that genus, a few additional species of *Hypseloconus* Berkey have been described.

Nothing has been added to the knowledge of the poorly known *Ozarkoconus* Heller, but the prominent ornamentation that it displays may indicate that it should not be in this class, though the view of Stinchcomb (1986) is that it might be a monoplacophoran; *Orthoconus* Stinchcomb bears longitudinal ornament.

It is also appropriate to note that the Middle Ordovician *Pollicina* Holzapfel was assigned to the Monoplacophora (Knight, 1952). That classification was subsequently accepted by Knight and Yochelson (1960) and followed by others in several later publications. Kisselev (1994) redescribed the type species, placing it within the presumed molluscan class Xenoconchia. Recently, Evans and Cope (2003) placed specimens assigned to that species within the Tergomya. In considering various possible assignments of the genus, they refer to earlier comments by Yochelson. The original remark was "The genus is probably an open-coiled gastropod which deviates only slightly from the plane of bilateral symmetry (Yochelson, unpublished observation)" (Peel and Yochelson, 1984, p. 218). The unpublished examination of the lectotype cited above has been bolstered with examination by Yochelson of Middle Ordovician topotypes or near topotypes from Estonia that more clearly show an asymmetric whorl profile. To that may be added the issue of functional morphology, namely the sea floor; the problem would be compounded if the animal crawled on the inclined surface of a boulder or a stromatolite. If the interpretation of *Pollicinia* as a member of the Gastropoda is accepted, the high, conical tergomyans are not known to range above the Early Ordovician period.

The order Cambridoidea was questionably placed in the Monoplacophora. The three genera considered therein fall within the proposed extinct molluscan class Stenothecoida. That placement is yet another point of contention not pertinent to this study.

In this section, we will also compile the generic names of Tergomya proposed since 1960 from the Late Cambrian–Early Ordovician interval that are known to us. If any such taxa have been missed, we hope that readers will notify us. A number of other genera have been proposed as monoplacophorans, primarily from older Cambrian rocks, and also a few from the mid-Paleozoic, but to mention them herein would further expand the issue of where to assign curved and coiled shells, another subject not pertinent to this examination of Berkey's species. An arrangement somewhat more biologic than chronologic may be of use to later investigators and we have attempted that below.

Among what was in 1960 the order Tryblidioidea, *Proplina* is the only genus of concern here. Stinchcomb (1986) described several species of *Proplina* from the Late Cambrian–Early Ordovician period exposed in the Ozark Uplift of Missouri. He added another genus to the Proplininae. *Ozarkplina* from the Late Cambrian Eminence Formation is an elongate proplinid whose muscle scars are extended toward the lateral margins of the aperture. The lower part of the Eminence Formation has yielded the trilobite *Calvinella* (Stinchcomb, 1986, p. 607), indicating an age of about mid-Trempealeauan stage (Sunwaptan; Howell and others, 1944).

To continue with this group, Webers and others (1992) raised the taxon to family rank, and described another species of *Proplina*. They added to the Proplinidae *Proconus* and *Ellsworthoconus* from the Late Cambrian Minaret Formation of Antarctica. The top of this unit is dated by trilobites as Late Dresbachian stage (Idamean) and is slightly older than the Taylors Falls assemblage. *Proconus* was judged allied to *Proplina*, but was more elongate and showed less curvature of the dorsal surface, along with rugosities of the shell. In contrast, *Ellsworthoconus* was strongly arched but with little overhang of the aperture and essentially no curvature below the apex.

Stinchcomb and Angeli (2002) added two more genera from the Missouri outcrops. The Late Cambrian *Potosiplina* may eventually be determined to be a subjective synonym of *Cosminoconella* Webers, Pojeta, and Yochelson. *Cosminoconella* was not certainly placed in a higher taxon, but was differentiated because of its pronounced longitudinal ornament. On the other hand, *Titanoplina* from the Early Ordovician Gasconade Formation, should certainly stand. It is a low, wide shell and is a remarkable form on examination. The largest proplinids heretofore known were from the Silurian of Gotland. These older specimens are at least three times as large.

In the *Treatise on Invertebrate Paleontology* (Moore, 1960) classification, the Tryblidiodia was followed by the order Archinacelloidia, to which the Hypseloconidae were questionably assigned. Two genera questionably assigned to the family, *Ozarkoconus* and *Pollicina*, have been mentioned above, leaving only *Hypseloconus* to be considered. Additional species have been added to the genus and new genera have been named and assigned to the family.

Stinchcomb (1986) raised the rank to superfamily as the Hyseloconellacea [sic] and added material to previously described species. He then assigned five new genera to the Hypseloconidae, four of which are also from the lower part of the Eminence Formation. *Cambrioconus* may be one of the most bizarre of the hypseloconids. The apex is near the narrower end of the aperture and the form has an exceedingly long aperture. This seems to be an example of the general rule that extreme examples of older named genera are commonly judged as new forms, in contrast to the alternative of expanding the concept of the genus. *Orthoconus* Stinchcomb is closer to the traditional concept of *Hypseloconus* because it is a high, gently curved cone, but it bears longitudinal lirae; as noted by the author, such ornamentation is extremely uncommon in hypseloconids. *Cornuella* Stinchcomb is distinctly curved and shows prominent growth lines; Stinchcomb noted its similarity to certain cephalopod siphuncular fillings, another challenge to classification. Both these last two genera are more elongate and less strongly curved than *Protoconus* of Stinchcomb (1986)—now *Proteroconus*—that will be considered in the systematics section. Although the number of related new genera from one formation is surprising, after examination of his types, we are satisfied that all of his proposals are biologically significant.

The last of these five, *Gasconadeoconus* from the Gasconade Formation, is a high cone also developing an elongate aperture, but with an apex closer to central than in *Cambrioconus*. The early stages show slight compression near the narrow end of the aperture and comparison with specimens from the Smith Basin Limestone (Flower, 1968) may be warranted when a detailed study of the hypseloconids is undertaken.

Gayneoconus Stinchcomb and Angeli (2002) from the Late Cambrian Potosi Formation has an overall shape like that of *Hypseloconus*, but is readily differentiated by prominent, wide growth rugosities at almost all growth stages. Stinchcomb (unpub. data, 2003) suggested that *Wildernessia*, unassigned to an order by Stinchcomb and Angeli, might form a link between the Proplinidae and the Hypseloconidae. It is a large shell with a strongly hooked apex. Though the morphology is bizarre, it may be a hypseloconid. Whatever the systematic placement of *Wildernessia* may be, its occurrence in the Early Ordovician Roubidoux Formation is too late for it to be a link between these family groups.

Shelbyoceras Ulrich and Foerste (in Bridge, 1931) was not mentioned among the *Treatise on Invertebrate Paleontology* (Moore, 1960) Monoplacophora. The appropriate classification of this genus has been a challenge for years, as one of the features of the genus is septation of the apical area, but these septa are solid and lack a siphuncle, or another kind of opening. Stinchcomb and Echols (1966) transferred several species of that genus to *Hypseloconus*. Subsequently, Yochelson and others (1973) placed *Shelbyoceras* in synonymy with *Hypseloconus*. Stinchcomb (1980) removed it from synonymy, clearly demonstrated the septation, and noted that its abundance and stratigraphic distribution in the Ozark region differed from that of *Hypseloconus*. We concur that the genus should be recognized and also agree that the septation is an important morphologic feature.

Yochelson and others (1973) placed emphasis on the presence of septa as a step preceding the formation of a siphuncle in the line leading to the Cephalopoda. The distribution of septa has been studied for some Cambrian Hyolitha (Syssoiev, 1973) and similar methodology might be applied to the shelbyocerids; the septate early portion of the shell has been referred to [in translation] as a "gas chamber," but we doubt that hyoliths or shelbyocerids generated any gas in the apical region (for a consideration of what might happen to a septate, orthoconic cephalopod that did not develop cameral deposits to counterbalance gas-filled chambers, see Flower, 1957, p. 834).

As regards septation, the Late Cambrian genus *Knightoconus* Yochelson, Flower, and Webers (1973) from Antarctica differs from *Shelbyoceras* in that *Knightoconus* is wider, has a more elongate aperture, and a lower cone. At the time, additional specimens of *Knightoconus* were described, and the genus was placed under the Hypseloconidae (Webers and others, 1992, p. 197); *Shelbyoceras* was not then discussed.

Archeoconus Stinchcomb (1986), from the Eminence Formation and *Ulrichoconus* Stinchcomb and Angeli (2002), from the slightly older Bonneterre Formation of the Ozark region have added to the diversity of septate, high, conical forms. *Biloboconus* Stinchcomb and Angeli, from the Eminence Formation, is reported as yet another septate form, though the type material is less satisfactory than with the other genera.

Although the apical chambers are described by some workers as being gas filled, even if this were so, the absence of the siphuncle would preclude any gas–water exchange. We continue to hold the view that the primary function of the septa was to shorten the soft tissue relative to the length of the shell. In the light of the diversity of these early septate mollusks, we accept Stinchcomb's view that septation is an important morphologic feature in the tergomyans. Should future systematists concur, it is appropriate to note that *Shelbyoceridae* Stinchcomb (1986, p. 622) was proposed under the Hypseloconellacea [sic].

This next brings us to *Kirengella* Rosov (1968; p. 1427), described from the Late Cambrian of the southern part of the Siberian platform. It is a relatively broad, low cone with a rugose exterior and noteworthy for the presence of five pairs of muscle scars in the type species, the only one included in the original description. Because of the well-preserved muscle scars, it was significant to the interpretation of Yochelson and others (1973). In brief, if the largest set of paired scars is assumed to be at the anterior, the curvature of the shell is toward the posterior rather than toward the anterior as in *Proplina*. In a revision of the Monoplacophora, Starabogatov (1970) placed the genus in a new family, the Kirengellidae.

The order Kirengellida was subsequently named (Rosov, 1975) and included three families. As with most of the rearrangements of the Monoplacophora, emphasis was placed on the arrangement of muscle scars and less consideration was given to overall shape. The first family, the Kirengellidae of Starabogatov, included *Scenella* Billings, *Kirengella* Rosov, and *Moyerokania* Rosov (1970). This Early Ordovician form from Siberia was more or less conical and compared by the author to *Archaeophialia*. The second family, Romaniellidae (new in that paper), contained three genera, the first of which is *Romaniella* Doguzhayeva (1972). This Early Ordovician genus was a strongly arched, high "limpet" more likely a proplinid or tryblinid; the author added the Early Ordovician species to *Kirengella*. *Nyella* Rosov (named in that paper), also from the Early Ordovician, had yet a different muscle pattern, but again may be a "limpet" with the largest muscle scar near the concave surface. The last genus included in the family was *Hypseloconus,* and the author was in error in not using Hypseloconidae as the family name. Finally, the third family was the Archaeophialidae of Knight and Yochelson (1958), containing only the type genus.

To change the sequence briefly, under the heading of Monoplacophora, Flower (1968) described several forms from the Early Ordovician Smith Basin Limestone of New York. *Yochelsonella* Flower (1968, p. 25) is strongly compressed laterally with a subcentral apex and no indication of curvature or a possible anterior-posterior differentiation of the aperture. Flower also described two new species that he assigned to *Archinacella* and a new species of *Palaeacmaea*. We have not examined the types, nor topotypical material, and can only make tentative comments. The *Palaeacmaea* may fit within the concept propounded by Webers and Yochelson (1999) that this genus is not a mollusk, though some species assigned to it may be molluscan. Flower's (1968) two species of *Archinacella* may belong in *Proplina*; whether they are senior synonyms of species of the same age proposed by Stinchcomb (1986) is an issue for others to pursue.

In connection with describing a new species of *Kirengella*, Webers and others (1992, p. 195-196) discussed the order and family. At that time *Yochelsonella*, through a print error given as *Yochelsoniella*, was transferred to the Kirengellidae. Several named species of *Hypseloconus* and other specimens assigned to the genus were also transferred to *Kirengella*. More recently, Stinchcomb and Angeli (2002), studying material from Missouri, assigned three previously named species to *Kirengella*. In addition, they named a new species from the Roubidoux Formation, which may be the youngest known representative of the genus. They also named *Ironalia* from the Bonneterre Formation and placed it in this family. The specimen has a very low cone that is broadly oval. As a result of transfers and this new genus, the concept of the Kirengellidae has been greatly expanded.

Finally, Byalyv (1973) described two new genera from Lower Ordovician rocks of Siberia, which he assigned to the Monoplacophora. *Multifariites* is a tiny bellerophontiform shell and need not be discussed further, except to note that in mode of coiling it may be closely related, or even congeneric with the North American Late Cambrian *Owenella* Ulrich and Scofield. The somewhat older *Lenaella* is a conical shell. It is similar to *Kirengella* in shape, but was differentiated by its author from that genus by the presence of eight pairs of muscle scars. Like *Kirengella,* it was described with only the type species and we are not aware of subsequent literature that has assigned any additional species.

To consider a higher level of classification, Horny (2002) produced an illustrated catalogue of many type specimens from Bohemia, including those that had earlier been placed in the Monoplacophora. He used Tergomya as a class term and divided the material under discussion into the orders Tryblidiida and Cyrtonellida. Included among the latter are two

Early Ordovician genera of bilaterally symmetrical coiled forms; discussion of them is not useful to this inquiry.

To return to the main aspect of this subject, several authors using different approaches to phylogeny either specifically or tacitly placed the Monoplacophora in a central position as being the closest to the hypothetical ancestral mollusk. There are also a variety of interpretations of what fossils constitute the Monoplacophora. For example, "It is now obvious that monoplacophorans radiated in a variety of ways during the Cambrian and that *Neopilina* and *Verma* are most conservative examples of the class (Runnegar, in press)" (Runnegar, 1983, p. 145). As an alternative, if one accepts the view of Peel (1991) that the Tergomya should be separated from other taxa placed in the Monoplacophora, the occurrence of the oldest fossils known to date is early Late Cambrian.

If one accepts both the view of the Tergomya propounded by Peel (1991) and the view of the Gastropoda propounded by Runnegar (1983), it produces a paradox. The apparently derived forms, that is the gastropods, appear in the fossil record tens of millions of years before their presumed ancestral form, the Tergomya. Peel's (1991) concept of a discrete group, rather than a "wastebasket" of various shapes seemed well founded. We follow Knight putting the weight of evidence on the Late Cambrian age of the Gastropoda and leave this possible paradox for future investigators.

A SURVEY OF EARLIER DESCRIBED NORTH AMERICAN LATE CAMBRIAN–EARLY ORDOVICIAN TERGOMYA SPECIES

In discussion, Berkey (1898, p. 278-279) made reference to a number of Paleozoic limpet or patelliform genera, which at that time were all judged to be Gastropoda. He noted "The tendency among American paleontologists until recently was to place many unlike forms in the genus *Metoptoma*, Phillips, 1836. Since 1872, however, as new forms have been studied, distinctions have been made which allow of a considerably more complete subdivision." He then went on to briefly consider *Metoptoma* Phillips, *Lepetopsis* Whitfield, *Scenella* Billings, *Stenotheca* Hicks, *Conchopeltis* Walcott, *Archinacella* Ulrich (Ulrich and Scofield, 1897), *Tryblidium* Lindström, and *Helcionopsis* Ulrich (Ulrich and Scofield, 1897).

Although, especially in the last half century, there have been numerous papers considering the Monoplacophora and the Tergomya and naming new taxa, no one has prepared a catalogue of the species and genera. The only index of which we are aware is the listing of North American species by Bassler (1915). He was influenced by E.O. Ulrich and employed the systemic ages of Ozarkian and Canadian to various fossils within his catalogue of Ordovician and Silurian forms. Thus, some taxa that currently would be considered Late Cambrian are listed in this catalogue. This index contains some strange details in the light of present-day understanding of correlation. For example, the Calciferous age was used by Walcott, and his earlier paper on the Saratoga Springs, New York fauna is indexed by Bassler, along with his later work (Walcott, 1912b) in which the age is listed as Ozarkian or Upper Cambrian. Other early papers in which Walcott described mollusks as Late Cambrian in age are not indexed. Curiously enough, part of Berkey's work is referenced and part of it is not. As one example, *Hypseloconus* Berkey is listed (Bassler, 1915, p. 656-657), but the only species under that heading is *H. recurvus* (Whitfield), yet this listing includes references to Berkey's work and to subsequent republication of his illustrations. Berkey's new species of the genus are not listed. Incomplete as this index may be, it is the only starting place for older papers and does cover much of the literature known to us.

The following material is simply a guide to provide limited aid to future investigators of early Paleozoic North American species and includes some observations on specimens and other opinions gleaned only from the literature. In no way does this constitute any formal reassignment or synonymy, and for some of the names we can only call attention to the point that they were transferred from one genus to another by Bassler (1915). Literature references to species names mentioned in passing may be found by consulting Bassler's work.

The genera mentioned by Berkey should first be considered, and several eliminated from further discussion. Bassler did not list *Lepetopsis* because it is of Mississippian age. *Helcionopsis* was not reported by Bassler as occurring below the Middle Ordovician. *Conchopeltis* has no known species older than Middle Ordovician and the presence of tentacles removes it from the Mollusca. Only one species of Middle Ordovician age was listed by Bassler under *Stenotheca*. Berkey (1898) suggested that this genus and *Palaeacmaea* Hall and Whitfield were too poorly known to be judged of higher than subgeneric rank. Knight (1952) assigned *Palaeacmaea* to the Monoplacophora. As mentioned, Webers and Yochelson (1999) removed that genus from the Mollusca and questionably placed it in the Cnidaria.

The remaining genera are *Archinacella*, *Metoptoma*, *Scenella*, and *Tryblidium*. For some described species, Bassler followed the published literature, but for other species he reassigned them to other genera. Although he contributed no study to their morphology, these transfers have nomenclatural standing and must be taken into account by a future investigator. To begin, Bassler (1915, p. 1306-1308) listed or transferred to *Tryblidium* eleven species which are of pre-Middle Ordovician age.

Tryblidium? *acutum* Whitfield is illustrated as having an apex overhanging the margin, and a low, rounded shape. It may be a *Proplina*, but the apparently flattened area below the apex is anomalous and suggests that this might be one shell of a brachiopod. It is from the Fort Cassin, Vermont area and therefore is close to the Early–Middle Ordovician boundary.

Tryblidium barabuensis (Whitfield) will be discussed in the Systematics section under *Proplina.* It was collected from Eikie's quarry near Baraboo, Wisconsin. The holotype is in the collections of the Museum of Paleontology, University of California, Berkeley, and is numbered 1211.

Tryblidium cornutaformis (Walcott) from the "Calciferous" strata at Saratoga Springs, New York is now the type species of *Proplina.* For details see Knight (1941). The unit is now considered Late Cambrian in age.

Tryblidium hyrie (Billings) was obtained from the second limestone in the conglomerate at Levis, Quebec, and its stratigraphic position of ?Ozarkian cannot be relied upon. More than two decades ago Yochelson examined the holotype and paratypes (Geological Survey of Canada [GSC] number 789a-d). He noted that there were no visible muscle scars. In general terms, this species has a tryblidiform shape and at the time was judged "…a low *Proplina*."

Tryblidium niobe (Billings; GSC number 781) and *Tryblidium nycteis* (Billings; GSC number 467) are both from the "Calciferous" strata, though at different localities. Judging from Billings' (1862) drawings and a brief examination of the type specimens by Yochelson, there is no obvious reason to have two specific names. The general shape of both is like that of *Proplina*.

Tryblidium ovale Whitfield is from the Beekmantown Formation on Lake Champlain in Vermont. The specimen is large and relatively narrow and might fall within *Pilina* Lindström. Muscle scars are preserved and should be restudied.

Tryblidium ovatum Whitfield is also from the Beekmantown Formation on Lake Champlain in Vermont. The specimens illustrated show prominent muscle scars. During a brief examination, Yochelson confirmed the presence of at least six pairs and noted "...may fit into *Bipulvina*" (Yochelson, unpub. data). The difference in shape from that of *T. ovale* supports Whitfield's interpretation that these are two distinct species at the same locality.

Tryblidium patulum Cleland is from the Calciferous of New York. As illustrated by line drawings, the species is enigmatic. It is reported by Cleland from a single specimen and at least superficially resembles a *Proplina*.

Tryblidium reptorum Sardeson is from the Shakopee Dolomite of Minnesota. As illustrated by line drawings, the species does not have the apex overhanging the aperture and therefore may not be a *Proplina*. The assignment to *Tryblidium* deserves reinvestigation, and the species might fit within *Archinacella.*

Tryblidium retrorsum (Whitfield) is from Eikie's quarry, near Baraboo, Wisconsin, with an age of "Ozarkian (Mendota)." This may be a relatively high-coned species of *Proplina*, but there is a suggestion of a reversal of curvature near the apex; a reversal of curvature has been observed in a number of specimens of *Knightoconus* (Webers and Yochelson, 1989). The type specimen is in the Museum of Paleontology, University of California, Berkeley.

Bassler transferred three species to *Archinacella*. *A. pileolum* (Whitfield) is from the Beekmantown Formation of New York. Judging from the illustrations, it is based on tiny specimens that have the general shape of *Proplina*. *Archinacella similis* (Whitfield) is from Eikie's quarry, near Baraboo, Wisconsin and fits reasonably well into that general form. However, the concept of *Archinacella* is based primarily on the muscle scars. Based on a study of a plaster cast, Whitfield's species may be an extremely low-coned *Proplina*, approaching *Pilina* in shape, or even a member of the latter genus; the type of this species is in the Museum of Paleontology, University of California, Berkeley. *Archinacella simplex* (Billings), from the "Calciferous" judging from its drawing, might be a relatively high-coned *Proplina*.

Scenella? *alta* (Whitfield) as illustrated (Whitfield, 1889, pl. 7, Figs. 12, 13), from the Beekmantown Formation, appears to be a hypseloconid, and if so is one of the youngest representatives of that group. The cross-section is smoothly ovoid and presumably from the drawing, it is wider toward the convex side and narrower toward the concave. If this is interpreted in keeping with the curvature of *Proplina*, the convex surface would be anteriorward and the concave surface posteriorward.

Tryblidium conicum Whitfield, also from the Beekmantown Formation at Ft. Cassin, Vermont, was transferred by Ulrich and Scofield (1897) to *Scenella*, where it then became a junior homonym. Bassler (1915, p. 1139) renamed it *Scenella cassinensis*. This species may be particularly important in that the steinkern shows paired muscle scars (Whitfield, 1886), yet apparently it has never been reillustrated nor studied. The apex is more or less subcentral and the cone is relatively low as in *Kirengella*.

Scenella orithyia (Billings) was collected from the "Calciferous" at Phillipsburg, Quebec. The holotype (GSC number 773) was recorded by Yochelson as a hypseloconid. The pear-like compression shown by Billings in his cross-sectional view is not an artifact. The orientation of the cross section is not clear. One may speculate from Billings' drawing that the narrowing of the shell is toward the anterior; if so, the specimen would thus be narrower toward the convex side. Clearly this species should be compared to *Scenella*? *alta*.

Scenella? *veneillia* (Billings) was obtained from limestones number 1 and number 2 at Point Levis, Quebec. The holotype and paratype (GSC numbers 787 and 787a) are recorded by Yochelson as "...defiantly hypseloconic, and not curved at all" (Yochelson, unpub. data), though there is no mention of the curious elongate ridges illustrated by Billings in the apertural area.

After reassignment by Bassler (1915), four species remained in *Metoptoma.* Three of these are questionably from the Ozarkian, that is limestone number 2 at Point Levis, Quebec; the fourth is significantly younger.

Metoptoma augusta Billings was not illustrated in Billings (1862). In a brief examination, Yochelson did not indicate the specimen number of the holotype, but recorded that it was a steinkern and appeared similar to a "...wide *Knightoconus*" (Yochelson, unpub. data). On that slim basis it was subsequently transferred to *Kirengella* (Webers and others, 1992, p. 196).

Several other poorly known species of *Metoptoma* were mentioned by Webers and others (1992) as possible representatives of *Kirengella*. *Metoptoma anomala* Billings is illustrated, but the shape is not consistent with that of a tergomya. Years ago, Yochelson examined the holotype (GSC number 786) and determined that it was a *Matthevia*. If so, it is probably of Trempealeauan (Sunwaptan) age and if all the specimens from limestone number 2 were obtained from the same limestone block, they would probably be younger than the material of Berkey and approximately equivalent to the fauna described by Walcott (1912b) from Saratoga Springs, New York. *Metoptoma melissa* Billings was not illustrated by Billings. The type lot (GSC numbers 776a-e) was noted by Yochelson as having a pyramidal shape like *Kirengella*, but otherwise, "...not showing much" (Yochelson, unpub. data).

In addition, Walcott (1890) described two species from the "Upper Cambrian Sandstone (Middle horizon)" that he questionably assigned to *Metoptoma*. *Metoptoma*? *minneiskanensis* Walcott (1890, p. 267) is from Minneiska, Minnesota. Two specimens were originally catalogued as USNM number 23844, but they have since been separated. They do not appear to be conspecific. The specimen bearing a green diamond and now catalogued as holotype (USNM number 23844) does not resemble the illustration. The second specimen now catalogued as a paratype (USNM number 312515) appears to be the original of Walcott's drawing. Both specimens are steinkerns, though on 312515 the impression of growth lines may be present. It is a relatively high *Proplina* and shows some similarity to Berkey's Gen.? sp.?. The other specimen, USNM number 23844, is much higher and close to *Proplina convexa* (Berkey), but has a steeper dorsum. The material is not adequate to discuss further.

Walcott (1890, p. 267) also described *Metoptoma*? *peracuta* from Spofford's Bluff, Wisconsin. The illustrated specimen, another smaller, loose individual, and two small fragments on matrix are catalogued as USNM number 312516; another piece of matrix under this number showing an external impression does not have the features that would group it with the others. The species is a hypseloconid, and although the apexes of both specimens are broken, the smaller one is 3 millimeters wide and it is unlikely that it was septate. The overall shape is very close to that of *Hypseloconus cylindricum* Berkey, but that species may be slightly more compressed. No precise comparison can be made with the limited material at hand.

Webers and Yochelson unsuccessfully attempted to locate the collecting site in Minnesota, but until such time as better preserved topotypical material may be collected, we suggest that both of Walcott's names be confined to use with the type lots.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier

Discussion: The last comprehensive summary of Paleozoic Gastropoda is more than four decades old (Knight and others, 1960). We follow it for the two genera discussed below. Our use of the -acea ending for a superfamily, rather than the currently recommended use of -oidea, indicates that the classification is old. We recognize that as soon as a classification is published it starts to become outdated; we deliberately have used the formal subdivisions within the class from the same publication. Some speculations for consideration in preparing any future revision of this 1960 classification have been presented (Yochelson, 1984).

Two of the molluscan species described by Berkey would likely fall under the general definition of gastropods. Each is now represented by a single specimen and there is no reason to assume that Berkey had more in his collection. Accordingly, the material at hand is insufficient to pursue a major study of Late Cambrian North American anisostrophically coiled shells. The concept of "Paragastropoda," loosely defined as snail-like shells that are assumed not to have undergone torsion of the soft parts, is intriguing and impinges on one of Berkey's specimens, but the scanty material provides no new information on the subject.

In keeping with his unstated view of a morphologic series of forms, Berkey described the three-dimensionally coiled forms following that of the bilaterally symmetrical shells. We have reversed this order. No phylogenetic significance should be read into this reversal. Our notion is simply to move from forms known only from scarce material to those that are better preserved or better represented in the collection.

Family Onycochilidae

Discussion: The Onycochilidae and Macluritidae were placed by Knight, Batten, and Yochelson (1960) within the Macluritacea, but to discuss this higher level classification is extremely far beyond the bounds of this work. Whether any or all of these forms are truly sinistral or hyperstrophic ("ultra-dextral") is a speculation in the realm of theoretical morphology. Until such time as more specimens, and especially better preserved specimens of *Scaevogyra* are described, this line of inquiry cannot be profitably pursued and we leave it to others to confirm or refute the revisions suggested below.

Subfamily Scaevogyrinae

Discussion: Knight and others (1960, p. I-187) grouped *Scaevogyra* with three others, and questionably another genus within the Scaevogyrinae. Although the genus *Kobayashiella* may be related to *Scaevogyra*, almost certainly the other three genera, all significantly younger, are not allied. This subfamily was combined with the Onychochilinae into the Onychochilidae. Within that subfamily, *Matherella* and *Matherellina* show some similarities to *Scaevogyra* and to a lesser extent *Kobayashiella*. These four genera have in common a Late Cambrian range, and although rare, are more common in the Trempealeauan (Sunwaptan) stage.

When the *Treatise on Invertebrate Paleontology* (Moore, 1960) classification was being prepared, considerable emphasis was placed on the sinistrality of these forms, but other morphologic details and differences in their stratigraphic ranges were given less emphasis. It seems at least equally plausible, and perhaps somewhat more logical, to place these Late Cambrian sinistral forms together and raise the Scaevogyridae to the rank of family and reconsider the placement of the stratigraphically younger genera remaining within the Onychochilidae. If there is one feature that holds this concept of a reconstituted Onychochilidae together, it is that the genera are rare and little studied. Unfortunately, nearly the same may be stated for any possible rearranged and raised Scaevogyridae. The comments above are informal suggestions, and not nomenclatural actions.

Genus *Scaevogyra* Whitfield, 1878

Type species: *Scaevogyra swezeyi* Whitfield, 1878, p. 62; for details see Knight (1941, p. 306).

Discussion: In his original description of the genus, Whitfield (1878) named three species, which were subsequently redescribed and figured (Whitfield, 1882). All three of these were reported from "Eikie's quarry" about seven miles east of Baraboo, Wisconsin. Subsequently, the type species has been reported from a variety of localities in rocks of Late Cambrian age in the southeastern and south-central United States.

Seemingly, the other two Whitfield species have been ignored for a century. Both differ from the type species in being relatively high-spired. Accordingly, *S. obliqua* Whitfield and *S. elevata* Whitfield are herewith transferred to *Matherella* Walcott. It is likely that at least one of Whitfield's species might be placed in synonymy when that genus is studied critically.

***?Scaevogyra swezeyi* Whitfield**

Figure 3A

Scaevogyra minnesotensis Berkey, 1898, p. 286, pl. 20, Fig. 26.

Discussion: Berkey illustrated his species with a line drawing at natural size having both the apertural and apical areas restored, though the author clearly indicated parts he had restored. The holotype is a steinkern on a piece of sandstone about 10 by 10 centimeters. No exterior with growth lines is preserved and there is just enough of the whorl

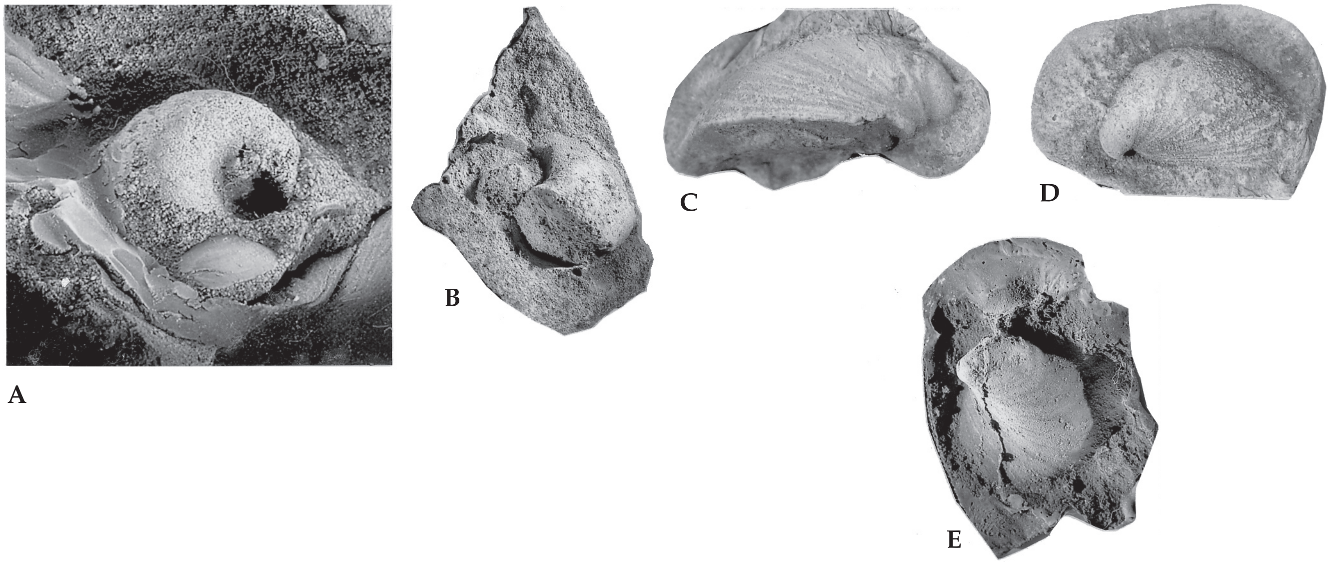


Figure 3. Gastropoda and Tergomya; all material was coated with ammonium chloride prior to photography.

A. ?*Scaevogyra swezeyi* Whitfield. Slightly oblique view of a plastic cast of the holotype of *S. minnesotensis* Berkey (1898, pl. 20, Fig. 26), showing the gradual expansion of the whorl on the lower part of the photograph; the sinistral coiling may be observed within the umbilicus. AMNH (American Museum of Natural History) number 22280, x 2½.

B. ?*Sinuopea sweeti* (Whitfield). Slightly oblique view of a plastic cast of the holotype of *Euomphalus strongi* Whitfield, var. *sinistrorsus* Berkey (1898, pl. 20, Fig. 23; pl. 21, Fig. 9), showing expansion of the whorl on the right side and the impression of a narrow umbilicus; the umbilical impression of the earlier whorl is within the roughened area of the umbilical opening near the center of the photograph. AMNH number 22281, x 1.

C. *Proplina*? *cornutiformis*. Presumed right lateral view of the wax impression, for which no original exists, but closely matching the opposite side of the material in Figure 3D. AMNH number 22278, x 2.

D. *Proplina*? *cornutaformis* (Walcott). Latex cast of the presumed left lateral view of the holotype of *Tryblidium aduncum* Berkey (1898, pl. 20, Figs. 27, 28), showing the growth lines and the apex overhanging the aperture. AMNH number 22278, x 2.

E. Gen.? sp.? of Berkey (1898, pl. 20, Fig. 20; pl. 21, Fig. 15). Slightly oblique presumed left lateral view of a latex impression of an incomplete specimen that Berkey interpreted as having dextral coiling, but which may be the apical portion of a *Proplina*. AMNH number 22295, x 1.

preserved to demonstrate the sinistral coiling. A plastic cast of the type specimen (AMNH number 22280) is illustrated herein and comparison with the holotype indicates that no details of shape were lost in the casting.

Although Berkey indicated in his drawing that coiling was to the left, he did not comment on this feature in his description. From what little can be discerned of the features of the holotype, there is no justification for maintaining his form as a distinct species, and placing the name tentatively within the type species is a matter of nomenclatural housekeeping. The alternative would be to restrict the name to use with Berkey's holotype, pending the unlikely discovery of better topotypical material. Because that prospect is slight, this synonymy seems more acceptable, if only to call attention to Berkey's remark concerning correlation.

Prior to his description of a new species of *Scaevogyra*, Berkey (1898, p. 286) made this comment. "Inasmuch as all the species of *Scaevogyra* so far described belong to the Baraboo fauna as reported by Whitfield, there is additional evidence in this St. Croix dalles occurrence of the essential identity of the two faunas as a whole and indirectly of the unbroken continuity of the strata to which they all belong." Inasmuch as the "Magnesian limestone" (Black Earth Member) is now considered to be within the Trempealeauan (upper Sunwaptan) stage, the question mark on assignment of the holotype should also be interpreted to indicate that the stratigraphic range of the species is uncertain. In western Utah, specimens identified as *S. swezeyi* occur in limestone of Trempealeauan (Sunwaptan) age. In Missouri, the genus is known to date only from the Potosi or Eminence Formations, both of Trempealeauan (Sunwaptan) age (B. Stinchcomb, unpub. data, 2003).

Whitfield's original illustrations show *S. swezeyi* with an expanding aperture, not unlike a miniature tuba. Knight (1941) indicated a slight flare of the aperture, but it may be that this too is an exaggeration. The gastropod shell is of knife-edge thinness at the growing aperture and thickens inward, so that steinkerns that are not broken at the aperture appear to flare. Specimens of *Scaevogyra* that are not preserved as steinkerns appear to be very rare.

Family Sinuopeidae

Discussion: At the time the *Treatise on Invertebrate Paleontology* classification was prepared (Knight and others, 1960), one assumption was that a sinus, a U-shaped bend in the growth lines, was closely allied to a parallel-sided slit, so that growth lines are interrupted and cannot be traced along the outer whorl face, whereas the growth lines indicating a sinuate aperture are not interrupted. Thus, all Paleozoic sinuate gastropods, ranging in age from Late Cambrian through Permian, were placed within the Sinuopeidae and divided into three subfamilies. In that classification, little consideration was given to the age of specimens within the Paleozoic and no emphasis was placed on the general shell shape. The details of the shape of the sinus were also little considered.

Subfamily Sinuopeinae

Discussion: Three genera were included in this taxon, two of which are Late Silurian in age. The one feature that they have in common is that none are low-spired. If, as a first approximation, one reorganizes the genera in the family by age, the next youngest genus in the family, *Chepultapecia* Ulrich (in Weller and St. Clair, 1928), is Early Ordovician in age. Because that genus is low-spired and quite different in overall shape, there is no reason to assume that these two genera are related, nor is there any strong reason to assume that the middle and late Paleozoic genera in this group are necessarily related even at the family level.

Genus *Sinuopea* Ulrich

Type species: *Holopea sweeti* Whitfield, 1880, p. 48; for details see Knight (1941, p. 321).

Discussion: The type species was described from the "Potsdam" Formation of Wisconsin. As might be expected in a sandstone matrix, most specimens are steinkerns. Knight (1941) illustrated an external mold showing a broad, shallow sinus on the whorl. We have examined topotype specimens from Osceola Mills, Wisconsin, and can confirm the presence of the broad sinus. At the time the *Treatise on Invertebrate Paleontology* (Moore, 1960) classification was prepared, *Sinuopea* was judged to range from Late Cambrian to Early Ordovician in age. Because of the poor material available for study, we have not made any attempt to examine Early Ordovician specimens to confirm the presence of the genus in younger rocks.

?*Sinuopea sweeti* (Whitfield)

Figure 3B

Euomphalus strongi Whitfield, var. *sinistrorsus* Berkey, 1898, p. 287, pl. 20., Fig. 23; pl. 21, Fig. 9.

Discussion: The illustration given by Berkey is a line drawing somewhat restored and in our view restored incorrectly. It is not immediately obvious from his illustration that this is different from ?*Scaevogyra swezeyi* discussed above, for both are restored as coiling in the same sinistral direction and as being extremely low-spired. As with the above species, the Berkey material is incomplete. One may argue that the specimen is sinistral, as Berkey implied with his name, but interpretation as a dextrally-coiled shell, moderately high-spired, and having a moderately well-rounded whorl profile, is somewhat more convincing. As such, it resembles the typical steinkerns of *S. sweeti*. Two incomplete steinkerns in the former University of Minnesota collection support the interpretation of dextral coiling.

The type specimen is on a piece of sandstone approximately 8 by 7 centimeters and sunken below the surface. Deep within the cavity the base of an early whorl may be seen that shows a few curved growth lines, confirming the dextral coiling. A plastic cast of the type specimen (AMNH number 22281) is illustrated herein. It does not show the growth lines, because they are well hidden by the sunken surface of the type and could not be photographically illustrated. As a consequence of the paucity of the material and the poor preservation, nothing more can be gleaned. Just as was the decision with ?*S. swezeyi* discussed above, the synonymy is more of a "housekeeping" matter to simplify the literature, than a true step forward in understanding the early gastropods.

The reassignment proposed herein provides a link to the Late Cambrian sandstones that outcrop at Osceola Mills, Wisconsin. However, the range of *Sinuopea* is essentially unknown. Examination of the general area by Webers and Yochelson did not find any fossiliferous layers exposed.

Euomphalus strongi Whitfield (1878) itself was assigned to *Sinuopea* by Bassler (1915, p. 514), but it deserves restudy. From the drawings (Whitfield, 1882, pl. 4, Figs. 1, 2), the species does appear to be a *Straparollus* (*Euomphalus*), but if so, it is older than any other member of the genus. Future investigators should note that the type of this species was not obtained from the Eikie's quarry locality in Wisconsin, nor was it collected by Whitfield.

Class Tergomya Horny

Discussion: As with the Gastropoda, the last comprehensive summary of what was then termed the Monoplacophora is more than four decades old. "In the *Treatise* [of] *Invertebrate Paleontology* Knight and Yochelson (1960) included within the Class Monoplacophora three orders which are now assigned by many workers to three distinct molluscan classes" (Peel, 1991, p. 159). In the face of such a comment it seems foolhardy to use any taxonomic subdivisions within the class, let alone formally modify any of the names in the literature or propose new ones. The material in the Berkey collection certainly does not provide a sufficient basis for any major revisions or rearrangements.

The subfamily name Proplininae Knight and Yochelson (1958) is in the literature, along with Hypseloconidae Knight (1956). Kirengellidae was proposed by Starabogatov (1970, p. 17) in a comprehensive reclassification of Monoplacophora. In our judgement, it may not be a step forward to use any family level taxa for the Tergomya described below, for that may further complicate a future comprehensive review of the systematics of this class.

We are aware that *Proplina* was assigned to the Tergomya, whereas *Hypseloconus* was placed in the Cyrtomya of Horny. The latter genus was not included in the reorganization of the Monoplacophora proposed by Starabogatov (1970). Notwithstanding that, we are placing *Hypseloconus* in the Tergomya at this time as a matter of practicality. That genus does not fit well into either the Tergomya or the Cyrtomya. Many of the genera currently placed in the Cyrtomya are strongly curved to coiled in form. Whether this group will achieve the status of an extinct class or the included genera will be reassigned is unknown. Until there is a careful restudy of this concept, it seems prudent to set it aside without comment. Were it to be used here as a major heading, this might imply that we have automatically accepted it as of class rank. In fact, most of the currently included genera are significantly younger and *Hypseloconus* may be the only Late Cambrian genus included in the concept.

Considerable emphasis has been placed on the bilaterality of the tergomya shell, but at least one Early Ordovician genus, *Cyrtenellopsis* Yochelson (1958, p. 8-9), is asymmetrical in the early growth stages. Were it not for this feature, the form would fit well into the general concept of *Proplina*.

Genus *Proplina* Kobayashi

Type species: *Metoptoma cornutiforme* Walcott, 1879, p. 129; for details see Knight (1941, p. 274).

Discussion: Walcott's original description of this species in 1879 was not supplemented by illustrations. Subsequently, the species was assigned to *Tryblidium* (Walcott, 1912b), the description was revised slightly, and three specimens were illustrated by photographs. The Late Cambrian Hoyt Limestone near Saratoga Springs, New York is only locally fossiliferous and to the best of our knowledge no topotype specimens have been described.

Insofar as we can determine, Berkey used the generic assignment of new species to *Tryblidium* for spoon-shaped shells in which the apex overhung the apertural margin. The height of the shell and the relative curvature of the dorsum were judged as specific characters. The type of this genus is from the Silurian of Gotland, Sweden, and is a nearly flat shell with prominent rugosities (for details see Knight, 1941, p. 364). It is understandable that Berkey employed that generic name, for "In conformity with the facts just noted bearing upon specific variability, it is deemed best to include a greater range of forms within this genus than has been at times customary" (Berkey, 1898, p. 279).

"In many forms, obtained from the Cambrian rocks especially, no muscle attachment can be located. Those which show such impressions present a circle of paired scars around the cone. ... In the earlier forms which are well enough preserved to show muscle scars the number is six. As it now stands, however, the form of the shell is the chief and almost the only feature offering a basis for a classification of many specimens" (Berkey, 1898, p. 280).

Stinchcomb (1980) illustrated, but did not discuss in any detail, two steinkerns showing six pairs of muscle scars, with the pair closest to the apex being significantly larger. These specimens are from the Early Ordovician Gasconade Formation of Missouri. We have compared his figured specimens with the type lot. His later illustration (Stinchcomb, 1986, text figures 2.4-2.5) of another steinkern shows the prominent muscle scars particularly well preserved. There may be some slight difference in the degree of curvature of the dorsum from that of the type lot, but until such time as a detailed morphometric study is done of the various species of *Proplina* to assess the degree of individual variation of the logarithmic spiral expansion of the shell, we are satisfied that the Missouri material is correctly identified as Walcott's species. We recognize that this is a long stratigraphic range for the species.

Yu Wen and Yochelson (1999) described somewhat differently shaped muscle scars from Late Cambrian shells that were attributed to *Pilina* Koken because the form was so little arched. The largest pair of scars was, like *Proplina*, closest to the apex, and was interpreted as associated with the radular apparatus. From what is known of *Proplina*, *Pilina*, and *Tryblidium*, we are confident that the shell apex is near or overhanging the anterior of the aperture. Unfortunately no muscle scars are known from Late Cambrian shells of comparable form; the caution used in description simply reflects this lack of knowledge, not concern that the interpretation of anterior and posterior may be flawed.

Proplina is used herein for those species that have a more or less oval aperture, a more or less arched dorsum, and an apical area that extends over the margin of the aperture, thereby exhibiting a slight degree of concave curvature of this surface below the apex. With more detailed data on these Late Cambrian species, the genus assumes slightly more importance within the Tergomya.

Berkey's species of *Tryblidium* were arranged in the following order: *rectilaterale, convexum, barabuensis* (Whitfield), *extensum, corpulentum,* and *aduncum*. We suspect that this order was in keeping with Berkey's concept of a systematic change in the shell shape. No inner meaning should be attributed to the arrangement of species below.

Four of Berkey's taxa from Taylors Falls are assigned to the genus with greater or lesser certainty. Among present day asymmetrically coiled gastropods, it is uncommon to have more than one or two species of the same genus at a single locality. In a few locations there may be more, for example neritaceans clinging to rocks or pilings where there is a considerable tidal range.

It is unlikely that this comment can be translated with any confidence to the Taylors Falls fossils. More likely the large number of named species assigned to *Proplina* is related in part to the paucity of specimens, for little is known of individual variation within a species. Equally, this large number of species is related to the need for study of more and better specimens before any attempt is made to define and establish any new genera.

Proplina? cornutaformis (Walcott)

Figures 3C, 3D

Metoptoma cornutaforme Walcott, 1879, p. 129.

Tryblidium aduncum Berkey, 1898, p. 282, pl. 20, Figs. 27, 28.

Tryblidium cornutaforme Walcott, 1912b, p. 203, pl. 41, Figs. 12-14.

Proplina cornutaformis Knight, 1941, p. 272, pl. 4, Fig. 21-2c.

Proplina cornutaformis Yochelson, 1958, p. 11-13, Figs. 10-13.

Proplina cornutaformis Stinchcomb, 1980, text figures 1A-1B.

Proplina cornutaformis Stinchcomb, 1986, p. 609-611, Figs 2.4-2.5.

Description: Strongly curved, bilaterally symmetrical shells, rapidly expanding, laterally compressed, and with distinct, relatively strong growth lines.

Discussion: Berkey's holotype material (AMNH number 22278) consists of a small block of sandstone in which there is an external impression of somewhat less than half of the fossil. From this a wax impression, and later three latex impressions, were taken. Two other wax impressions are associated with the holotype, but there is no external impression from which they were taken; one of these bears the same number as the holotype piece. These last two impressions are of a shell that shows less surface detail but is slightly more complete than the holotype, though the impression also does not reach the midline of the shell. It is possible that at one time Berkey had two fragments of an external mold and one has been lost.

Berkey's illustration is of the presumed right side of a specimen, whereas the external mold is of a presumed left side, thus supporting the view that another piece was originally available.

Berkey (1898, p. 282) compared this species to "*T. (Metoptoma) erata* Billings." This species was not illustrated by Billings and is from Middle Ordovician strata at Paquette Rapids, Quebec. We have not studied the type material in order to comment on the comparison.

We have observed one topotype specimen of the type species in the collections of the National Museum of Natural History that has distinctly impressed growth lines, like those in Berkey's specimen. We have questioned the specific reassignment of Berkey's species because the fragmentary nature of the material does not provide a definitive concept of the shape.

Stinchcomb (1986) described several new species of *Proplina* from the Early Ordovician Gasconade Formation in Missouri. To summarize, *P. meramecensis* appears wider and is more strongly curved than *P. cornutaformis*. In contrast, *P. sibeliusi* is so low and broad as to approach the Late Cambrian species that Yu Wen and Yochelson (1999) assigned it to *Pilina*. Stinchcomb (1986) described two additional species from the Late Cambrian Potosi Formation of Missouri. Both *P. suttoni* and *P. inflatus* are higher and correspondingly have a less elongate aperture than *P. cornutaformis*.

Lochman and Hu (1962) described *P. loganensis* from the Late Cambrian Pilgram Formation of Montana. We suspect that the three available specimens probably are the same as Walcott's species. Unfortunately, they are all smaller than the type lot of that form and no detailed comparison can be made.

We should mention that Berkey also described a genus and species indeterminate, on page 287 (Berkey, 1898) of his work and illustrated it with both a line drawing and a photograph (Fig. 3E; AMNH number 22295). From its position in the publication following *Euomphalus*, one may assume that he considered it a three-dimensionally coiled gastropod. The specimen is an external impression on a thick, hand-sized piece of sandstone. In contrast to other material in the Berkey collection, this is nearly black on the exterior. From that we infer it may have been a weathered piece on the exterior of the outcrop and it may have been collected prior to Berkey starting his investigations.

From the external impression both a wax cast and a latex cast had been made; presumably Berkey used the wax. These impressions are of a large and quite incomplete shell that may be interpreted in several ways. In the interpretation favored here, this form may be the apical area and part of the side of a large *Proplina*. Growth lines are closely spaced and simple. From what comparison may be made, it is probably closer to *P. suttoni* Stinchcomb than to any other species. Until such time as more comparable material is obtained from Taylors Falls, nothing further can be gleaned from it, except that it is another demonstration of the diversity of species in this fauna.

Proplina corpulentum (Berkey)

Figures 4A1, 4A2

Tryblidium corpulentum Berkey, 1898, p. 281-282, pl. 20, Figs. 21, 22.

Description: A bilaterally symmetrical shell expanding uniformly from near the apical area, low, and uniformly curved. Dorsum is gently arched. Apex and aperture are unknown. Growth lines are simple, distinct, but not prominent.

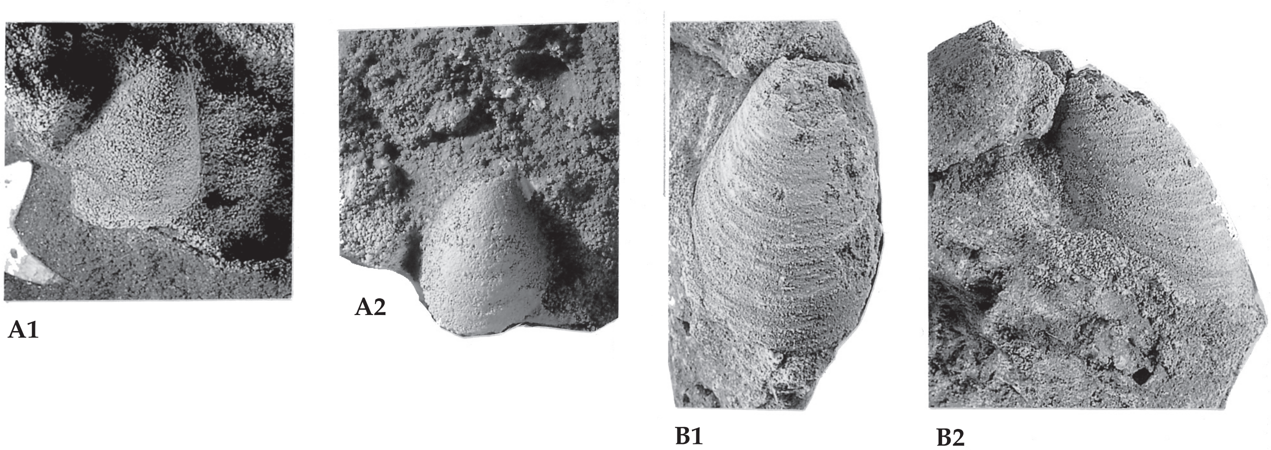


Figure 4. Tergomya; all specimens were coated with ammonium chloride prior to photography.

A1. *Proplina corpulentum* (Berkey). Slightly oblique dorsal view, showing growth lines, of the holotype of *Tryblidium corpulentum* Berkey (1898, pl. 20, Figs. 21, 22). AMNH number 22277, x 2½.

A2. Dorsal view showing the general shape, x 2½.

B1. *?Proplina extensum* (Berkey). Dorsal view of the holotype of *Tryblidium extensum* Berkey (1898, pl. 20, Figs. 16, 17). AMNH number 22276, x 2.

B2. Presumed left lateral view, x 2.

Discussion: The holotype material (AMNH number 22277) is a fragment of sandstone on which a single specimen occurs. The maximum preserved length is just over 10 millimeters and the maximum width is 7 millimeters. The apical area is covered by matrix and the shell is broken away at the apertural edge. It is impossible to precisely determine the shape of the aperture or the position of the apex relative to the apertural edge. Having stated that, the general rate of expansion, relative width, and degree of curvature strongly suggest assignment to *Proplina*.

In view of the incompleteness of the material, it is suggested that use of the specific name be limited to the holotype. This is not meant to imply that it should not have been differentiated by Berkey. Despite the small size of the specimen, it is relatively wider than ?*P. extensum* and significantly lower-coned than ?*P. convexum*. It differs little, if at all, from *P. cornutiformis* as used herein, but nothing is to be gained by placing it in synonymy except to make interpretation of that species slightly less certain. In the former University of Minnesota collection are two specimens about 6 and 12 millimeters in length, respectively. Both are steinkerns and provide no data other than general shape. Because of their small size, they might belong to this species.

Berkey compared his species to "*T.* (*Metoptoma*) *simplex* Billings," of interest only in an historic sense for the consideration of *Metoptoma* as a subgenus.

?Proplina barabuensis **(Whitfield)**

Not Illustrated

Metoptoma Barabuensis Whitfield, 1878, p. 60.

Metoptoma Barabuensis Whitfield, 1882, p. 195, pl. 3, Figs. 16, 17.

Metoptoma Barabuensis Chamberlin, 1883, p. 142, Fig. 26.

Metoptoma barabuensis Sardeson, 1896, p. 97.

Tryblidium barabuensis Berkey, 1898, p. 281.

Tryblidium (*Metoptoma*) *barabuensis* Berkey, 1898, pl. 20, Figs. 18, 19.

Tryblidium barabuensis Sardeson, 1903, p. 479, Fig. 2.

Tryblidium barabuensis Grabau and Shimer, 1909, p. 604, Figs. 802e, 802f.

Tryblidium barabuensis Bassler, 1915, p. 1306.

Discussion: The specimen discussed and perhaps illustrated by Berkey is one of two molluscan specimens described by him that are not from Taylors Falls, Minnesota. The fossil was collected by Sardeson (1896) at Osceola Mills, Wisconsin, associated with numerous *Sinuopea sweeti* (Whitfield). Presumably, the prime reason for including it in his publication was biostratigraphic. "*Tryblidium barabuensis* (Whitfield), is identified from the Jordan sandstone while related forms *T. convexum*, n. sp., and *T. extensum*, n. sp., are from the marginal conglomerates of the Dresbach. Therefore the range exhibited by these similar species is about 200 feet." (Berkey, 1898, p. 291).

Whitfield's type species from Baraboo, Wisconsin may fit into the generalized definition of *Proplina* given above, and is herewith questionably transferred to that genus. A formal redescription of that species must await a restudy of the holotype, housed at the Museum of Paleontology, University of California, Berkeley.

As discussed under ?*Proplina convexum*, the material from the AMNH (number 22274) currently labeled as *Tryblidium barabuensis* was correctly noted by a later unknown investigator as not matching Berkey's figures, and is not part of the type lot of that species. Presumably over the years, the specimen from Osceola Mills, Wisconsin has been lost. Equally, it may have been loaned to Berkey by Sardeson, who maintained his own collection, separate from that of the University of Minnesota (Weiss, 2000).

?Proplina extensum **(Berkey)**

Figures 4B1, 4B2

Tryblidium extensum Berkey, 1898, p. 281, pl. 20, Figs. 16, 17.

Description: Elongate, low, rugose shells; apical area is unknown, shorter slope is unknown; longer slope of dorsum is very gently curved; shell is seemingly low and uniformly arched laterally; growth lines are rugose, simple in outline, slightly irregular in spacing, but generally separated by about 1 millimeter.

Discussion: The available material (AMNH number 22276) consists of a small block of sandstone to which the holotype is attached. Notwithstanding the limited nature of what could be observed, Berkey did not hesitate to outline the aperture and the presumed right side.

Berkey (1898, p. 281) noted "This specimen is defective, but is sufficiently complete to allow restoration of all missing parts. It forms an important step in the morphologic series." His first sentence is clear, though his conclusion may be argued, but his second sentence is enigmatic. It may be that Berkey saw the various species he assigned to *Tryblidium* as a series of forms that did not intergrade but ranged from low to ever higher shells with a concomitant change in the position of the apex and with variation in the shape of the aperture. It is because of the incompleteness of the holotype that the generic assignment is given with question.

When one compares specimens showing the external form with steinkerns, it is like comparing a peeled orange to one that is whole. Each reveals a different sent of characters, but those that are on the exterior vary more in a subtle manner. In its display of muscle scars, ?*Proplina convexum*, discussed below, is like the peeled form, whereas with its rugosities, ?*P. extensum* is like the exterior of the orange. Depending on the thickness of the shell, a steinkern may differ significantly in shape from that of a form showing the exterior. Fortunately among the Tergomya, this does not appear to be a significant factor for most genera. Berkey compared ?*P. extensum* to a Middle Ordovician form described by Sardeson (1896), but noted differences. We concur that these two species are distinct.

This species may be the same as *Proplina arcua* (Stinchcomb, 1986) from the Late Cambrian Eminence Formation of Missouri in terms of low rate of expansion and distinct lateral compression. The illustrated specimens are smooth and show no growth lines. The type species of *Proplina* is relatively smooth on the exterior, as are several species assigned to it. What significance, if any, is to be placed on growth irregularities is uncertain, but we judge that a questionable assignment to the genus is appropriate, and prefer not to place the Stinchcomb species, which is from a different stratigraphic interval, in synonymy.

Although mollusks are considered as growing continuously, that can only be viewed as a generalization in opposition to the molting of arthropods. Each growth line indicates a pause in deposition of shell material. Rugosities and more elaborate extensions of the apertural edge in living gastropods indicate a longer pause in shell enlargement. The rugosities of this species are thickenings of the apertural edge, but why the animal paused in growth and whether such pauses were linked to any cycle of the water is unknown.

In bearing distinct rugosities, this species is closest to *Proplina rutfordi* Webers, Pojeta, and Yochelson. That species may be more wedge-shaped, but close comparison of the overall form cannot be made due to the inadequate nature of Berkey's type.

Proplina convexum (Berkey)

Figure 5

Tryblidium convexum Berkey, 1898, p. 280, pl. 20, Figs. 24, 25; pl. 21, Fig. 18.

Description: Distinctly curved, slightly arched, elongate specimens with a short slope below the apex; dorsum is elongate, smoothly and gently curved, seemingly following the arc of a large circle; lateral slopes are more strongly arched and seemingly slightly compressed; the short slope varies from little arched to distinctly curved; details of the exterior are unknown.

Discussion: The issue of the type specimen of this species is not straightforward. A relatively large specimen in the Berkey collection (AMNH number 22274) on one of the largest pieces of sandstone in the collection, consists of an external mold and a steinkern. The interior of the external mold shows no details. The two pieces fit extremely close, suggesting the shell was thin. A plastic cast of the steinkern has a label with it identifying it as the type and original of Figure 24 of Berkey (1898). A second label in the box with this specimen indicates that number 22274 is the type. Another included piece of paper in the same box bears a "2." and three lines "length—40 millimeters/height—20 millimeters/ apical angle—90 x 60" and has similar handwriting to a few of the labels that may have been written by Berkey. In general size and shape, the specimen approximates the drawing on plate 20, Figures 24 and 25 of Berkey (1898), and it may also match the reduced photograph on plate 21, both of which are cited as *Tryblidium convexum*.

As one complication, the length given on that label nearly matches that of a latex cast of a slightly smaller specimen labeled "Metoptoma barabuensis Whitf." and this note also might have been written by Berkey. To confuse matters further, this second cast also bears number 22274. Berkey used a certain amount of imagination in reconstructing his drawings, but one could argue that this might match the side view and outline drawings on plate 20, Figures 18 and 19 of Berkey (1898), listed on the caption as *Tryblidium* (*Metoptoma*) *barabuensis*.

We are satisfied that the two specimens are conspecific. Our speculation is that because both have the same number they were catalogued as cotypes (Berkey's types are not listed in the early catalogue of the AMNH collections [Whitfield and Hovey, 1898]). Later, apparently the absence of a Berkey specimen labeled as the original of *Tryblidium barabuensis* was noted and it was assumed that the larger specimen fit the illustration of that species. Still later, another party noted that the specimen did not closely match the drawing and included a note to that effect with the smaller specimen.

Accordingly, to avoid any future uncertainty we hereby designate the larger specimen under AMNH number 22274 as lectotype of *Proplina convexum* (Berkey; Fig. 5C). The smaller specimen under

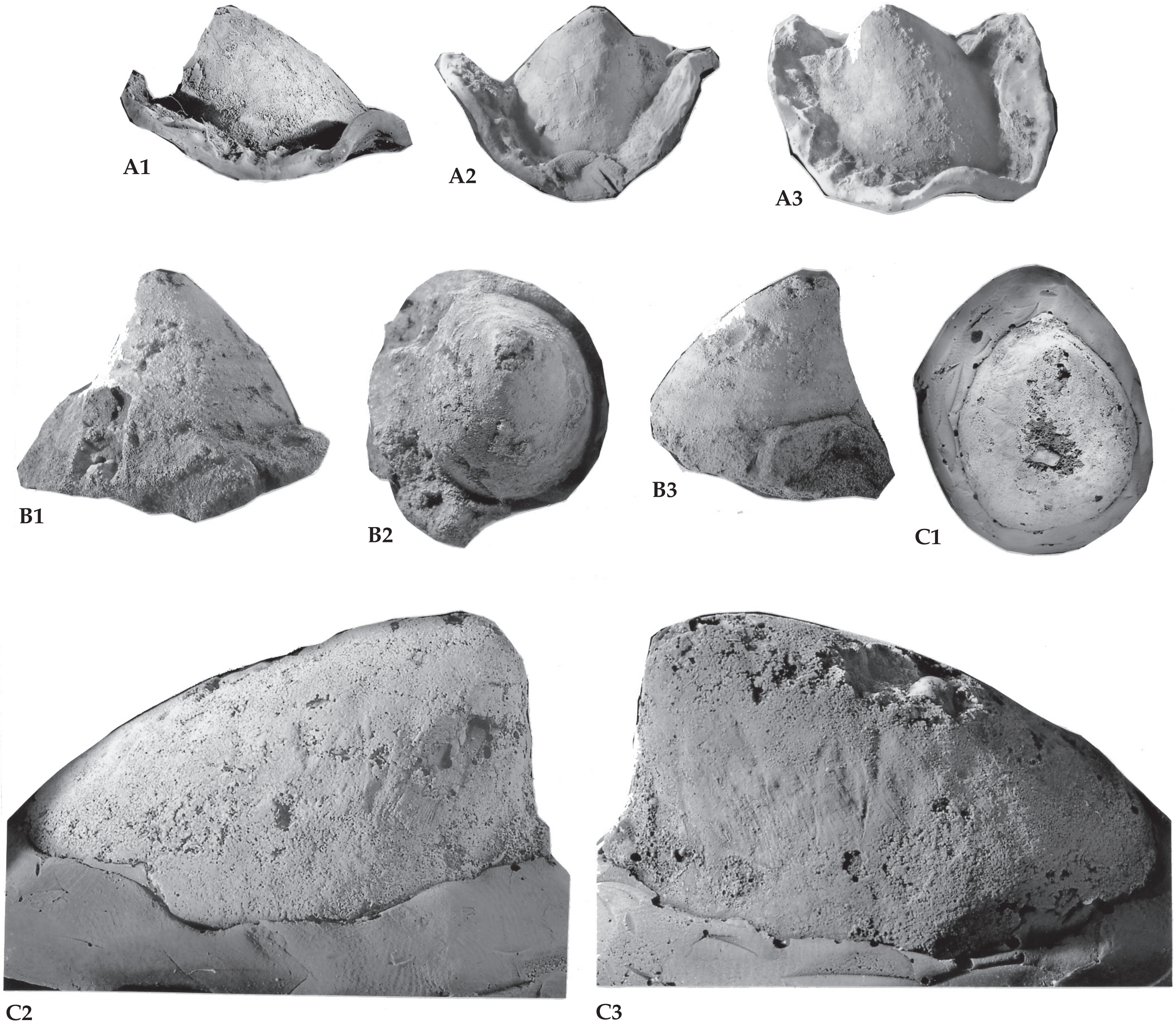


Figure 5. Tergomya, ?*Proplina convexum* (Berkey); all material was coated with ammonium chloride prior to photography.

A1. Presumed left lateral view of a latex cast of the lectoparatype, also AMNH number 22274, x l.

A2. Presumed right side view, x 1.

A3. Slightly oblique dorso-left lateral view, x 1.

B1. Presumed left lateral view of the topotype, USNM (United States National Museum) number 521875, x 1.

B2. Dorsal view, x 1.

B3. Presumed right lateral view, x 1.

C1. Dorsal view of plastic cast of the lectotype of *Tryblidium convexum* Berkey (1898, pl. 20, Figs. 24, 25; pl. 21, Fig. 18). AMNH number 22274, x 1.

C2. Presumed right lateral view showing possible muscle scars or current markings, x 2½.

C3. Presumed left lateral view showing several possible muscle scars or current markings, x 2½.

the same number is designated as a paralectotype (Fig. 5A). Both are casts of steinkerns. The former University of Minnesota collection contains one steinkern that is referred to as this species. It is slightly larger than the lectotype and it shows the profile of this species well (Fig. 5B).

Berkey made a comparison of this species to *Metoptoma niobe* Billings. As illustrated (Billings, 1862, Fig. 39), the type is a broken specimen lacking the apex. What is left of the short slope appears straight and that may be the feature that led to the comparison. Berkey also suggested that this species was similar to *Metoptoma barabuensis* Whitfield, but that species has a slightly narrower apical angle and may have had the apex extending a short distance beyond the aperture.

This species approaches the upper limits of *Proplina* in that the apex of the two steinkerns is so close to the margin of the aperture that one may argue that the apex does not overhang the inner shell layer, thereby providing a spurious whorl profile.

The issue of muscle scars deserves discussion. Berkey mentions that six pairs of scars are known in what might be interpreted from his writing as typical of *Tryblidium*. His description of this species includes the comment "There are traces of six pairs of muscle scars in this form" (Berkey, 1898, p. 280). His illustration of the presumed right side of the larger specimen shows six elongate scars.

We have examined the lectoparatype and cannot find any undoubted scars present on either lateral slope. On the presumed left lateral slope of the lectotype, there are traces of what may be two muscle scars, and perhaps a third closer to the apex (Fig. 5C3). On the basis of the two presumed faint scars on the left slope, we can convince ourselves that at least one similar feature is present on the right slope.

As a result of our examination, we are convinced that Berkey's drawing of such detail is incorrect in two regards. First, there is no evidence of six scars, and second, in his drawing he illustrated the right side of the specimen where the evidence of scars is even weaker than on the presumed left side. The presumptive scars are more or less triangular and below show several elongated narrow ridges. Muscle scars of a similar nature have been described from another species of *Proplina* (Stinchcomb, 1980, 1986).

Because there is both an external mold and a steinkern of the type specimen, there is no question that the shell is extremely thin. In the light of this morphologic feature, the presence of such prominent muscle scars might be viewed as anomalous. An alternative interpretation cannot be dismissed. The dorsal surface of the steinkern is broken away almost at the center, and within this area a small pebble may be seen (Figs. 5C1, 5C3). Its presence indicates currents stronger than those which carry only sand. One can equally interpret the two most prominent impressions on the lateral slope as current shadows or markings behind an obstacle (Allen, 1982). Within a conelike shell, current patterns must have been exceedingly complex and several sand grains coarser than those forming most of the matrix would have been sufficient to cause such lineations. Thus, we are unable to judge whether these features are true muscle scars or spurious features.

To add one further complication, Rosov (1968) indicated that on the type species of *Kirengella* the shell was relatively thick and growth lines developed into short flanges. In the final analysis, ?*P. convexum* differs considerably from *Kirengella* in having the apex strongly eccentric rather than subcentral. It is more conservative to question its assignment to *Proplina* than to transfer it to *Kirengella* or to propose a new genus.

The only *Proplina* species of Berkey preserving a rugose exterior, ?*P. extensum*, is more elongate and lower than this species. The overall shape differs from that of the more curved *P. cornutaformis*, especially in the position of the apex and the much higher, less arched shell.

Genus *Kirengella* Rosov

Type species: *Kirengella ataktchica* Rosov, 1968, p. 1428, Figs. 2, 3.

Discussion: *Kirengella* is used herein for moderately high conical species that have an aperture varying among species from moderately narrow to more or less widely oval and an apex which varies in position from subcentral to near the apertural margin, but does not overhang it. Curvature of both concave and convex surfaces is slight. The assignment of laterally compressed forms among others, is an expansion of the original generic concept.

Kirengella stabilis (Berkey)

Figure 6

Hypseloconus stabilis Berkey, 1898, p. 286, pl. 19; Figs. 25, 26, pl. 21, Fig. 6.

Hypseloconus cf. *H. stabilis* Berkey Stinchcomb, 1980, p. 46, text figures 1K-1O.

Kirengella stabilis Webers, Pojeta, and Yochelson, 1992, p. 196.

Kirengella stabilis Stinchcomb and Angeli, 2002, p. 969.

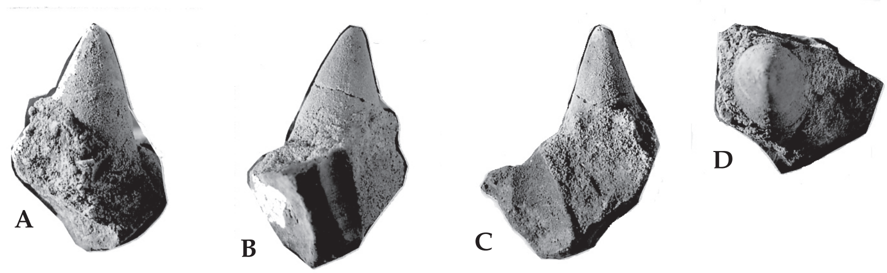


Figure 6. *Kirengella stabilis* Berkey; the specimen was coated with ammonium chloride prior to photography.

A. Presumed right lateral view of the holotype of *Hypseloconus stabilis* (Berkey, 1898, pl. 19, Fig. 25; pl. 21, Fig. 6). AMNH number 22260, x 1.

B. Presumed posterior view, x 1.

C. Presumed left lateral view, x 1.

D. Apical view, x 1.

Description: High, conical shells with a moderately well rounded aperture; apex is unknown; apertural area is not far removed from a subcentral position; both longer and shorter surfaces are essentially straight; sides are well rounded; surface of the steinkern is seemingly smooth; details of the outer surface are unknown.

Discussion: The type and only known specimen (AMNH number 22260) is a steinkern. In the absence of any growth lines, among other external features, one cannot determine the inclination of the apex relative to the cone. There is a difference in inclination between the two primary slopes of the cones, but it is so slight as to suggest that the apex was close to central in position. There is no indication of curvature, although the earliest stages of the steinkern are not preserved. The broken specimen is about 2 centimeters high and there is no indication of a ring-like bulge on the slopes. From this one may speculate that either the specimen was originally much higher-coned or it is a relatively small individual.

Ulrich and Bridge (1931) named two *Hypseloconus* species of interest from the Van Buren Formation of Missouri. Stinchcomb (1986, p. 609) has noted the difficulty of recognizing this name in terms of a rock formation, despite the fact that a characteristic fauna is widespread, and he accordingly treats these fossils as a zone within the Early Ordovician Gasconade Formation. The material of *H. compressus* cannot be located in the collections of the National Museum of Natural History, but it seems to be a distinctly arched, relatively narrow cone. A paratype of *H. ozarkensis* (USNM number 83533-b) and assigned specimens described by Stinchcomb in 1986 (USNM numbers 313575 and 313576) suggest that this species has essentially no curvature and has the apex near the narrower end of the oval. It seems to have the same relative width as *K. stabilis*, but is a lower cone and concordantly has a more elongate aperture.

In a later work, Stinchcomb and Angeli (2002) redescribed both these species. They also transferred *Gasconadoconus expansus* Stinchcomb (1986) to *Kirengella* and described a new species of the genus. *Kirengella stabilis* differs from *K. expansus* in being more compressed laterally, and from *K. oregonesis* Stinchcomb and Angeli in showing even less curvature of one slope.

Stinchcomb (1980) illustrated specimens from the Late Cambrian Davis Formation of Missouri that he compared to *Hypseloconus stabilis* Berkey. We can confirm the presence of two areas of compression on the steinkern on his largest specimen (USNM number 252279) and the presence of muscle scars as indicated on his illustrations. On both this specimen and another illustrated one (USNM number 252278), the muscle scars have been inked to bring out the pattern of these slight impressions in the rather coarse, sugary matrix that is actually present. A third illustrated specimen (USNM number 252276) shows several faint depressions on a lateral slope, but whether these are muscle tracks cannot be confirmed. The specimens themselves have a broader angle and a correspondingly longer slope from the apex than in *K. stabilis*, but this may be a matter of individual variation rather than two different species. In any event, assignment of this species to *Kirengella* removes a form bearing muscle scars from *Hypseloconus*.

As with ?*H. cylindricus*, Berkey (1898, p. 286) indicated that this specimen might be considered as a representative of *Scenella*, but again as in the case of that species we have decided against that assignment. *Kirengella stabilis* is a little closer to the general form of *Scenella* than ?*H. cylindricus,* but is not close to the low oval cone; we attribute this questionable assignment by Berkey to the paucity of literature on Cambrian mollusks that was available to him. Insofar as we can observe, Berkey's type specimen and the specimens mentioned above all have straight slopes on both the anterior and posterior, whereas the type of *Hypseloconus* is curved. All these forms are significantly higher cones than the type of *Kirengella*.

The general shape of this species is closely similar to that of *Archeoconus missouriensis* Stinchcomb (1986). That genus was established for elongate forms with a narrow oval aperture and a subcentral apex. We cannot demonstrate septation in Berkey's species, perhaps because it is juvenile. Until the significance of slight curvature as a major characteristic is clarified, we prefer to recognize that this species is probably not a *Hypseloconus,* but equally we prefer not to questionably transfer it to *Archeoconus* or to name a new genus.

?Kirengella rectilateralis (Berkey)

Figure 7

Tryblidium rectilaterale Berkey, 1898, p. 280, pl. 20, Figs. 29, 30; pl. 21, Fig. 17.

Description: A high, conical shell with one side essentially vertical and the other inclined about 20° from vertical; the shorter surface of the shell is seemingly slightly compressed and the longer surface of the shell is seemingly moderately well rounded; growth lines are seemingly simple and closely spaced.

Discussion: As noted in his generic discussion of *Tryblidium*, Berkey did not assign this species to *Hypseloconus* because the apex apparently did not overhang the aperture. In our interpretation, the inclination of the simple smooth aperture is such that the apex is just within the margin rather than just outside. The height of the cone relative to the width reinforces this transfer.

Berkey's type specimen (AMNH number 22273) is on a large, cobble-sized piece of sandstone with the specimen within a depression on one side of the piece. Berkey (1898, p. 280) commented "Shell thin, as indicated by space between cast and mould," but it is difficult to determine whether this specimen is a steinkern or an external mold. We concur that the shell is probably thin, but this is uncertain. Our best interpretation is that the type is a steinkern and the marking seen on the illustrated plastic cast are reflections of internal aspects of the shell.

A

B

Figure 7. Tergomya, *?Kirengella rectilateralis* (Berkey); the cast was coated with ammonium chloride prior to photography.

A. Presumed right lateral view of a plastic cast of the holotype of *Tryblidium rectilaterale* Berkey (Berkey, 1898, pl. 20, Figs. 29, 30; pl. 21, Fig. 17). AMNH number 22273, x 1.

B. Slightly oblique view of the presumed anterior of the cast, x 1.

Berkey noted that no muscle scars were preserved, an observation we can confirm, though if this were an external mold, no muscle scars would be seen. About two-thirds of the distance between apex and aperture, a slight bulge in the profile occurs. This may be seen on part of one side of the cast, but because of the incomplete nature of the specimen, it is impossible to determine whether this is a ring extending around the specimen. Examination of the holotype suggests that the apex may come to a point, though without making another cast it cannot be demonstrated.

This species is so much higher-coned than the type species of *Kirengella* that we judge it appropriate to question the generic assignment. On the other hand, it does not show curvature that would place it within *Hypseloconus*. *Kirengella pyramidalis* Webers, Pojeta, and Yochelson also has the apex close to one end of the aperture, but it is lower and wider than this species. A steinkern in the former University of Minnesota collection is more similar to that species than to ?*K. rectilateralis*, but it is smaller and so poorly preserved that even a questionable generic assignment is uncertain.

Hypseloconus washingtonensis Stinchcomb (1975) from near the middle of the Bonneterre Formation of Missouri was transferred to *Kirengella* by Webers and others (1992, p. 196). Examination of the type lot

(USNM numbers 118643-118645) indicates that it is a broad, low cone, the apex being within the apertural region and about one-third of the distance between the narrower and wider ends of the aperture. As noted by the author, no muscle scars are preserved.

Genus *Hypseloconus* Berkey

Type species: *Hypseloconus recurvus* (Whitfield) var. *elongatus* Berkey, 1898; for details see Knight (1941, p. 157).

Description: High, gently curved cones having a moderately wide oval aperture. The apex is seemingly without septa. The outer surface is ornamented only by growth lines. The curvature of the shell is distinct, but for less than one-quarter of a whorl. The aperture is not greatly elongated.

Discussion: In his general remarks, prior to the formal naming of *Hypseloconus,* Berkey (1898, p. 279) commented that some material collected "...comprises conical shells with the apex bent backward. The curve from anterior to posterior (broader) margin is therefore concave rather than convex as in *Tryblidium*. Muscle scars are similar to *Tryblidium* as indicated on the casts. This group is in fact united with *Tryblidium* through *T. rectilaterale*, n. sp. but is separated into a new genus because of the direction of development which is toward *Eccyliomphalus* rather than toward *Patella* and on account of the radically different form which at once develops in this line." *Eccyliomphalus* is an open-coiled gastropod, which is coiled nearly in a single plane and has a whorl profile that is only slightly asymmetrical. It would have been logical for Berkey to assume he was dealing with the ancestor of such a strange form of snail.

We do not judge that there is any sort of morphological gradation between *Proplina* and *Hypseloconus*. However, Berkey's interpretations of anterior and posterior and the direction of curvature in the two genera appear to be reasonable assumptions.

The issue of muscle scars has been noted previously. Knight (1941, p. 158) was clear that he saw no muscle scars. We have reexamined the two numbered specimens Knight cited and presumably the additional specimens/casts to which he alluded. We also see no evidence of paired muscle scars.

As a result of the efforts of Stinchcomb (1980, 1986), much more is now known of the diversity of hypseloconids. We suspect that older reports of Early Ordovician occurrences of *Hypseloconus* will eventually be determined to be representatives of closely allied genera, but not of the genus in a restricted sense.

Hypseloconus elongatus Berkey

Figure 8

Hypseloconus recurvus (Whitfield), var. *elongatus* Berkey, 1898, p. 284-285, pl. 17, Fig. 1; pl. 19, Figs. 1, 2; pl. 21, Figs. 2, 11-14, 21.

Hypseloconus elongatus Knight, 1941, p. 137-138, pl. 5, Figs. 1a-1c.

Hypseloconus recurvus Lochman and Hu, 1962, p. 440, pl. 69, Figs. 29-35.

Hypseloconus recurvus Stinchcomb, 1980, text fig. 1-G.

Not *Hypseloconus recurvus* Stinchcomb, 1986, p. 617, Figs. 4-10.

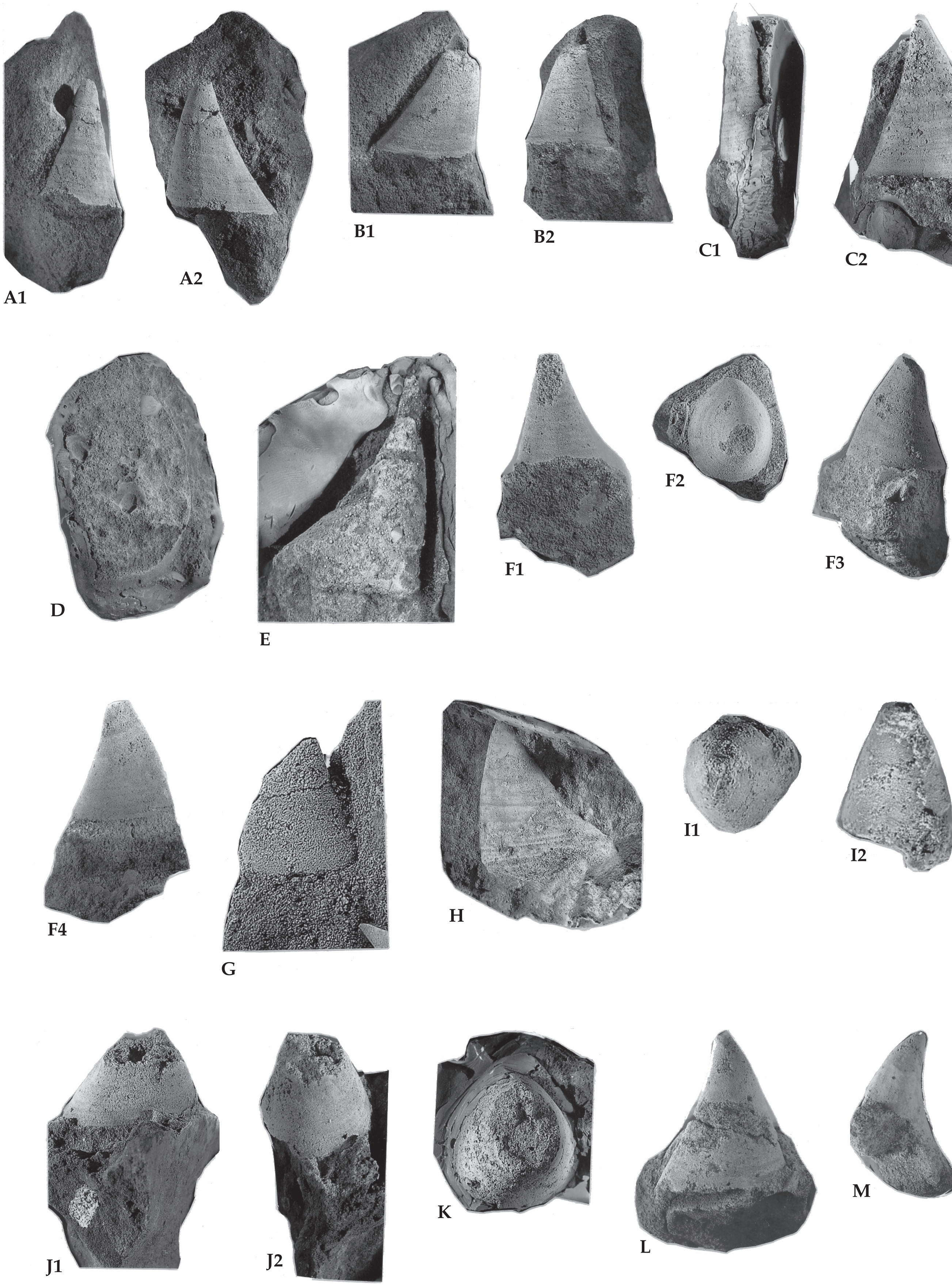
Description: High, gently arched, relatively slender cones. Apex is without septa. Ornaments are restricted to growth lines only. The interior of the shell is without striations or ribs, but with a faint, ringlike depression in large specimens. Curvature is distinct, but relatively slight. Aperture varies from relatively narrow to moderately wide such that the whorl cross-section approaches subcircular. Aperture is nearly a uniform oval, varying from distinctly to only slightly smaller at one end.

Discussion: Berkey's collection of fossils, at least those remaining, is quite small, yet almost half of it is composed of specimens referred to as this species. When the University of Minnesota specimens are added, nearly two-thirds of the available material from Taylors Falls refers to this species. When the few additional type specimens of other *Hypseloconus* that he named are included, it is obvious that this genus predominates in the biota.

In our judgement, all specimens of *Hypseloconus* in the collections except those labeled as types of other species belong to this species. Supplemental specimens formerly in the University of Minnesota collection are all referred to as this species.

Knight (1941) commented on the problem involved in Berkey's use of the specific name with and without that of his new variety; in the synonymy, references to Whitfield's species as such are not listed. Knight then treated Berkey's variety as a species. Actually, Berkey mentioned three additional varietal names, though these were not described. On plate 21, Figures 11-14 of Berkey (1898), he mentions that the photographs are of three different forms, though these variety names are not given in the figure captions. For nomenclatural purposes, these three names have no standing and will be ignored.

What is surprising is that Knight designated as the holotype a specimen photographed by Berkey,


A1
A2
B1
B2
C1
C2
D
E
F1
F2
F3
F4
G
H
I1
I2
J1
J2
K
L
M

but which we wonder whether he was able to relate without question to any of the specimens in the collection. Berkey's (1898) plate 17 is a montage of several pieces of rock piled together for a photograph, to show one well-preserved trilobite and presumably, to demonstrate the abundance of *Hypseloconus* by including four specimens. Knight was much concerned with the term "type," but "Two generic types" as used in the caption must refer to trilobite and mollusk, respectively, with no deeper meaning.

The collections of the AMNH include the two paratypes illustrated by Knight (1941; AMNH numbers 22269 and 22279) at twice natural size, plus nine other specimens that also should be part of the type lot. The first of these specimens illustrated by Knight (Fig. 8A) has with it a label, in what may be Berkey's handwriting, indicating that it is the figure on the upper right of that plate and that it is "var. triangulatus;" it also may match the outline on plate 19, Figures 15 and 16 of Berkey (1898), though the absence of the apical area creates some doubt with this match. The second paratype illustrated by Knight (Fig. 8B) has a similar label indicating that it is the upper left figure of that plate and the original of Figure 16 on plate 21 of Berkey (1898); the apex of the specimen has broken away since it was illustrated. Neither label has any linkage to Berkey's outline drawings on plate 19 (Berkey, 1898) and because no matrix is indicated on these outlines, it is impossible

Figure 8. Tergomya, *Hypseloconus elongatus* Berkey; all material was coated with ammonium chloride prior to photography.

A1. Presumed anterior view of the paratype. AMNH number 22269, x 1.

A2. Presumed left lateral view (Berkey, 1898, pl. 17, upper right; Knight, 1941, pl. 5, Fig. 1c), x 1.

B1. Presumed right lateral view of the paratype (Berkey, 1898, pl. 17, upper left; pl. 21, Fig. 16; Knight, 1941, pl. 5, Fig. 1b, but with the apical portion broken away). AMNH number 22279, x 1.

B2. Presumed anterior view, x 1.

C1. Presumed anterior view of a plastic cast of the holotype (Berkey, 1898, pl. 17, lower right; pl. 19, Figs. 1, 2; Knight, 1941, as part of pl. 5, Fig. 1a). AMNH number 22267A, x 1.

C2. Presumed right lateral view, x 1.

D. Apical view of a latex cast of the paratype, the largest specimen, preserving essentially only the outline of the aperture (Berkey, 1898, pl. 19, Fig. 31). AMNH number 22268, x 1.

E. Presumed right lateral view of a plastic cast of the paratype (Berkey, 1898, pl. 19, Figs. 29, 30). AMNH number 22257, x 1.

F1. Presumed posterior view of the paratype (Berkey, 1898, pl. 19, Figs. 3, 4). AMNH number 22262, x 1.

F2. Apical view; the lighting is from the right rather than the upper left, x 1.

F3. Presumed left lateral view, x 1.

F4. Presumed right lateral view, x 1.

G. Presumed left lateral view of the paratype (Berkey, 1898, pl. 19, Figs. 27, 28). AMNH number 22256, x 2.

H. Presumed left lateral view of a latex cast of the paratype (Berkey, 1898, pl. 19, possibly Figs. 21, 22). AMNH number 22272A, x 1.

I1. Apical view of the paratype (Berkey, 1898, pl. 21, Fig. 13). AMNH number 22272B, x 2.

I2. Presumed left lateral view, x 2.

J1. Presumed right lateral view of the paratype (Berkey, 1898, pl. 19, possibly Figs. 7, 8). AMNH number 22270, x 1.

J2. Apical view, x 1.

K. Apical view of a plastic cast of the paratype (Berkey, 1898, pl. 19, possibly Figs. 24, 25). AMNH number 22259, x 1.

L. Presumed right lateral view of a moderately well preserved topotype. USNM number 521876, x 1.

M. Presumed left lateral view of a topotype; although the anterior is broken away, the long curve of the posterior provides a suggestion of the great length of the aperture of this specimen. USNM number 521877, x 1.

to state what figures might be represented. Both show closely spaced, well-preserved growth lines, whereas it is uncertain if growth lines are indicated on Berkey's outlines, rather than shading to attempt to illustrate the degree of curvature of the shell.

Two other specimens were shown by Berkey (1898) to the lower right of his photograph forming plate 17. The same picture appears on plate 21, Figure 21 with the note "(type)" in that caption. The specimen to the left was designated as the holotype by Knight (1941), though one can argue that because two specimens are shown he should have used lectotype and paralectotype in his designations. A small sandstone block (AMNH number 22267), approximately 6 by 8 centimeters, bears an excellent external impression of a relatively narrow specimen, plus a second slightly wider specimen. Presumably to avoid confusion between the two specimens, a plastic cast (Fig. 8C) has AMNH number 22267A on the back. The AMNH label lists it as the source for the two photographic illustrations and the drawing on plate 19, Figures 1 and 2 of Berkey (1898), and that it was illustrated by Knight; the specimen is narrower than shown in the apertural outline. Not all the specimens have Columbia University labels with them, but of those that do, three are marked "Hypotype" and this specimen is one of those three. It is impossible to match this specimen to Berkey's photographs with total certainty, but we judge even with this residue of uncertainty that this specimen is a good candidate for holotype and therefore assume that it has that role in nomenclature and that Knight selected the correct specimen. The specimen shows simple growth lines and has the apex preserved. It is moderately compressed and slightly curved. Thus, it is intermediate among the wide variation in degree of curvature shown by the specimens available to us in the type lot.

In addition to the photographs, Berkey used outline drawings of the apertures and lateral views to illustrate additional specimens of this species. All the lateral views have the apex of specimens curving from right toward the left, and the apertural outlines have the narrower end to the right, consistent with Berkey's interpretation of the narrower end of the aperture as anterior. We concur with his assumption that the lateral views he presented are of the right side and have used this assumption in our figure captions with the qualifier "presumed."

Some of remaining seven specimens might be matched to the drawings, but because Berkey drew only outlines without matrix, there is a further degree of uncertainty in any attempt to match them. The ovals to indicate the shape of the aperture, in our view, are less realistic than the lateral outlines, though we concur in general with the conclusion that they show considerable variation in the width of the shell and correspondingly, the degree of curvature at the presumed anterior.

There are two reasonably certain assignments of specimens to drawings. A large fragment of an apertural area (AMNH number 22268; Fig. 8D) can be matched to plate 19, Figure 31 of Berkey (1898), as the largest representative of the species. The illustration of the latex cast shows the shell to the right, but in the lower part of photograph where the shell has been peeled away from the steinkern, that part of the aperture is more clearly observed on the type specimen. One large specimen plastic cast (AMNH number 22257) formed the basis for plate 19, Figures 29 and 30 of Berkey (1898). It is on a fist-sized piece of sandstone to which is attached another *Hypseloconus*, a poorly preserved specimen. Like the other replicas compared, the plastic cast (Fig. 8E) is accurate; included with it is a label indicating that this is one of Berkey's undescribed varieties. Almost as likely, a specimen lacking the apex (AMNH number 22262; Fig. 8F) might be the original for plate 19, Figures 3 and 4 of Berkey (1898), though the AMNH cataloguer expressed some question.

In addition, a small specimen (AMNH number 22256; Fig. 8G) could be the original of plate 19, Figures 27 and 28 of Berkey (1898); it includes a pencil label indicating these drawings, plus another label in the same handwriting suggesting it was a new species, but it is difficult to reconcile the partially matrix-covered presumed right lateral part of this specimen with the drawing by Berkey, unless he reconstructed the outline from the other side. One external impression (AMNH number 22272A) bears some similarly to Figures 13 and 14 of Berkey (1898), or it might match Figures 21 and 22, an assignment tentatively suggested by the anonymous cataloger. The latex cast illustrated (Fig. 8H) reproduces the shape accurately, but does not show the growth lines quite as sharply as they are on the external mold; it is uncertain that a better illustration could be provided from the external mold itself. One other possible match is even less certain. A small specimen (AMNH number 22272B; Fig. 8I) bears an AMNH label indicating plate 21, Figure 13 (Berkey, 1898), but it seems at least as good a match as the original of Figures 7 and 8.

A broken specimen lacking the juvenile portion of the shell (AMNH number 22270; Fig. 8J) was questioned by the cataloger as the original of plate

19, Figures 7 and 8 (Berkey, 1898), and we are equally uncertain. The plastic cast of another equally incomplete individual (AMNH number 22259; Fig. 8K) was questioned as the original of plate 19, Figures 24 and 25 (Berkey, 1898), but likewise cannot be matched with any of the drawings. Two specimens from the University of Minnesota collections (Fig. 8L, M) complete our illustration of this species.

The reason for this tedious discussion is to indicate that some of the specimens illustrated by Berkey are no longer available for study. In particular, this concerns the drawing of Figure 23 on plate 19, which is shown by Berkey (1898) as having faint longitudinal markings. Berkey (1898, p. 283) noted "Several of these specimens have a well defined slightly depressed area extending completely or almost completely round the cast usually about one-fourth to one-third the distance from the base to apex. ... It is therefore added as a character of the genus,—that the muscle attachments form a circle of six pairs of scars considerably above the aperture and parallel to it." Berkey did not mention the markings on Figure 23 as representing discrete muscle scars and as demonstrated, we are unable to match this drawing to any of the specimens. All we can state concerning the presence or absence of discrete scars is that none of the specimens examined give any indication of them. Likewise, on more than a dozen specimens from the University of Minnesota collection, no scars are to be seen. In order to present a fair argument, it must be stated that not all specimens are well enough preserved to show such features, if they are present. On the other hand, the topotype specimen (USNM number 278642) illustrated by Stinchcomb (1980) is excellent and we do not see any muscle scars. After examining the type lot at Columbia University, Knight (1941, p. 158) commented: "I am forced to conclude that the supposed muscle scars are a combination of radial undulations and adventitious scratches on specimens coupled with bands of growth and that they have been misrepresented in the drawings." The originals of those specimens, which are illustrated here by casts, were carefully examined to see if any muscle scars were present and again none were seen.

Despite the statements by Berkey, we therefore cannot accept that the presence of muscle scars is part of the description of the species. Likewise, if the specimen, which Knight (1941, p. 157) designated as holotype is accepted as such (a course we follow here), the specimen is an external mold. Even if muscle scars were present, they could not be observed on this specimen. Until such time as topotypical specimens might be collected that show muscle scars, we consider the discussion on this point closed. Other species which have been assigned to the genus and from which scars have been reported should be reexamined to see if they are attributed correctly to this genus.

In addition to the type specimens, the AMNH collection contains five other lots of numbered *Hypseloconus*, a total of eight specimens. This further reinforces the predominance of that genus in the faunule. In particular, AMNH number 22293 is a cross-section and bears with it a note that this is the specimen used by Berkey to measure shell thickness. By way of comparison, a sheet of typing paper has the same thickness as the shell. Two other collections are given new species names by Berkey, but are not included in his publication. These further testify to the high degree of individual variation within the species.

Specimens from the former University of Minnesota collection show a comparable degree of variation in the degree of curvature and hence the relative length of the aperture. Two specimens (Figs. 8L, M), one similar to the holotype and one showing much curvature relative to other specimens, are illustrated.

Hypseloconus elongatus is less strongly arched than the approximately coeval *H. bonneterrense* Stinchcomb. We did not observe any muscle scars on the illustrated specimens of that species, nor did the author note any.

Stinchcomb (1986) also described and illustrated as *Hypseloconus recurvus* material from the lower part of the Gasconade Formation in Missouri (USNM numbers 333577, 333578).

Despite the use of Whitfield's specific name, we are convinced that Stinchcomb intended to identify these as the type species *H. elongatus*, a view strengthened by his 1980 usage of that name. Stinchcomb recognized the long stratigraphic ranges indicated by his identification of Early Ordovician specimens and viewed the genus as morphologically conservative.

There is variation in the type lot from Taylors Falls, but in our judgement the Gasconade Formation material should not be included in Berkey's species, for it is more strongly curved, narrower, and has a slightly more elongate aperture; we leave it specifically unassigned.

The three specimens illustrated by Lochman and Hu (1962; USNM numbers 138261a-c) as *H. recurvus* (Whitfield) are all broken from limestone, and show that the shell is thin. Two are significantly smaller than any of the specimens from Taylors Falls, but insofar as they can be compared might be conspecific. The third specimen is somewhat larger and suggests that the concave slope might not be quite as strongly curved as some specimens in the type lot, though this may be within the range of individual variation.

Metoptoma recurvus Whitfield, from Eikie's quarry, was transferred to *Hypseloconus* by Berkey and may have one of the points by which he judged that fauna to be similar to that of Taylors Falls. That species has a more elongate aperture than any of the specimens of *H. elongatus*.

***Hypseloconus cornutiformis* Berkey**

Not Illustrated

Hypseloconus cornutiformis Berkey, 1898, p. 285, pl. 19, Figs. 11, 12.

Discussion: The material on which this name is based apparently is no longer among the type material of Berkey that was transferred to the American Museum of Natural History. It is probable that it no longer exists. As described and illustrated, this species is a strongly curved, elongate cone. The apical area apparently was lost, but the reconstruction of Berkey seems accurate, and if so, the curvature extends through nearly one-quarter of a whorl. The outline of the cross section is distinctly oval, with the longer convex side being at the more strongly compressed area of the oval.

We do not question the validity of this species as one extreme morphologic variant of the hypseloconid group. Although the same argument for shell stability made in connection with ?*Proteroconus capuloides*, discussed below, may apply here, the proportions of the aperture are different, being somewhat wider than in that form, and the shell might have been held erect. As illustrated, it has a lower angle of log curvature than that species, and seems to have a slower rate of whorl expansion. Unfortunately, the supplemental material of *Hypseloconus* from the University of Minnesota and the National Museum of Natural History do not contain any specimens that show such strong curvature. Under the circumstances, we suggest that the name be restricted to use with the type material and effectively eliminated from further consideration.

Stinchcomb (1975) named *Hypseloconus bonneterrense* from near the upper part of the Bonneterre Formation in Missouri, though on his stratigraphic column this is indicated as *H. recurvus*. This species differs from the illustrations of the type species in being more strongly curved. The curvature is comparable to that illustrated for *H. cornutiformis*. However, *H. bonneterrense* has both a wider and more elongate aperture than Berkey's enigmatic form. *Cornuella parva* Stinchcomb is similar in curvature but is much smaller, and slightly more compressed.

***?Hypseloconus cylindricus* Berkey**

Figure 9

Hypseloconus cylindricus Berkey, 1898, p. 285-286, pl. 19, Figs. 9, 10.

Description: Elongate cones with essentially no curvature; the shell is very little curved, the apertural area is slightly compressed laterally with little differentiation of anterior and posterior; the profile of the sides is interrupted by a wide bulge on the steinkern seemingly closer to the aperture than to the apex; growth lines and details of the exterior are unknown.

Discussion: Three specimens (AMNH numbers 22264A, 22264B, and 22264C) are in one box that includes a label of holotype. Inasmuch as Berkey did not designate type material as such, we take this opportunity to designate number 22264A as the lectotype; it matches the illustration of Berkey. The other two specimens are designated as paralectotypes.

Specimen number 22264C (Fig. 9B) is a fragment, wider than the lectotype. Like the lectotype it shows a laterally elongate bulge on the steinkern at about the same general position as in the lectotype, though it is almost impossible to see on the photograph. For the distance at which it can be observed, the feature is continuous and when taken in conjunction with the lectotype, suggests that the depression in the shell may have been a continuous ringlike feature. The third specimen (number 22264B) is larger in diameter, but just overlaps the broken lower portion of the lectotype. Allowing for some breakage at the apertural end, a height of about 45 millimeters is suggested; this would place the ring-like bulge at near two-thirds of the distance from apex to aperture.

The apertural outline reconstructed by Berkey is of a small, laterally compressed oval, with little differentiation at the ends, but slightly narrower at the longer side of the specimen. This is in keeping with the extremely limited curvature of the species.

The smaller paralectotype lacks the apex and is broken at a diameter of 3 millimeters. The break is irregular. One cannot categorically rule out the absence of septa, but the small width of the apical portion makes it seem unlikely that any were present.

Berkey suggested that the species might possibly be considered a *Scenella*, but the great height and

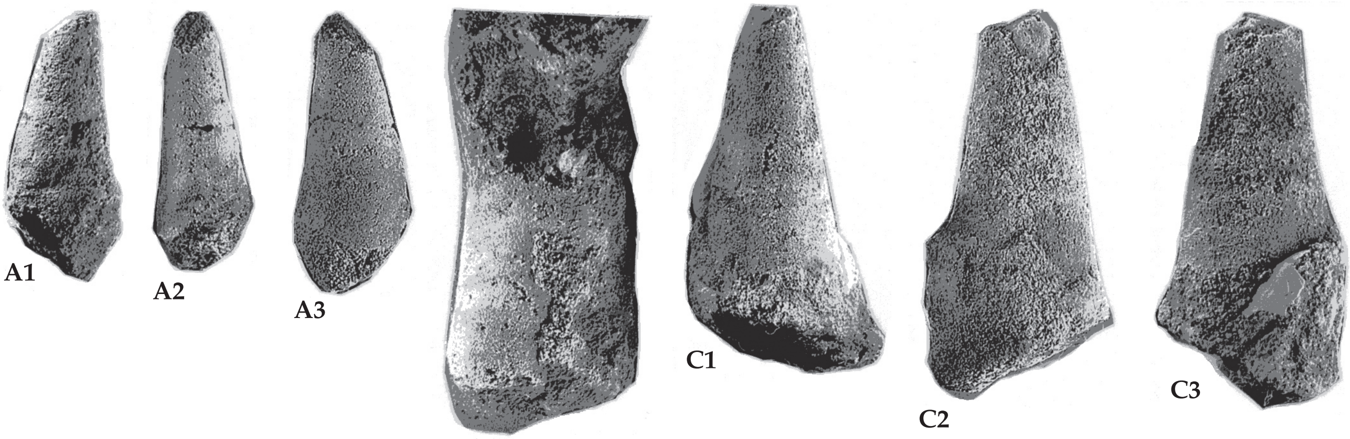


Figure 9. Tergomya, ?*Hypseloconus cylindricus* Berkey; all specimens were coated with ammonium chloride prior to photography.

A1. Presumed left lateral view of a paralectotype. AMNH number 22264C, x 2.

A2. Presumed anterior view, x 2.

A3. Presumed right lateral view, x 2.

B. Presumed lateral view of a fragmentary paratype closely bonded to the matrix. AMNH number 22264B, x 2.

C1. Presumed posterior view of the lectotype (Berkey, 1898, pl. 19, Figs. 9, 10); a faint indentation may be seen about midway on the specimen. AMNH number 22264A, x 2.

C2. Presumed right lateral view, x 2.

C3. Presumed left lateral view, x 2.

overall resemblance to other species of *Hypseloconus* argued against this assignment. The apertural outline reconstructed by Berkey is of a small, laterally compressed oval with little differentiation at the ends, but slightly narrower at the longer side of the specimen. This is in keeping with the extremely limited curvature of the species. Because of the slight curvature and the corresponding relatively short aperture, ?*H. cylindricus* is readily distinguished from *H. elongatus.* Also, although comparisons are difficult, this species may also have a slightly narrower aperture. The high cone and narrow aperture readily separate it from *Kirengella stabilis*.

This species is remarkably close to *Orthoconus striatus* Stinchcomb from the Eminence Formation, the type and only known species of that genus. Examination of the holotype and paratype (USNM numbers 339834 and 339829) show that the proportions are similar. Berkey's specimens lack the longitudinal ornament, which is one of the prime features that led to differentiation of that genus (B. Stinchcomb, unpub. data, 2003).

In more general terms, ?*Hypseloconus cylindricus* also has proportions like some of the species assigned to *Shelbyoceras.* One of the features of that genus is the presence of apical septation, as in *Knightoconus*, but *Shelbyoceras* is slimmer. We cannot conclusively rule that septa might be present in ?*H. cylindricus*, but from the small diameter of the preserved portion of the apex, this may be likely; a counter argument is that these may be small specimens, rather than broken fragments of large individuals, and septation may not have developed in small specimens. Were septa present, this species would be transferred to *Shelbyoceras*. Accordingly, it seems prudent to question the generic assignment.

Curiously enough, the specimens also resemble the siphuncular deposits of some orthoconic cephalopods. Were this material of Ordovician age, such an interpretation would have to be considered. Although the fossil record continues to contain surprises, from what is known of the record of the early cephalopods, it seems reasonable to suggest that the Taylors Falls locality is older than the oldest known cephalopod and certainly older than the oldest known orthoconic form (Yochelson and others, 1973; Webers and Yochelson, 1989).

Proteroconus Stinchcomb

Protoconus Stinchcomb, 1986, *not* Yu Wen, 1979.

Proteroconus Stinchcomb, 1996, p. 339.

Type species: *Protoconus eminence* Stinchcomb.

Description: "High cornucopia-shaped shell with apex projecting over anterior apertural margin and terminating in a sharp point. Aperture and shell cross section ovate, presumed anterior margin acute, posterior margin broadly rounded" (Stinchcomb, 1986, p. 621).

Discussion: Stinchcomb described the genus, with a single included species, as part of the Hypseloconidae. The type lot was from the lower part of the Eminence Formation, above the Potosi Formation, and in the *Calvinella* zone. This would place the type species near the middle of the Trempealeauan (upper Sunwaptan) stage.

In discussion, Stinchcomb noted longitudinal ornaments that he referred to as striations, but these are widely spaced, low ridges. The best-preserved paratype in the type lot (USNM number 369967, published as number 306913) is also the most complete, and shows the ornament well. Depending on the angle at which one observes the specimen, an argument may be made that the curvature is very slightly asymmetric. Until more specimens are collected to confirm or disprove this notion, the genus should stay with the hypseloconids, as originally described, despite the fact of the apex overhanging the apertural edge.

There is remarkable similarity between *Proteroconus* and *Cosminoconella* and they may be congeneric.

?Proteroconus capuloides (Berkey)

Figure 10

Hypseloconus capuloides Berkey, 1898, p. 285, pl. 19, Figs. 19, 20.

Description: Laterally compressed, strongly curved shells; apex is unknown; shell is curved for about one-quarter of a whorl following a relatively large angle of logarithmic curvature; shell is strongly compressed laterally; exterior details are unknown.

Discussion: The only known specimen (AMNH number 22261) closely matches Berkey's drawings and there is no question as to its status as holotype. The specimen is a steinkern and shows a minor degree of apertural flaring, interpreted as the thinning of the shell as it approaches the growing edge of the aperture. This is therefore a complete specimen, but whether it is mature and ceased growth is unknown.

The apex is broken, but as restored by Berkey the shell may have completed at least one-third of a whorl. It thus appears to be much closer to an open-coiled gastropod than a curved cone; the curvature is more apparent than even in the illustrations of the larger *Hypseloconus cornutiformis*. The strong lateral compression, such that the lateral slopes are nearly parallel, reinforces this appearance of pronounced curvature. The extremely narrow aperture is the principal distinction between *Proteroconus eminence* and ?*P. capuloides*. It is possible that this species and genus may be in some way related to the poorly

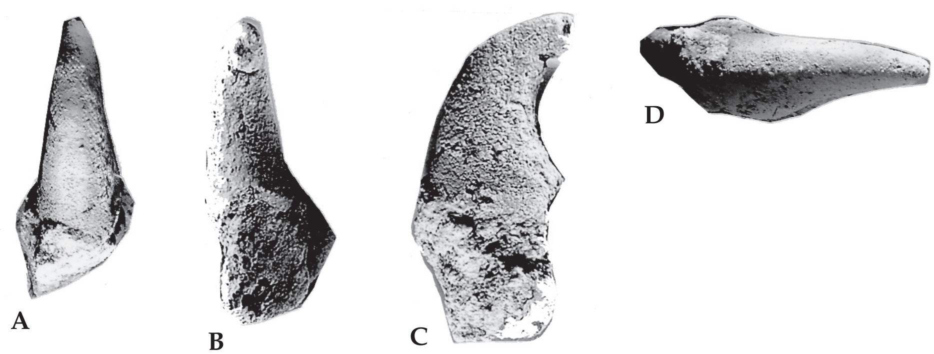


Figure 10. ?*Proteroconus capuloides* (Berkey); the specimen was coated with ammonium chloride prior to photography.

A. Presumed anterior view of the holotype of *Hypseloconus capuloides* (Berkey, 1898, pl. 19, Figs. 19, 20), if interpreted as a hypseloconid. AMNH number 22261, x 2½.

B. Presumed posterior view, x 2½.

C. Presumed left lateral view, x 2½.

D. Presumed exterior view, if interpreted as an open-coiled gastropod, x 2½.

known Late Cambrian forms that have been described as or assigned to *Pelagiella*.

Because the outer surface is unknown, there is no information on whether longitudinal lirae are present; this is one reason for questioning assignment to the genus. There is no indication of ridges and troughs on the steinkern, so assignment to the Helcionelloidea is unlikely. Lochman and Hu (1962, p. 440-441) recovered two tiny specimens from the Pilgram Limestone of Montana that they assigned to the Coreospiridae (USNM numbers 138262a-b); the prominence of the troughs and ridges in such tiny specimens suggests that (even allowing for preservation of the steinkern in sandstone) if any comparable features were present, then they would be observed.

The steinkern might be bilaterally symmetrical, but it is small enough so that if there was some slight deviation from a plane of symmetry, then it would not be discernible. When viewed from both the concave and convex sides, the specimens suggest minor asymmetry, but if any deviation from bilaterality is present, it is very slight. In the final analysis, this species may belong to another genus, but the available material is inadequate to seriously consider such a step.

Lochman (Lochman and Duncan, 1944) described *Hypseloconus simplex* from the Aphelaspis zone of the Pilgram Limestone in Montana. The holotype (USNM number 127025) is remarkably close to Berkey's type, allowing for the different preservation in limestone, but has a few broad ridges and troughs on the medial part of the concave surface.

As a complication, Shaw (1956) described *Hypseloconus simplex simplex* and named *Hypseloconus simplex erectus* from the Dry Creek Shale in Wyoming as part of an *Aphelaspis* zone faunule; both named forms were collected from thin limestones separated by seven feet of shale. We have not examined Shaw's material, but from his photographs we cannot determine any obvious distinctions between the two forms. Subsequently, Lochman and Hu (1962, p. 440) described *H. simplex simplex,* again from Montana, and the small steinkern illustrated (USNM number 138264) would be difficult to differentiate from Berkey's species.

Class ?Helcionelloidea

Discussion: A question mark is used with this assignment for two reasons. First, whereas Tergomya seems to be generally accepted as a class name replacement for a portion of the Monoplacophora, it is not clear that any consensus has been established in regard to the acceptance and general morphologic limits of this class. Indeed, to the best of our knowledge, neither name has appeared in a textbook of paleontology, which by some standards may be the hallmark of acceptance of new high-level taxa to the general body of knowledge. One specialist in the group considers that the helcionelloids fall within the Gastropoda (Parkhaev, 2002), whereas another supports the concept of class Helcionelloidea (Gubanov, 2000). We judge this class proposal to be an acceptable concept, but the available material scarcely provides the basis for making that decision.

Second, if the class proposal is generally accepted, we cannot be certain at this stage that the taxon considered below should be included. One incomplete specimen is not sufficient for an informed opinion at this high a taxonomic level. Counterbalancing that, a genus of helcionelloids has been described from the Early Ordovician period, considerably extending the range of this presumed class.

New genus, undescribed

Discussion: Berkey (1898, p. 285) had doubt as to describing his new species *Hypseloconus franconiensis* under that genus. "This form might possibly be placed with the genus *Eccyliomphalus*. But on account of the series with which it is associated it seems preferable to describe it with them as a representative of one of the extremes of variation in the genus." We concur with Berkey to the extent that this species is not a *Hypseloconus*. The species in question is more strongly curved than ?*Proteroconus capuloides* and has a more elongate aperture. It is understandable how Berkey might have an interpretation of his species of *Hypseloconus* as a series of steps with ever increasing curvature to eventually reach the shape of that of a gastropod.

Another species is pertinent to this issue. As part of his brief discussion of *Scaevogyra*, Berkey (1898, p. 286), transferred *Platyceras primordiale* Hall to that genus. Because this was a formal nomenclatural action, it deserves comment. Presumably, this action was based on Berkey's interpretation of a seemingly slight sinistral twist to the coiling. From what is now known of *Scaevogyra*, assignment of Hall's species to the genus is implausible. *Scaevogyra* is distinctly coiled in three dimensions, whereas the specimen attributed to Hall's species is so close to bilaterally symmetrical, that it is bellerophontiform in shape.

Sardeson (1903) transferred Hall's species back to *Platyceras*. For more than half a century it has been recognized that *Platyceras* does not occur in the Cambrian period (Knight, 1952), though it is widespread and diverse through most of the Paleozoic. The generic term was used in connection with Cambrian mollusk shells or presumed mollusk shells that are strongly hook-shaped but do not complete a full whorl. Grant (1965, p. 105) transferred *Platyceras primordiale* to *Pelagiella* Mathew. This is almost an equally inappropriate assignment for the species.

Specimens of "*Platyceras*" *primordiale* Hall are locally abundant in Wisconsin. So many shells are present on bedding planes that they are almost certainly in a death assemblage. Despite their abundance, these have never been carefully studied, perhaps because specimens are steinkerns firmly attached to the matrix on one side. Although the type material has not been studied and the locality data are vague, it is likely that Hall may have collected his specimens at Saddle Mountain, about 15 miles east of Black River Falls, Wisconsin. The geographic feature has the Wonewoc Formation at its base and is capped by the Tunnel City Sandstone, which is likely the stratigraphic unit in which this fossil is abundant.

There is no question in our minds that this material constitutes a new genus. It will require careful study to determine whether it is bilaterally symmetrical or slightly asymmetrical. The form suggests strong similarities to the Late Cambrian compressed bellerophontiform shells. Whether this is a bellerophontid that is not fully coiled, or one that is open-coiled, or yet quite another category cannot be speculated on at this time. The only clear statement we can make is that this is probably a significant shell form in the general scheme of univalve morphology.

"?Hypseloconus" franconiensis Berkey

Figure 11A

Hypseloconus franconiensis Berkey, 1898, p. 285, pl. 19, Figs. 17, 18; pl. 21, Fig. 10.

Description: Small shell, strongly curved and strongly compressed laterally; apex is unknown; shell is coiled and completes about three-quarters of a whorl; aperture is elongate and so strongly compressed that the lateral sides are subparallel; growth lines and other details of the exterior are unknown.

Discussion: The holotype (AMNH number 2271) and only known specimen is primarily a steinkern, but it is broken at both ends; the external mold may be seen toward the apical portion and near one side of the broken aperture, a small part of the exterior may also be observed. Part of the steinkern is obscure, but by projecting the curvature forward one can observe that the aperture is elongated. The steinkern shows what might be a rugosity, but which we interpret as an accident of preservation. Despite the elongated aperture, we would therefore tend to rule out association of this species with the Helcionelloidea.

Where the steinkern is broken away in the apical area, a curved impression is visible. Unfortunately,

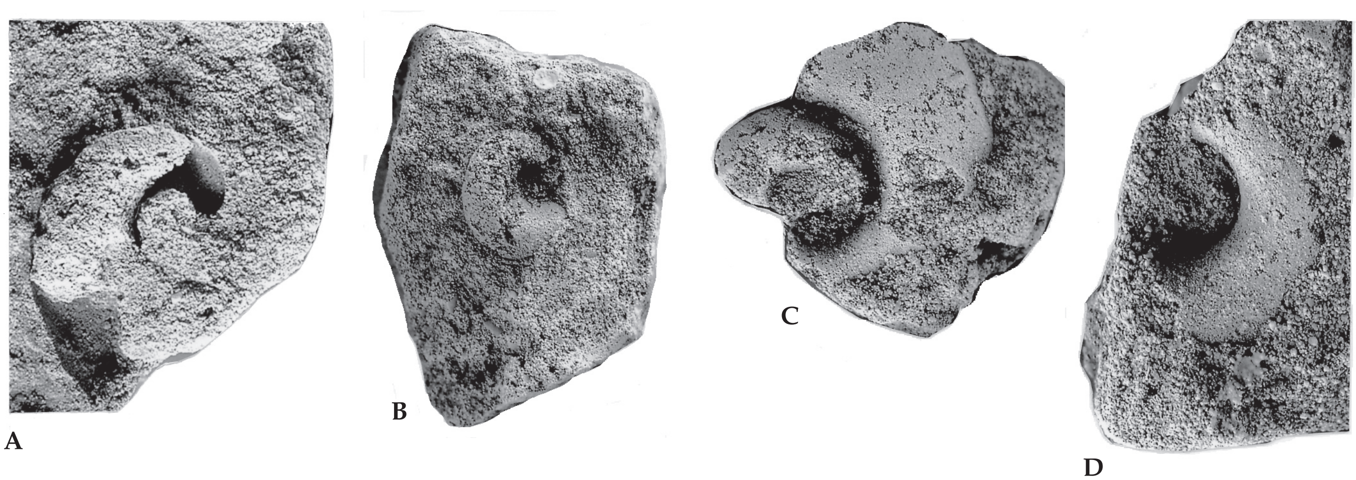


Figure 11. All specimens were coated with ammonium chloride prior to photography.

A. New genus undescribed, the holotype of *Hypseloconus franconiensis* Berkey (1898, pl. 19, Figs. 17, 18; pl. 21, Fig. 10). AMNH number 22271, x 2½.

B. ?"*Cloudia*" sp. Presumed right lateral view of a small specimen. USNM number 521878, x 2.

C. ?"*Cloudia*" sp. Presumed left lateral view of a specimen showing several whorls. USNM number 521879, x 2.

D. ?"*Cloudia*" sp. Presumed right lateral view of an incomplete specimen. USNM number 521880, x 2.

because this curvature is incomplete, several different interpretations are possible. If this specimen is part of an anisostrophically-coiled shell, the curvature might be part of an earlier whorl rising toward the apex. Based on examination of a similar feature in younger Paleozoic steinkerns, we prefer to interpret the curvature as the impression of a short apertural plug, or a septum near the apex. Neither interpretation can be proven from the material at hand and other interpretations are possible.

The exposed surface of the steinkern is rounded. Whether the small amount of the exterior surface exposed near the aperture has the same degree of inflation cannot be determined. The specimen may be bilaterally symmetrical, but if it is not, the deviation from a plane of symmetry is exceedingly slight. It does not seem feasible to attempt to remove the steinkern to see more of the external surface, for even if this could be done without breaking the steinkern, the external surface does not extend to the midline.

This is the second species described by Berkey that did not come from Taylors Falls, the first being the individual from Osceola Mills, Wisconsin, which he assigned to *Tryblidium Barabuensis*. Fortunately for this species, a specimen still exists from "The Franconia sandstone, Franconia, Minn." (Berkey, 1898, p. 285).

As discussed above, we judge this species to belong to a new genus. At the time the more abundant material from Wisconsin is investigated, we suggest that Berkey's holotype be compared to Hall's original material; Berkey's species may be a junior synonym.

Stinchcomb (1975) described *Hypseloconus bonneterrense* from Missouri. That species is strongly curved, though not so strongly as Berkey's species. The type specimens are much larger, but even allowing for this the species seems to be relatively wider. The Missouri *Hypseloconus* is bilaterally symmetrical so any association with the Late Cambrian "*Platyceras*" can be ruled out. Probably that species is unrelated, but the point should be reinvestigated when this form is studied in detail.

SUPPLEMENT TO SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Fossils from Taylors Falls, formerly at the University of Minnesota, include bilaterally symmetrical coiled specimens. Although the form was not described by Berkey, we judge it appropriate to include the taxon in this work. Like so many of the Taylors Falls specimens, the material is of indifferent quality, but provides considerable food for thought.

In the prior essay on classification, we alluded to the Bellerophontacea without providing much detail. In brief, these are a group ranging from the Cambrian to Triassic period, most of whose shells are bilaterally symmetrical, though a few deviate from symmetry. Because the majority of genera have a slit in the apertural lip, most students of Paleozoic Gastropoda consider these to be Gastropoda, allied to the Pleurotomariacea. Some workers, now currently in a minority, consider the bilateral symmetry to be more significant than the slit and have assigned all such bellerophontiform shells to the Monoplacophora.

A further complication ensues in that a few curved or coiled forms lack a slit but instead have a sinuate apertural lip. Some of these forms show multiple muscle scars, and in large part these taxa constitute the "Cyclomya," differentiated as part of the Monoplacophora (Horny, 1965). It is possible that the bellerophontiform shells include two independent groups, with the bulk of the specimens belonging to the Gastropoda (Yochelson, 1967). We assume that the material in question belong to the Gastropoda and defer the larger issues for reconsideration by others.

In the discussion by Knight (1952), which first drew general attention to the Monoplacophora, he postulated that bilaterally symmetrical gastropods preceded asymmetrical forms, though that point has been disputed (Yochelson, 1984, p. 262). Prior to Knight's seminal study on early evolution of the Gastropoda and the Monoplacophora, he published two short papers (Knight, 1947b, 1948) documenting the occurrence of Late Cambrian bellerophontaceans. In the first paper, he described one new species in the genus *Coreospira* Saito and added three new genera to the literature, each with a single species. In the second paper he added two more genera, again each monotypic, to the record. We have reexamined the specimens that he described.

Of the six genera of Late Cambrian bellerophontiform gastropods currently known, four may be readily eliminated from consideration. Both *Chalerostrepsis* and *Streposdiscus* have the last portion of the body whorl not in contact with the penultimate whorl. *Coreospira* and *Sinuella* have the outer whorl face distinctly flattened, somewhat different from the profile that may be gleaned from the Taylors Falls specimens.

Genus *Cloudia* Knight, 1947b

Type species: *Cloudia* Knight, 1947b, p. 6-7, pl. 2, Figs. 1a-e.

Discussion: Both *Cloudia* and *Anconchochilus* are characterized by a moderately well rounded whorl profile and accordingly, a moderately wide shell. They are most likely of Trempealeauan (Sunwaptan) age. *Anconchochilus* has a narrower umbilicus and on the basis of width of the umbilicus, rather than the whorl profile, the Taylors Falls material is questionably associated with *Cloudia*.

?"Cloudia" sp.

Figures 11B, C, D

Discussion: None of the three of the illustrated specimens have any growth lines preserved and none are complete. The largest may have been about 2.5 centimeters in diameter during life; the preserved portion shows no evidence of the body whorl becoming free. There is a suggestion that the cross section undergoes an ontogenetic change from moderately well rounded to more lanceolate; the lanceolate cross section, however, does not approach the sharpness of that in *Strepsodiscus*. An alternative but less likely interpretation that two distinct taxa occur, one with a more rounded cross section, cannot be ruled out.

The material demonstrates that Knight's investigations did not exhaust the amount of diversity to be found among Late Cambrian bellerophontiform mollusks. Beyond that, nothing further of substance can be gleaned. Despite the frustration of being unable to describe a new taxon from adequately preserved material, the absence of this form of shell in Berkey's collection is interesting.

The specimens donated by the University of Minnesota include one ?*Kirengella*, two ?*Proplina*, more than 18 *Hypseloconus*, one ?*Scaevogyra*, and three ?"*Cloudia*." All of these specimens were in a nearly continuously numbered sequence, and it is impossible to state when this form of curation was performed in the later history of the general collection. We do not know whether these specimens constitute a single collection from Taylors Falls or are the result of multiple collecting trips. It is possible that some of this material may have been deposited by Berkey, but if he had seen the ?"*Cloudia*" specimens they would have been included in his paper.

If one makes the assumption that these specimens constitute a single group, collected some time after Berkey completed his study, in a sense they reflect the distribution of Berkey's illustrated specimens described above. By that, we mean that *Hypseloconus* is abundant and other forms are rare.

Some of the present-day gastropods that inhabit a reefal environment have a "patchy" distribution. In the Ordovician reefal limestone of Dalarna, Sweden, and the Silurian of Gotland, Sweden, the distribution of some gastropods is relatively widespread, whereas others are restricted and "patchy" in local distribution. Such restriction is not necessarily related to the number of specimens, for collectors have obtained many specimens of a form on a single occasion and then, apparently, have never found it again. For example, the modern *Conus gloria maris*, the gastropod shell so rare that specimens once sold for a high price, is no longer a rare shell after abundant specimens were discovered at another locality in the twentieth century.

If one can draw any implication from the occurrence of these specimens of ?"*Cloudia*," it could be that the boulder-strewn sea floor at Taylors Falls had an equally patchy distribution, with *Hypseloconus* being relatively widespread and all other forms restricted to only one or two extremely local spots. This speculation remains to be tested, but it may be that differences in the community composition of gastropods that inhabit level bottom communities and those in reefal communities have had a very long history.

STRATIGRAPHIC MATTERS

Several different factors involve the utility of fossils in biostratigraphy. The primary ones, of course, are the relative abundance of the fossils themselves and the quality of their preservation. No matter how well a single shell is preserved, its rarity precludes the gathering of any data on individual variation within a species. No matter how well a steinkern displays muscle scars, it cannot yield information on the exterior. Our opinion is that in the Cambrian and especially the Early Cambrian period, too much emphasis has been placed on small steinkerns from insoluble residues and too little consideration has been given to their limitations.

In early Paleozoic rocks, mollusks are seldom well preserved, possibly as a result of their original aragonitic composition. In most rocks, they are uncommon to exceptionally rare, as illustrated by *Chippewaella* from the *Crepicephalus* zone of Wisconsin. It is known from a single specimen of the type and only known species. "This was the only gastropod uncovered during the splitting of over 200 kilograms of sandstone, which also yielded hundreds of trilobite cranidia and pygidia" (Gunderson, 1993, p. 1083).

Offshore, slightly deeper water sediments are more likely to be preserved than those deposited in nearshore, extremely shallow water. For the upper Mississippi River valley region, the Taylors Falls occurrence provides a window into a rarely preserved environment. This may be why, apart from the early Late Cambrian of Missouri, there do not appear to be any faunas in North America that are similar. Even with that example of another shallow water environment, the occurrence of many of these fossils among abundant digitate stromatolites of the Ozark region is very different from the sandstone matrix at Taylors Falls.

A secondary point concerning the utility of fossils is the degree of study expended on any group. In addition to their abundance in the Cambrian period, trilobites have attracted the attention of many professional and amateur paleontologists. Historically, the Paleozoic Mollusca have received little attention relative to the Brachiopoda and the Arthropoda. It is only fair to state, however, that any paleontologist who has a favorite group of fossils will note that more study of that group is needed. Conodonts have been shown to have a high degree of utility in dating rocks and they now dominate Paleozoic biostratigraphy, concomitant with a decline in systematics of megainvertebrates.

Even in the unlikely event of considerable additional detailed study, it seems to us unlikely that the Tergomya will ever be a significant element in determining the age of rocks. If there were no trilobites at Taylors Falls and no other ancillary stratigraphic evidence of relative age, even on the basis of what is now known, it might not have been possible for Berkey to determine with certainty a Late Cambrian age for the matrix of the conglomerate. The only approximately comparable fauna was that from Eikie's quarry in Wisconsin, and though some elements of the molluscan fauna are different, his view of a Late Cambrian age was reasonable. Had the rich molluscan fauna of the Ozark region of Missouri been known to Berkey for comparison, without the knowledge of the faunule at Eikie's quarry, he might have been able to date his fossils as Late Cambrian or less likely Ordovician. If relative abundance of a genus has significance in correlation, he might have tentatively correlated his fauna to that of the Bonneterre Formation, by reason of the large numbers of *Hypseloconus*, or to the Davis Formation, though that fossil assemblage was not discovered until the 1920s. Ultimately, honesty forces us to admit that all of this paragraph may be an example of hindsight improving vision.

A few tergomya species are known to range through most of Late Cambrian–Early Ordovician time, and in the appropriate facies, specimens may be common; with one or two exceptions, in the overlying rocks they are rare. Most species, and indeed some of the genera, are known from one or two specimens obtained at a single locality. One is left with the uncomfortable feeling that once a few basic shell forms were established, there was little environmental pressure or other possible causes for great diversification within the class, and thus little opportunity for the development of useful biostratigraphic markers. In rare situations, the Tergomya may have utility, but if comparisons are to be made to other classes of the Mollusca, the changes through time in this class are better compared to the model of the Scaphopoda than to that of the Cephalopoda.

SPECULATIVE MATTERS

In contrast to their biostratigraphic limitations, the tergomyans have provided many opportunities for paleobiologically-oriented studies. The last half-century has seen development of a large body of literature on these Paleozoic mollusks and it is still growing. Inasmuch as there are published conflicting views as to whether the type species of *Hypseloconus* has discrete paired muscles scars or not—a point which ought to be able to be resolved by observation—it is understandable that there are so many different views on more theoretical concepts concerned with Monoplacophora and the permutations of that concept.

Disparity and diversity

Some paleobiologists are interested in the patterns shown by fossils in both space and time. Among other aspects of such studies, concepts of diversity and disparity are in the literature. Diversity is used in a variety of manners, but seems to be of more utility in comparing one fauna to another. Brachiopod beds in Late Ordovician strata in the Cincinnati area contain thousands of specimens, but very few genera and species of that phylum along with exceedingly rare representatives of other phyla. Some of this distribution of forms may be due to sorting and to accumulation in death assemblages, though clearly there must have been adjacent life assemblages in which these thousands of brachiopods flourished. Likewise, most of the occurrences of fossils in the Late Cambrian sandstones of the upper Mississippi River valley are similar to the example cited above of possible death assemblages, substituting trilobites for brachiopods. In contrast, the Taylors Falls fauna shows no lithologic evidence of sorting and may be closer to a former life assemblage than the two comparisons listed above. If nothing else, the variety of shapes and sizes of the fossils suggest that severe sorting did not occur before the shells were entombed.

In the Mill Street conglomerate at Taylors Falls, elements of three phyla—Arthropoda, Brachiopoda, and Mollusca—are encompassed within a small number of specimens. Among the Mollusca, at least two classes are present. Among the Tergomya, a larger number of genera are present than were recognized by Berkey more than a century ago. Comparable to the greater refinement in dating the rocks, this is due to more precision in defining similarities and differences among specimens. By almost any measure of diversity, the Taylors Falls assemblage appears to have been highly diverse.

Wagner (1995a) used diversity to express difference through time in connection with study of the evolution of early gastropods. As a smaller sample to consider in searching for evolutionary patterns, the Tergomya are certainly more diverse in Ordovician and Silurian rocks than in Late Cambrian rocks. In a different approach to evolutionary considerations, Wagner (1995b) has considered the early diversification of gastropods. Once again the Tergomya as represented in the Taylors Falls fauna show essentially all the morphologic diversity to be found throughout their total geologic range.

Disparity is a more elusive concept. "There is no consensus on a definition of disparity, less still an agreed method for measuring it" (Wills, 2001, p. 57). We assume that one use of the concept is a comparison of fossil groups through time. From the Middle Ordovician to the recent, and even in many areas of Lower Ordovician rocks, gastropods are exceedingly common and tergomyans are rare; no tergomyans are known from the late Paleozoic, Mesozoic, and only from the Pleistocene epoch of the Cenozoic. We judge this to be a significant disparity within the phylum. In light of the joint occurrence of gastropods and tergomyans at localities from Late Cambrian through Silurian age, we suspect that the reason for this change was not related to facies, that is habitat differences, but is a phenomenon of evolution.

Muscles and other presumed soft parts

To move to another subject, by virtue of muscle scars seen in other species, we are confident that the Taylors Falls *Proplina* species did not undergo torsion. The muscle scars in the species assigned to *Kirengella* equally support this view. We attribute the absence of muscle scars in *Hypseloconus* to a thin shell and a need to fuse the muscles for better control of an awkward shell. To approach this matter from another aspect, whether the apex points forward or backward in these early, bilaterally symmetrical shells is related to the geometry of the shell itself and not necessarily to any twisting of the soft parts.

As discussed earlier, it is presumed that some Tergomya had similar habits to limpet gastropods, and genera such as *Pilina* and *Tryblidium* had a broad foot that when extended, was not much larger than the covering shell. Of the two, *Proplina* is a higher shell, but still is close in external shape to living capuliform gastropods and therefore may have had almost as large a foot. In contrast, the higher cones, best exemplified by *Hypseloconus*, are all significantly taller and most are slightly curved. Regardless of the degree of curvature of the apex, all have a relatively broad aperture. Despite the larger bulk of soft parts within the shell and presumably a higher center of gravity, the broad aperture again implies a large surface on the sole of the foot.

Following this line of reasoning, one might argue that *Hypseloconus cornutiformis*, unstudied here because the type has been lost, may not have had such a broad foot; Berkey's drawing indicates a narrow aperture. This would have increased the problem of stability in such a large shell. Open-coiled gastropods are judged to be sessile rather than mobile. Such shell forms are known in the Early Ordovician and they might have occurred earlier. An intriguing thought is that Berkey's species might have been the oldest open-coiled snail.

For smaller, relatively strongly curved shapes such as that of ?*Proteroconus capuloides*, interpretation of how the shell may have been positioned during life is more difficult. Whether one judges curved and coiled bellerophontiform shells to be monoplacophorans or gastropods, there seems to be tacit agreement that they were positioned bilaterally on the foot. Linsley (1977) developed several laws concerning the mode in which the shell is carried by a gastropod in motion, but cautioned that the "laws" did not apply to limpet gastropods in which the shell effectively functions as a tent covering most of the foot when it is moving and all of the foot when it is at rest. Apart from the two specimens first described in the systematics section (*?Scaevogyra swezeyi* and *?Sinuopea sweeti*), a fairly confident assumption may be made that the shells of the bilaterally symmetrical mollusks were positioned upright on the foot.

Concern about the soft parts of Cambrian fossils recalls the vigorous debate of several generations of paleontologists as to whether the ammonites might have had two or four gills.

"If the shells are believed to have curved or coiled over the head they are termed *exogastric*; if they are believed to have curved backwards away from the head they are said to be *endogastric'*.

"To avoid confusion, we recommend that the 'endogastric' coiling of a gastropod be renamed *gyrogastric* coiling, for it results from torsion, a developmental process that destroys the symmetry of the body. In an endogastric cephalopod the anus lies on the concave side of the shell, but in all gastropods the anus is on the convex side of the shell; there is no change in shell curvature, only a change in orientation of the shell and visceral mass on the head-foot" (Runnegar and Jell, 1976, p. 115). We cannot see the merit in introducing the term gyrogastric for it simply provides unnecessary terminology for unproven assumptions. Flower (1955) discussed both endogastric and exogastric coiling in cephalopods; Mutvei (1957), in his Figure 7, reconstructed the soft parts of fossil nautiloids all with gills in the same relative position, but with different curvature and different position for attachment of the muscles.

Symmetrical and asymmetrical shell forms

In our view, more emphasis should be placed on "old-fashioned" studies of detailed morphology of the hard parts of fossils to provide new data, which might then be used for speculation. Mathematical models of the three dimensional coiling of gastropods have been developed and refined. A number of papers have analyzed the typical three-dimensional coiling of the gastropod shell, but relatively little attention has been paid to the Paleozoic limpets. The ratio of length of the aperture to the length of the apical area, ranging from overhanging the aperture to well within the cone, has been suggested as an illustration of evolutionary change within the Tergomya (Starabogatov, 1970), but this seems to be a strained approach to an implausible conclusion.

Ackerly (1989) attempted to compare the curvature of selected mollusks and may have been the only paleontologist to consider the morphometrics of fossil limpets. He made a useful first effort by employing a "moving reference model" and developed illustrations of the various shapes resulting from varying four components: translation, rotation, dilation, and whorl expansion. "...Variation in this component [allometry in direction of translation] is rather common in monoplacophorans" (Ackerly, 1989, p. 158). This sweeping conclusion is based on representatives of seven genera, one of which, *Pollicina*, is not a monoplacophoran. None of his reconstructed sketches shows the apex, the most critical part of the logarithmic spiral, and all were based on drawings taken from the *Treatise on Invertebrate Paleontology* (Moore, 1960). In the specimens we have examined in connection with this study, if there is any allometric growth in the various species, it is not immediately apparent.

A next logical step in the study of these curved, bilaterally symmetrical Paleozoic mollusk shells may be more sophisticated computer modeling of the various shapes as a basis for greater precision in the delineation of species. A particularly important and challenging part of such an effort would be quantification of the angle of tangency of the logarithmic spiral for each of the species. If one can model both the convex and the concave curvature, the longitudinal profile of each species may be described and compared more precisely, and the range of the angle of log coiling might then be determined for each genus. The degree of arching of the lateral surfaces at right angles to the plane of symmetry may also be helpful in defining species, but we judge that it would not be as critical.

In a purely qualitative approach to the transition from straight cephalopods to coiled ones, Flower (1955) suggested that whereas slightly curved shells are found, there are none known that have a logarithmic spiral, which would allow them to complete most of one whorl. In Flower's interpretation, it would have been essentially impossible for a cephalopod to function with such a shell shape. He referred to the change from slightly curved to distinctly coiled and the absence of any examples of intermediate shapes as a saltation, or abrupt jump; in more modern terminology, the forms that have not been found lie within "forbidden morphospace." This insight of Flower in the context of Raupian morphospace might explain why the apex in *Proplina* and many of the broad, low shells is presumably anterior and that of *Hypseloconus* and comparable conical forms is presumably posterior. There may be an upper limit to the curvature of *Proplina* and a lower limit to the curvature of *Hypseloconus*, with a gap between the two. Accordingly, we propose that no continuous series of slight changes in the curvature of the logarithmic spiral angle will be found, but rather there will be discontinuities.

As another notion to be tested, we suggest that the septation of *Shelbyoceras* and its allies would have lowered the center of gravity, resulting in less curvature of the shell and a slightly smaller area of the aperture than in *Hypseloconus*. Dr. R.M. Linsley (unpub. data, 2002) cut open the apical region of a variety of living septate gastropod shells and has never found any fluid within the septate portion; he therefore surmises that they may have been gas-filled. The removal of fluid from a chamber by the soft parts of any organism may occur in several ways and need not be related to any generation of gas to increase buoyancy—as in cephalopods—but would result in lowering the center of gravity of the animal.

The shape of the bilaterally symmetrical tergomyans may be considered as the result of two logarithmic curvatures, the difference between them establishing the relative width of the elongate aperture. In connection with a euomphalacean gastropod with such a low spire that it coiled almost in a single plane, Yochelson (1971) attempted to explain the open-coiled shape qualitatively. He saw it as the degree of logarithmic curvature establishing the overall shape, but the width of the individual whorl determining whether the body whorl impinged on the preceding whorl. For those species such as *Proteroconus eminense* (Stinchcomb), which may grow through almost half a whorl but are not coiled, exploration of this view may be useful.

At the same time, one should not expect perfect bilateral symmetry in every shell, for one is dealing with former living animals and they conform to the laws of biology, not the rules of geometry. At least one Late Cambrian bellerophontacean (Knight, 1947b) displays slight asymmetry both to the right and to the left, yet it is more easily interpreted as a shell carried upright on the body than as one inclined in the typical asymmetrical gastropod mode. Among the Helcionelloidea, several genera exhibit slight asymmetry. Just as in the example propounded by Flower (1955), there may be minor deviations from bilateral symmetry without any major consequences, but there is a fundamental distinction between this minor variation and coiling of the shell through several whorls.

Class-level evolution within the Mollusca

As discussed earlier, the acceptance of the concept of Monoplacophora was a dramatic change in understanding the history of the Mollusca. On a smaller scale, it was a paradigm shift, not unlike that from fixed continents to plate tectonics. After some years, the concept of Monoplacophora has served its time and has been abandoned by some workers in favor of Helcionelloidea and Tergomya, with a few of the genera in the Monoplacophora still not certainly assigned. The question raised here is whether the Tergomya in turn should be replaced by a different concept of a molluscan class or classes.

In a discussion of the relationship of shell form and locomotion rates, Linsley (1978, p. 193) began his exposition by asking that the reader "... imagine a preposterous snail carrying an elongate straight shell over its dorsal surface. This shell obviously presents a large cross-sectional area, relative to the volume of the shell, for the fluid movement to act against if the animal tries to move. .... A great deal of energy would have to be expended to prevent this shell from tipping over during locomotion."

Hypseloconus is not quite characterized by the symmetrical cone having a circular aperture suggested by Linsley for "a preposterous snail," but it is a high cone and in some sense preposterous in shape. The broad oval aperture and slight differentiation between the two ends of the oval may be ascribed to the shell containing bilaterally symmetrical soft-parts and especially a distinct head, rather than a radially symmetrical organism. To jump several steps, the assignment of *Hypseloconus* to any phylum other than Mollusca seems very unlikely.

After many years of being classified as a gastropod, *Hypseloconus* was transferred to the Monoplacophora and now presumably is part of the Tergomya. If it is a tergomya, the shape is dramatically different from others. First, it is tall, second it seems to have a thin shell and thus lacks muscle scars, and third, if interpretations of anterior and posterior are correct, the slight curvature is toward the posterior. These morphological features all argue for placement at some taxonomic level distinct from more characteristic tergomyans.

We can envision the first outlines of a revision of the Tergomya. As one major division, there is the low and broad, thick-shelled forms that gave rise to the original concept of the Monoplacophora. The second major division would be the high and narrower forms, some with thick shells and others thin. Partly on the basis of a thick shell, the kirengellids might form one group, and partly on the basis of septation, the shelybyocerids might form a second. The hypseloconids might then constitute a third group, lacking both the features, but having the morphologic feature of slightly more obvious curvature of the shell. This is not quite the arrangement suggested by Rosov (1975) with his proposal of the Order Kirengellida.

If reliance may be placed on the notion that the largest pair of muscle scars are anterior and if one can with confidence transfer this interpretation from the kirengellids to the other two groups, the difference in direction of curvature of the shell between the two divisions becomes significant. Whether it is significant enough to warrant the rank of orders within the Tergomya or the abandonment of that class in favor of two new class-rank terms requires more data and study.

The Late Cambrian Taylors Falls faunule is molluscan dominated, but it is strikingly different from a Late Ordovician faunule, which is also molluscan dominated. Much of that difference lies in the presence of abundant *Hypseloconus*. The relative value of facts and the relative value of models has been argued and will continue to be argued. The great abundance of high conical forms during a short time interval, relatively early in the history of the Mollusca and the subsequent rapid decline toward extinction argue theoretically that this group may be another "failed experiment" in evolution. That the "fact" of *Hypseloconus* is supported by a model of adaptive radiation makes the fact more interesting, but does not necessarily prove the speculations on reclassification mentioned above.

The level of any taxon is not related to the number of included lower taxonomic units. One can propose an extinct class or an extinct phylum based on few or even one genus. The issue is not the proposal of any new high-level taxon, but its acceptance by others. The issue of extinct molluscan classes seems no longer to be a subject of interest to many paleontologists.

Whether one emphasizes similarities or differences in the continuity of life depends in part on one's personal views, and the temper of the time. The pendulum swings between splitters and lumpers at all taxonomic stages and it seems to be moving toward similarity rather than differentiation. In our private opinion, *Hypseloconus* and its allies may be different enough from other Late Cambrian–Early Ordovician Mollusca to warrant consideration of class rank. In a more formal approach, we prefer to simply state the differences in shape from other Mollusca that we have observed and not propose any further action at this time

High-level evolution within the Mollusca

Because specimens coiled in three dimensions occur in the Taylors Fall fauna, the associated tergomyans could not have been ancestral to the Gastropoda. At this stage of our understanding of older forms we have no strong beliefs as to which shells may or may not have included torted soft-parts. In the absence of belief, we prefer to follow the suggestions of Knight and other earlier workers, and guess that torsion may have appeared abruptly in a larval stage. Whether the egg that produced such a guessed-at novel larva came from an older shell that was broad and low or one that was a high cone, seems insignificant at this state of our knowledge.

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REFERENCES

Ackerly, S.C., 1989, Kinematics of accretionary shell growth, with examples from brachiopods and mollusks: Paleobiology, v. 15, p. 147-166.

Allen, J.R.L., 1982, Sedimentary structures: Their character and physical basis: Amsterdam, Elsevier Scientific, v. 2, 663 p.

Austin, G.S., 1969, Paleozoic lithostratigraphic nomenclature for southeastern Minnesota: Minnesota Geological Survey Information Circular 6, 11 p.

Baker, R.W., Cordua, W.S., Middleton M.D., and Williams, I.S., 1989, Paleogeography and structure of the St. Croix River valley: 53rd Annual Tri-State Geological Field Conference Guidebook, 72 p., 1 pl.

Bassler, R.S., 1915, Bibliographic index of American Ordovician and Silurian fossils: U.S. National Museum Bulletin 92, 2 v., 1521 p.

Bell, W.C., Feniak, O.W., and Kurtz, K.E., 1952, Trilobites of the Franconia formation, southeastern Minnesota: Journal of Paleontology, v. 26, p. 175-198.

Berg, R.R., 1953, Franconian trilobites from Minnesota and Wisconsin: Journal of Paleontology, v. 27, p. 553-568.

———1954, Franconia Formation of Minnesota and Wisconsin: Geological Society of America Bulletin, v. 65, no. 9, p. 857-882.

Berg, R.R., Nelson, C.A., and Bell, W.C., 1956, Upper Cambrian rocks in southeast Minnesota, *in* Sloan, R.E., ed., Lower Paleozoic geology of the Upper Mississippi valley: Geological Society of America Annual Meeting, Minneapolis, Minn., Field Trip 2 Guidebook, p. 1-13.

Berkey, C.P., 1897, Geology of the St. Croix Dalles: The American Geologist, v. 20, p. 345-383.

———1898, Geology of the St. Croix Dalles, III: Paleontology: The American Geologist, v. 21, p. 270-294.

Billings, E., 1862, 2.—On some new species of fossils from the Calciferous, Chazy, Black River, and Trenton Formations [part]: Geological Survey of Canada, p. 25-51. [The 426 p. major work of Billings "Palaeozoic Fossils" was published in 1865 but earlier portions of the work were printed in 1861, 1862, and 1865. The 1862 and 1865 texts are identical].

Boardman, R.S., Cheetham, A.H., and Rowell, A.J., eds., 1987, Fossil invertebrates: London, Blackwell Scientific, 713 p.

Bockelie, T.G., and Yochelson, E.L., 1979, Variation in a species of "worm" from the Ordovician of Spitsbergen: Norsk Polarinstitut Skriffter, v. 167, p. 225-237.

Byalyv [Bjaly], V.I., 1973, [New Early Ordovician monoplacophorans of Siberia]: Paleontologicheskii Zhurnal [Paleontological Journal], v. 3, p. 42-47 [English translation].

Byers, C.W., 2001, Sequence stratigraphy at the turn of the century: E.O. Ulrich's Ozarkian System in Wisconsin: Geoscience Wisconsin, v. 18, p. 43-48.

Cavaleri, M.E., Mossler, J.H., and Webers, G.F., 1987, Field trip guidebook for the Upper Mississippi Valley, Minnesota, Iowa, and Wisconsin: Minnesota Geological Survey Guidebook 15, 185 p.

Chamberlin, T.C., 1883, General geology: Wisconsin Geological Survey Volume 1, 300 p.

Clarkson, E.N.K., 1998, Invertebrate paleontology and evolution (4th ed.): London, Blackwell Scientific, 452 p.

Cuvier, G.F., 1798, Tableau elementaire de l'histoire naturelles des animaux: Paris, Baudouin, 710 p.

Dake, C.L., 1930, The geology of the Potosi and Edgehill quadrangles: Missouri Bureau of Geology and Mines, v. 23 (2nd series), 233 p.

Dall, W.H., 1893, The phylogeny of the Docoglossa: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 45, p. 285-287.

Dalziel, I.W.D., and Dott, R.H., Jr., 1970, Geology of the Baraboo District, Wisconsin: Wisconsin Geological and Natural History Survey Information Circular 14, 164 p.

Doguzhayeva, L.A., 1972, [New Tremadocian monoplacophorans from the Urals]: Paleontologicheskii Zhurnal [Paleontological Journal], v. 6, no. 1, p. 20-24 [English translation].

Dott, R.H., Jr., 1974, Cambrian tropical storm waves in Wisconsin: Geology, v. 2, p. 243-246.

Dzik, J., 1991, Is fossil evidence consistent with traditional views of the early metazoan phylogeny, *in* Simonetta, A., and Conway Morris, S., eds., The early evolution of Metazoa and the significance of problematic taxa: Cambridge, Cambridge University Press, p, 47-56.

———1994, Evolution of "small shelly fossils" assemblages: Acta Palaeontologica Polonica, v. 39, p. 247-313.

Evans, D.H., and Cope, J.C.W., 2003, Systematic position of *Pollicina corniculum* (Eichwald, 1860) (Mollusca, Tergomya) from the Middle Ordovician of the United Kingdom: Palaeontology, v. 46, pt. 1, p. 139-149.

Fedonkin, M.A., and Waggoner, B.M., 1997, The late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism: Nature, v. 388, p. 868-871.

Feng, W., Mu, X., and Kouchinsky, A.V., 2001, Hyolith-type microstructure in a mollusc-like fossil from the Early Cambrian of Yunnan, China: Lethaia, v. 34, no. 4, p. 303-308.

Flower, R.H., 1955, Saltations in nautiloid coiling: Evolution, v. 9, p. 244-260.

———1957, Nautiloids of the Paleozoic, *in* Ladd, H.S., ed., Treatise on marine ecology and paleoecology, volume 2, paleoecology: Geological Society of America Memoir 67, p. 629-652.

———1968 [1969], Part II. Fossils from the Smith Basin Limestone of the Fort Ann region, New York: New Mexico Bureau of Mines and Mineral Resources Memoir 22, p. 23-27.

Frederickson, E.A., 1949, Trilobite fauna of the Upper Cambrian Honey Creek Formation: Journal of Paleontology, v. 23, p. 341-363.

Grabau, A.W., and Shimer, H.W., 1909, 1910, North American index fossils: New York, A.G. Seiler and Company, 2 v., 1762 p.

Grant, R.E., 1965, Faunas and stratigraphy of the Snowy Range Formation (Upper Cambrian) in southwestern Montana and northwestern Wyoming: Geological Society of America Memoir 96, 171 p.

Grout, F.F., and Aldrich, H.A., 1965, Memorial to Charles Peter Berkey (1867-1955): Geological Society of America Bulletin 73, Proceedings, p. P.45-P.51.

Gubanov, A.P., 2000, Evolution of the earliest molluscs: Uppsala, Sweden, Uppsala University, Ph.D. dissertation, 28 p.

Gunderson, G.O., 1993, New genus of Late Cambrian gastropod: Journal of Paleontology, v. 67, p. 1083-1084.

Horny, R.J., 1963, Lower Paleozoic Monoplacophora and patellid Gastropoda (Mollusca) of Bohemia: Sborník Ústredního Ústavu Geologického, v. 27, p. 7-83.

———1965, *Cyrtolites* Conrad, 1838 and its position among the Monoplacophora (Mollusca): Sborník Národního Muzea V Praze, v. 21B, no. 2, p. 57-70.

———1997, Ordovician Tergomya and Gastropoda (Mollusca) of the Anti-Atlas, Morocco: Acta Musei Nationalis Pragae Series B, Natural History, v. 53, no. 3-4, p. 37-78.

———2002, Ordovician Tergomya and isostrophic Gastropoda (Mollusca) of Bohemia: Types and referred specimens in the collections of the National Museum, Prague Czech Republic: Acta Musei Nationalis Pragae Series B, Natural History, v. 57, no. 3-4, p. 69-102.

Howell, B.F., Bridge, J., Deiss, C.F., Edwards, I., Lochman, C., Raasch, G.O., and Resser, C.E., 1944, Correlation of the Cambrian formations of North America: Geological Society of America Bulletin, v. 55, p. 993-1003.

Kisselev, G.N., 1994, [The systematic position of the Lower Palaeozoic mollusc '*Cyrtolithes*' *corniculum* (Eichwald, 1860) (Xenoconchia, Toxeumorphorida): Ruthenica, v. 4, p. 35-37.

Knight, J.B., 1941, Paleozoic gastropod genotypes: Geological Society of America Special Paper 32, 510 p.

———1947a, Bellerophont muscle scars: Journal of Paleontology, v. 21, p. 264-267.

———1947b, Some new Cambrian bellerophont gastropods: Smithsonian Miscellaneous Collections, v. 105, no. 17, 11 p.

———1948, Further new Cambrian bellerophont gastropods: Smithsonian Miscellaneous Collections, v. 111, no. 3, 6 p.

———1952, Primitive fossil gastropods and their bearing on gastropod classification: Smithsonian Miscellaneous Collections, v. 117, no. 13, 56 p.

———1956, New families of Gastropoda: Journal of the Washington Academy of Sciences, v. 46, p. 41-42.

Knight, J.B., Batten, R.L., and Yochelson, E.L., 1960, [Paleozoic gastropod descriptions], *in* Moore, R.C., ed., Treatise on invertebrate paleontology: Volume I, Mollusca 1: Lawrence, Kansas, University of Kansas Press, p. I169-I324.

Knight, J.B., and Yochelson, E.L., 1958, A reconsideration of the Monoplacophora and the primitive Gastropoda: Proceedings of the Malacological Society of London, v. 33, no. 1, p. 37-48.

———1960, Monoplacophora, *in* Moore, R.C., ed., Treatise on invertebrate paleontology: Volume I, Mollusca 1: Lawrence, Kansas, University of Kansas Press, p. I77-I84.

Kouchinsky, A., 2000a, Shell microstructures in Early Cambrian molluscs: Acta Palaeontologica Polonica, v. 45, p. 119-150.

———2000b, Skeletal microstructures of hyoliths from the Early Cambrian of Siberia: Alcheringa, v. 24, p. 65-81.

Landing, E., Geyer, G., and Bartowski, K.E., 2002, Latest Early Cambrian small shelly fossils, trilobites, and Hatch Hill dysaerobic interval on the Québec continental slope: Journal of Paleontology, v. 76, p. 287-305.

Landing, E., and Narbonne, G.M., 1992, *Scenella* and a chondrophorine (medusoid hydrozoan) from the basal Cambrian (Placentian) of Newfoundland: Journal of Paleontology, v. 66, p. 338.

Lemche, H., 1957, A new living deep-sea mollusc of the Cambro-Devonian class Monoplacophora: Nature, v. 179, p. 413-416.

———1972, The discovery of *Neopilina*, *in* Jenkins, M.M., The curious mollusks: New York, Holiday House, p. 195-201.

Lindström, G., 1884, On the Silurian Gastropoda and Pteropoda of Gotland: Kongliga Svenska Vetenskaps-Akademiens Handlinger, v. 19, no. 6, 250 p.

Linsley, R.M., 1977, Some "laws" of gastropod shell form: Paleobiology, v. 3, p. 196-206.

———1978, Locomotion rates and shell form in the Gastropoda: Malacologia, v. 17, no. 2, p. 193-206.

Linsley, R.M., and Kier, P.M., 1984, The Paragastropoda: A proposal for a new class of Paleozoic Mollusca: Malacologia, v. 25, no. 1, p. 241-254.

Lochman, C., 1958, *Sulcocephalus* Wilson 1948 to replace *Berkeia* Resser 1937, and *Burnetiella* to replace *Burnetia* Walcott 1924: Journal of Paleontology, v. 32, no. 1, p. 247.

Lochman, C., and Duncan, D.C., 1944, Early Upper Cambrian faunas of central Montana: Geological Society of America Special Paper 54, 177 p.

Lochman, C., and Hu, Chung-Hung, 1962, An *Aphelaspis* zone faunule from Logan, Montana: Journal of Paleontology, v. 36, no. 3, p. 431-441.

Ludvigsen, R., and Westrop, S.R., 1985, The new upper Cambrian stages for North America: Geology, v. 13, p. 139-143.

Marek, L., and Yochelson, E.L., 1976, Aspects of the biology of *Hyolithes* (Mollusca): Lethaia, v. 9, p. 65-82.

Moore, R.C., ed., 1960, Treatise on invertebrate paleontology: Volume I, Mollusca 1: Lawrence, Kansas, University of Kansas Press, p. I1-I351.

Moore, R.C., Lalicker, C.G., and Fischer, A.G., 1952, Invertebrate fossils: New York, McGraw-Hill, 766 p.

Mossler, J.H., 1987, Paleozoic lithostratigraphic nomenclature for Minnesota: Minnesota Geological Survey Report of Investigations 36, 36 p., 1 pl.

Mutvei, H., 1957, On the relations of the principal muscles to the shell of *Nautilus* and some fossil nautiloids: Arkiv för Mineralogi och Geologi Kungliga Svenska Vetenskapsakademien, v. 10, no. 2, p. 219-254.

Nelson, C.A., 1951, Cambrian trilobites from the St. Croix Valley: Journal of Paleontology, v. 25, p. 765-784.

Ohdner, N.H., 1960, Some notes on the classification of Gastropoda: Proceedings of the Malacological Society of London, v. 34, p. 250-254.

Parkhaev, P.Y., 2001, The functional morphology of the Cambrian univalved Mollusks—Helcionellids: Paleontologicheskii Zhurnal, v. 5, p. 20-26. [English translation in Paleontological Journal, v. 35, no. 5, p. 470-475.}

———2002, [Phylogenesis and the system of the Cambrian univalved mollusks]: Paleontologicheskii Zhurnal, v. 1, 2002, p. 27-39. [English translation in Paleontological Journal, v. 36, no. 1, p. 25-36.]

Peel, J.S., 1991, Functional morphology of the Class Helcionelloidea nov. and the early evolution of the Mollusca, *in* Simonetta, A., and Conway Morris, S., eds., The early evolution of Metazoa and the significance of problematic taxa: Cambridge, Cambridge University Press, p. 157-177.

Peel, J.S., and Yochelson, E.L., 1984, Permian Toxeumorphorida from Greenland: An appraisal of the molluscan class Xenoconchia: Lethaia, v. 17, p. 211-221.

Pojeta, J., Jr., and Runnegar, B., 1976, The paleontology of the rostroconch mollusks and the early history of the phylum Mollusca: U.S. Geological Survey Professional Paper 968, 88 p.

Pojeta, J., Jr., Runnegar, B., Morris, N.J., and Newell, N.D., 1972, Rostroconchia: A new class of bivalve mollusks: Science, v. 144, p. 264-267.

Rasetti, F., 1954, Internal shell structures in the Middle Cambrian gastropod *Scenella* and the problematic genus *Stenothecoides:* Journal of Paleontology, v. 28, p. 59-66.

Raup, D.M., and Stanley, S.M., 1971, Principals of paleontology: New York, W.H. Freeman and Company, 481 p.

Resser, C.E., 1935, Nomenclature of some Cambrian trilobites: Smithsonian Miscellaneous Collection, v. 93, no. 4, 46 p.

———1937, Third contribution to nomenclature of Cambrian trilobites: Smithsonian Miscellaneous Collection, v. 95, no. 22, 29 p.

Rosov, S.N., 1968, [A new genus of Late Cambrian molluscs of the class Monoplacophora (southern part of the Siberian platform)]: Doklady Academy of Sciences of USSR, v. 183, p. 214-217. [English translation by American Geological Institute.]

———1970, [*Moyerokania*, a new Siberian Early Ordovician monoplacophoran]: Paleontologicheskii Zhurnal, v. 2, p. 254-257 [English translation].

———1975, [A new order of the Monoplacophora]: Paleontologicheskii Zhurnal, v. 1, p. 39-43 [English translation].

Runnegar, B., 1980, Hyolitha: Status of the phylum: Lethaia, v. 12, p. 21-25.

———1981, Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs: Lethaia, v. 14, p. 311-322.

———1982, The Cambrian explosion: Animals or fossils?: Journal of the Geological Society of Australia, v. 29, p. 395-411.

———1983, Molluscan phylogeny revisited, *in* Roberts, J., and Jell, P.A., eds.: Association of Australasian Palaeontologist Memoir 1, p. 121-144.

Runnegar, B., and Jell, P.A., 1976, Australian Middle Cambrian molluscs and their bearing on early molluscan evolution: Alcheringa, v. 1, p. 109-138.

Runnegar, B., and Pojeta, J., Jr., 1974, Molluscan phylogeny: The paleontological viewpoint: Science, v. 186, p. 311-317.

Runnegar, B., Pojeta, J., Jr., Morris, N.J., Taylor, J.D., Taylor, M.E., and McClung, G., 1975, Biology of the Hyolitha: Lethaia, v. 8, p. 181-191.

Russell-Hunter, W.D., 1979, A life of invertebrates: New York, McMillan Publishing Company, 650 p.

Salvini-Plawen, L., 1980, A reconsideration of systematics in the Mollusca (phylogeny and higher classification): Malacologia, v. 19, no. 2, p. 249-278.

Sardeson, F.W., 1896, The fauna of the Magnesian series: Bulletin of the Minnesota Academy of Natural Sciences, v. 4, p. 92-105.

———1903, The phylogenetic stage of the Cambrian Gastropoda: Journal of Geology, v. 11, p. 469-492.

Shaw, A.W., 1956, A Cambrian *Aphelaspis* fauna from Steele Butte, near Boulder, Wyoming: Journal of Paleontology, v. 30, p. 48-52.

Scheltema, A., 1978, Position of the class Aplacophora in the phylum Mollusca: Malacologia, v. 17, p. 99-109.

Starabogatov, Y.I., 1970, [Systematics of early Paleozoic Monoplacophora]: Paleontologicheskii Zhurnal, v. 3, p. 6-17 [English translation].

Steiner, G., and Salvini-Plawen, L., 2001, *Acaenoplax*—polychaete or mollusc?: Nature, v. 414, p. 601-602.

Stinchcomb, B.L., 1975, Paleoecology of two new species of Late Cambrian *Hypseloconus* (Monoplacophora) from Missouri: Journal of Paleontology, v. 49, p. 416-421.

———1980, New information on Late Cambrian Monoplacophora *Hypseloconus* and *Shelbyoceras* (Monoplacophora): Journal of Paleontology, v. 54, p. 45-49.

———1986, New Monoplacophora (Mollusca) from the Late Cambrian and Early Ordovician of Missouri: Journal of Paleontology, v. 60, p. 606-626.

———1996, Change of monoplacophoran genus *Protoconus* to *Proteroconus* due to homonomy: Journal of Paleontology, v. 70, p. 339.

Stinchcomb, B.L., and Angeli, N.A., 2002, New Cambrian and Lower Ordovician monoplacophorans from the Ozark Uplift, Missouri: Journal of Paleontology, v. 76, p. 965-974.

Stinchcomb, B.L., and Echols, D.J., 1966, Missouri Upper Cambrian Monoplacophora previously considered cephalopods: Journal of Paleontology, v. 40, p. 647-650.

Sutton, M.D., Briggs, D.E.G., Siveter, David J., and Siveter, Derek J., 2001a, An exceptionally preserved vermiform mollusc from the Silurian of England: Nature, v. 410, p. 461-463.

———2001b, Reply [*Acaenoplax*- polychaete or mollusc?]: Nature, v. 414, p. 602.

Syssoiev, V.V., 1973, [Some features of gas chamber growth in Early Cambrian hyoliths]: Paleontologicheskii Zhurnal, v. 3, p. 53-58 [English translation].

Tasch, P., 1973, Paleobiology of the invertebrates: Data retrieval from the fossil record: New York, John Wiley and Sons, 946 p.

Ulrich, E.O., and Bridge, J., Jr., 1931, Description of species—Gastropoda, *in* Ulrich, E.O., Foerste, A.P., and Bridge, J., Jr., Systematic paleontology, *in* Bridge, J., Jr., Geology of the Eminence and Cardareva quadrangles: Missouri Bureau of Geology and Mines, 2nd series, v. 24, p. 186-207.

Ulrich, E.O., and Scofield, W.H., 1897, The Lower Silurian Gastropoda of Minnesota: Minnesota Geological Survey Final Report, v. 3, pt. 2, p. 813-1081.

Wagner, P.J., 1995a, Diversity patterns among early gastropods: Contrasting taxonomic and phylogenetic descriptions: Paleobiology, v. 21, p. 410-439.

———1995b, Testing evolutionary constraint hypotheses with early Paleozoic gastropods: Paleobiology, v. 21, p. 248-272.

Walcott, C.D., 1879, Descriptions of new species from the Calciferous formation: 32nd Annual Report of the New York State Museum of Natural History for 1879, p. 129-131.

———1890, Descriptions of new forms of Upper Cambrian fossils: Proceedings of the United States National Museum, v. 13, p. 266-279.

———1912a, Cambrian Brachiopoda: U.S. Geological Survey Monograph 51, pt. I, 872 p.

———1912b, No. 9—New York Potsdam-Hoyt fauna: Smithsonian Miscellaneous Collections, v. 57, no. 9, p. 251-300.

Wanenmacher, J.M., Twenhofel, W.H., and Raash, G.O., 1934, Paleozoic strata of Baraboo area, Wisconsin: American Journal of Sciences, 5th series, v. 28, p. 1-30.

Webers, G.F., and Yochelson, E.L., 1989, Late Cambrian molluscan faunas and the origin of the Cephalopoda, *in* Crame, J.A., ed., Origins and evolution of the Antarctic biota: Geological Society of London Special Publication 47, p. 29-42.

———1999, A revision of *Palaeacmaea* (Upper Cambrian) (?Cnidaria): Journal of Paleontology, v. 73, p. 589-607.

Webers, G.F., Pojeta, J., Jr., and Yochelson, E.L., 1992, Cambrian Mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctica, *in* Webers, G.F., Craddock, C., and Splettstocesser, J.F., eds., Geology and paleontology of the Ellsworth Mountains, West Antarctica: Geological Society of America Memoir 170, p. 181-248.

Weiss, M.P., 2000, Fredrick William Sardeson, geologist: 1866-1958: Minnesota Geological Survey Bulletin 48, 200 p.

Weller, S., and St. Clair, S., 1928, Geology of Ste. Genevieve County, Missouri: Missouri Bureau of Geology and Mines, 2nd Series, v. 22, 352 p.

Wenz, W., 1939, Gastropoda; Allgemeiner Teil und Prosobranchia, *in* Schindewolf, O.H., ed., Handbuch der Paläozoologie: Germany, v. 6, 7 pts., 1639 p.

———1940, Ursprung und frühe Stammes-geschichte der Gastropoden: Archiv für Molluskunde, v. 72, p. 1-10.

Whitfield, R.P., 1878, Preliminary descriptions of new species of fossils from the lower geological formations of Wisconsin: Annual report of the Wisconsin Geological Survey for 1877, p. 50-77.

———1880, Descriptions of new species of fossils from the Paleozoic of Wisconsin: Wisconsin Geological Survey Annual Report for 1879, p. 44-71.

———1882, Part III, Palaeontology, *in* Geology of Wisconsin, volume 4, 1873-1879: Wisconsin Geological Survey, p. 163-363.

———1886, Notice of geological investigations along the eastern shore of Lake Champlain, conducted by Prof. H.M. Seeley and Prest. Ezra Brainard, of Middlebury College, with descriptions of the new fossils discovered: American Museum of Natural History, Bulletin 8 [Article XVII], p. 293- 345, pls. 24-35 [During the early days of publication of this series, articles were numbered and combined in bulletins, which in turn were combined into volumes; Volume 1 of the Bulletin is dated from 1881-1886].

———1889, Observations on some imperfectly known fossils from the Calciferous sandrock of Lake Champlain, and descriptions of several new forms: American Museum of Natural History, Bulletin 2 [Article III], p. 42-65, pls. 9-13. [Volume 2 of the Bulletin is dated from 1887-1890].

Whitfield, R.P., and Hovey, E.O., 1898, Catalogue of the type and figured specimens in the palaeontological collection of the geological department, American Museum of Natural History: American Museum of Natural History, v. 11, no. 1, p. 1-72.

Wills, M.A., 2001, Morphological disparity: A primer, *in* Adrian, J.A., Edgecombe, G.D., and Lieberman, B.S., eds., Fossils, phylogeny, and form—an analytical approach: New York, Kluwer Academic/Plenum Publishers, p. 44-144.

Winchell, N.H., 1886, Revision of the stratigraphy of the Cambrian in Minnesota: Minnesota Geological and Natural History Survey, 14th Annual Report, p. 325-337.

Yochelson, E.L., 1958, Some Lower Ordovician monoplacophoran mollusks from Missouri: Journal of the Washington Academy of Sciences, v. 48, p. 8-15.

———1967, Quo Vadis *Bellerophon*?, *in* Teichert, C., and Yochelson, E.L., eds., Essays in paleontology and stratigraphy: In honor of R.C. Moore: Lawrence, Kansas, University of Kansas Press, Department of Geology Special Publication 2, p. 141-161.

——— 1971, A Late Devonian gastropod and its bearing on problems of open coiling and septation, *in* Dutro, J.T., Jr., ed., Paleozoic perspectives: A paleontological tribute to G. Arthur Cooper: Smithsonian Contributions to Paleobiology, no. 3, p. 231-241.

———1978, An alternative approach to the interpretation of the phylogeny of ancient Mollusca: Malacologia, v. 17, p. 165-171.

———1979, Early radiation of Mollusca and Mollusc-like groups, *in* House, M.R., ed., The origin of major invertebrate groups: New York, Academic Press, Systematics Association Special Volume 12, p. 323-358.

———1984, Historic and current considerations for revision of Paleozoic gastropod classification: Journal of Paleontology, v. 59, p. 259-269.

———1988, A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: The oldest known example of the Superfamily: New Mexico Bureau of Mines and Mineral Resources Memoir 44, p. 195-200.

———1999a, Molluscs: Minor molluscan classes, *in* Singer, R., ed., Encyclopedia of paleontology: Chicago, Fitzroy Dearborn Publishers, p. 762-764.

———1999b, Molluscs: Overview, *in* Singer, R., ed., Encyclopedia of paleontology: Chicago, Fitzroy Dearborn Publishers, p. 754-761.

———2000, Concerning the concept of extinct classes of Mollusca; or what may/may not be a class of mollusks: American Malacological Bulletin, v. 15, no. 2, p. 195-202.

Yochelson, E.L., Flower, R.H., and Webers, G.F., 1973, The bearing of the new late Cambrian monoplacophoran genus *Knightoconus* upon the origin of the Cephalopoda: Lethaia, v. 6, p. 275-309.

Yochelson, E.L., and Gil Cid, D., 1984, Re-evaluation of the systematic position of *Scenella:* Lethaia, v. 17, no. 4, p. 331-340.

Yochelson, E.L., and Nuelle, L.M., 1985, *Strepsodiscus* (Gastropoda) in the Late Cambrian of Missouri: Journal of Paleontology, v. 59, p. 1305-1319.

Yonge, C.M., 1960, General characters of Mollusca, *in* Moore, R.C., ed., Treatise on invertebrate paleontology, Volume I, Mollusca 1: Lawrence, Kansas, University of Kansas Press, p. I3-I36.

Yu Wen, 1979, Earliest Cambrian monoplacophorans and gastropods from western Hubei and their biostratigraphic significance: Acta Paleontologica Sinica, v. 18, p. 230-270.

———1990, The first radiation of shelled molluscs: Palaeontologia Cathayana, v. 5, p. 139-170.

Yu Wen, and Yochelson, E.L., 1999, Some Late Cambrian mollusks from Lianong Province, China: Records of the Western Australian Museum, v. 19, p. 379-389.

Zittel, C. von, 1900, Textbook of paleontology; translated by C.R. Eastman. Volume 1: New York, McMillan Company. [This volume was published in two parts, the first in 1896; the Mollusca occur in both parts].

APPENDIX

AGE OF THE BERKEY COLLECTION FROM TAYLORS FALLS, MINNESOTA

A.R. Palmer

Reexamination of the original trilobite specimens, now in the American Museum of Natural History (AMNH), described by Berkey from Taylors Falls, was undertaken to clarify the age of the sample because Berkey's original identifications included *Ptychoparia calymenoides* Whitfield (subsequently *Menomonia calymenoides*). This species is a characteristic trilobite of the *Crepicephalus* zone and thus several zones older than the other trilobites in the sample, which represent the *Elvinia* zone. This suggested either the Berkey collection was mixed or something was misidentified.

The problem was misidentification of the specimen identified as "*P. calymenoides*." This is an articulated thorax and pygidium associated with cranidia now assigned to *Camaraspoides berkeyi* (Resser). The thorax is a normal ptychoparioid thorax with a pygidium that seems to be the same as several isolated pygidia in the same collection. True *calymenoides* has a much longer thorax with a tiny pygidium, quite unlike the one figured by Berkey.

The majority of the AMNH specimens are assignable to *Camaraspoides berkeyi* (Resser). They are internal and external molds in dark red sandstone and not associated with any other trilobites, but all parts are present. The glabella and border furrow are well defined on both the internal and external molds. One AMNH specimen (number 22432) of the same lithology consists of several internal molds assignable to *Camaraspis convexus* that look very similar to *Camaraspoides berkeyi*, and one external mold that shows the nearly effaced exterior furrows typical of *convexus*.

The types of *Agraulos hemisphericus* Berkey, later synonymized with *Camaraspis convexus* (Whitfield); *Cheilocephalus stcroixensis* Berkey; and *Berkeia typica* Resser, originally figured by Berkey as *Agraulos convexus* var. B; are in a slightly more brownish sandstone, but both lithologies show scraps of molluscs. Nelson (1951, p. 774) noted that the *Berkeia typica* specimens are "associated with...many gastropods." *Camaraspus convexus, Cheilocephalus stcroixensis,* and *Berkeia typica* are all very distinctive *Elvinia*-zone forms, so one can be pretty comfortable with that being the age of the associated molluscs.

Camaraspoides berkeyi has a complicated nomenclatural history. Berkey illustrated two varieties that he assigned to Whitfield's *Agraulus* [sic] *convexus*. Neither one seems to belong to that species, whereas his specimen of *Agrualus* [sic] *hemisphericus* has been correctly synonymized with *convexus*. Berkey's form A was renamed by Resser as *Modocia berkeyi* in 1935. Frederickson (1949) recognized that the generic assignment was not correct and named a new genus *Camaraspoides*, based on *berkeyi*. Grant (1965) incorrectly, in my view, synonymized *Camaraspoides* with *Camaraspis*. The Berkey collection contains internal molds of the type species of both *Camaraspis convexus* and *Camaraspoides berkeyi*. These are similar, which may account for the lumping, but external molds show that they are two separate species (see note above) and there is no particular reason to lump the genera without further study beyond the scope of this appendix. Thus, in my revised faunal list below, I show *Camaraspoides berkeyi* instead of *Camaraspis berkeyi*, which is the last published binomial.

In 1937, Resser renamed Berkey's *Agraulus* [sic] *convexus* var. B as *Berkeia typica*, type species of a new genus *Berkeia*. Lochman in 1958 mistakenly stated that *Berkeia* should be synonymized with *Camaraspis* because *Camaraspis*, based on Whitfield's (not Berkey's) *convexus*, was an older name. But *Berkeia* is based on Berkey's misidentification of specimens as *convexus* and Lochman's (1958) argument is invalid. Thus *Berkeia typica* is a valid species and genus.

The faunal list and age for Berkey's specimens should now be:

Elvinia zone

Berkeia typica Resser (Berkey's *Agraulus* [sic] *convexus* var. B)

Camaraspoides berkeyi (Resser) (Berkey's *Agraulus* [sic] *convexus* var. A and most probably the specimen he identified as *Ptychoparia calymenoides*)

Camaraspis convexus (Whitfield) (Berkey's *Agraulus* [sic] *hemisphericus*)

Cheilocephalus stcroixensis Berkey