STATE GEOLOGICAL SURVEY OF KANSAS, BULLETIN 38

1941 REPORTS OF STUDIES, PART 4, PAGES 121-163, PLATES 1-3

JUNE 30, 1941

# UPPER PENNSYLVANIAN GASTROPODS FROM KANSAS

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## ILLUSTRATIONS



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## Abstract

A molluscan fauna collected in north-central Kansas from the Deer Creek limestone of the Shawnee group, upper Pennsylvanian (Virgil) in age, contains bellerophontid and other gastropods that excellently show apertural characters and some features of shell structure.

Study of specimens of *Euphemites* indicates that the prismatic shell layer, secreted by an anterior border region of the mantle, is marked on the outer side by growth lines and covered externally by a thin smooth shell layer, here named perinductura, formed by a backward reflection of the outer edge of the mantle and partly by a longitudinally ribbed inductura deposited by the posterior and lateral parts of the mantle. Some species of *Euphemites* show the presence of another distinct shell layer that is deposited over part of the inductura. This layer is named the coinductura. The "obsolescence" of revolving ridges on a portion of the last whorl of *Euphemites*, not previously well explained, is seen to belong inherently both to old and young individuals. The smooth area is covered only the noncostate perinductura, whereas the costate area is formed by the inductura or by the inductura and coinductura.

A new bellerophontid genus, *Knightites*, which is represented in the collections by nearly all growth stages, is especially characterized by a series of paired tubular projections bordering the slit band. These hornlike structures are believed to mark the loci of incurrent streams of water that bathed the ctenidia and osphradia. Mature or gerontic specimens of this genus and of some other bellerophontids in the collection show a thick inductura that is much more strongly curved transversely than the underlying shell of the preceding whorl.

A new species that is assigned to *Warthia*, previously known from Permian rocks of Asia, seems to be the first determination of the occurrence of this genus in North America. Two new species of *Bellerophon* are described.

## Introduction

Pennsylvanian and Lower Permian rocks of Kansas are rich in their content of marine invertebrate fossils. The general nature of the faunas is well known through the work of Prosser (1894, 1895), Beede (1898-1902), Beede and Rogers (1899-1908), Girty (1915), Newell (1931-1937), Williams (1937), and others, but very much work remains to be done in studies of all groups. Comparative study of specimens obtained from many different stratigraphic horizons has shown that various loosely defined species actually represent a succession of more or less closely related forms that can be differentiated into more narrowly defined species having stratigraphic usefulness. Also, paleo-ecologic studies of special interest are encouraged in Kansas because of the presence in Pennsylvanian and Permian deposits of this region of remarkably well defined cyclic successions of beds. The sedimentary rock cycles and their contained fossils can be identified reliably as representing several contrasting environments that are associated with advance and retreat of shallow seas.

It is the purpose of this paper to describe some of the molluscan fossils that, during the last few years, have been collected from an upper Pennsylvanian limestone at a locality near Lawrence, Kansas. A reason for selection of these fossils is the nature of their preservation, which permits observation of structural features. A new genus and several new species of bellerophontid gastropods are distinguished but description of these new forms seems intrinsically less important than study of the significance of morphologic characters that are observed in them.

*Source of material.*—The described fossils were all collected from the upper portion of the Ozawkie limestone member of the Deer Creek formation in a cut on U.S. Highway 40, 9.4 miles west of Lawrence. The outcrop is located in the NW¼ SW¼ sec. 22, T. 12 S., R. 18 E., Douglas county, about three miles south of Lecompton. A section of the Deer Creek beds near this place has been published (Moore, 1932, p. 52; 1936, pp. 48, 182). The Deer Creek formation is in the middle part of the Shawnee group, which forms the middle main division of the Virgil series, upper Pennsylvanian. The Shawnee group is especially characterized by the prominence of escarpment-making limestone formations. The fossil-bearing zone is about 500 feet above the base of the Virgil strata and about 600 feet below the boundary that is accepted in Kansas as marking the base of the Permian system (Moore, 1936, p. 12; 1940, p. 300).

The thickness of the Ozawkie limestone in the highway cut mentioned and in nearby areas is about 5 feet. The lower one-half of the member consists of massive blue-gray brown-weathering limestone that contains numerous fusulinids, associated with some brachiopods, bryozoans, and other invertebrates. The upper one-half of the member is an oolitic rock, bluish in unweathered condition, but readily altered to yellow brown by exposure. Parts of the rock are very hard, and although fossiliferous, the unweathered well preserved structural characters. The fauna is a molluscan as-limestone does not yield good specimens. Locally, the limestone disintegrates in such a manner that good fossils may be freed from the matrix. Care in collecting and preparing the specimens often yields complete individuals having undistorted form and unusually semblage in which gastropods predominate, the abundance of bellerophontids being a speciaaly noteworthy feature. Several pelecypods, fragments of a few cephalopods, and some brachiopods have been collected, but these are a minor element of the fauna.

The mollusk-bearing oolitic part of the Ozawkie limestone represents one of the recessional phases of the Ozawkie cyclothem (cyclic succession of deposits) in the lower part of the Deer Creek formation. As indicated by study of numerous cyclothems in the Pennsylvanian-Permian strata of Kansas, it is clear that fusulinid-bearing limestones represent the most widespread typically marine environment in the succession of beds. The oolitic gastropod-bearing rock of the upper Ozawkie is a local deposit, although it is known to extend about 50 miles along the general line of the north-trending outcrop. Fossils are observed at many places in this part of the Ozawkie member, but they are not abundant and in general they are somewhat poorly preserved.

*Type specimens.*—In accord with cogent suggestions of Simpson (1940) in a recent discussion of philosophic viewpoints and procedure in taxonomy, only a single type for each new species is designated. This type specimen serves the function of name-bearer. My previous practice in descriptions of new species, like that of many other paleontologists, has been to select a holotype and to designate all other specimens of the new species studied as paratypes. The labeling of some specimens as paratypes and the recognition of various other categories of subsidiary types seem to serve no useful purpose, however. Simpson rightly observes that the concept of a species, genus, or other classificatory group of organisms essentially involves subjective elements, even though it is presumably based on careful observation of objective data. It is reasonable to conclude that interpretations of the norm of a species and the range of its variations should be based, not on comparisons with a single type or a small group of types, variously designated, but on all known individuals that are deemed referable to the species in question. This collective representation of a classificatory unit, such as a species, Simpson designates as a hypodigm, meaning sample or example. Only a single fixed type is needed and this is for the purpose of fixing the name. The considerations advanced by Simpson seem to be sound, and general adoption of his viewpoint may be expected to clarify and simplify some features of taxonomy in paleontologic studies.

*Acknowledgments.*—For the collection of many specimens, supplementing those obtained by me, I am indebted to associates in the University of Kansas—Ralph H. King, Allen Graffham, Russell M. Jeffords, and Maurice Wallace. Mr. Graffham discovered the first good specimens that are here described as *Knightites* and aided in freeing specimens from the matrix. I am indebted also to J. Brookes Knight, of Princeton University, for suggestions concerning the origin of some structural features of these gastropods, and for the contribution of notes, which he has permitted me to publish. To J. Marvin Weller, of the Illinois Geological Survey, special thanks are due for the loan of specimens of his *Euphemites callosus*.

## DESCRIPTION OF SPECIES

### Class Gastropoda

Subclass Prosobranchia Cuvier; Order Archaeogastropoda Thiele; Superfamily Bellerophontacea Wentz
Family Bellerophontidae McCoy

### Genus Bellerophon Montfort, 1808

This well known genus of Paleozoic gastropods includes subglobular to laterally someewhat compressed shells, coiled in a plane, expansion toward the aperture being at a regular rate. The surface is smooth except for the presence of growth lines. A short to moderately deep narrow slit having parallel sides indents the margin of the outer lip, and a slit band that is commonly somewhat elevated above adjoining parts of the shell is traceable around the last whorl to the point where it is covered by the inductura (Knight, 1931, p. 180). In most species the inductural layer is very thin and its surface is perfectly smooth. Its adapertural margin is not strongly sinuate, as in genera such as *Euphemites,* but extends in a gently curved line across the shell at a distance of about three-fourths of a whorl from the outer lip. A narrow, partly open umbilical depression may be present, or this area may be filled by thickening of the shell at the lateral edges of the aperture, including extensions of the inductural layer.

*Genotype.*—*Bellerophon vasulites* Montfort, Middle Devonian, Germany.

*Discussion.*—The wide distribution of shells that are assigned to *Bellerophon,* both stratigraphically and geographically, coupled with the general simplicity of shell structure and a somewhat poor preservation of these fossils in very many instances, makes difficult a reliable differentiation of species having stratigraphic value. Nevertheless, a considerable diversity of form exists in this group of shells, and at least in cases where reasonably well preserved specimens are available, they may be differentiated and classified satisfactorily. Among described species of *Bellerophon* in Carboniferous rocks of North America, a majority are unrecognizable, because of the lack of published illustrations or the very inadequate nature of figures that are given, coupled with unavailability of type materials, and an absence up to the present time of critical comparative study of this group of mollusks. A monographic work on American bellerophontids, similar to that by Weir (1931) on the British and Belgian Carboniferous Bellerophontidae, is greatly needed. I have hesitated to describe specimens of *Bellerophon* from the Deer Creek limestone as belonging to new species, but do so because they seem not to be referable to any described species.

*Occurrence.*—Ordovician to Triassic, world wide.

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EXPLANATION OF PLATE 1

*(All figures 2 times natural size)*

*Bellerophon singularis*, n. sp., from the Ozawkie limestone member, Deer Creek formation, 9.4 miles west of Lawrence, Kansas.

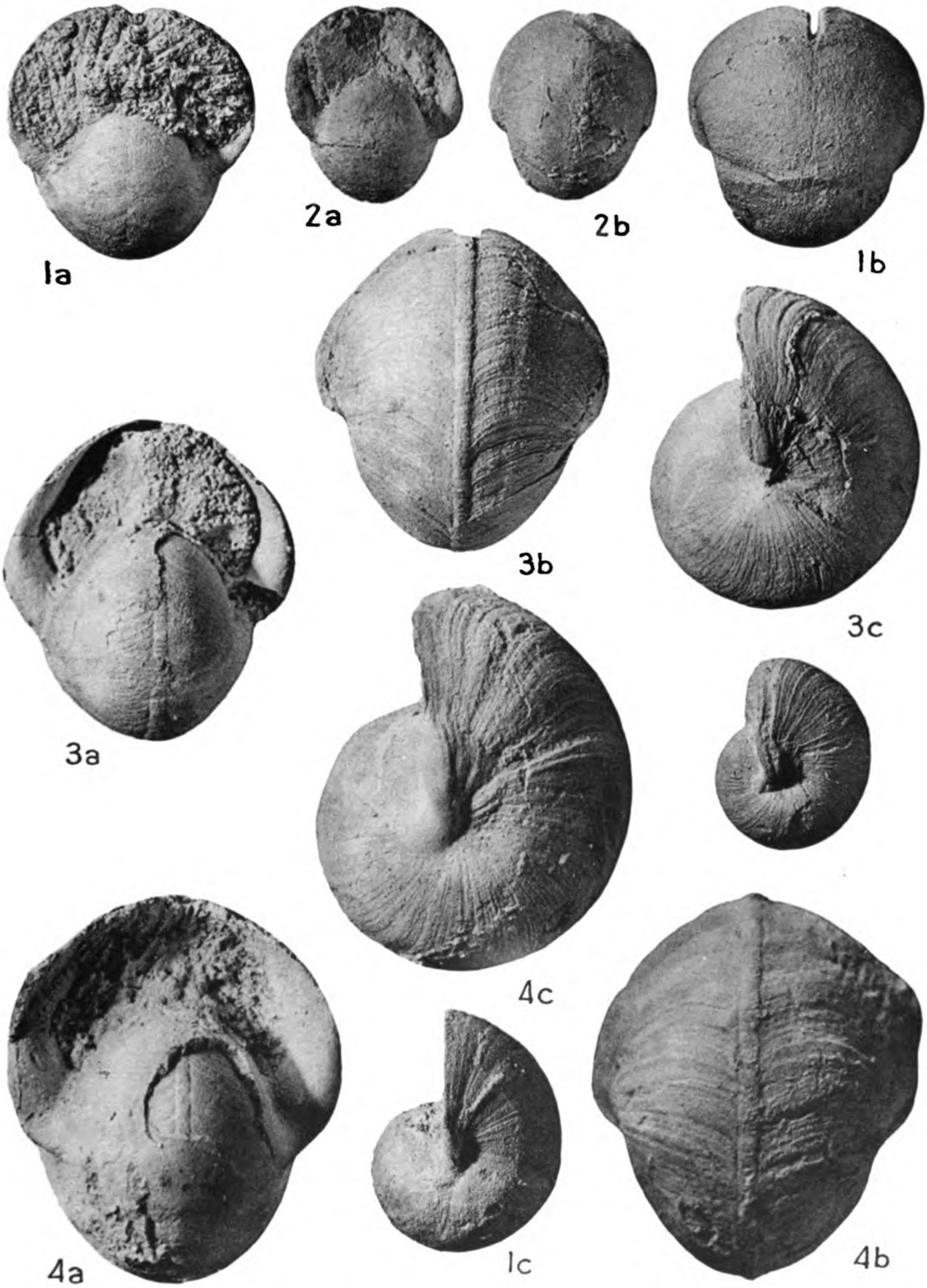
*1a-c*—Type specimen (Univ. of Kansas no. 32696), a very well preserved individual having complete apertural margin. *a,* Bottom view, showing broad transverse curvature and outline of the aperture. *b,* Top view, showing the deep narrow slit and absence of a very distinct slit band. *c,* Side view.

*Bellerophon graphicus*, n. sp., from the Ozawkie limestone member of the Deer Creek formation, 9.4 miles west of Lawrence, Kansas.

*2a-c*—An immature shell (Univ. of Kansas no. 3295J), bottom, top, and side views.

*3a-c*—The type specimen (Univ. of Kansas no. 32695), a nearly perfect adult shell. *a,* Bottom view showing apertural features and a part of the inductura. *b,* Top view, showing the prominent, slightly elevated slit band, and growth lines. *c,* Side view.

*4a-c*—The largest observed specimen (Univ. of Kansas no. 32695B). *a,* Bottom view, a part of the inductura broken away showing thickness of this layer. *b,* Top view. *c,* Side view.




Moore, Pennsylvanian Gastropods

### Bellerophon graphicus, n. sp.

**Plate 1, figures 2a-d, 3a-c, 4a-c; text figure 6C**

The shells assigned to this species are medium in size, slightly compressed laterally, the whorls expanding evenly, the aperture strongly crescentic, and the umbilicus closed. The greatest width of the shell is equal to about 85 percent of the greatest length, and the height of the aperture equals 30 percent of the greatest length. The surface is marked by closely spaced, slightly uneven growth lines that run almost straight from the umbilicus to a point within a few millimeters of the position of the slit band, whence they curve gently and evenly backward to the margin of the band. The slit band is gently convex transversely, and it is elevated above the surface of adjoining parts of the shell. The margin of the shell along the outer lip is very thin except in the region of the umbilicus, where it is markedly thickened. On the inner side of the aperture at a point directly opposite from the slit, the inductura has a thickness of about 0.6 mm, as measured on a specimen slightly larger than the type, but toward its margin the inductura thins gradually to a feather edge.

The collection of Ozawkie fossils from the locality west of Lawrence contains more than three dozen specimens that are referred to this species. They range in size from that of very immature individuals about 3 mm in greatest diameter to an observed maximum of 26.8 mm. Measurements of the type specimens are: greatest width, 20 mm; greatest length, 22.2 mm; height of aperture in plane of coiling, 6.1 mm; depth of slit, 5 mm; width of slit, 1.4 mm. The largest specimen has a greatest width of 22.8 mm and a length of 26.8 mm; height of aperture in plane of coiling 8.2 mm.

*Discussion.*—Among described forms, this new species seems most closely to resemble *Bellerophon crassus wewokanus* Girty (1915, p. 164, pl. 19, figs. 1-3). The aperture of the Deer Creek specimens clearly differs in outline from that of the Oklahoma specimens, which show an abrupt lateral expansion in the region of the umbilicus, producing an angulation in the outline of this part of the shell, and ratio of the width of the aperture in the plane of coiling to greatest length of the shell amounts to about 45 percent as compared to about 30 percent in *B. graphicus*. The appearance of *B. graphicus* in apertural view somewhat closely resembles species of *Waagenella*, such as *W. dumonti* (D'Orbigny) (Wenz,

p. 105) and W. *rownhamensis* Weir (1931, p. 816), but these shells are distinguished by a crescent-shaped callus that extends laterally from the aperture over the area of the umbilicus. No such deposit is present on the Kansas specimens.

*Occurrence.*—Ozawkie limestone member of the Deer Creek formation, sec. 22, T. 12 S., R. 18 E., 9.4 miles west of Lawrence, Kansas.

*Type.*—University of Kansas no. 32695.

### BELLEROPHON SINGULARIS, n. sp.

Plate 1, figures 1a-c

The shell described under this name has a subglobular outline. It is evenly rounded transversely so that curvature in this plane is about the same as in the plane of coiling. The aperture is broadly crescentic in outline, the lateral margin curving outward somewhat abruptly from the umbilical region, which is closed by lateral extension of the inductural deposits. The surface is smooth except for faintly marked growth lines. The slit band is not elevated, being observable, in fact, only on close scrutiny. The slit is narrow and deep. The inductural layer is very thin and confined to the inner parts of the shell, its anterior margin nearly a full whorl from the margin of the aperture. This is clearly shown by the type specimen, which is a perfect individual having all of the margin of the outer lip well preserved. Except for a slight backward curve near the slit band, the margin is almost perfectly straight, a feature that is shown also by the growth lines.

Dimensions of the type specimen are as follows: greatest width, 16.8 mm; greatest length in plane of coiling, 17.4 mm; height of aperture, 7mm; depth of slit, 6 mm; width of slit at base, 0.6 mm.

*Discussion.*—The shell that is here described is readily differentiated from associated specimens of *Bellerophon graphicus* by its greater relative breadth, flatter transverse curvature, and absence of a raised slit band. The ratio of the height of aperture to the greatest length is more than 40 percent as compared with about 30 percent in *B. graphicus*. The outline of the shell of *B. singularis* resembles illustrations of *B. crassus wewokanus* Girty, but the lateral margins project less abruptly from the umbilical areas, and the raised character of the slit band, which is clearly evident in Girty's specimens, is absent in *B. singularis*.

*Type.*—University of Kansas no. 32696.

*Occurrence.*—Ozawkie limestone member of the Deer Creek formation, sec. 22, T. 12 S., R .18 E., 9.4 miles west of Lawrence, Kansas.

## Genus Euphemites Warthin, 1930

*Euphemus* McCoy, *1844*, Synopsis of characters of the Carboniferous limestone fossils of Ireland, p. 25; ———, Waagen, *1880*, Palaeontogia Indica, ser. 13, vol. 1, p. 163; ———, DeKoninck, *1883*, Musee Roy. Hist. Nat. Belgique, Ann., vol. 8, p. 154; ———, Weir, *1931*, Roy. Soc. Edinburgh, Trans., vol. 56, p. 841.

*Euphemites* Warthin, *1930*, Oklahoma Geol. Survey, Bull. 53, p. 44; ———, King, R. H., *1940*, Jour. Paleontology, vol. 14, p. 150.

*Description.*—This genus comprises tightly coiled, highly involute shells of subglobular form that are small to medium in size. The aperture is not expanded. The anterior margin is indented by a comparatively shallow slit, lateral margins being characterized by deposits that overlap and conceal the umbilicus, and the posterior margin being marked by an inductura or callus that bears parallel revolving ridges. The spirally costate shell layer termed inductura (Knight, 1931, p. 180) commonly extends backward and upward so as to cover most of the first half of the last whorl; the remaining part of the last whorl is smooth, or marked somewhat faintly by revolving grooves and ridges, and in some sepcies it bears pairs of nodes bordering the slit band.

*Genotype.*—*Bellerophon urii* Fleming (1828, p. 338), designated by Waagen (1880, p. 163).

*General discussion.*—As originally proposed, McCoy's genus *Euphemus* included a somewhat heterogeneous group of shells, none of which was designated as genotype. From the species mentioned by McCoy, Waagen (1880, p. 163) selected *Bellerophon urii* Fleming to serve as genotype, and he restricted the genus to gastropods having characters like that of *E. urii*. Particularly distinguished by the revolving costae or lirae that cover the first part of the last whorl, the genus comprises a homogeneous, widely distributed group of forms that occurs in beds of Carboniferous and Permian age. Warthin (1930, p. 44) introduced the name *Euphemites* to replace McCoy's *Euphemus* because the latter term has been proved to be a homonyn. This fact was overlooked by Weir

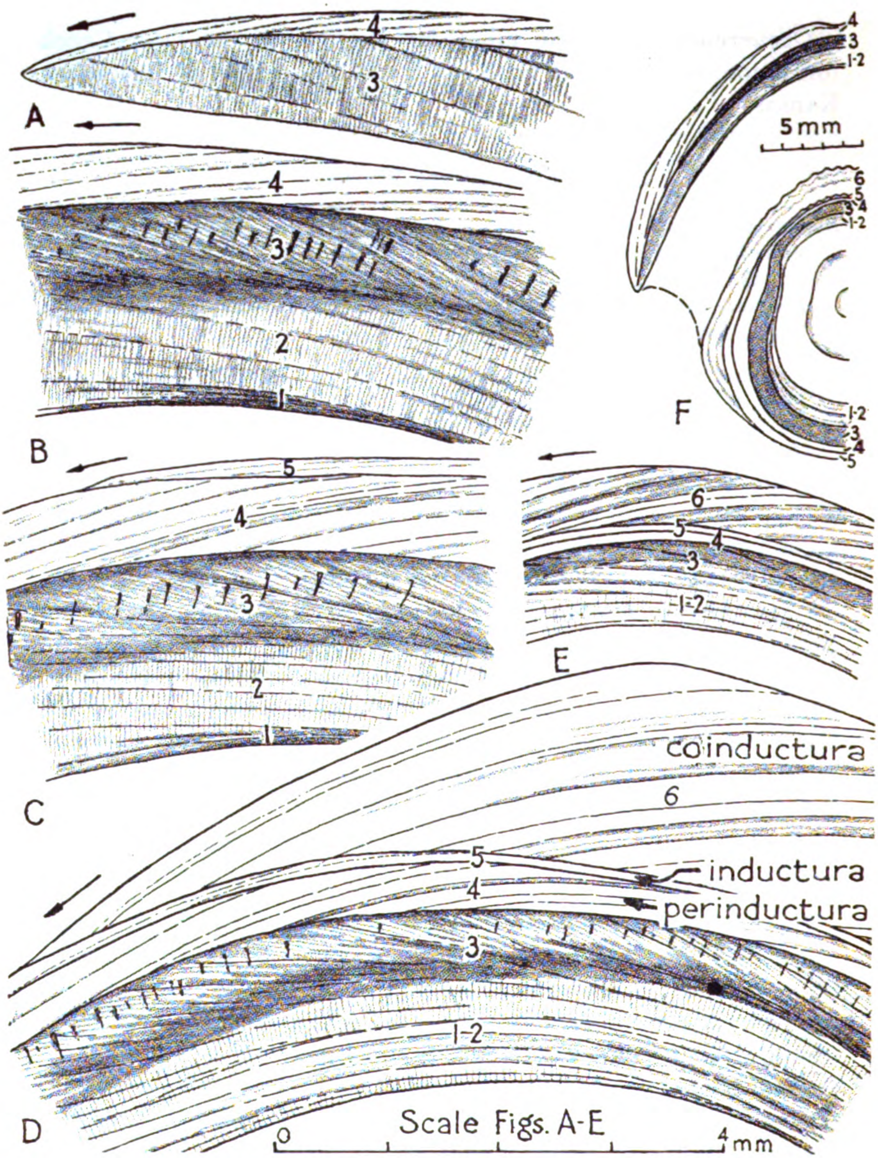



FIG. 1. Shell structure of *Euphemites*, camera lucida drawings from polished section of *E. callosus* (Weller) (*A-E*) from Illinois, a paratype, and from thin section of *E. vittatus* (McChesney) (*F*) from Texas. *A*, Median longitudinal section beginning at the base of the slit and showing structure in the slit band; cverlapping lamellae of the relatively thick prismatic layer 3

(1931, p. 841) in his monograph on British and Belgian Carboniferous Bellerophontidae.

Interest in the study of *Euphemites* attaches especially to origin of the difference in markings of the spirally ribbed and the relatively smooth portions of the last whorl. Almost universally these features have been regarded as distinctive peculiarities of surface ornament that are attained in the mature shell. It is indicated by some (Grabau and Shimer, vol. 2, p. 621) that the spiral ribs of the inner lip of the aperture do not extend beyond more than part of the preceding whorl, but transverse sections of any specimen show that the spiral markings actually extend back to the innermost whorl. Weir (1931, p. 841) reports that very young examples of *E. urii*, about 1 mm. in diameter, have prominent revolving ribs that fail to reach the anterior margin of the dorsum. Koken (1899, p. 393) regarded the spiral costae as formed by a scalloping of the mantle edge, the smooth part of the shell in adult specimens indicating a disappearance of the scalloped nature of the mantle edge when maturity of shell growth was attained. This, of course, does not agree with evidence that specimens of any size show a partially smooth last whorl, unless this is broken away. Waagen, and later, DeKoninck regarded the spiral markings as columellar in nature, for they were thought to correspond to the spiral grooves and ridges on the columella of some gastropods. Patently, however, the ribs of *Euphemites* are not confined to a columella and in some cases they extend dorsally to within less than a half whorl of the anterior lip of the aperture. King (1940, p. 150) states that "in all species except *E. callosus* (Weller) the inner lip is formed by the outer surface of the preceding volution without

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**indicate its formation by the marginal portion of the mantle inside the shell, whereas the overlapping lamellae of the thin smooth periductura (4) show that it was deposited by a reflected portion of the mantle outside of the shell. *B,* Median longitudinal section beginning 18 mm back of the slit; internally formed shell layers (1-3) are clearly differentiated from the externally formed perinductura (4). *C,* Similar section beginning 27 mm back of the slit, showing margin of the inductura (5) which bears longitudinal costae. *D,* Similar section beginning 53 mm back of the slit, which is about three-fourths of the outer whorl, showing all of the shell layers; the thick coinductura (6) is sharply distinct from subjacent inductura (5) and a definite line separates this layer from the perinductura (4). *E,* Similar section beginning 83 mm back of the slit. Relative positions of these sections are indicated on Fig. 4B. *F,* Transverse thin section of part of the shell of *E. vittatus* showing layers.**

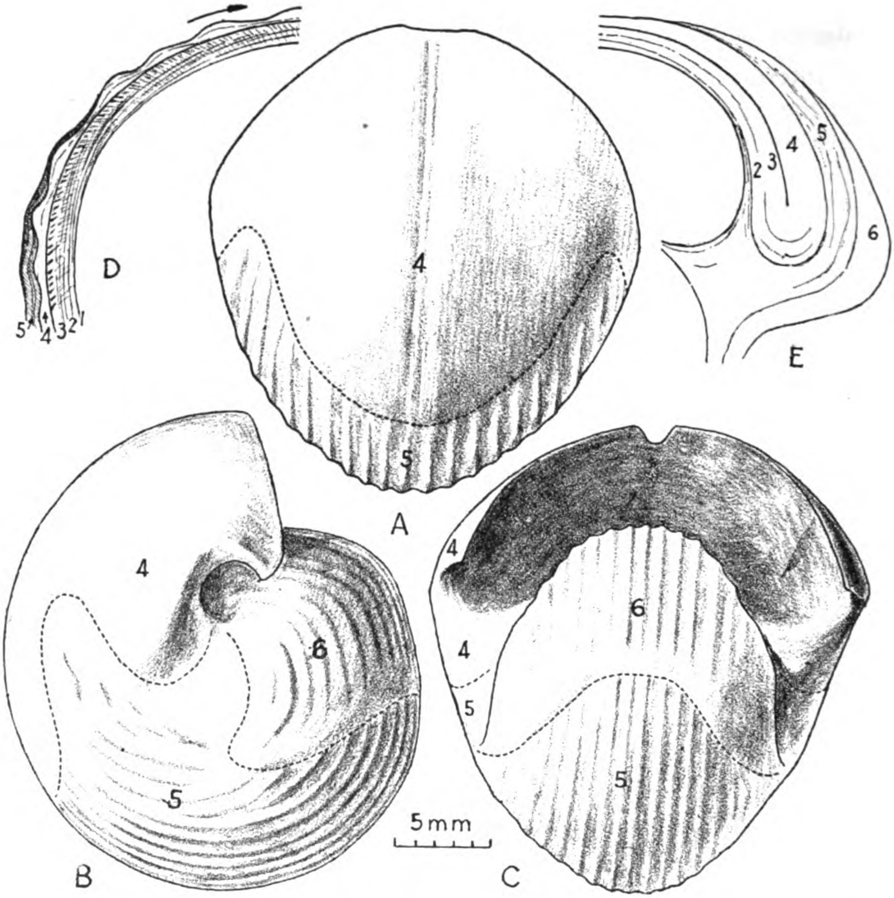


FIG. 2. External views of an early adult specimen of *Euphemites callosus* (Weller), a paratype, from Pennsylvanian rocks of Illinois, showing surface distribution of the smooth perinductura (4), the thin costae-bearing inductura (5), and the thick coinductura (6). *A*, Top view, position of the slit band indicated by a depression but no growth lines observable on the perinductura. *B*, Side view, showing adapertural extensions of the inductura (5) and coinductura (6) on the sides of the shell. *C*, Bottom view. *D*, Longitudinal section of part of the last whorl of a specimen of *E. callosus*, through nodose swellings that border the slit band, showing that the nodes are due to variation in thickness of shell layer no. 4 (perinductura). Arrow points toward aperture. *E*, Transverse section of part of the shell, joining that shown in D. The section indicates very clearly the thickening of layers toward the umbilicus and equivalence of layer no. 4, formed on the outside of the shell, to the main inside layers of the shell.

callosity of any sort" and it is evident from his description of the spiral markings on several forms of this genus that the ribs are thought to be external features of ornamentation, which differ in no essential way from the spiral markings of *Bucanopsis* or those of various pleurotomarids. These views King now recognizes to be erroneous. They were based on an inadequate understanding of the mode of constructing the shell in *Euphemites*.

The most detailed study of the shell structure in a species of *Euphemites* and the only one that seems to explain correctly the various peculiarities of the shell in this genus, is a contribution by J. Marvin Weller (1930). This paper is devoted to description of unusually well preserved specimens belonging to a new species of *Euphemites,* which he named *Euphemus callosus,* from lower Pennsylvanian rocks of Illinois. Weller's specimens, some of which even retain color markings, clearly reveal structural elements of the shell when studied in sections. An innermost very thin layer (designated no. 1 by Weller) seems to represent the nacreous lining of the shell interior, presumably secreted, as in other mollusks, by the surface of the mantle beginning a short distance back from its margin (figs. 1B,C). Next to this thin layer, proceeding toward the exterior of the shell, Weller recognizes two somewhat indistinctly divided layers that are characterized by gently inclined overlapping laminae. The laminae slope outward toward the exterior in the direction of shell growth, that is, toward the aperture. The structural attitude and overlap of elements in this part of the test plainly show that they are constructed by parts of the mantle lying within its margin, and also inside the growing edge of the shell aperture. The deeper of the two layers (Weller's no. 3) has a prismatic structure, the prisms of calcite being arranged normal to the planes of the overlapping laminae. The other layer (no. 2) is distinguished by a slight difference in color and seemingly by absence of a prismatic structure; it thins adaperturally and, according to Weller, disappears at a distance of 10 or 12 mm from the margin of the aperture (figs. 1A-E). Study of the specimen sectioned by Weller and of other sections prepared by me indicates that layer no. 2 is not a distinct structural element of the shell. It has a fine prismatic or fibrous nature that may be seen also in adjoining layers and where color distinctions happen not to be present, there is little basis for recognizing layer no. 2.

Next outside of the layers described is another (no. 4) composed of thin, overlapping laminae that slope adaperturally inward (figs. 1A-E). This layer extends to the very margin of the aperture and its structure shows that it must have been deposited by a portion of

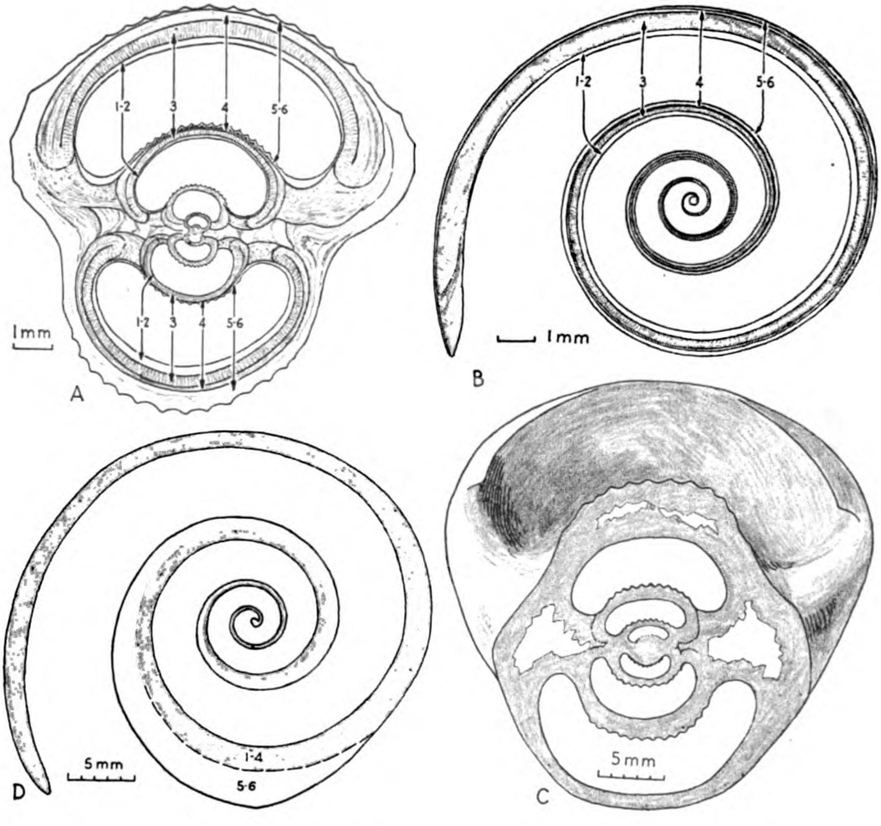


FIG. 3. Sections of the shell of *Euphemites,* showing shell layers. *A,* Transverse thin sections of a well preserved specimen of *E. vittatus* (McChesney), from the Wayland shale, upper Pennsylvanian of Texas. *B,* Median longitudinal section of another shell belonging to *E. vittatus,* also from the Wayland shale. *C,* Transverse section of *E. graffhami,* n. sp., from the Deer Creek limestone near Lawrence, Kansas.; crystal-lined cavities in the umbilical and inductural regions are incidental features that indicate solution of aragonitic shell substance during fossilization; different shell layers not clearly distinguishable. *D,* Median longitudinal section of another example of *E. graffhami* showing the abrupt thickening of the shell by inductural deposits (5-6).

the mantle that was turned backwards around the shell margin so as partly to cover the exterior of the test (fig. 4B). In parts of the shell, Weller distinguishes two additional layers, which he believes are made by posterior portions of the mantle. First is a thin layer (no. 5) that is recognizable mainly because it carries revolving costae or lirae like those extending backward on the outer surface of inner whorls (figs. 1C-E, 2A-C, 4A). In specimens studied by Weller, this layer is reported to extend to within about one-third volution of the apertural margin. The outermost layer (no. 6), on parts of the shell, is a relatively thick costae-bearing deposit, composed of thin laminae inclined adaperturally inward. This layer thins and disappears at a distance of about two-thirds of a volution from the aperture (figs. 1D-E, 2B-C, 4A-B).

Surface characters of the last half whorl in various species of *Euphemites* are obscurely described and figured in some cases and they seem to show variation in others. Referring to some specimens, definite statement can be made that this part of the shell is perfectly smooth, lacking detectable growth lines, and showing no sign of the presence of a slit band. This smoothness, especially that across the position of the slit band, is very difficult to explain unless one understands fully the mode of building the shell. Some examples reveal the position of the slit band indistinctly or clearly but the lateral portions of the shell near the aperture lack markings of any sort (figs. 4A-B). A few shells belonging to *Euphemites* show plainly marked growth lines that cross the band and adjacent areas, which are otherwise smooth (Weller, 1930, pl. 2, figs. 1a, 7d; King, 1940, pl. 24, fig. 5c). Weir (1931, p. 845), in describing specimens of *E. urii* (incorrectly spelled *E. urei* by him) notes that a smooth area extending backward about 15 mm. from the shell margin has a surface that is "ornamented only with faint curved lines of growth," but these are not visible on his illustrations. The explanation of one figure of this species (Weir, 1931, pl. 9, fig. 7), which plainly shows the slit band and growth lines, is given as "shell with spiral lirae stripped off showing . . . concrescent ornament underlying the lirate columellar callosity."

This summary of characters observed in previous studies of species belonging to *Euphemites* serves to direct attention to significant features shown by specimens of the new species here described.

*Perinductural shell layer.*—All specimens of *Euphemites* that have been studied by me show differentiation of the shell into parts that are formed on the inside and on the outside, respectively, of the surface defined by the trace of the growing edge of the shell. The successively superposed laminae of inside layers (nos. 1 to 3 as designated by Weller) slope adaperturally outward. The laminae of outside layers, on the other hand, are inclined adaperturally inward. The line of separation between the inner and outer groups of layers is very sharp in the cross section of some shells.

One of the outside layers (Weller's no. 4)—hereafter called the perinductura—extends to the margin of the shell aperture. It forms a continuous cover that reaches laterally to the umbilical areas and that surrounds each of the whorls. Exposed parts of the surface of this layer generally are smooth but faint growth lines may be visible. Sections of the shell of *Euphemites callosus*, cut through the nodelike swellings that occur as a row on each side of the slit-band area, reveal the fact that the protuberances are due solely to locally increased thickness of layer no. 4 (fig. 2D). There are no corresponding undulations in the subjacent shell layers. Several specimens of *E. graffhami*, n. sp., show clearly some features of the structure of this layer. Growth lines on the smooth exterior of the shell near the margin of the outer lip are seen to be the edges of thin laminae that dip into the shell in adapertural direction, that is, toward the growing edge, rather than away from it (pl. 2, fig. 1d). Obviously, these laminae were deposited by an anterior part of the mantle that was turned back on the outside of the shell along the outer lip. Thus, a shell layer was deposited that covers externally the relatively thick prismatic layer secreted by the marginal parts of the mantle lying just inside of the apertural edge. Even though the reflected outer part of the mantle is narrow, it builds a continuous cover or epitheca that is laid on the prismatic shell layer, plastering and concealing the exterior of the latter. The mode of construction of this epithecal cover and its relation to the shell as a whole are much like those of the periostracum,—the horny outer covering of the shell in many mollusks that is very rarely preserved in fossils. Neglecting the periostracum, the surface of the prismatic layer normally forms the exterior of the shell in gastropods, and it shows growth lines. The outer surface of the prismatic layer (Weller's no. 3) in *Euphemites* also shows distinct growth lines, but these lie underneath the covering layer that has been described. On some specimens of *Euphemites*, such as examples of *E. vittatus* (McChesney) from the Wayland shale of Texas (pl. 2, fig. 7), it is easy to demonstrate the growth lines of the prismatic layer (with edges of laminae facing away from the aperture) by chipping away part of the outermost layer close to the aperture. Some slightly broken specimens in our collection clearly show these features of the shell without mechanical preparation, fragments of the covering layer in the outer smooth portion of the shell being broken away so as to reveal the surface of the next lower shell layer, prominently marked by growth lines. For sake of clearness it should be stated that all of this discussion relates to the smooth part of the *Euphemites* shell, at or close to the apertural margin, and not to the costate region that begins some distance back from the margin.

The morphologic significance of the covering shell layer that is formed of adaperturally inward sloping laminae indicates the desirability of a special designation for it. Knight (1931, p. 180) has proposed the very useful term *inductura* (Latin—a covering) for the shell layer in gastropods that is "nearly always found covering the parietal wall and that in some cases is thickened to form a callus in the region of the inner lip of the aperture." For the outer shell layer formed by the reflected edge of the mantle along the outer lip of the aperture in *Euphemites* and some other gastropods, the name *perinductura* (Latin—a complete covering) is here proposed. The perinductura is a continuous shell layer on all the whorls, whereas the inductura covers only inner whorls and never more than a part of the last whorl. The perinductura is layer no. 4, as described by Weller (1930) and shown in accompanying diagrams (figs. 1-5) given in this paper.

The perinductura of some shells may be as thick as the prismatic layer on which it rests, but commonly it is much thinner than this layer, at least in the median portion of each whorl adjacent to the slit band. In longitudinal sections of well preserved shells the perinductural layer is commonly distinguishable clearly around each whorl back to the small inner ones, where it is reduced to a very thin film. It is sharply defined also in transverse sections of the shell, being separated from adjoining layers by a cleanly marked line. Inasmuch as the perinductura is formed only by the marginal anterior and anterolateral parts of the mantle that are bent back over the outer lip, this layer may be regarded as en-

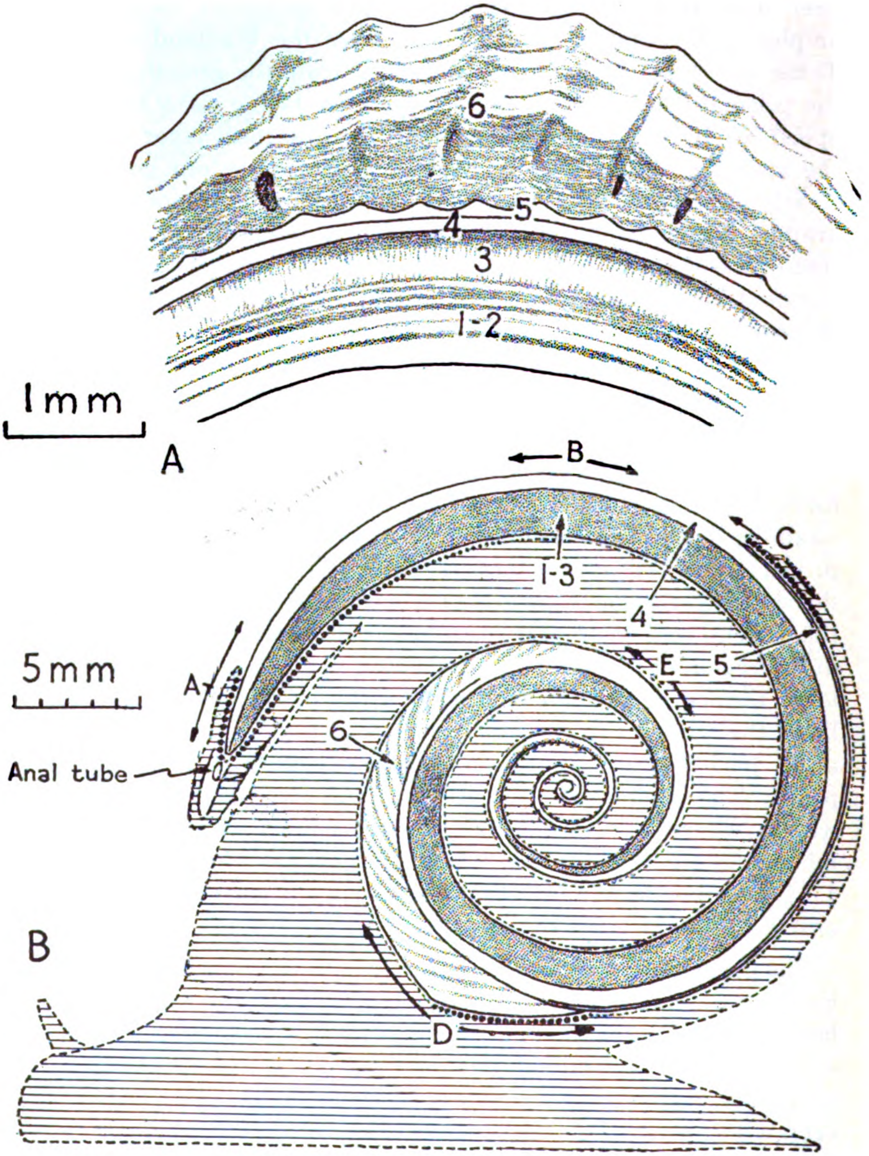


**Fig. 4.** Sections of the shell of *Euphemites*. *A*, Camera lucida drawing of part of a transverse section of the shell of *E. callosus* (Wheller), in the region of the thick coinductura, about three-fourth of a volution from the margin of the aperture; openings in the lower part of layer 6, located in the positions of the costae, are connected by curved lines of superposed crenulations with

tirely distinct structurally from other elements of the shell. In a sense this is true, but transverse sections (figs. 2E, 3A) reveal an abrupt curvature of the laminae of the perinductura near the umbilicus so as to join the layers secreted by the mantle on the inner side of the shell. This is readily understandable and expectable. It indicates that shell layers 2 and 3, which are not clearly distinguishable from one another, are secreted by parts of the mantle inside the shell in continuity with layer 4 (perinductura), which is secreted by reflected marginal parts of the mantle all along the front and sides of the outer lip.

Sections of the perinductural layer of some specimens of *Euphemites callosus* show a prismatic or fibrous structure that crosses the inclined laminae approximately at right angles. This structure is very well defined in some laminae but less clearly marked in others, which are darker and seemingly denser. The direction of inclination of the fibrous structure seen in the perinductura is sufficiently different from that of the layer beneath the perinductura to make distinction easy, and it may be more evident than the dissimilar slopes of component laminae of the two layers.

*Inductural shell layer.*—The inductura of *Euphemites* is a costae-bearing shell layer. The costae are rounded or sharp-crested ridges that run longitudinally around the whorls, but those of the umbilical regions may be discontinuous and the segments may be somewhat offset one from another. The laminae slope adaperturally inward in manner and degree corresponding almost exactly to structure of the perinductura. Notwithstanding this similarity of structure, the boundary between inductura and perinductura is very sharp, as seen in sections of the shell, because these layers are formed by entirely different parts of the mantle. The boundary between the layers is not sharp, however, as seen in surface views of the shell, because the feather-edge of the front margin of the inductura makes this edge imperceptible

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the surface ridges developed on this layer. *B*, Diagram showing location of the detailed drawings of shell structure given in Fig. 1 and showing inferred regions of active shell secretion by parts of the mantle (indicated by enlarged dots); there seem to have been four chief shell-secreting areas, one extending backward from the outer margin of the aperture on the inside of the shell (layers 1-3), another just outside the edge of the aperture (perinductura), a third on the outside of the shell at the top and sides (thin costate inductura), and a fourth in the position of the inner lip (coinductura).

except as defined by fading of the costae. The inductura is very thin in some species of *Euphemites* but thick in others. It may be less than one-half as thick as the perinductura, which is the case in *E. callosus* (fig. 1), or it may be much thicker than the perinductura, as seen in *E. vittatus* and *E. graffhami*. The inductura may show an inclined fibrous or finely prismatic structure, like that of the perinductura.

Transverse sections of the inductural shell layer in specimens of *E. vittatus* (fig. 3A) show the existence of small tubelike cavities running longitudinally at the base of this layer beneath the costae. The inductura is a wavy layer having nearly uniform thickness along the ridges and grooves, rather than one having notably greater thickness along the ridges. The part of the mantle that secreted the inductura of *Euphemites* must have borne folds running longitudinally, and unless there was excess deposition of shell substance beneath the upraised parts of the mantle, or unless localized evenly spaced areas of the mantle were more active in shell-making, hollow spaces would be formed beneath the costae. The terminations of the inductural costae at the growing edge of this layer do not show any openings, however, in so far as I have been able to observe, and this indicates that normally the inductura is a solid layer.

The front edge of the inductura extends within one-half of a volution from the outer lip in some species of *Euphemites,* such as *E. regulatus,* n. sp., and *E. vittatus*. Well-preserved examples of *E. graffhami* show that the front margin of the inductura is three-fourths of a volution from the outer lip. Transverse sections of *E. callosus* and *E. vittatus* indicate the presence of especially thick inductural deposits in the umbilical region. The side walls of the shell where whorls adjoin are principally built by the inductura.

*The coinductural shell layer.*—The thick deposits that Weller designated as shell layer no. 6 are a very distinct structural element, as indicated by studies of *Euphemites callosus* (figs. 1E, F, and 4A). The laminae of this layer slope forward toward the aperture in the manner of foreset beds of a delta and each lamina is overlapped adaperturally by later-formed laminae. The line of division between the laminae of layer no. 6 and the subjacent inductura is perfectly sharp. The laminae of the inductura also are inclined toward the aperture but at much lower angle than in the case of laminae of layer no. 6. Thus, the inductural laminae suggest bottomset beds of a delta. One might suppose that the laminae of these two layers are connected in the manner of deltaic bottomset deposits, but this is definitely not the case in *E. callosus*. Layer no. 6 overlies the inductura disconformably. If deposits were formed by parts of the mantle between the areas of active shell secretion that respectively produced the inductura and the thick layer above it (fig. 4B), resorption must have removed such shell material before layer no. 6 was laid down.

The name *coinductura* (Latin, cum (co)—in association with, inductura—covering) is suggested for the shell layer that in species such as *Euphemites callosus* covers part of the inductural deposits. The coinductura is chiefly developed as a callus on the inner lip of the aperture but it extends laterally over parts of the umbilical region and it seems to be continuous with thin deposits on the inside of layers nos. 2 and 3,—that is, part or all of the obscurely differentiated layer no. 1 (fig. 3A). The surface of the coinductura is marked by revolving costae, that correspond in general features to the longitudinal ridges of the inductura, but the number and position of the costae on the two layers may not be the same (fig. 4A). Commonly the coinductural costae become faint or disappear before the front edge of this layer is reached (figs. 2B, 2C), so that the ridges of the coinductura and inductura are not confluent even in the case of their approximate equivalence in size and spacing. In some shells the costae of the coinductura are fewer in number and they are more widely spaced than those of the underlying inductura. This is shown both by examination of the surface of the shell and by transverse sections (fig. 4A). Another feature that may be seen in some transverse sections is the presence of open spaces beneath the costae, but they do not occur beneath all of them and the manner in which they interrupt the wavy laminae of the coinductura suggests that the openings are due to a peculiar localized resorption or to solution.

The uppermost parts of the successively deposited laminae of the coinductura are inclined slightly less steeply than the median and lower parts. Each lamina is terminated upward and backward from the aperture, without being extended in the manner of topset beds of a delta. This indicates that the area of shell secretion by this part of the mantle is restricted to a comparatively narrow transverse belt corresponding to the "front of the delta." If deposits were made back of this front, toward the interior of the shell, these were resorbed before fossilization, but there is no evidence at all to support the hypothesis of such deposition and resorption.

### EUPHEMITES GRAFFHAMI, n. sp.

Plate 2, figures 1a-d, 2, 3a-b, 4a-b, 5a-b, 6a-b; text figures 3C-D.

Description of this species is based on study of about a dozen specimens that range in greatest diameter from about 15 to 37 mm.

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#### EXPLANATION OF PLATE 2

*(All figures, except 1d and 7, 1.5 times natural size)*

*Euphemites graffhami*, n. sp., from the Ozawkie limestone member of the Deer Creek formation, west of Lawrence, Kansas.

*1a-d*—Type specimen, K.U. no. 32691. *a*, Top view showing the perinductura exfoliated from the anterior part of the slit band but extending across it in part of the view. *b*, Side view, showing closed umbilicus, angulated projection at lateral margin of the outer lip of the aperture, growth laminae of the perinductura, and the thick callus marked by costae. *c*, Bottom view, showing form of aperture and the clearly differentiated area of the callus, which is synonymous with inductura in this species. *d*, Small portion of surface of the perinductura, enlarged to show edges of laminae that slope adaperturally (in direction of arrow).

*2*—Specimen 32691-B, top view, perinductura exfoliated in the region of the slit band, which reveals the growth lines of the prismatic shell layer (no. 3).

*3a,b*—Specimen 32691-I, an individual of average size having complete apertural margins. *a*, Bottom view, showing sinus, the thin edge of the outer lip of the aperture and thick, rounded lateral margins; callus well developed but costae indistinct. *b*, Side ciew, showing geniculation produced by the callus and the "ear" at outer lateral edge of the aperture.

*4a,b*—Specimen 32691-G, a very robust shell. *a*, Top view, showing the smooth perinductura. *b*, Side view, outer lip broken.

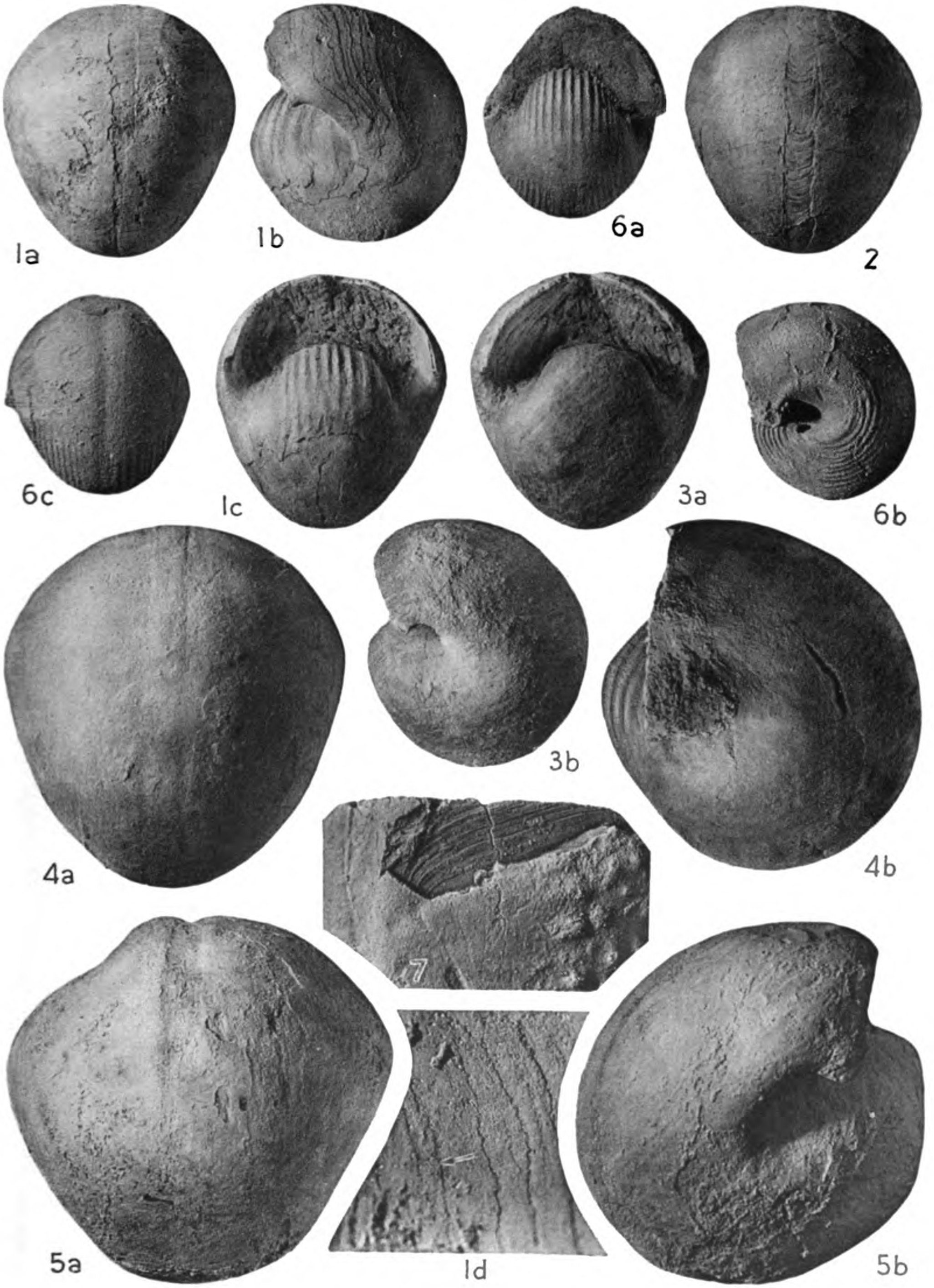
*5a,b*—Specimen 32691-C, the largest observed individual, a broad shell. *a*, Top view, the slit band entirely covered by the perinductura, but its position clearly shown by a depression. *b*, Side view, the outer margin of the aperture complete.

*Euphemites regulatus*, n. sp., from the Ozawkie limestone member of the Deer Creek formation, west of Lawrence, Kansas.

*6a,b*—Type specimen, K.U. no. 32692, a part of the outer lip broken away. *a*, Bottom view, showing the transverse outline of the shell ,and the costate areas of the inductura with smooth zone between the callus (layer 6) and the anterior thin portion (layer 5) of the inductura. *b*, Side view, showing umbilical region; costae and smooth perinductura.

*Euphemites vittatus* (McChesney), a specimen from the Wayland shale member of the Graham formation, Cisco group, 1 miles south of Gunsight, Texas.

*7*—A small portion of the shell near the margin of the aperture, showing the perinductura and inductura broken away from part of the prismatic shell layer (no. 3), which shows growth lines (enlarged).




Moore, Pennsylvanian Gastropods

The average size of mature individuals, therefore, is large for the genus. The shell is subglobular, greatest width being approximately equal to the longest diameter in the plane of coiling. The surface of the shell is evenly curved transversely except for a slight flattening on the dorsum, which shows by a faint depression the position of the slit band. Except for faint growth lines, the last three-fourths of the outer whorl is smooth. The aperture is low and arcuate. The outer lip is very thin at the edge and the lateral extremities project in an angular manner; the remainder of the lip is nearly straight except for the sinus in the position of the slit band. The sinus is about 7 mm wide at the front and 7 mm deep, narrowing posteriorly to the width of the slit band, which is about 3 mm. Backward from the apertural margin the shell increases in thickness to about 2 mm in areas adjoining the slit band and to 4 mm or more in areas low on the sides toward the umbilicus. The inner lip is formed by a thick callus that bears revolving grooves and ridges. Typically, the grooves are broad smooth-bottomed shallow furrows, but in some specimens they contain faint subsidiary ridges. The costae between the furrows are sharply rounded transversely but not strongly elevated. Those on slopes toward the umbilicus become increasingly faint but they are continuous adaperturally to the margin of the callus. The considerable thickness of the callus in the region of the inner lip and its abrupt adapertural thinning produces a nearly right-angled geniculation near the beginning of the last whorl.

All of the smooth part of the outer volution seems to be formed by the surface of the perinductura. The upper edges of the laminae of this layer belong to successively later-formed laminae as one approaches the margin of the shell aperture and the laminae are inclined toward the aperture. The structure is that which is typical of the perinductura, although it also characterizes the inductura. Of course, the area close to the aperture can be covered only by perinductura, but on parts of the shell extending back from about one-half of a volution from the outer lip, the smooth surface conceivably might be formed by an inductural layer overlying the perinductura. If so, such supposed inductura bears no costae and there is no perceptible division between it and the perinductura. Recrystallization of the shell substance makes study of cross sections valueless for differentiation of these layers. No evidence is seen that an inductura reaches adaperturally beyond the margin of the thick costate area of the inner lip of *Euphemites graffhami*. Also, no reason except position seems to be given for classifying the thick costae-bearing shell layer as coinductura, or as combined inductura and coinductura. Therefore, it will be regarded as a thick inductura.

The inductura of *Euphemites graffhami* has a laminated structure that corresponds exactly to that of the perinductura, except for steepness of slope of the laminae. The inclination of the laminae is adaperturally inward and overlap of the laminae is toward the aperture. In *E. graffhami,* the margin of the inductura is strikingly sinuate; from a position at the slit band that is fully three-fourths of a whorl from the outer lip of the aperture, it curves to the proximity of the lateral margin of the aperture, extending around and beyond the umbilical region.

Measurements of the type and of three other representative specimens are given in the following tabulation.

*Measurements of Euphemites graffhami, n. sp., in millimeters*

| | Type | 60871B | 60871C | 60871H |
|---|---|---|---|---|
| Greatest width | 21.3 | 22.0 | 37.0 | 33.0 |
| Greatest diameter in plane of coiling | 23.4 | 23.5 | 36.0 | 32.7 |
| Height of aperture | 6.7 | 6.5 | 7.8 | 7.1 |
| Width of slit band | 2.5 | 2.5 | 3.0 | 2.3 |

*Discussion.*—The smoothly rounded subglobular form and large size of *Euphemites graffhami,* as well as the unusual thickness of added shell layers in the region of the inner lip, are points of resemblance to *E. callosus* (Weller), which occurs in rocks of late Des Moines age in Illinois. Peculiarities of the costate markings of the inductura and coinductura, and the occurrence of paired nodes along the slit band of *E. callosus* serve readily to differentiate Weller's species. Also, the perinductura forms a much greater part of the shell surface in *E. graffhami* than in *E. callosus*. The presence of differentiated inductural and coinductural areas in *E. regulatus,* n. sp., distinguishes it from the species here described. No other described *Euphemites* seems to be sufficiently similar to this form from the Deer Creek limestone to make additional comparisons necessary.

*Type.*—Type, University of Kansas, no. 60871, collected by Allen Graffham. Other specimens studied, nos. 60871B, C, E, F, D, H, I, J, K, and L.

*Occurrence.*—Upper part of the Ozawkie limestone member, Deer Creek formation, Shawnee group, Virgil series, Pennsylvanian; locality 3269, on U.S. highway 40, 9.4 miles west of Lawrence, Kansas.

### Euphemites regulatus, n. sp.

**Plate 1, figures 6a-b**

Four specimens of *Euphemites* in the collection from the Ozawkie limestone clearly belong to a species that is distinct from *E. graffhami*. They differ from examples of the latter, including small juvenile shells, in the outline and relative thickness of the shell, lack of prominent shell deposits in the umbilical region, and especially by characters of the inductural layers. As in *E. callosus,* two inductural layers, besides the perinductura, are distinguishable. The lower one, the inductura proper, reaches adaperturally within about one-fourth volution of the margin of the outer lip. The surface of this layer is marked by low, even-spaced, distinct revolving ribs that extend farthest forward on the lateral slopes. The upper layer, which is the coinductura, forms a barely perceptible callus, the margin of which is slightly more than one-half a volution from the aperture. Most of the surface of this layer is marked by strong, somewhat sharp-crested, evenly spaced ribs, but these die out in the direction of shell growth so that a zone at the front of the coinductura is smooth. This smooth zone separates the respective ribbed areas of the inductura and coinductura. Comparison of the costate portions of the shell show that the number and position of the ribs in the two areas do not quite match. There are more and finer ridges on the inductura than on the coinductura. The latter has about 9 distinct ridges on each side of the center line, whereas 12 or 13 are counted in corresponding parts of the former.

The nearly smooth area that separates the ribbed inductural and coinductural surfaces may be explained as a filling of the grooves in the inductura by marginal deposits of the coinductura so as to obliterate the costate markings of the lower layer. At the same time one must presume that ribs of the coinductura do not extend to the very edge of this deposit. Alternatively, it is possible that ridges of the inductura may be resorbed in a belt just in front of the advancing coinductura, making a smooth surface that is covered "disconformably" by coinductura. Recrystallization of the shell prevents determination of contacts between layers by study of cross sections. No indication of any resorption of shell layers has been seen, however, in sections of other species of *Euphemites*.

The thin perinductura extends over all the anterior part of the shell, concealing growth lines on the prismatic layer. The position of the slit band is shown by a faint but distinct depression that has well marked borders in the area of the periductura and in the region of the inductura, where it is bounded by broad, low ridges. The markings that show the position of the slit band disappear, however, where they meet the margin of the coinductura.

The lateral margins of the aperture are formed by the thin sharp angled edge of the shell, and the lateral extremity of the outer lip is somewhat strongly produced. These characters give a side view of the shell a different appearance from that produced by the thick rounded margin at the sides of the aperture in *Euphemites graffhami*.

Measurements of the type specimen of *Euphemites regulatus* are: greatest width 17.5 mm, diameter 19.5 mm, height of aperture 5.8 mm. The ribs on the callus are 0.6 mm apart, and the height of the ribs above adjoining furrows is only about 0.2 mm.

*Discussion.*—Specimens of *Euphemites graffhami* are distinctly broader and less strongly rounded transversely than shells belonging to *E. regulatus*. Immature individuals belonging to *E. graffhami*, smaller than the type of *E. regulatus*, show these distinctions of configuration as well as do the largest specimens of *E. graffhami*. Definite absence of a costate inductura in advance of the margin of the callus in *E. graffhami* distinguishes this species from *E. regulatus*.

*Euphemites callosus* differs from *E. regulatus* in transverse profile, in the greater prominence and wider spacing of the costae, and in the strongly marked thickening of the coinductura. The position of the slit band is not defined in *E. callosus* in any part of the inductural region, although it is well marked in the area of the perinductura.

Among described species, *Euphemites regulatus* seems most closely to resemble examples that have been identified by R. H. King (1940) as belonging to *E. vittatus* (McChesney). Numerous specimens in our collection that have been identified as *E. vittatus* were obtained from the Wayland shale member of the Graham formation in north-central Texas. These resemble the new species here described in general form and markings, except that ribs of the Texas specimens are less regular and somewhat more elevated and widely spaced, the umbilical slopes being marked by numerous discontinuous costae, also. The Texas specimens show no clearly marked differentiation of areas representing inductura and coinductura and there is no perceptible shell thickening in the form of a callus.

*Type.*—Type specimen, University of Kansas no. 32692.

*Occurrence.*—Upper part of the Ozawkie limestone member, Deer Creek formation, locality 3269, on U.S. highway 40, 9.4 miles west of Lawrence.

## Genus Warthia Waagen, 1880

This genus comprises Upper Carboniferous and Permian bellerophontids of small size, subglobular or laterally slightly compressed form, the umbilicus closed, and the surface entirely smooth except for very faint growth lines. The outline of the shell closely corresponds to that of *Euphemites* in that there is no increase in the rate of expansion of the shell near the aperture, and lateral margins of the aperture are produced in an angular manner. There is a moderately deep sinus that broadens anteriorly, but there is no true slit or slit band and the shell bears no longitudinal costae.

*Genotype.*—*Warthia brevisinuata* Waagen.

*Occurrence.*—According to Wentz (1938, p. 108) *Warthia* is known only from Upper Carboniferous and Permian rocks of India and Australia. The new species here described under the name *Warthia kingi* seems unquestionably to belong to this group and thus extends records of occurrence of the genus to include North America.

### Warthia kingi, n. sp.

**Plate 3, figures 11a-b, 12a-c, 13a-b; text figure 5**

Some of the bellerophontid shells in the Deer Creek collection are separated from the rest by their smoothly rounded but laterally compressed form, small average size, and the presence along the anterior midline of the outer lip of a sinuate depression that is both wider and distinctly more flaring than the true slit depressions, as seen in *Bellerophon* and *Euphemites*. A thin perinductura covers all the shell exterior concealing growth lines on the surface of the prismatic shell layer. Very well preserved specimens, in which the perinductural layer is complete, are perfectly smooth or they bear extremely faint growth lines. The perinductura is partly exfoliated on one specimen (fig. 5), so that the surface of the underlying layer may be seen. This layer bears strongly marked growth lines that show successive positions of the apertural sinus. An inductural layer, if present, cannot be distinguished on any of the specimens at hand.

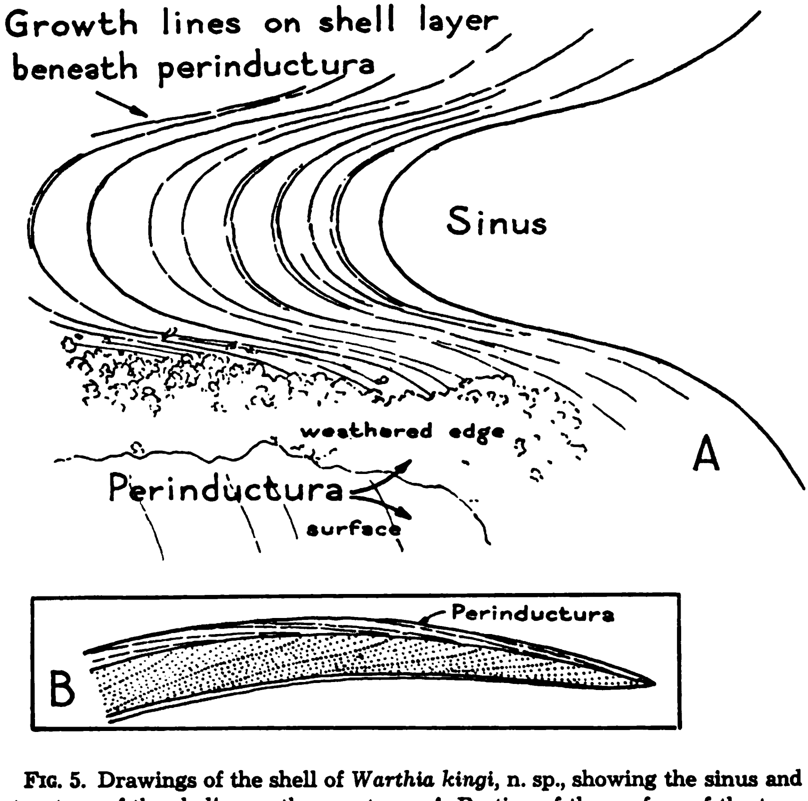



FIG. 5. Drawings of the shell of *Warthia kingi*, n. sp., showing the sinus and structure of the shell near the aperture. *A*, Portion of the surface of the type specimens showing the sinus and growth lines on the outside of the prismatic shell layer in an area that has been uncovered by exfoliation of the perinductura. *B*, Diagram of the shell near the aperture, showing inner shell layer covered by a thin perinductura.

Measurements of the type specimen follow: greatest width, 10.5 mm; greatest length, 12.3 mm; height of aperture, 3.5 mm. A specimen that was longitudinally sectioned (pl. 3, fig. 13b) has a greatest length of 14 mm. and height of aperture of 4 mm.

*Discussion.*—The new species here described generally resembles the genotype species, *Warthia brevisinuata,* and also *W. polita* Waagen, from the upper Productus limestone of India. Adult examples of the Kansas species are somewhat larger, the sinus is slightly less flaring, and the lateral margins of the aperture are more angular than in the forms described by Waagen. The shape of the shell of *W. kingi* is readily distinguished from that of associated specimens of *Bellerophon,* but resemblance in outline to *Euphemites* is so marked that one of the specimens was sectioned and a part of the matrix of the interior of the shell removed in order to determine positively the presence or absence of a costate inductural layer. Conceivably such a layer might be present and yet not reach to a point where it would be visible at the aperture of the shell. No such costate layer exists in the shells under consideration.

This species is named for my associate, Ralph H. King, of the University of Kansas, who has published a number of papers on Pennsylvanian fossils and who aided in collection of the specimens from the Deer Creek limestone.

*Type.*—University of Kansas no. 32694. We have four additional specimens.

## Genus KNIGHTITES, n. gen.

A new genus of bellerophontid gastropods that is introduced here has about 4 volutions in mature specimens, an open umbilicus, the aperture moderately expanded at nepionic (embryonic) stage and broadly flaring in gerontic (old age) stage. The surface of juvenile shells is cancellated, evenly spaced revolving lirae of two or more orders in size being crossed approximately at right angles by close-spaced corrugations and growth lines. The revolving ornamentation becomes progressively weaker toward the aperture in gerontic specimens and the transverse marks, especially growth lines, progressively stronger. The slit and slit band are prominent. They are bounded laterally by faint to moderately strong ridges that in ephebic (adult) and gerontic stages of shell growth bear paired tubular hornlike projections that are directed obliquely forward. The inductura is thin and smooth, its margin retracted adapically in crossing the region of the slit band and extended adaperturally on the sides of the initial part of the last whorl. Late neanic (adolescent) and ephebic shells show an abrupt thickening of inductural deposits back from the margin of

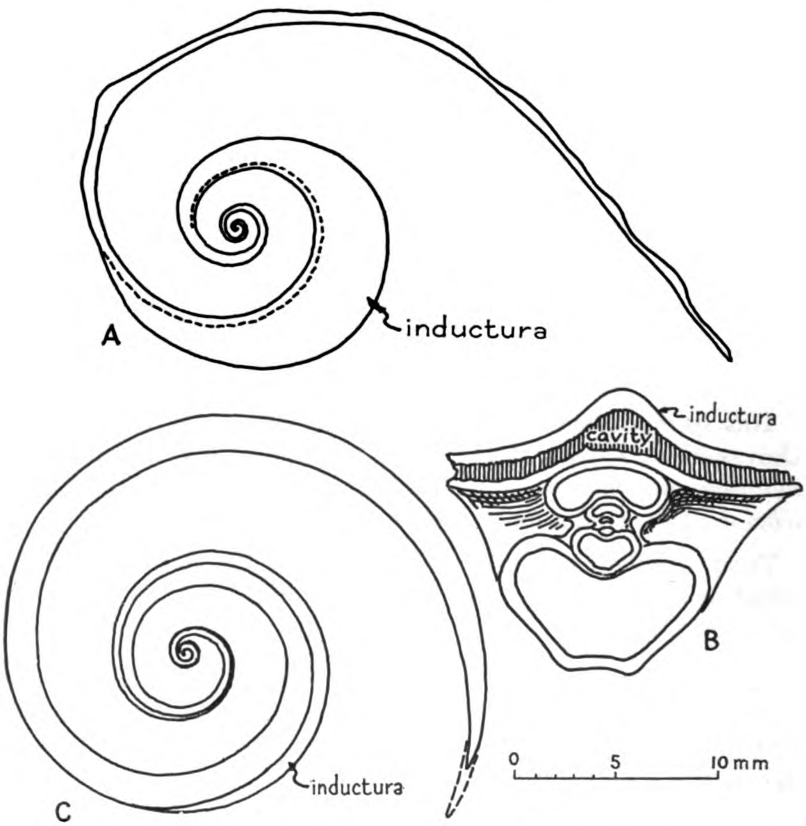



FIG. 6. Sections of the shell of *Knightites* and *Bellerophon*, from the Deer Creek limestone near Lawrence, Kans. *A*, Median longitudinal section of a moderately large specimen of *Knightites multicornutus*, n. gen., n. sp., showing the flaring last whorl and thick callus. *B*, Transverse section of part of another specimen of this species showing the sharply elevated nature of the median area of the callus and the cavernous nature of this deposit, probably a peculiarity due to weathering. *C*, Median longitudinal section of the shell of *Bellerophon graphicus*, n. sp., showing even expansion of the whorls and moderate thickness of the inductural layer (callus).

the inductura. In some specimens the adapertural margin of the inductura is sharp, but recrystallization of the shell layers prevents determination of structure by means of thin sections. The inductura is greatly thickened, especially in the central part, so that its surface is arched much more sharply than the transverse cross section of the preceding whorl on which it rests.

*Genotype.*—*Knightites multicornutus*, n. sp., Deer Creek limestone, Virgil series, Pennsylvanian, northeastern Kansas.

*Discussion.*—The most interesting character of this gastropod is the appearance of paired tubular hornlike projections of the shell after the animal attained an ephebic growth stage. The horns are arranged in pairs on opposite sides of the slit band and they occur in regularly spaced positions longitudinally. The most prominent horns lie nearest to the aperture. Their size diminishes backward from the aperture until they are reduced in size to mere knobs or large tubercles, and excepting the pair of projections nearest to the aperture, the shell seems not to be perforated in these places. The significance of the paired prominences is discussed in later paragraphs contributed by J. Brookes Knight, who examined these gastropods during a visit to Lawrence in July, 1940. His interpretation of them given orally at some length was revised in letters sent to me subsequently. I appreciate greatly Mr. Knight's kindness in contributing to this study and in permitting me to use his discussion and sketch illustrations.

Almost as interesting as the spinelike projections of the mature shell just noted, is the change in appearance of these bellerophontids from juvenile to ephebic and gerontic stages in their growth. The young specimens have a strongly marked cancellated ornamentation, only a slightly expanded aperture, and they reveal no sign at all of the protuberances arranged at intervals along the slit band. Gerontic specimens, on the other hand, have very weak or even obsolete revolving ornamentation, accentuated corrugations or growth lines, a broadly flaring aperture, and, most distinctive of all, several pairs of strongly protuberant knobs or horns. Given these two extremes, it is hardly to be guessed that they represent a single species. Indeed, during preparation and first study of the specimens, I was sure that they represented two distinct species. The group of nearly five dozen specimens of this gastropod that is now available for study allows no question as to the development of the broadly flaring cross-wrinkled horn-bearing shells out of the cancellated small shells that lack knobs or horns. All gradations between the extremes are seen. Attainment of the ephebic stage in *Knightites multicornutus* seems logically defined as being marked by the first appearance of low paired spouts adjacent to the slit band. Such specimens may be less than one-fourth as large as the most robust gerontic individuals. The first-formed of the paired openings are raised only a little distance above the adjacent shell surface, and they are directed anteriorly almost in the plane

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### Explanation of Plate 3

*(All figures, except 9, 1.5 times natural size)*

*Knightites multicornutus*, n. sp., from the Ozawkie limestone member of the Deer Creek formation, west of Lawrence, Kansas.

*1a,b*—A rotund juvenile specimen (no. 32693X), showing undepressed slit band. *a*, Top view. *b*, Side view.

*2a,b*—A slightly larger specimen (no. 32693AJ), showing elevation of borders of the slit band. *a*, Top view. *b*, Side view, showing open umbilicus.

*3a,b*—An immature specimen (no. 32693AH) showing strong riblike elevations at the margins of the slit band. *a*, Top view. *b*, Side view.

*4*—An immature specimen (32693M) that shows well-marked transverse and logitudinal lines.

*5a,b*—A shell (no. 32693Q) in which the rounded elevations at the sides of the slit band are produced in a pair of short spouts at the anterior margin. *a*, Top view. *b*, Bottom view.

*6a-d*—The type specimen (no. 32693), an adult individual having well developed hornlike spouts and showing the anterior margin of the aperture almost completely. *a*, Top view. *b*, Front view, showiing the deep narrow slit and the horns. *c*, Side view. *d*, Bottom view, showing the elevated callus and smooth inductural extension covering the reticulate external ornamentation of the shell.

*7*—A specimen (no. 32693Y) that has barely attained the ephebic stage, projecting horns at the plane of the aperture; top view.

*8a-c*—A gerontic individual (no. 32693H), showing the broad expansion of the aperture and the obsolescence of the longitudinal markings. *a*, Bottom view. *b*, Side view. *c*, Top view.

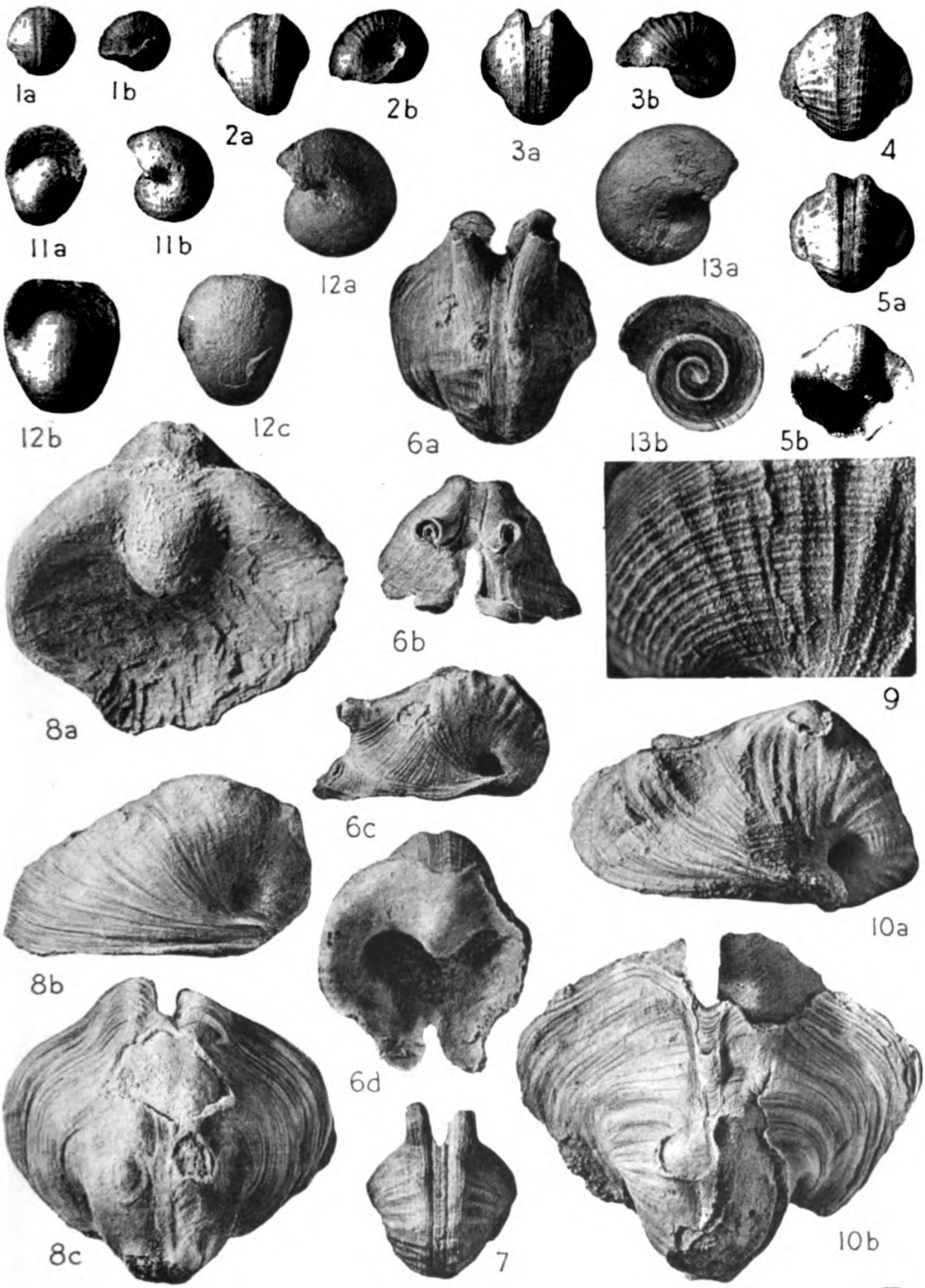
*9*—A part of the surface of an early adult shell showing longitudinal costae and cross wrinkles, enlarged.

*10a,b*—A gerontic shell (no 32693C), which is the largest observed individual, showing obsolete longitudinal markings, horns broken away. *a*, Side view. *b*, Top view.

*Warthia kingi*, n. sp., from the Ozawkie limestone member of the Deer Creek formation, west of Lawrence, Kansas.

*11a,b*—A small specimen (no. 32694C) having nearly complete aperture. *a*, Bottom view. *b*, Side view.

*12a-c*—The type specimen (no. 32694), showing smooth surface of the shell without slit band, lack of an umbilical cavity, and general resemblance of the shell to *Euphemites* except in the absence of a costate inductura. *a*, Side view. *b*, Bottom view. *c*, Top view.


1a
1b
2a
2b
3a
3b
4
11a
11b
12a
13a
5a
12b
12c
6a
13b
5b
6b
9
8a
6c
10a
8b
6d
8c
7
10b

of the growing shell surface. Later-formed passageways are more prominently elevated and are directed also somewhat laterally as well as upward. Resemblance of the young shells of *Knightites* to specimens of *Bucanopsis* should be noted.

### KNIGHTITES MULTICORNUTUS, n. sp.

Plate 3, figures 1ab, 2ab, 3ab, 4, 5 ab, 6a-d, 7, 8a-c, 9, 10ab; text figures 5AB

General characters of this species are given in description of the genus. Attention is directed here to features shown by shells grouped according to relative age. Three ontogenetic stages may be differentiated, but it is natural that the lines between these groups are not very sharply defined.

*Immature stage.*—Juvenile shells, ranging in maximum dimension from slightly less than 5 mm to about 10 mm, are distinguished by their small size but mainly by the lack of paired prominences at the borders of the slit band near the aperture. One or two of the smallest observed specimens may represent a nepionic stage, but most of them are classifiable as neanic individuals. Shells of this group are not distinguishable from examples of *Bucanopsis,* and accordingly these young individuals of *Knightites* may be said to represent a *Bucanopsis* stage. Seemingly, *Knightites* was developed out of *Bucanopsis.*

About thirty specimens in our collection represent the immature stage of *Knightites multicornutus.* Together they form an unbroken series that passes into the horn-bearing shells, and except for this transition there would be no basis for excluding them from assignment to the genus *Bucanopsis.* The rotund form and somewhat even expansion of the whorls of the very young specimens correspond almost exactly to these characters as represented in *Bucanopsis meekiana* (Swallow) and *B. textilis* Hall. The reticulate ornamentation is proportionately a little coarser than in that of the first mentioned species, and more like that of Hall's species. It is noteworthy that the cross markings of the smallest shells are not angulations or wrinkles, but are comparable to the revolving lirae. The slit band is slightly elevated and is bordered by two shallow furrows.

Shells slightly larger than the smallest observed individuals, having a length and width of about 7 and 6 mm respectively, show somewhat more strongly defined cross markings that consist of angulated wrinkles. The furrows that border the slit band are well marked, but the median part of the band is not elevated (pl. 3, figs. a,b). Larger immature shells show a gradually strengthened elevation of the shell at the margins of the furrows along the slit band. At length, the slit band comes to be developed as a flat depressed strip bordered by low ridges (pl. 3, figs. 2a, b, 3a, b, 4) and accentuation of the ridges leads to development of short spouts that are lifted only very slightly upward from the spirally revolving shell surface.

The apertural region of young shells of *Knightites multicornutus* is not more expanded than the normal increase in size of the growing whorls. The outer lip of the aperture is nearly straight, but near the umbilicus on each side it is reflected upward. This part of the lips is below and behind the umbilicus so that the umbilical areas are broadly open at all stages. The adapertural margin of the smooth inductura is well marked on most specimens. It is broadly sinuate, receding farthest from the aperture in the median region, which in young specimens is not more sharply curved transversely than the profile of the next preceding inner whorl. The thin nature of the inductura is shown both by the close conformance of its surface to the shape of the whorl that it covers and by slightly weathered and incomplete specimens, in which this layer is seen to be little more than a film of shell.

*Mature stage.*—Shells of *Knightites multicornutus* that may be classed as representing early to late ephebic growth stages have a greatest length ranging from about 10 to 25 mm. Some specimens, 10 to 15 mm in greatest length, bear a single pair of spoutlike projections and the horns are only very slightly raised (pl. 3, figs. 5a, b, 7). Several middle to late ephebic shells, like the type specimen (pl. 3, figs., 6a-d) show the position of two or more pairs of horns, those farthest back from the outer lip being marked by scars or prominent tubercles. The horns tend to be lifted more distinctly from the shell surface, rather than being carried forward in a line tangent to the curvature of coiling. Also, as shown by the type specimen, the horns may diverge sidewards from the slit band.

The aperture tends to expand in a somewhat bell-like manner, and the margin becomes slightly uneven. Back from the margin of the inductura toward the interior of the shell there is a somewhat abrupt thickening of layers formed by a part of the mantle near the inner lip. This makes a prominence over the slit band (pl. 3, fig. 16, text figs. 5b) and it may be equivalent to the coinductura, as observed in *Euphemites*. If so, it is not sharply and definitely differentiated from the inductura as in *Euphemites callosus*.

Surface ornamentation shows a gradually wider spacing of the cross wrinkles than in immature specimens, and this is accompanied by a gradual weakening of the revolving lirae.

*Gerontic stage.*—Specimens classed as gerontic have a maximum dimension of about 25 mm to more than 40 mm. Half a dozen pairs of horns or strong nodes are present along the slit band, the distance between successive pairs being as much as 15 mm in some specimens. The apertural region is notably expanded and marked by irregular, closely crowded growth lines. The inductura is strongly thickened in the median portion so as to be elevated prominently, the transverse curvature of the raised portion being distinctly sharper than that of the whorl beneath it (pl. 3, fig. 8a; text fig. 5B). The adapertural margin is strongly and somewhat narrowly indented where it crosses the slit band of the preceding whorl, and superposition of shell laminae having outer edges in the same position makes the margin abrupt. The lateral region near the umbilicus is spread out as a broad gently curving surface, and it is also much thickened by successive shell layers. The umbilicus is open.

Almost every large specimen that happens to be broken across the thickened shell area regarded as inductura or one that is sectioned in this region shows a cavity extending through part of the shell that one naturally supposes to be solid (text fig. 5B). The evenness and lateral extent of the opening in some individuals are such as to suggest the building of a thin shell layer arched over another one but touching it only at the margins. The surfaces of the opening are not smooth and they may be lined with small crystals. A longitudinal section of one specimen (text fig. 5A) shows solid shell in the thickened, abruptly arched area of the inductura, except for a few small irregular crystal-filled spaces. The openings are evidently due to solution of a part of the shell, probably originally aragonite, in the course of fossilization.

Measurement, in mm, of the type specimen and of a large gerontic specimen are as follows. Type (no. 32693): height, 13.5; length (anteroposterior), 23; length of aperture, 10.5; width of aperture, 21.5; width of slit band, 1.2 to 1.5; depth of slit, 7.5; diameter of tubular projection, 2.4. Gerontic specimen (no. 32693B): height, 22; length, 40.5; length of aperture, 15; width of aperture, 34.5.

*Occurrence.*—Ozawkie limestone member, Deer Creek formation, upper Pennsylvanian, 9.4 miles west of Lawrence, Kansas.

*Type.*—Type, University of Kansas no. 32693.

## Physiological Significance of Paired Tubular Prominences in Bellerophontids

By J. Brookes Knight

The following paragraphs are from letters by J. Brookes Knight and are published with his permission.

I have been thinking a good deal about that two-pronged bellerophontid you showed me in Lawrence and as a result I have changed my ideas somewhat as to the point of egress of the water currents. When I was in Lawrence I had *Haliotis* strongly in mind as the only living rhipidoglossate with provision for extrusion for the anal tube about which anything is known as to the course of the aerating water current. But I should have remembered that *Haliotis* is highly atypical in respect to the fact that its limpet-like mode of life and explanate shell have required the development of an enormous muscle of attachment athwart what is the path of the outgoing water currents, as they are known in such not distantly related groups as the Trochidae and Turbinidae. In *Haliotis* the water currents enter under the anterior margin of the mantle on both sides of the row of tremata, which is homologous to the slit and selenizone of the pleurotomarians and, presumably, of the bellerophontids. The currents then pass over the osphradia and ctenidia, which in *Haliotis* lie on each side of the row of tremata, and then, instead of passing backward through the mantle cavity and out at the right posterior margin, they are blocked in that direction by the muscle and so they turn and pass out through the tremata instead. The anal tube is extruded through one of the tremata.

There are three living species of *Pleurotomaria* but they are excessively rare and their anatomy is as yet imperfectly known. So far as I am aware, nothing is known of the path of the aerating water currents in their mantle cavities, but as they as very similar in all respects to the Trochidae, except in the possession of a slit for the extrusion of the anal tube, and perhaps a more symmetrical development of the ctenidia and associated organs, it is reasonable to suppose that the water currents follow much the same path that they do in the Trochidae. The only modification that should be expected are such as might be required by the presence in *Pleurotomaria* of two well developed osphradia and ctenidia and by the presence of an anal slit. Of course, the modification is from the probably more primitive pleurotomarian condition to the trochid condition, in which the right ctenidium (and associated organs) are reduced and the anal slit does not appear, modifications that are carried much further in the more advanced groups.

In the trochids, the water currents enter the mantle cavity under the anterior margin, perhaps a little left of dead center, pass over the (topographically) left ctenidium with its osphradium, pass across the mantle cavity and out under the right-posterior margin of the shell close to the point where the outer lip joins the parietal wall. I have actually watched the ingress and egress of the water currents in living specimens of the trochid genus *Margarita.* Where there is some remnant of the right ctenidium, presumably there is some incoming current too under the right-anterior margin, but I am not certain of this. The anal tube lies within the mantle cavity and the excreta are carried out with the currents, which have already aerated the left ctenidium and perhaps the right. In *Pleurotomaria* with its two well developed ctenidia (although I remember that in the living forms the right is slightly reduced) and the slit for the protrusion of the anal tube, one would expect that the incurrent water would enter under the margin, principally to the left of and anterior to the slit, but probably posterior to the slit as well, and that after aerating both gills it would pass out under the right posterior margin, just as it does in the trochids and in the great majority of prosobranchs. The left posterior is occupied by the parietal wall of the preceding whorl, and the mantle cavity is much reduced in that quarter. One should understand that left, right, anterior and posterior are relative to the living animal, not to the artificial conventional orientation adopted by English-speaking and German conchologists.

Now, we have no living bellerophontids, but there is good reason to suppose that the bellerophontids are prosobranchs that have undergone *torsion,* as all living gastropods have, but which have not taken the next step, the development of *asymmetry,* which also characterizes all living gastropods. The shells of the bellerophontids are, with few minor exceptions, quite symmetrical. Besides, all bellerophontids, (except a very few questionable ones) have a sinus, notch, notch-keel, or a slit presumably for the same purpose that these same features serve in the pleurotomariids,—namely, for the extrusion of an anal tube. It seems reasonable to suppose,

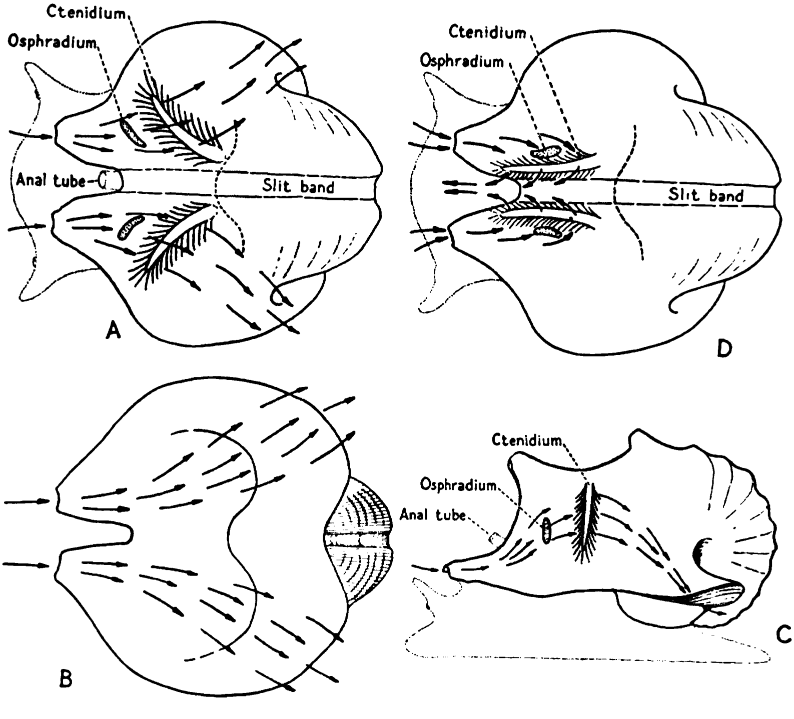



FIG. 7. Diagrams illustrating inferred physiologic features of *Knightites multicornutus*, n. gen., n. sp., (drawn from sketches prepared by J. Brookes Knight). *A*, Top view of shell (represented as transparent so as to show some of the soft parts); the ctenidia and osphradia lie on the inner surface of the mantle in the mantle cavity where they were bathed by water currents, diffuse or concentrated, that are believed to have entered the shell through the paired hollow projections on opposite sides of the slit and to have emerged at the posterolateral margins of the aperture (direction of water currents shown by arrows). *B*, Apertural view of empty shell showing course of water currents. *C*, Side view of shell (represented as transparent), position of some soft parts and water currents suggested. *D*, Top view of shell (represented as transparent) showing inferred course of water currents based on the hypothesis that circulation of currents in *Knightites* corresponds to that of *Haliotis*.

then, that the aerating currents entered the mantle cavity in a more or less diffused current under the anterior margin of the shell on both sides of the slit or in homologue passed upwards and backwards in two streams over the paired and symmetrically developed osphradia and ctenidia, and finally downward and outward over the postero-lateral wings of the margin, that is to say over, or rather under, the columellar part of the margin on each side (fig. 7A-C). The chief interest in your remarkable form is that it seems to confirm this supposition, at least in respect to the point of entry, for what we seem to have is a periodical development at late ephebic stages of paired incurrent siphons in the mantle margin on each side of the slit, and the recording of these siphons as paired incurrent canals developed on the shell margin. These incurrent canals are in most respects homologous to the incurrent canals developed in other groups of prosobranchs. They differ principally in that they seem to have been developed periodically in response to some physiological cycle which I can only guess at, whereas commonly such canals are permanent post-nepionic features. (Written from Lake Tahoe, California, July, 1940).

*Subsequent note.*—Since writing on the bellerophontid shells that you are naming *Knightites,* I have taken occasion to review the remarks and ideas given to you last summer when I had no means of checking anything. I am not able to confirm some of them by corroborative observations from nature. For example, the end of the anal tube in dead specimens of *Haliotis* and *Pleurotomaria* lies at the inner end of the row of tremata or slit precisely in position to be protruded, and the end of the tube is free from the mantle as if to facilitate such protrusion (Dall, 1889, p. 402), but I have been unable to find any record that this protrusion actually occurs. In fact, the best account of living *Haliotis* (Liverpool Marine Biology Committee, Memoir 29) indicates that the end of the tube seemingly is not protruded. In *Haliotis,* of course, the faeces would be carried out directly with the outgoing currents that pass through the tremata, without need for protrusion of the anal tube, —whether or not the movement of the currents is normal for slit-bearing Rhipidoglossa, or, as postulated in my letter, whether it is peculiar to *Haliotis* and is necessitated by the blocking of the right side of the mantle cavity by the tremendous muscle.

In *Pleurotomaria,* if the end of the anal tube is not actually protruded (as Dall has postulated and as I have always believed), then there is no use for the slit, unless it is for egress of the used and fouled water from the mantle cavity, just as in *Haliotis.* If this is the case, as it well may be, then the picture of the probable course of the water currents in the mantle cavity of *Pleurotomaria* and of the bellerophontids according to my previous suggestion (see discussion above and text figures 6A-C) must be reconsidered.

That the tubelike horns of *Knightites* are incurrent canals is most probable, whatever the way in which the currents made their exit from the shell. I still think that the course of these currents was probably about as indicated in my previous sketches (text figs. 6A-C). Observational evidence in support of these views, however, seems to be less clearly given in the literature than I thought. I have no reason to modify my remarks on the aerating currents in the trochids or in general as regards gastropods that lack a slit.

A sketch of *Knightites* in dorsal view, which I have prepared (text fig. 6D), indicates the inferred path of currents on the hypothesis that the water circulation in this genus may be surmised from study of *Haliotis.* According to the haliotid hypothesis, supplementary currents could have entered the mantle cavity at other points around the margin of the shell, as they do in *Haliotis.* Reconstruction of *Knightites* following this pattern places the osphradia outside of the ctenidia, which is the more usual position. How important this may be is uncertain. One may even question the existence of well developed osphradia in gastropods of such primitive nature as the bellerophontids. These organs seem much more diffused and less highly organized in primitive gastropods than in advanced types.

Perhaps the truth may be found between the two extremes suggested. That is to say, a part of the outgoing water may have passed out of the slit to flush away the faeces while another part, perhaps the largest part, passed backwards. In *Haliotis* not all the outgoing currents pass through the tremata; a part passes out under the right margin of the shell and there seem to be no currents passing backwards, as in most gastropods, probably because of the interference of the large muscle that blocks the way.

Very remarkable are the many different devices among living gastropods for reaching out as if to grab clean water for the pallial cavity and for getting rid of fouled water without contaminating the incoming water. Incurrent siphons, recorded by canals or notches in the shell, seem to have developed independently in different stocks. These passageways were formed generally by the margin of the mantle. There are other tricks, also, such as the siphon-like folds in the propodium of the Naticidae and lappet-like structures in other groups. Various structures are provided for the outgoing currents, and we find in the turrids, which are wholly unrelated to slit-bearing Rhipidoglossa, a perfectly good slit and selenizone. The motive force for the currents normally is provided by cilia. (Princeton University, April, 1941).

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