# GASTROPODA AND MONOPLACOPHORA OF THE SOLSVILLE MEMBER (MIDDLE DEVONIAN, MARCELLUS FORMATION) IN THE CHENANGO VALLEY, NEW YORK STATE

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# INTRODUCTION

THE IMPRESSIVE WORK of James Hall during the last century has certainly acquainted most paleontologists with the abundant and diverse molluskan faunas of the Hamilton Group in New York State. It is no small testimony to Hall's work that, with few exceptions, students of mollusks have not, nearly a hundred years later, undertaken monographic revision of the Hamilton mollusks.

Several years of collecting in Hamilton rocks of the Chenango Valley have revealed very few new molluskan species, but have made available for study large, well-preserved populations.

Recent exposures of the Solsville shales and calcareous siltstones contain an extremely diverse molluskan fauna. Zones of calcareous siltstones in the Solsville are often leached so that they provide a mold fauna with fine replication of delicate ornament. The mollusks of the shale facies often retain shell material with recognizable microstructure. Many Hamilton gastropod species that were previously known only from distorted, poorly preserved specimens have been recovered in such quantity and condition as to permit valuable ontogenetic comparisons.

In the present paper we have, in addition to reviewing systematically the Solsville gastropods and monoplacophorans, attempted to analyze the phylogenetic and ontogenetic information retrieved. We believe that the present study will point out the opportunity and need for additional reexamination of the Hamilton faunas of New York State.

Most of the systematic descriptions were prepared by Rollins. Eldredge assumes responsibility for *Ruedemannia trilix* (Hall) and *Glyptotomaria* (*Dictyotomaria*) *capillaria* (Conrad). The section on *Bembexia sulcomarginata* (Conrad) was prepared by Eldredge and Spiller.

Abbreviations used are: A.M.N.H., the American Museum of Natural History, Department of Invertebrate Paleontology; N.Y.S.M., New York State Museum; U.S.N.M., United States National Museum, Smithsonian Institution.

Initials used with a number alone refer to localities. Initials used with the abbreviation "No." refer to catalogued specimens.


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## GENERAL STRATIGRAPHY

The Hamilton Group in the Chenango Valley of New York poses many unsolved stratigraphic problems resulting from complex facies mosaics associated with the early growth of the Catskill Delta. The only detailed stratigraphic study in the Chenango Valley was that of Cooper (1930). Cooper used the name Marcellus in the sense of Vanuxem (1840). The lower limit of the Marcellus is the top of the Onondaga limestone and the upper limit, the base of the Mottville.

In the Chenango Valley the members of the Marcellus Formation, in ascending order, are the Union Springs limestone and shale, the Cherry Valley limestone, the Chittenango black shale, the Bridgewater shale, the Solsville calcareous shale and sandstone, and the Pecksport shales and siltstones. The Bridgewater, Solsville, and Pecksport members, as noted by Cooper (1930, p. 132), undergo a striking and rather abrupt facies change to the west of the Chenango Valley, where all three are represented by the rather uniform dark gray Cardiff Shale.

The area covered in the present report straddles the facies changes noted by Cooper (fig. 1). As such, exact stratigraphic placement of the sequence treated herein is somewhat tenuous in terms of Cooper's terminology. On the basis of the contained fauna, the sequence most

closely corresponds to Cooper's Solsville unit, although several of the exposure localities are farther west than the presumed limit of the Solsville (Cooper, 1930, p. 134). Certain elements of the Solsville fauna (i.e., *Nephriticeras maximum*, *Paracyclas lirata*, *Gosselettia triquetra*, *Cornellites flabellum*, and so on) were considered by Cooper to represent a unique Hamilton assemblage. These species are equally conspicuous in the exposures treated in the present study.

TABLE 1

| | Locality Register |
|---|---|
| A.M.N.H. 3012 | Road cut on east side of Swamp Road, 0.5 mile south of intersection with Gill Road, Morrisville, New York, 7½′ quadrangle |
| A.M.N.H. 3013 | Small abandoned quarry on east side of Swamp Road, 1.0 mile south of intersection with Gill Road, Morrisville, New York, 7½′ quadrangle |
| A.M.N.H. 3014 | Small abandoned quarry on west side of Old County Road, 1.6 miles south of intersection with Gill Road, Morrisville, New York, 7½′ quadrangle |
| A.M.N.H. 3015 | Abandoned and covered quarry on west side of Cole Road, 0.2 mile south of intersection with U.S. Route 30 and Morrisville Station, New York; Munnsville, New York, 7½′ quadrangle |
| A.M.N.H. 3016 | Small road cut on south side of U.S. Route 20, 0.2 mile east of intersection with Route 46 at Pine Woods, New York; Munnsville, New York, 7½′ quadrangle |
| A.M.N.H. 3017 | Small abandoned quarry on southeast side of Center Road, 1.5 miles south of intersection with U.S. Route 20; Oriskany Falls, New York, 7½′ quadrangle |

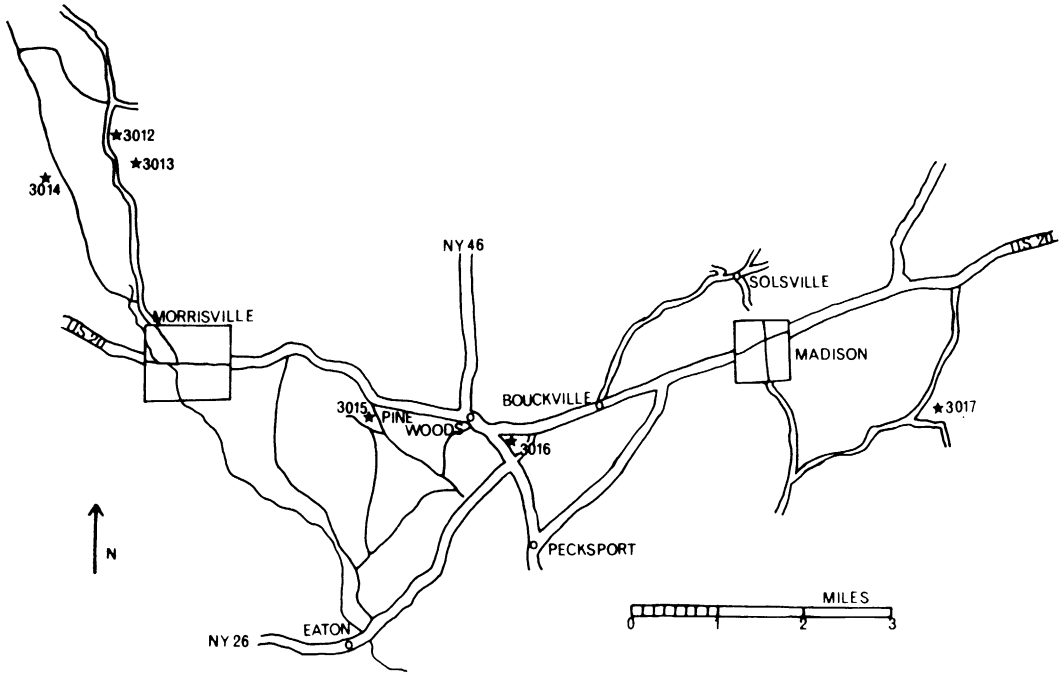


FIG. 1. Collecting localities of the Solsville in the Chenango Valley, central New York State. See table 1 for detailed description of localities.

TABLE 2

A.M.N.H. Locality and Facies Distribution of Species

| Species | 3012 | 3013 | 3014 | 3015 | 3016 | 3017 |
|---|---|---|---|---|---|---|
| *Bembexia sulcomarginata* (Conrad) | C[a] | C[a]R[b] | C[a] | C[a] | R[b] | C[a] |
| *Cyrtonella mitella* (Hall) | R[b] | C[b] | R[b] | R[b] | — | R[b] |
| *Glyptotomaria* (*Dictyotomaria*) *capillaria* (Conrad) | — | C[b] | R[b] | — | R[b] | — |
| *Gyronema lirata* (Hall) | — | R[a] | — | — | — | — |
| *?Holopea hebe* (Hall) | — | C[b] | R[b] | — | R[b] | — |
| *Mourlonia subzona*, new species | — | R[b] | — | — | — | — |
| *Murchisonia* (*Murchisonia*) *micula* Hall | — | C[b] | — | — | R[b] | — |
| *Murchisonia* (*Murchisonia*) sp. | — | R[b] | — | — | — | — |
| *Naticopsis* (*Naticopsis*) sp. | — | R[b] | — | — | — | — |
| *Palaeozygopleura hamiltoniae* (Hall) | C[a]R[b] | C[a]R[b] | C[a]R[b] | C[a] | R[b] | C[a]R[b] |
| *Patellilabia* (*Phragmosphaera*) *lyra* (Hall) | — | R[c] | — | — | — | — |
| *Platyceras* (*Platyceras*) *erectum* (Hall) | — | C[b] | R[b] | — | — | — |
| *Platyceras* (*Platyostoma*) sp. A | — | R[b] | — | — | — | — |
| *Platyceras* (*Platyostoma*) sp. B. | — | R[b] | — | — | — | — |
| *Platyceras* (*Orthonychia*) sp. | — | R[b] | — | — | — | — |
| *Praematuratropis ovatus*, new genus and new species | — | R[c] | R[a] | R[a] | — | R[a] |
| *Ptomatis rudis* (Hall) | — | — | — | — | — | R[a] |
| *Retispira leda* (Hall) | R[c] | R[c] | R[c] | R[a] | R[b] | R[c] |
| *Ruedemannia trilix* (Hall) | R[a] | R[a]C[b] | R[c] | — | — | — |
| *Sinuitina brevilineatus* (Conrad) | — | R[b] | — | — | — | — |
| *Trepospira* (*?Angyomphalus*) *peneglabra*, new species | — | R[b] | — | — | — | — |
| *Tritonophon rotalinea* (Hall) | — | R[b] | — | — | — | — |

[a] Found in calcareous gray shales, with shell preserved.
[b] Found as molds in weathered calcareous siltstone.
[c] Found in both of above situations.
*Symbols:* C, common; R, rare.

# SYSTEMATIC PALEONTOLOGY

## CLASS **GASTROPODA** CUVIER, 1797

## ORDER **ARCHAEOGASTROPODA** THIELE, 1925

## SUPERFAMILY **BELLEROPHONTACEA** M'COY, 1851

## FAMILY **BELLEROPHONTIDAE** M'COY, 1851

## SUBFAMILY **BUCANIINAE** ULRICH AND SCOFIELD, 1897

### GENUS **TRITONOPHON** ÖPIK, 1953

(=*Kokenospira* (*Tritonophon*) Öpik, 1953)

TYPE SPECIES: *Tritonophon trimetra* Öpik, 1953.

DIAGNOSIS: Small, distinctly trilobate bellerophontaceans, with wide shallow U-shaped sinus generating obscure selenizone; ornament consisting of faint growth lines with distinct, numerous revolving lirae.

**Tritonophon rotalinea** (Hall), 1879
Figure 2A, B

*Bellerophon rotalinea* HALL, 1879, p. 115, pl. 26, fig. 8.
*Nylanderina rotalinea* (Hall): BOUCOT, 1967, p. 9, pl. 2, fig. 12.

DESCRIPTION: This small species is characterized by a strongly trilobed whorl profile, relatively unexpanded aperture, numerous distinct spiral lirae, and a wide shallow U-shaped sinus presumably generating a selenizone. The strongly developed median lobe is flattened dorsally, has steep but convex lateral flanks, and is very wide, forming more than one-half of the total shell width. The more rounded lateral lobes are separated from the median lobe by a pair of depressions, the loci of relatively widely spaced spiral lirae. Obscure growth lines indicate that the shallow U-shaped sinus and obscure selenizone extend the total width of the median lobe, bordered by distinct spiral lirae. The selenizone is ornamented by five to six spiral lirae, including the bordering lirae. Trilobation is more pronounced in later ontogenetic stages. The umbilici are phaneromphalous, with rounded lirate slopes. Collabral ornament is represented only by very faint growth lines. The spiral ornament consists of numerous, unevenly spaced lirae, closer together on the flanks of the median and lateral lobes. The shell structure and inductura are unknown.

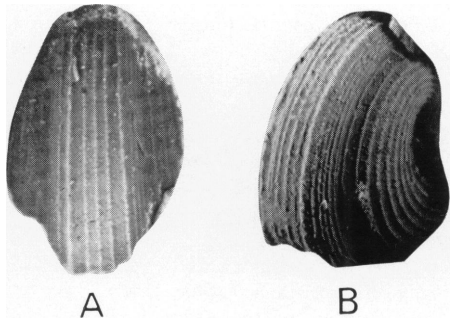


FIG. 2. *Tritonophon rotalinea* (Hall), from A.M.N.H. 3013. A. Dorsal view of latex cast showing very faint growth lines and shallow U-shaped sinus, A.M.N.H. No. 28821. ×16.0. B. Oblique lateral view of latex cast, A.M.N.H. No. 28822. ×6.0.

DISCUSSION: Boucot (1967) established the genus *Nylanderina* for those trilobed bellerophontaceans possessing a V-shaped sinus on the median lobe, coarse spiral ornament, and no selenizone. He assigned two Devonian species, *Bellerophon rotalinea* Hall, 1879 and *Nylanderina goldringae* Boucot, 1967, to this genus, stating that the former could be distinguished by its coarser spiral ornament.

Boucot (1967, p. 9) mentioned the similarities between *N. goldringae* and *Kokenospira* (*Tritonophon*) *trimetra* Öpik, 1953, from the Silurian of Australia, and stated that *Nylanderina* might be synonymous with *Tritonophon*. But since Öpik (1953, p. 20) reported a "short and wide U-shaped slit notch" in *K.* (*Tritonophon*) *trimetra*, Boucot elected to establish the genus *Nylanderina*. Illustrations of the type specimens of *N. goldringae* (Boucot, Cumming, and Jaeger, 1967, pl. 3, figs. 1–4) do not suggest a V-shaped sinus. Indeed, a U-shaped emargination of the type described by Öpik for the subgenus *Tritonophon* is indicated.

There is no doubt that *Bellerophon rotalinea* Hall lacks the V-shaped sinus attributed to *Nylanderina* and possesses, instead, a short and wide U-shaped sinus that probably generates a selenizone. Collabral ornament in this species is extremely obscure, consisting only of very faint

growth lines. Although the Cardiff specimens are moderately well preserved, it is impossible to continuously trace the growth-line pattern from the lateral flanks to the median lobe.

*Bellerophon hermitei* Oehlert and Davoust, 1879, from the Devonian of France, is morphologically quite similar to *Tritonophon rotalinea* and illustrations of the former suggest a U-shaped sinus generating a selenizone. *Bellerophon hermitei* apparently belongs to the genus *Tritonophon* and differs from *T. rotalinea* by being more lenticular and possessing a narrower and more angular median lobe.

The taxonomic position of *K.* (*Tritonophon*) remains in doubt. *Tritonophon* is here elevated to generic rank as the accentuated trilobation of this taxon is quite different from the bluntly angular whorl profile of *Kokenospira*. If *Tritonophon* possesses a true selenizone, it should be removed from the Sinuitidae and placed in the Bellerophontidae, possibly with the subfamily Bucaninae. It is interesting that a similar taxonomic fate has befallen the genus *Plectonotus* Clarke (Saul, Boucot, and Finks, 1963). It is most unfortunate that the types of *Tritonophon trimetra* Öpik were lost by fire (Yochelson, 1968, written commun.).

Boucot and Saul (Saul, Boucot, and Finks, 1963. p. 1047) erroneously stated that "Knight, Batten and Yochelson (1960, p. 1175) placed *Tritonophon* Öpik, known from the Lower Silurian of Victoria, Australia, in the synonymy of *Plectonotus*." In that work *Tritonophon* was placed in synonymy with *Bucanella* (*Bucanella*), not with *Plectonotus*.

The entire group of trilobed bellerophontaceans is in dire need of careful taxonomic revision.

MATERIAL: Twelve specimens, from A.M.N.H. 3013.

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF *Tritonophon rotalinea* (HALL)

| | Specimen A.M.N.H. No. 28821 | Specimen A.M.N.H. No. 28822 |
|---|---|---|
| Total Width | 1.6 | 3.22 |
| Median Lobe Width | .92 | 1.84 |
| Selenizonal Width | .69 | .92 |

SUBFAMILY **KNIGHTITINAE** KNIGHT, 1956

GENUS **RETISPIRA** KNIGHT, 1945

TYPE SPECIES: *Retispira bellireticulata* Knight, 1945.

**Retispira leda** (Hall)

Figure 3A–E

*Bellerophon leda* HALL, 1861, p. 30; 1862, p. 58; 1875, pl. 13, fig. 1; 1876, pl. 24; 1879, pl. 23, figs. 2–16.

*Bucanopsis leda* (Hall): KNIGHT, 1944, p. 443, pl. 178, fig. 23.

DESCRIPTION: This rather large species has a moderately expanded aperture and is phaneromphalous. The adult whorl expands rapidly with a gently rounded profile, somewhat flattened dorsally. The anterior apertural lip possesses a moderately shallow and wide U-shaped sinus that generates a wide selenizone which, in early whorls, is flush with the shell surface but, in maturity, is slightly elevated. A rather thin striatopustulate inductura is restricted to the immediate parietal region. The collabral ornament consists in some specimens of lirate growth lines and, in others, broad ill-defined undulations on the mature whorl surface. The spiral ornament consists of subequally spaced lirae, often with three to four intercalated threads, even on the selenizone. In general, the spiral ornament is more subdued in the earlier growth stages. Throughout ontogeny, the selenizone width remains relatively constant, but the spacing of lunulae is variable. The shell microstructure is complex crossed-lamellar.

DISCUSSION: *Retispira* is readily distinguishable from all other knightitinid genera by its relatively unexpanded aperture and its smooth, thin parietal inductura. Juvenile specimens of *Retispira* species, however, are often morphologically inseparable from immature specimens of other knightitinids (Yochelson, 1960). This has led previous workers (Yochelson, 1960; Knight, Batten, and Yochelson, 1960) to include *Retispira* as a subgenus of *Knightites*. As the immature individuals of all the Knightitinae are remarkably similar, there seems no more reason for placing *Retispira* with *Knightites* than with *Patellilabia*. It seems preferable to refer it to a separate genus on the basis of its adult morphology.

*Retispira* closely resembles *Bucanopsis*, but has a simple inductural layer and lacks the ridge on

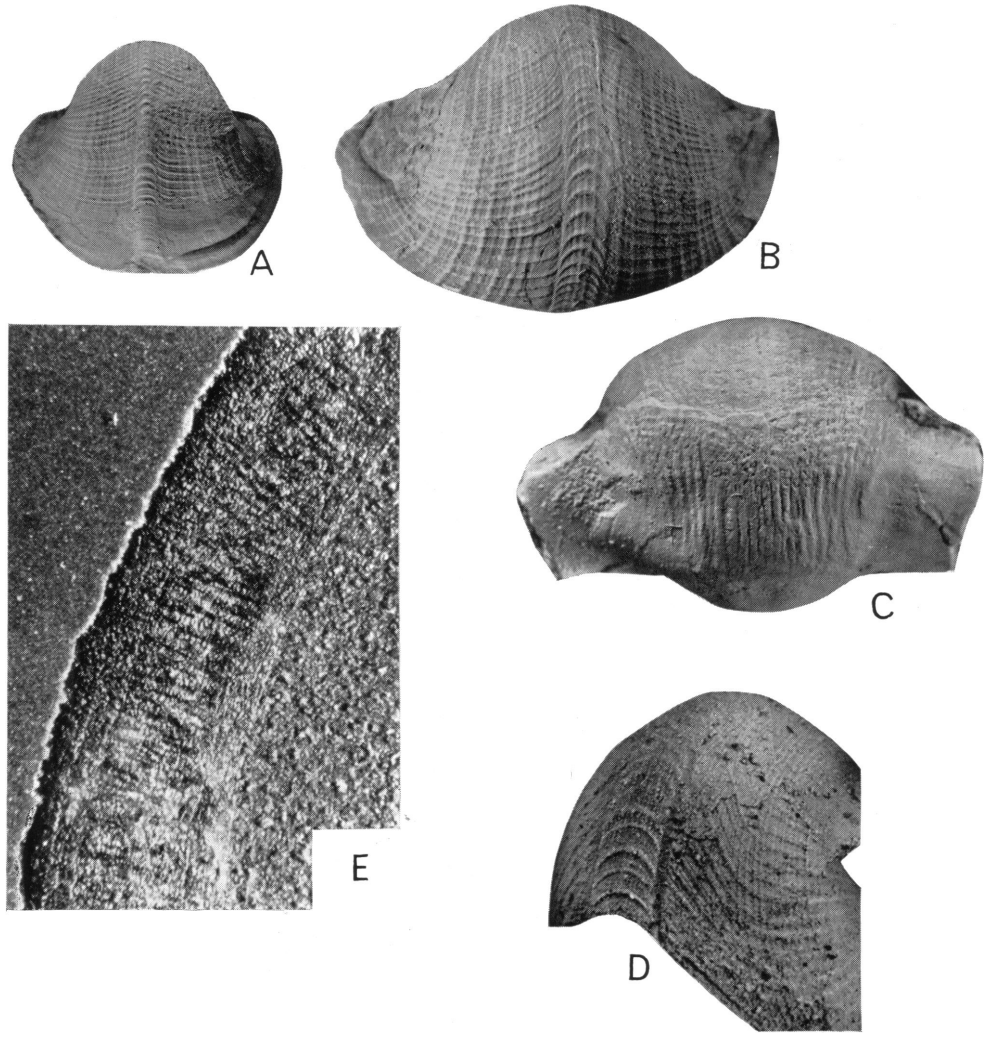


FIG. 3. *Retispira leda* (Hall). A. Dorsal view; note transition from preservation of shell to composite mold, from A.M.N.H. 3017, A.M.N.H. No. 28828. ×1.5. B. Dorsal view of mature specimen, from A.M.N.H. 3012, A.M.N.H. No. 28829. ×3.0. C. Apertural view; note thin striatopustulate inductura, from A.M.N.H. 3017, A.M.N.H. No. 28830. ×4.0. D. Oblique dorsal view of immature specimen, latex cast; note width of selenizone, from A.M.N.H. 3016, A.M.N.H. No. 28831. ×12.0. E. Stained and etched polished transverse section showing complex crossed-lamellar shell microstructure, from A.M.N.H. 3017, A.M.N.H. No. 28894. ×25.0.

the floor of the inner whorl, a diagnostic feature of the latter genus. The older literature is replete with *Bucanopsis* species that are referable to *Retispira*, and it is even not unusual to find misinterpretation of these genera in the recent literature (e.g. Ellison, 1965, p. 146). As currently treated *Bucanopsis* ranges from Ordovician through Silurian and *Retispira* only occurs in rocks from Devonian through Permian age.

In the literature, the number of species of the genus *Retispira* approaches 60. Undoubtedly, there are many synonyms in this vast array of species and the initial impression is one of dismay over the lack of morphological discreteness for many of the described forms. This confusing pattern has certainly resulted from a number of factors: the long stratigraphic range of the genus *Retispira*, its wide geographic distribution and, most of all, the stabilization upon a basic ornament pattern of nearly equal collabral and spiral

elements, but with great ontogenetic variability. Attempts to subdivide *Retispira* species into groups based on ornament patterns have met with little success. The intergradation is too complete (see Yochelson, 1960, p. 242). Although *Retispira* species typically display a smooth, thin inductura, a few are distinctive in the possession of massive parietal deposits [e.g. *R. imbricatus* (Weir) and *R. striatus* (Fleming)]. These might profitably be placed in a separate subgenus of *Retispira*.

A few species, such as *R. leda* (Hall) possess a thin, but ornamented inductura. Others, such as *R. girtyi* Yochelson and *R. lyelli* Gemmellaro, as figured by Wanner (1922, pl. 151, fig. 7) are slightly compressed and widely phaneromphalous.

There are very few *Retispira* species in the Devonian and the genus achieves its greatest representation, in terms of number of species, in the Carboniferous and Permian. Besides *R. leda* (Hall), the only Devonian species of *Retispira* that we can find in the literature are *R. denckmanni* (Clarke), *R. retifera* (Talent), *R. vogulicus* (Tschernyschew) and *R. elegans* (d'Orbigny). All these species are quite alike in the possession of collabral and spiral ornament of about equal weight and are close to the type species, *R. bellireticulata* Knight. *Retispira leda* (Hall) can apparently be distinguished from these species on the basis of its striatopustulate parietal inductura.

The specimens of *R. leda* (Hall) available in this faunal study provide instructive insights into aspects of bellerophontacean ontogeny and preservation.

*Retispira leda* (Hall) exhibits striking change in ornament emphasis throughout ontogeny. The "typical" reticulate ornament of retispirids is a result of equal development of collabral and spiral elements and is not achieved in *R. leda* until the later growth stages (fig. 3B, D). Specimens in which the earlier whorls can be observed (usually as a result of breakage of later whorls) display restriction of distinct spiral ornament to the lateral whorl surfaces. Over the dorsal whorl surface the spiral elements are either very subdued or nonexistent. The selenizone margins, however, are strongly developed.

The initial mantle folds apparently developed laterally on the mantle skirt, becoming accentuated and more numerous throughout ontogeny. The rate of increase in number of spiral elements cannot be determined, but allometric growth of the mantle must have been present until later ontogeny. The obscure spiral threads present in early whorls in the dorsal region are the intercalated threads of the adult ornament. The coarser spiral elements (lirae), then, first developed laterally and eventually were present over the whole shell, adjacent lirae having three or four intercalated spiral threads.

Bivariate plots of selenizone width versus whorl width in several bellerophont species (Rollins, 1967) display allometric development of the selenizone width, a rapid increase in early ontogeny, and a lesser rate of increase in later growth stages. The same pattern has been observed in Paleozoic pleurotomarians (Eldredge, 1968). Thus, the mantle cleft, responsible for generation of the anterior slit in the shell, attains the bulk of its adult width very early in ontogeny. This reflects the early morphogenetic development of the rectal complex. In studies of the ontogeny of recent marine prosobranchs, the rectal tract is one of the earliest developing organ systems. This allometric widening of the mantle cleft (as indicated by selenizonal width) is most striking in *R. leda* (Hall).

The well-preserved specimens of *R. leda* (Hall) available in the present study invite comparison with commonly compressed representatives of that species, widely distributed in the Middle Devonian siltstones and shales of North America. When dorsal compression in bellerophontaceans occurs, the result is a drastic accentuation of aperture width, a situation which has often been responsible for inaccurate description of species in the literature. An excellent case in point is Hall's broad morphological conception of *R. leda* (see Hall, 1879, p. 110). On the other hand, dorsal compression has, at times, been useful in interpreting the nature and extent of parietal deposits. Such features often are reflected in reentrant "chinks" or sutural grooves after dorsal compression (see Knight, 1945).

McAlester (1962, pp. 69–73) has discussed the mode of formation and interpretation of composite molds of bivalves preserved in shale. A unique character of composite mold formation in bivalves is the superposition of external shell ornament upon the muscle scar patterns of the inner shell surface. Creation of a composite mold requires sedimentary compaction during or after the removal of original shell material.

As they lack dorsal muscle scars, bellero-

phontaceans do not suffer superposition of muscle scars and external ornament under conditions of composite mold formation. The elevation of the selenizone, however, is sometimes affected. If the inner shell surface is reflexed slightly to the outside of the shell, as is often the case in the inner area immediately beneath the sinus and selenizone, a specimen preserved as a composite mold is likely to have a selenizone of exaggerated elevation, replete with the normal external ornament. Because the elevation of the selenizone is a commonly employed taxonomic character at the species level, the same care must be taken in the recognition and evaluation of the effects of composite mold preservation, as is often accorded the distortional effects of compressional preservation in shale. On a single specimen from A.M.N.H. 3017 can be seen a gradation from retention of shell (replaced) to composite mold preservation (fig. 3A). The changes of ornament emphasis on this specimen from one preservational mode to the other is striking.

MATERIAL: Fifteen specimens from A.M.N.H. 3017; two specimens from A.M.N.H. 3016; one specimen from A.M.N.H. 3012; two specimens from A.M.N.H. 3015.

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF *Retispira leda* (HALL)

| | Total Width | Total Height | Selenizone Width |
|---|---|---|---|
| A.M.N.H. No. 28829 | 17.45 | 11.21 | 1.65 |
| A.M.N.H. No. 28830 | 19.30 | 15.10 | 2.20 |
| A.M.N.H. No. 28832 | 20.60 | 17.10 | — |
| A.M.N.H. No. 28832 | 15.10 | 13.30 | — |
| A.M.N.H. No. 28832 | 20.30 | 14.30 | — |
| A.M.N.H. No. 28832 | 16.80 | 11.15 | — |
| A.M.N.H. No. 28832 | 20.85 | 13.90 | — |
| A.M.N.H. No. 28832 | 18.10 | 14.55 | — |
| A.M.N.H. No. 28832 | 19.35 | 12.15 | — |
| A.M.N.H. No. 28832 | 17.60 | 11.80 | — |

## GENUS **PATELLILABIA** KNIGHT, 1945

TYPE SPECIES: *Patellilabia tentoriolum* Knight, 1945.

### SUBGENUS **PATELLILABIA (PHRAGMOSPHAERA)** KNIGHT, 1945

*Bellerophon* (in part) of HALL, 1861, p. 31 and 1879, p. 94.

*Bucanopsis* (in part) of ULRICH AND SCOFIELD, 1879, p. 853.

*Patellostium* (in part) of several authors.

*Phragmostoma* of CLARKE, 1904, p. 322; 1909, p. 139; not HALL, 1861.

*Carinaropsis* (in part) of CLARKE, 1904, p. 323, 427.

TYPE SPECIES: *Patellilabia (Phragmosphaera) lyra* (Hall), 1861 (=*Phragmosphaera miranda* Knight, 1945).

DIAGNOSIS: Bellerophontid gastropods with flaring to explanate apertures; ornament dominantly spiral but in some cases with gentle wavelike collabral undulations; parietal inductural deposit centrally massive, thinner laterally, and in many cases, anteriorly attenuated and flattened; short to moderately long slit generating narrow convex selenizone; shell microstructure probably complex crossed-lamellar.

DISCUSSION: A recent taxonomic revision of the Knightitinae (Rollins [MS.(b)]), supports transfer of the genus *Phragmosphaera* Knight from the Carinaropsinae to the Knightitinae as a subgenus of *Patellilabia* Knight. *Patellilabia (Phragmosphaera)* differs from *P. (Patellilabia)* by not possessing a pronounced knoblike parietal tooth and in having a convex selenizone not situated in a medial dorsal trough.

*Patellilabia (Phragmosphaera)* resembles certain species of *Bucanopsis*, but is distinguishable by its lack of a spiral ridge on the floor of the inner whorl.

### **Patellilabia (Phragmosphaera) lyra** (Hall), 1861
Figure 4A–E

*Bellerophon lyra* HALL, 1861, p. 31; 1862, p. 59; 1876, pl. 24; 1879, p. 113, pl. 23, figs. 1, 17–20.

*Phragmosphaera miranda* KNIGHT, 1945, p. 338, pl. 49, figs. 2a–e.

DESCRIPTION: This medium-sized bellerophontiform species possesses a flaring, but nonexplanate, aperture with a massively developed parietal inductura, anteriorly attenuated into a shelf. The parietal shelf is thickest centrally below the spire and is commonly pustulate on the ventral surface. The broad aperture is subcircular and reflexed slightly upward (dorsally) along the posterior margin. A rather narrow convex selenizone is generated by a shallow anterior sinus culminating in a short U-shaped slit. Ornament is dominantly spiral, consisting of numerous lirae, often with intercalated threads. Collabral ornament consists of only faint growth lines. The adult whorl profile, except for the slightly elevated selenizone, is smoothly shield-shaped. The early whorls are

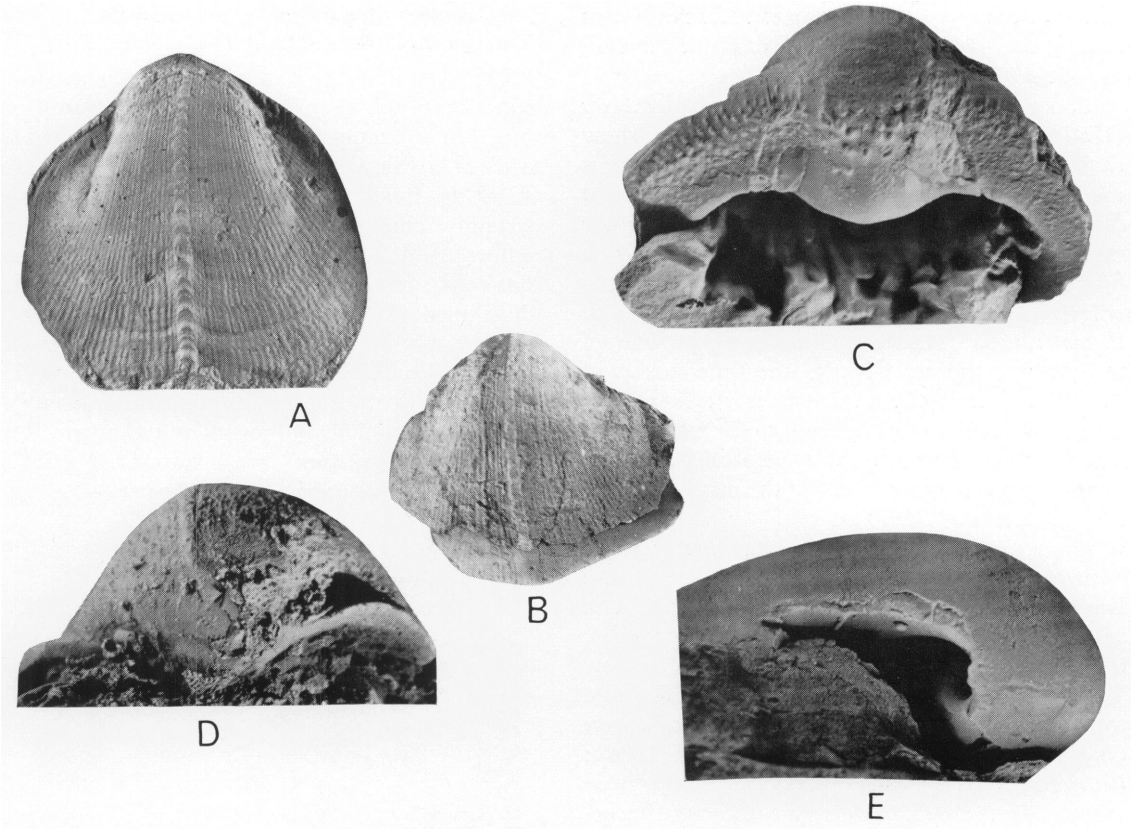


FIG. 4. *Patellilabia* (*Phragmosphaera*) *lyra* (Hall). A. Holotype, dorsal view showing sutural grooves, from Hamilton beds, Fultonham, New York, N.Y.S.M. No. 9150. ×2.0. B, C. A.M.N.H. No. 28824. B. Dorsal view. ×1.5. C. Apertural view showing pustulate parietal deposits. ×4.0. D. Posterior view of young individual showing reflexed apertural margin, latex cast, A.M.N.H. No. 28825. ×3.0. E. Lateral view of steinkern; note extent of former parietal inductural deposit, A.M.N.H. No. 28826. ×3.5. B–E from A.M.N.H. 3013.

unknown. The shell microstructure is apparently complex crossed-lamellar.

DISCUSSION: When Knight (1945) established the genus *Phragmosphaera*, he selected and described, as the type species, *P. miranda* a form that he believed represented a new species from the West Brook member of the Middle Devonian Tully Formation of New York State. The holotype and one paratype of *P. miranda* clearly show the sutural grooves which Knight thought were produced by an apertural diaphragm. He was able to prepare the other paratype, preserved in shale, so that it displayed an apertural diaphragm which he concluded could not be an accident of preservation. Knight suspected that *P. miranda* might eventually fall into synonymy with *P. lyra* (Hall), 1861. He was unable to locate Hall's types but thought that Hall's specimens of *P. lyra* were more strongly lirate than *P. miranda*.

A single specimen from the type lot of *Bellerophon lyra* Hall has been located in the New York State Museum collections in Albany (N.Y.S.M. No. 9150). The specimen, from the "Hamilton beds" at Fultonham, New York, appears to be one of Hall's illustrated specimens (Hall, 1879, pl. 23, figs. 19, 20) and is herein designated lectotype (see fig. 4A). Examination of this specimen and comparison with the types of *P. miranda* leaves little doubt that the forms are conspecific. The lectotype of *P. lyra* (Hall) displays the sutural grooves that suggested to Knight an apertural diaphragm and also possesses the peculiar spiral ornament of *P.*

*miranda*—lirae with intercalated threads [this pattern of spiral ornament is also found in *P.* (*Patellilabia*) *tentoriolum*].

The several undistorted specimens of *P. lyra* (Hall) collected at A.M.N.H. 3013 clearly show that the apertural diaphragm of that species is merely a great thickened parietal inductural deposit, massive over a bluntly rectangular central area and much thinner laterally. The function of this shelflike pad, as discussed elsewhere in the present paper in connection with *Ptomatis rudis* (Hall), was presumably one of muscle attachment. Clearly, the type species of *P.* (*Phragmosphaera*), at least, is more closely allied to the Knightitinae than to the Carinaropsinae. Furthermore, *P.* (*Phragmosphaera*) does not develop a ridge on the floor of the inner whorl as do most carinaropsinid genera.

Species referable to *P.* (*Phragmosphaera*) occur with wide geographic distribution from the Devonian to the Lower Carboniferous. The greatest concentration and variety of species, however, occur in the Upper Devonian of New York State, with at least four species assignable to this subgenus: *Phragmostoma chautauquae* Clarke, 1904; *Phragmostoma natator* Hall, 1862; *Bellerophon incisus* Clarke, 1885; and *Bellerophon triliratus* Hall, 1885. *Carinaropsis ithagenia* Clarke, 1904 may belong to this subgenus. *Carinaropsis victoriae* Chapman 1916, p. 81, pl. 2, figs. 13, 14, from the Devonian of Australia, closely resembles *Carinaropsis ithagenia* Clarke. *Phragmostoma diopetes* Clarke (1907, p. 192), from the Lower Devonian of Maine, is certainly referable to the subgenus *P.* (*Phragmosphaera*). None of the above species, nor any of the others mentioned by Rollins (1967), has close specific similarities with *P.* (*Phragmosphaera*) *lyra* (Hall).

MATERIAL: Five specimens from A.M.N.H. 3013.

## SUBFAMILY **BUCANELLINAE** KOKEN, 1925

### GENUS **SINUITINA** KNIGHT, 1945

TYPE SPECIES: *Tropidocyclus cordiformis* Newell, 1935.

#### **Sinuitina brevilineatus** (Conrad)

Figure 5A–D

*Bellerophon brevilineatus* CONRAD, 1842, p. 269, pl. 16, fig. 6; HALL, 1879, p. 107, pl. 26.

*Tropidocyclus brevilineatus* (Conrad): CLARKE, 1908, p. 229, pl. 17, figs. 7–16; CLARKE, 1909, p. 139, pl. 32, figs. 4–7.

"*Bucanella*" *brevilineatus* (Conrad): BOUCOT AND YOCHELSON, 1966, p. A 5, pl. 1, figs. 5, 6.

DESCRIPTION: This small species possesses a subcordate whorl profile and is phaneromphalous. The subacute dorsal periphery is marked by a distinct lira and grades smoothly, but with a slight to moderate concavity, into the rather strongly convex lateral whorl surfaces. The whorl profile abruptly enters the umbilici where flangelike circum-umbilical carinae are usually developed. The aperture is poorly known, but presumably has a height about equal to its width. As suggested by growth lines, the anterior apertural lip has a rather wide and deep V-shaped sinus. The inductura is unknown. The lateral whorl surfaces are ornamented by distinct subequally spaced collabral costae that

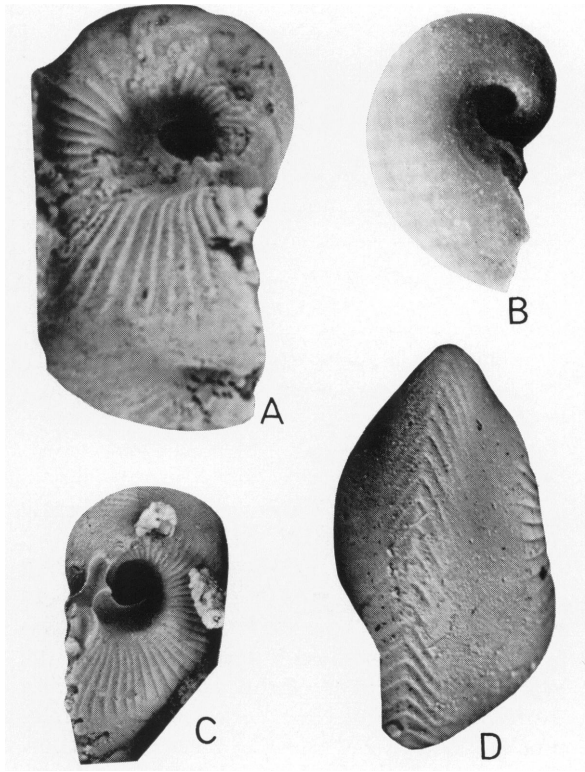


FIG. 5. *Sinuitina brevilineatus* (Conrad), from A.M.N.H. 3013. A. Lateral view of latex cast, A.M.N.H. No. 28816. ×13.0. B. Steinkern showing obscure columellar muscle scar. A.M.N.H. No. 28818. ×5.0. C. Lateral view of latex cast, A.M.N.H. No. 28817. ×7.0. D. Dorsal view of latex cast showing V-shaped sinus and median lira, A.M.N.H. No. 28819. ×10.0.

extend dorsally from the umbilici to a little less than one-half the distance to the dorsal periphery, where they are reduced to abaperturally reflexed growth lines that become costate again, however, on the periphery flanks.

DISCUSSION: The reduced midlateral collabral ornament of *S. brevilineatus* renders that species distinguishable from most other species of *Sinuitina*. An unpublished species from the Lower Mississippian Wassonville limestone of southeastern Iowa also possesses restricted lateral ornament but differs from *S. brevilineatus* in having a narrower sinus and flatter, nonlirate dorsal periphery, (Rollins [MS.(a)]).

Although Conrad's original description of *S. brevilineatus* (Conrad, 1842) was specific in designation of the restricted lateral ornament, subsequent workers have enlarged the conception of the species to include forms with continuous collabral costae and even spiral ornament (Hall, 1879; Clarke, 1908, 1909).

Nine specimens, unquestionably assigned to *S. brevilineatus, sensu stricto*, have been recovered from the Solsville shale. Hall (1879) described and figured specimens of *S. brevilineatus* that are apparently of comparable growth stages and exhibit, in some cases, restricted ornament, and in others, continuous ornament. Although the possibility of ontogenetic variation in the extent of lateral ornament cannot be ruled out, it seems likely that subsequent study of *S. brevilineatus*, as it is commonly understood, will reveal at least two distinct morphotypes that could profitably be separated at the species level.

A single steinkern (fig. 5B), apparently referable to *S. brevilineatus*, shows a narrow lateral groove that is probably a columellar muscle scar. Similar bellerophontacean muscle scars were reported by Knight (1947) and Rollins (1967).

Boucot and Yochelson (1966), in a study of the Paleozoic gastropods of the Moose River Synclinorium, northern Maine, provisionally referred *S. brevilineatus* (Conrad) to the genus *Bucanella* Meek. They stated that they were following the custom of the past several decades, i.e., assignment of "most trilobed Paleozoic bellerophontaceans to *Bucanella*" (Boucot and Yochelson, 1966, p. A 5). They suspected, however, that *S. brevilineatus* might have a selenizone, as was recently discovered in the genus *Plectonotus* (Saul, Boucot, and Finks, 1963). Indeed, at least two species of trilobed bellerophontaceans, *Bucanella mamontovensis* Butosova and *Bucanella gurjevskensis* Butosova, from the Middle Devonian, Kuznetz Basin, U.S.S.R., appear to possess a narrow selenizone (Butosova, 1960). *Bellerophon angulatus* Gueranger, 1853, from the Devonian of Sarthe, France (as figured by Oehlert and Davoust, 1879, pl. 15, figs. 6a–c), is very similar to the Russian species.

The relatively well-preserved specimens from the Solsville clearly show a V-shaped sinus on the periphery of the median lobe. No selenizone is present. Moreover, the degree of trilobation of *S. brevilineatus* shows considerable intraspecific variation. In view of the laterally compressed shape and circumumbilical carina, we consider *S. brevilineatus* more closely allied to *Sinuitina* than to *Bucanella*.

## GENUS **PTOMATIS** CLARKE, 1899

TYPE SPECIES: *Bellerophon patulus* Hall, 1843.

### **Ptomatis rudis** (Hall), 1861

Figure 6A–D

*Bellerophon rudis* HALL, 1861, p. 29; 1862, p. 57; 1873, pl. 23; 1879, p. 103, pl. 24, figs. 13–15.

DESCRIPTION: This species is large, with an explanate bell-shaped aperture. The shallow V-shaped anterior sinus is accentuated on the adult whorl surface by undulating widely spaced, but dorsally restricted, transverse rugae. Spiral lirae may be present, but are always obscure. The rapidly expanding adult whorl is quite steeply arched on both sides of a slightly developed median dorsal keel but becomes explanate laterally, forming a nearly circular aperture. The posterior margin of the aperture is reflexed abaperturally into a short, wide sinus subjacent to the spire. Pustulate or striatopustulate parietal inductural deposits are strongly developed and attenuated anteriorly into a broad parietal shelf, which is arched dorsally and thickened medially. The umbilici are not well known, but are presumed to be narrowly phaneromphalous as a result of the upward flare of the aperture. The shell microstructure and muscle scars are unknown.

DISCUSSION: *Ptomatis rudis* (Hall) is morphologically very close to *Ptomatis patulus* (Hall), a species that is widespread in the Middle Devonian siltstones of North America. *Ptomatis rudis* is distinguishable by its collabral rugae and lack of spatulate parietal depression, a feature that has been interpreted, in the latter species, as the locus of an incompletely retractable posterior

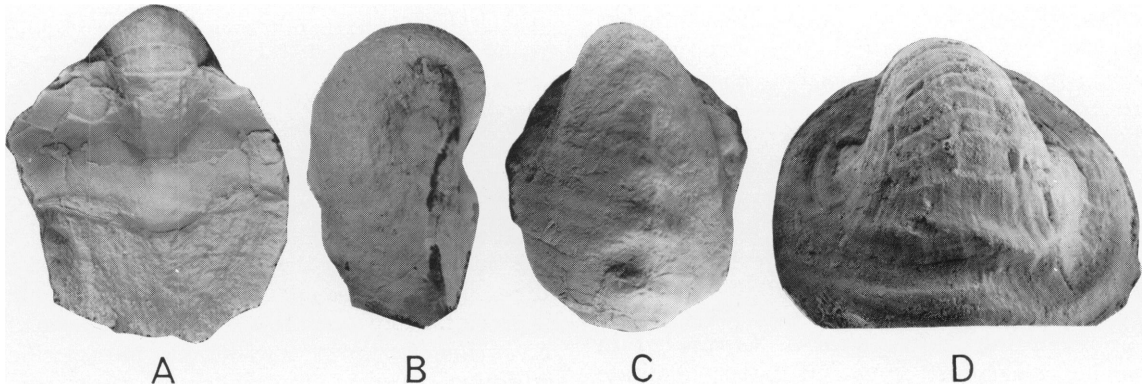


FIG. 6. *Ptomatis rudis* (Hall). A–C from A.M.N.H. 3017, A.M.N.H. No. 28847. A. Apertural view; note parietal extension. Approximately ×1.5. B. Lateral view showing collabral rugae. Approximately ×1.5. C. Dorsal view. Approximately ×1.5. D. Dorsal view of one of Hall's type specimens, Hamilton beds, Fultonham, New York, N.Y.S.M. No. 3251. Approximately ×1.0.

portion of the foot mass (Rollins, 1966, p. 3). However, one of the type specimens of *P. rudis* (N.Y.S.M. 3251) figured by Hall (1879, pl. 24, fig. 13) appears transitional in terms of ornament between *P. rudis* and *P. patulus*. For the present, it seems wise to retain these two forms as separate species.

Other species of *Ptomatis* have been reported from the Devonian of South America and South Africa. In every case, they are too poorly known to permit meaningful comparison with *P. rudis* and *P. patulus*.

The parietal shelf of *P. rudis* is not unique to that species. In fact, it occurs in most bellerophontaceans with widely explanate apertures and has been interpreted by Rollins [MS (b)] as a muscle attachment platform. It is tempting to suggest a modified benthic habitat for these forms. Most exhibit very rapidly expanding whorls and usually a whorl volume too restrictive for total retraction. Perhaps the shell was merely pulled down and positioned over the cephalopedal mass. In such a situation, better muscular leverage and control might be derived from more centrally attached muscles. During the last few years, the senior author has had the opportunity to examine hundreds of bellerophont steinkerns and all muscle scars observed have been on what might be called the "normal" bellerophontacean type (i.e., moderately tightly coiled, non-explanate apertures and no conspicuous parietal modifications, such as a platform or shelflike pad). On the other hand, no muscle scars have yet been observed on the dorsal lateral surfaces of the parietal platforms. This, however, is not too surprising in view of the general obscurity and low probability of preservation of bellerophontacean columellar muscle scars. It may be significant that one species, *Pharkidonotus labioreflexus* Sturgeon, discussed by Rollins (1967) has a muscle scar pair situated more within the columellar plane and extended only slightly upon the lateral shell wall. This same species develops a thick parietal pad.

The shell microstructure of *P. rudis* (Hall) has not been resolved because such an undertaking would destroy the only available specimen from the Solsville. The structure of *P. patulus* (Hall), however, is apparently complex crossed-lamellar (Rollins, 1967).

MATERIAL: One well-preserved specimen from A.M.N.H. 3017.

### FAMILY UNCERTAIN

DIAGNOSIS: Bellerophontaceans characterized by prominent keel throughout ontogeny; mature shell with extensively covered smooth inductura massively developed posteriorly; anal emargination a narrow short slit generating a slightly depressed selenizone.

### PRAEMATURATROPIS, NEW GENUS

TYPE SPECIES: *Praematuratropis ovatus*, new species.

DIAGNOSIS: *Praematuratropis* is distinguishable from other bellerophontacean genera in having

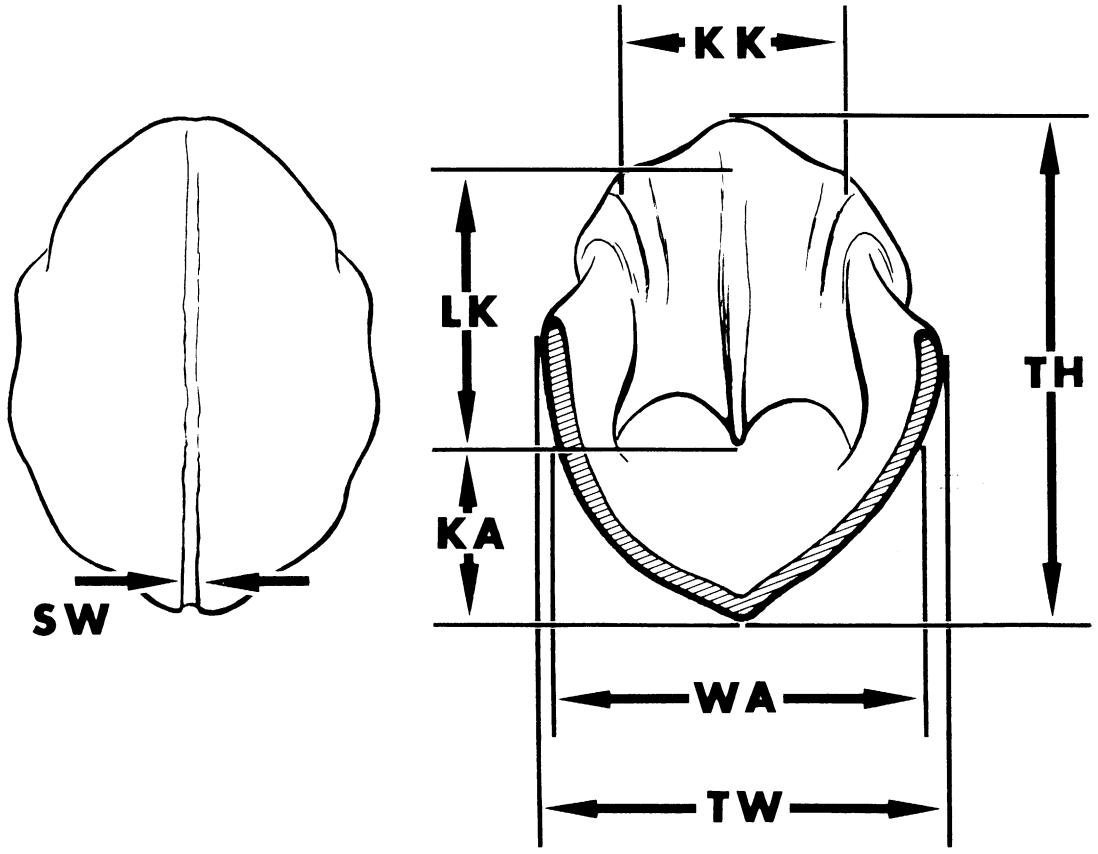


FIG. 7. Schematic illustrations of *Praematuratropis ovatus*, new species, showing the measured characters. *Abbreviations:* KA, distance from keel margin to anterior extremity of aperture; KK, distance between lateral ridges, measured with apertural orientation; LK, length of keel visible with apertural orientation; SW, selenizone width, measured on youngest portion of whorl; TH, total height, measured with apertural orientation; TW, total width, measured with apertural orientation; WA, apertural width, measured across aperture at keel margin with apertural orientation.

peculiar ovoid shape, conspicuous keel, and extensive inductura.

DESCRIPTION: This species is a rather small, involute bellerophontacean with bluntly ovoid or egg-shaped outline. The shell surface is smooth and lacks visible growth lines because of extensive inductural deposit; the inductura is very thin anteriorly, but becomes massive about one-half whorl back from the anterior margin, obscuring the selenizone and building in the parietal region a high narrow keel that is ontogenetically persistent. The parietal channels, or reentrants, extending anterolaterally toward the columellar axis are often developed; the inductural ridges occur parallel and subjacent to the keel in the lateral parietal regions. The anal emargination is a narrow short slit generating a slightly depressed selenizone. The microstructure of the inductura is crossed-lamellar with the primary lamellae oriented at right angles to the selenizone margins in the dorsal shell region. The microstructure of the primary shell wall is probably complex crossed-lamellar. The aperture is nonflaring, with straight lateral margins and rather strongly arched anterior lips. The muscle scars are unknown.

DISCUSSION: We are unable to assign this genus to any existing bellerophontacean subfamily, and following a trend recently endorsed by Horny (1963), we believe that this form is sufficiently distinct in its total morphology to be placed in a separate subfamily and possibly a separate family. We have not done the latter because we are aware of only one species of

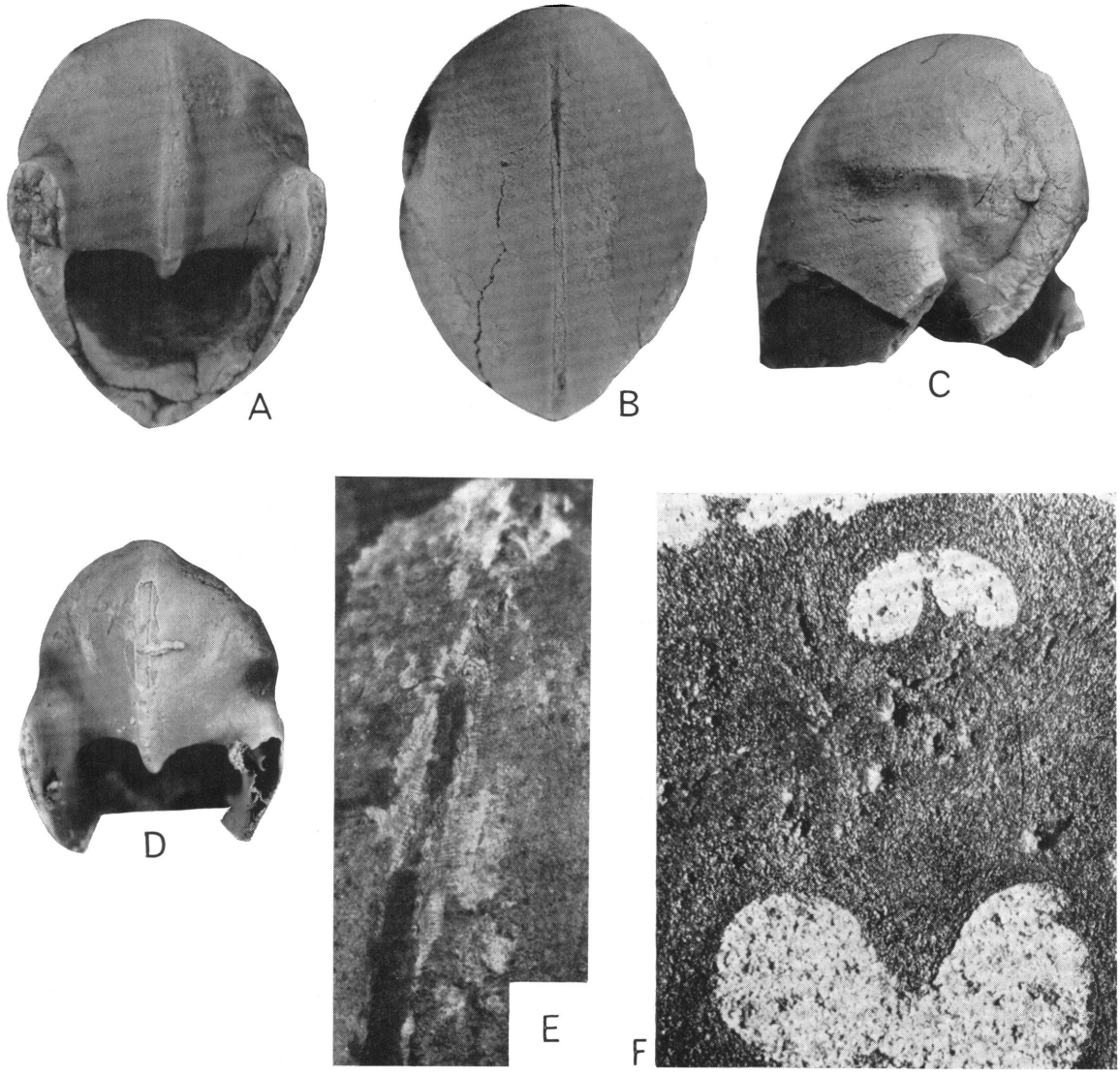


FIG. 8. *Praematuratropis ovatus*, new genus and species. A, B. Holotype, from A.M.N.H. 3017, A.M.N.H. No. 28833. A. Apertural view. ×4.0. B. Dorsal view. ×4.0. C. Paratype, oblique lateral view; note keel and parietal channel, from A.M.N.H. 3017, A.M.N.H. No. 28834. ×4.0. D. Paratype, apertural view of latex cast of small specimen, from A.M.N.H. 3013, A.M.N.H. No. 28838. ×4.0. E. Closeup of selenizonal region, showing crossed-lamellar shell structure with first order lamellae perpendicular to selenizone margins; note intersection of growth line and first order lamellae, from A.M.N.H. 3015, A.M.N.H. No. 28837. ×8.0. F. Paratype, etched and stained transverse section showing persistence of keel into early whorls, from A.M.N.H. 3017, A.M.N.H. No. 28839. ×50.0. Magnifications are approximate.

*Praematuratropis*. The involuteness and extensive inductura are reminiscent of the Euphemitidae whereas the keel calls to mind the Carinaropsinae. The keel in *Praematuratropis* is, however, more accentuated than that of any carinaropsinid, and it is not associated with a distinct platelike parietal extension.

It is difficult to believe that a morphological feature as pronounced throughout ontogeny as the keel of *Praematuratropis* would not have

functional significance. Indeed, this keel virtually divides the early whorls of *Praematuratropis* and must indicate some unusual organization of the soft anatomy of the animal. The extensive inductura suggests that, like the Euphemitidae, *Praematuratropis* possessed an extensive posterior mantle flap that, at times, virtually covered the entire shell. Unlike *Euphemites*, *Praematuratropis* probably possessed no additional anterior mantle flap which in the former genus was responsible for deposition of additional inductural layers (Moore, 1941; Yochelson, 1960). The pronounced keel certainly was responsible for limitation of the available space within the shell and this probably goes hand in hand with the evidence that the shell was internal. It is doubtful that there would have been enough room within the shell to permit total retraction.

**Praematuratropis ovatus,** new species
Figures 7, 8A–F

DESCRIPTION AND DIAGNOSIS: Same as for genus.

DISCUSSION: To date, only a single species of this unusual genus is known.

MATERIAL: Fifteen specimens from A.M.N.H. 3017; three specimens from A.M.N.H. 3013; four specimens from A.M.N.H. 3015; one specimen from the Pompey member of the Skaneateles Formation, at falls on Electric Light Stream, 2 miles southwest of Morrisville, New York.

## SUPERFAMILY **PLEUROTOMARIACEA** SWAINSON, 1840

## FAMILY **LOPHOSPIRIDAE** WENZ, 1938

## SUBFAMILY **RUEDEMANNIINAE** KNIGHT, 1956

### GENUS **RUEDEMANNIA** FOERSTE, 1914

TYPE SPECIES: *Ruedemannia lirata* (Ulrich), 1897.

**Ruedemannia trilix** (Hall), 1861
Figure 9A–D

*Pleurotomaria trilix* HALL, 1861, p. 17.

*Pleurotomaria trilix* HALL, 1879, p. 79, pl. 21, figs. 13–15.

*Lophospira trilix* GRABAU AND SHIMER, 1909, p. 637, fig. 864.

*Bembexia trilix* KNIGHT, in Shimer and Shrock, 1944, p. 457, pl. 184, figs. 27, 28.

*Ruedemannia trilix* CAMPBELL and ENGEL, 1963, p. 93.

TABLE 5
MEASUREMENTS (IN MILLIMETERS)[a] OF *Praematuratropis ovatus*, NEW SPECIES

| | TW | TH | WA | KA | LK | SW | KK |
|---|---|---|---|---|---|---|---|
| A.M.N.H. No. 28833 holotype | 11.35 | 14.60 | 11.00 | 4.80 | 7.60 | 0.45 | 5.20 |
| A.M.N.H. No. 28836 paratype | 9.70 | 13.85 | 9.90 | 5.50 | 6.20 | 0.80 | 5.10 |
| A.M.N.H. No. 28835 paratype | 12.25 | 15.10 | 11.70 | 5.15 | 8.00 | 0.85 | — |
| A.M.N.H. No. 28837 paratype | 9.30 | 13.95 | 8.70 | 5.65 | 6.40 | 0.75 | — |
| A.M.N.H. No. 28834 paratype | 10.20 | 13.05 | 9.75 | 4.65 | 5.50 | 0.65 | 4.50 |
| A.M.N.H. No. 28840 | 11.50 | 17.55 | 10.70 | 5.20 | 7.65 | — | 5.50 |
| A.M.N.H. No. 28840 | 10.65 | 16.80 | — | — | — | — | — |
| A.M.N.H. No. 28840 | 10.80 | 16.75 | 10.00 | 5.60 | 10.25 | — | 5.30 |
| A.M.N.H. No. 28840 | 12.40 | 16.80 | 12.35 | 6.20 | 6.10 | — | — |
| A.M.N.H. No. 28840 | 10.05 | 18.25 | 10.80 | — | — | 0.75 | — |
| A.M.N.H. No. 28840 | 14.05 | 14.10 | 13.70 | 5.60 | 5.20 | 0.70 | 5.30 |
| A.M.N.H. No. 28840 | 10.20 | 11.90 | 10.25 | 4.95 | 6.75 | — | — |
| A.M.N.H. No. 28840 | 10.60 | 14.05 | 10.30 | 5.20 | 6.00 | — | — |
| A.M.N.H. No. 28840 | 10.10 | — | 9.65 | — | 6.90 | — | — |
| A.M.N.H. No. 28840 | 9.40 | 19.75 | 8.65 | 5.25 | 7.35 | 0.75 | — |
| A.M.N.H. No. 28840 | — | — | — | — | — | — | — |
| A.M.N.H. No. 28840 | 11.70 | 15.50 | 10.85 | — | — | — | — |
| A.M.N.H. No. 28840 | — | — | — | — | — | 0.60 | — |
| A.M.N.H. No. 28840 | 13.15 | — | 13.75 | — | 5.75 | 0.75 | — |
| A.M.N.H. No. 28840 | — | — | — | — | — | — | — |
| A.M.N.H. No. 28840 | 9.40 | 14.10 | 8.90 | 5.60 | 6.80 | 0.55 | — |
| A.M.N.H. No. 28840 | 10.70 | 14.30 | 10.60 | 5.55 | 6.90 | 0.55 | 5.00 |

[a]See figure 7 for explanation of measurement symbols.

DESCRIPTION: The turbiniform carinate shell of this species consists of from five to six whorls and expands rapidly, the largest whorl comprising approximately one-half the total height of the shell. The upper whorl face, approximately 40 per cent of the total whorl height, is divided by a single strong carina into subequal upper and lower concave areas. The broad peripheral selenizone comprises about 20 per cent of the whorl height and is bounded by two thin spiral cords; a third, much stronger spiral cord in the center of the selenizone produces a pseudoconvex, noded interference pattern with the lunulae. The vertical concave outer whorl face is separated from the base by a distinct angulation produced by a heavy carina, above which a fainter spiral cord is sometimes developed. The suture is always situated on or slightly below the lower heavy carina. The anomphalous to minutely phaneromphalous base is flattened and bears a relatively fine spiral cord which is variably developed and sometimes absent. The aperture is subcircular.

The adapical moiety of the upper whorl face in many cases bears a small spiral ridge immediately below the suture. The collabral threads on the upper whorl face are prosocline and stronger on the adapical portion. The collabral elements of both the abapical portion of the upper whorl face and the lower whorl face swing back abaperturally, forming a V and indicating the relatively shallow extent of the sinus. Over the base the prosocline collabral threads are fainter.

In adult individuals the carinae are relatively less well developed, accounting for the smoother, less robust appearance of larger specimens. The protoconch, consisting of about three whorls, is smooth, with only faint growth lines visible. The first adult ornamental features to appear are two carinae, the upper in the position of the median carina of the adult selenizone on the periphery, and the lower corresponding to the large carina below the selenizone in adults. The collabral ornament is prosocline above the upper carina and opisthocline below, outlining a shallow V-shaped sinus on the immature whorls.

DISCUSSION: Campbell and Engel (1963, p. 93), who have recognized the true affinities of *R. trilix*, stated during the ontogeny of the Tournaisian species *R. bembexiformis* Campbell and Engel from New South Wales, that "the spiral threads on the whorls increase only slightly in prominence, and consequently the whorl profile in the early growth stages is much more rugged than in adults. The median thread of the selenizone actually decreases in size in the final whorl of the largest specimen. On the earlier whorls it is more than three times the size of the bounding carinae, and often forms the periphery of the whorl." A closely comparable diminution in robustness of the carinae is developed in large specimens of *R. trilix*, although most of the Solsville specimens are small and exhibit little ontogenetic change.

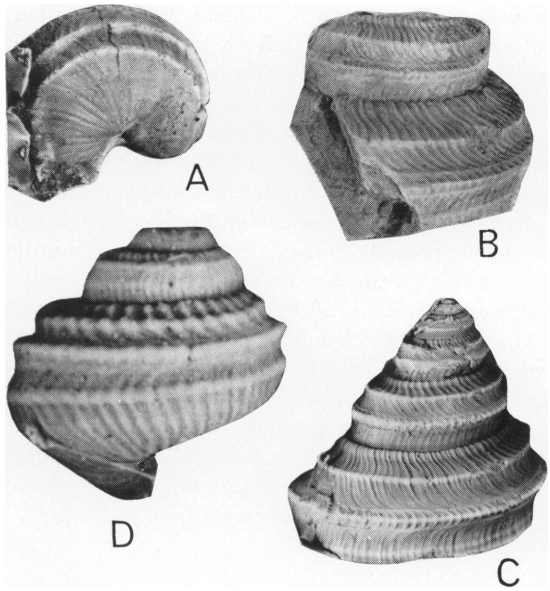


FIG. 9. *Ruedemannia trilix* (Hall). A. Basal view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28852. × 3.5. B. Lectotype?, side view, from Hamilton Group, Seneca Lake, New York, A.M.N.H. No. 5417. × 3.0. C. Oblique side view of large specimen, latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28853. × 2.5. D. Side view of very small specimen, latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28854. × 17.0.

Devonian and Lower Mississippian (Tournaisian) species of *Ruedemannia* are all very similar. Most differences involve the development of the smaller, secondary carinae on the upper and outer whorl faces. These carinae are variably developed even within samples from a single locality and cannot be considered profound specific differences. *Ruedemannia bembexiformis* possesses a second carina on the upper whorl face; a second carina is also variably developed on the upper whorl face of *R. strigillata* (Herrick) from the Tournaisian Waverly Group of Ohio (Hyde, 1953, p. 328). Another species, *R. bolivari*

(Kozlowski) from the middle Devonian of Bolivia, differs from *R. trilix* mainly in its lack of a carina on the base, its relatively finer collabral ornamentation, and its apparently greater maximum size. Although a carina is developed on the base of the Solsville *trilix* specimens and on Hall's figured specimens (1879, pl. 21, fig. 14, A.M.N.H. 4915/2, and fig. 15, A.M.N.H. 5417/2; see fig. 3B), individuals from other units of the Hamilton frequently lack this carina.

Additionally, Boucot and Yochelson (1966, p. A 9) have tentatively recognized *Ruedemannia* in the Emsian Tarrantine Formation of Maine. Although their specimens possess the shell form characteristic of *Ruedemannia*, poor preservation of their material prohibits any close comparison with *trilix*.

Diminution of robustness of the carinae produces a more rounded whorl profile in later whorls, and adult specimens approach the general shape and appearance of the type species *R. lirata* (Ulrich) from the Upper Ordovician of Kentucky.

The strongly gradate angular shape of the earlier whorls of *R. trilix* is strongly reminiscent of some species of *Worthenia* de Koninck. *Worthenia* was evidently derived from *Ruedemannia* by retention of the strong medial carina on the selenizone, addition of spiral threads on the upper and outer whorl faces and on the base, and diminution of the single carina of the upper and outer whorl faces. There thus seems to have been no simple relationship between the ontogeny of *Ruedemannia* and the evolution of *Worthenia* from *Ruedemannia* in the Mississippian.

MATERIAL: Thirty specimens from A.M.N.H. 3013; two specimens from A.M.N.H. 3014.

## FAMILY **PHYMATOPLEURIDAE** BATTEN, 1956

## GENUS **GLYPTOTOMARIA** KNIGHT, 1945

### SUBGENUS **GLYPTOTOMARIA**

### (**DICTYOTOMARIA**) KNIGHT, 1945

TYPE SPECIES: *Glyptotomaria* (*Dictyotomaria*) *scitula* (Meek and Worthen), 1861.

#### **Glyptotomaria (Dictyotomaria) capillaria** (Conrad), 1842

Figure 10A–F

*Pleurotomaria capillaria* CONRAD, 1842, p. 271, pl. 16, fig. 11.

*Pleurotomaria capillaria* HALL, 1879, p. 77, pl. 20, figs. 18–21.

*Gyroma capillaria* GRABAU AND SHIMER, 1909, p. 646, fig. 882.

*Bembexia capillaria* KNIGHT, in Shimer and Shrock, 1944, p. 457, pl. 184, fig. 30.

DESCRIPTION: The whorl profile of this turbiniform species changes throughout ontogeny and is intimately correlated with changes in ornament expression. The protoconch is rounded and consists of from two to three whorls. The selenizone, the first adult feature to appear, is nearly vertical and is located on the periphery slightly below midwhorl. The lowest spiral cord of the upper whorl face becomes increasingly pronounced and reaches the periphery in later whorls. The upper whorl face is rounded, and, in later whorls, becomes vertical between the lower spiral cord and the upper margin of the selenizone. The outer whorl face is vertical and separated from the flattened base by a rounded angulation.

The ornament initially consists solely of collabral cords. These are transected first by one, then eventually by three, four, or five spiral cords which quickly become equal in strength to the collabral elements and produce a dictyate pattern. In later whorls, the spiral elements become unequal and stronger than the collabral cords, producing a nodose effect. The selenizone is bounded by two strong spiral cords. The areas between these cords and the nearest spiral elements of the upper and outer whorl faces frequently lack collabral ornament and are generally broader than are the spaces between spiral elements elsewhere on the whorl. In the earliest whorls, the collabral cords on the upper whorl face are nearly orthocline near the suture, but are inflected at the lone spiral cord and become prosocline to the selenizone; in later whorls, there is no such sharp deflection, the collabral cords becoming prosocline gradually as the selenizone is approached. Immediately below the selenizone the collabral cords are opisthocline, becoming prosocline at the first spiral cord and sweeping back into a broad, shallow sinus on the base. The dictyate appearance is maintained over the base to the umbilicus in immature specimens, though the collabral elements thin and merge near the umbilicus; the spiral elements dominate in later whorls.

The moderately deep slit is quite broad initially and widens at a slower rate of growth

relative to the other shell dimensions. The selenizone is depressed and bears distinct, closely and regularly spaced lunulae in all but the earliest whorls. Sutures are impressed but not very deep. The columella is minutely phaneromphalous and the aperture, according to Hall, is subrhomboidal.

DISCUSSION: Hall (1879, pp. 77–78) noted the extreme variability of the ornament of this species. The extensive collection from the Solsville shows that the variability is determined entirely by a complex, but regular, series of ontogenetic changes. All ornament is at first collabral; then spiral cords appear, become equal in strength to the collabral cords to produce the dictyate pattern, and eventually dominate the collabral cords while becoming themselves unequal in strength. This dominance of the spiral ornament is seen in large individuals of other species of this subgenus, e.g. *Glyptotomaria* (*Dictyotomaria*) cf. *scitula* (Meek and Worthen) from the Vanport limestone of Ohio, figured by Sturgeon, 1964, pl. 32, figs. 9, 10, and *Glyptotomaria* (*Dictyotomaria*) *quadrilineatus* (Girty) of the Pennsylvanian McCoy Formation of Colorado (Girty, 1934, p. 257 and figs. 20–22).

The position of the suture in *capillaria* may vary greatly from specimen to specimen, ranging from directly below the selenizone to the base of the outer whorl face of the preceding whorl. Later species tend to add more spiral cords to the upper whorl face and increase its angle of slope, a trend culminating in the "bee-hive" shaped subgenus *G.* (*Glyptotomaria*) Knight of the Pennsylvanian and Permian. *Glyptotomaria* (*Dictyotomaria*) *quadrilineatus* of the McCoy Formation retains a whorl shape and ornament pattern closely similar to *G.* (*D.*) *capillaria*, and is likely a conservative descendant of the latter.

The only Devonian pleurotomarian with which *G.* (*D.*) *capillaria* may be confused is *Dictyobembix bella* Tyler from the Four Mile Dam limestone of Michigan (Tyler, 1965, p. 343, pl. 48, figs. 13–16). This somewhat unusual eotomarian differs from *G.* (*D.*) *capillaria* in possessing a narrow selenizone, apparently nonlunulate or only faintly so, somewhat above the periphery; upper whorl face ornament is similar to that of *capillaria*, but *Dictyobembix* possesses only spiral ornament below the selenizone.

A specimen tentatively referred by Hall to *G.* (*D.*) *capillaria* from the Onondaga ("Upper Helderberg") limestone of New York (Hall, 1879, pl. 12, fig. 25) is a poorly preserved steinkern possibly of an unusually gradate species of *Bembexia*.

### COMMENTS ON THE ORIGIN OF THE PHYMATOPLEURIDAE

According to Batten (1958, p. 210), the subgenus *G.* (*Dictyotomaria*) is ancestral to all the other phymatopleurid genera and first appears in the Meramecian Salem limestone of Indiana. An unpublished species from the Kinderhookian Wassonville limestone of Iowa (Rollins, 1963) and *G.* (*D.*) *capillaria* of the Cazenovia, Tioughnioga, and Taghanic Stages extend the range of the family down through the Mississippian into the Middle Devonian. Several specimens of *capillaria* from the Solsville are preserved with the earliest whorls, including the protoconch, intact. The sequence of whorl shape and ornamental changes leading to the adult features of *Dictyotomaria* sheds some light on the provenance of this subgenus.

The Phymatopleuridae probably arose from the Eotomariidae, specifically the tribe Eotomariides, *sensu* Knight, Batten, and Yochelson, 1960, p. I 204. These eotomarians commonly possess a concave selenizone at mid-whorl bounded by cords, the lower one of which forms the periphery. Spiral ornament is not universally present and is generally masked by the more dominant, omnipresent collabral ornament; *Dictyobembix* appears to be an exception. Phymatopleurids, on the other hand, typically have strong spiral ornament dominant over collabral, and the selenizone slightly below mid-whorl. Selenizone morphology is closely similar to that of the eotomarians, although the lunulae are more sharply developed in the Phymatopleuridae.

In terms of the first two post-protoconch whorls, *G.* (*D*). *capillaria* is an eotomarian, and in fact indistinguishable from *Bembexia* Oehlert. The selenizone is at mid-whorl and its lower bounding cord forms the periphery. Collabral ornament appears first, the first spiral cord to appear is slightly below the center of the upper whorl face, and the selenizone bears no lunulae; this complex of characters essentially defines *Bembexia*. In later whorls the number of spiral cords increases, and the whorl periphery consists of the vertical surface extending from the lowest of the spiral cords of the upper whorl face through the lower margin of the selenizone.

Thus, although typically phymatopleurid features appear early in ontogeny, the very earliest stages are distinctly eotomarian in nature; to the extent that ontogenetic information may shed light on phylogenetic relationships, knowledge of the early ontogeny of *G. (D.) capillaria* in our opinion greatly strengthens the belief that the phymatopleurids arose from the Eotomariinae via a genus close to *Bembexia*.

Several eotomarian species of the Middle Devonian acquired ornamental features approaching those developed in *capillaria*. *Dictyobembix bella*, with its close ornamental resemblance to *capillaria*, may represent the eotomarian stock close to that which gave rise to the phymatopleurids, but retained a whorl shape and selenizone morphology and position typical of the eotomarians.

*Bembexia adjutor* (Hall), from the Delaware limestone of Ohio, has two spiral elements on the upper whorl face and a dictyate pattern on the base of the earlier whorls. The upper spiral cord of the upper whorl face and the spiral cords on the base are apparently lost in later whorls. Thus the typical phymatopleurid ornamental patterns seem to have been developed gradually within the *Bembexia-Dictyobembix* stock.

MATERIAL: Twenty-five specimens from A.M.N.H. 3013; two specimens from A.M.N.H. 3014.

## FAMILY **EOTOMARIIDAE** WENZ, 1938

## SUBFAMILY **EOTOMARIINAE** WENZ, 1938

## TRIBE **EOTOMARIIDES** WENZ, 1938

### GENUS **BEMBEXIA** OEHLERT, 1888

### **Bembexia sulcomarginata** (Conrad), 1842

Figures 10J–M, 11

TYPE SPECIES: *Bembexia larteti* (Munier-Chalmas), 1876.

*Pleurotomaria sulcomarginata* CONRAD, 1842, p. 272, pl. 16, fig. 13; HALL, 1879, p. 69, pl. 19, figs. 8–17.

*Bembexia sulcomarginata* (Conrad): ULRICH AND SCOFIELD, 1897, p. 1001, fig. 6. KNIGHT, in Shimer and Shrock, 1944, p. 457, pl. 184, figs. 25, 26.

DESCRIPTION: The shell of this species consists of from five to seven whorls and expands rapidly, the final whorl comprising approximately one-half the total height of the shell. Although generally turbiniform, the shell form ranges from trochiform to gradate, reflecting ontogenetic and interpopulational variation in ornament expression and position of the suture. In the early whorls the suture is situated immediately subjacent to the selenizone and the shell form is turbiniform or slightly gradate. In larger specimens, the suture may progressively cover the selenizone and produce a trochiform shape.

The protoconch consists of from three to four whorls and is smoothly rounded. The selenizone is positioned at mid-whorl and is the first adult feature to appear. Two spiral cords appear next on the upper whorl face, the upper immediately below the suture, and the lower approximately midway up the upper whorl face. In later whorls the median cord becomes a prominent carina, dividing the upper whorl face bearing collabral ornament and a lower smaller nearly vertical surface which is smoothly concave. In the final whorls, this carina generally becomes obsolescent as it migrates toward the selenizone.

The slightly concave selenizone is bounded by spiral threads; although wide in the earlier whorls, it expands at a relatively slower rate than the rest of the whorl. Regularly spaced lunulae are variably developed and restricted to the final whorls. Initially vertical, the selenizone becomes inclined adapically, its lower margin forming the periphery of the whorl.

Although prosocline growth lines are generally developed on the upper whorl face above the carina in early whorls, the strength of collabral ornamentation varies in later whorls. In some specimens, prosocline lirae form at regular intervals, whereas in others, faint, closely spaced growth lines are developed. Large specimens from some populations lose all traces of collabral ornament. The collabral elements form radial nodes upon intersection with the spiral cord and carina of the upper whorl face.

The outer whorl face of the body whorl is gently rounded and generally bears a single spiral thread. The anomphalous base is indistinctly set off from the lower whorl face and is somewhat flattened. Faint growth lines marking a shallow sinus are generally present over the base. The aperture is ovoid.

DISCUSSION: Variation in position of the suture and strength of collabral and spiral ornamentation accounts for the striking differences seen, particularly in later whorls, between samples of *B. sulcomarginata* from different units of the Solsville. Specimens from the lower gray shale of the Solsville (fig 10K, M) are generally large and develop a moderate carina which dies out in

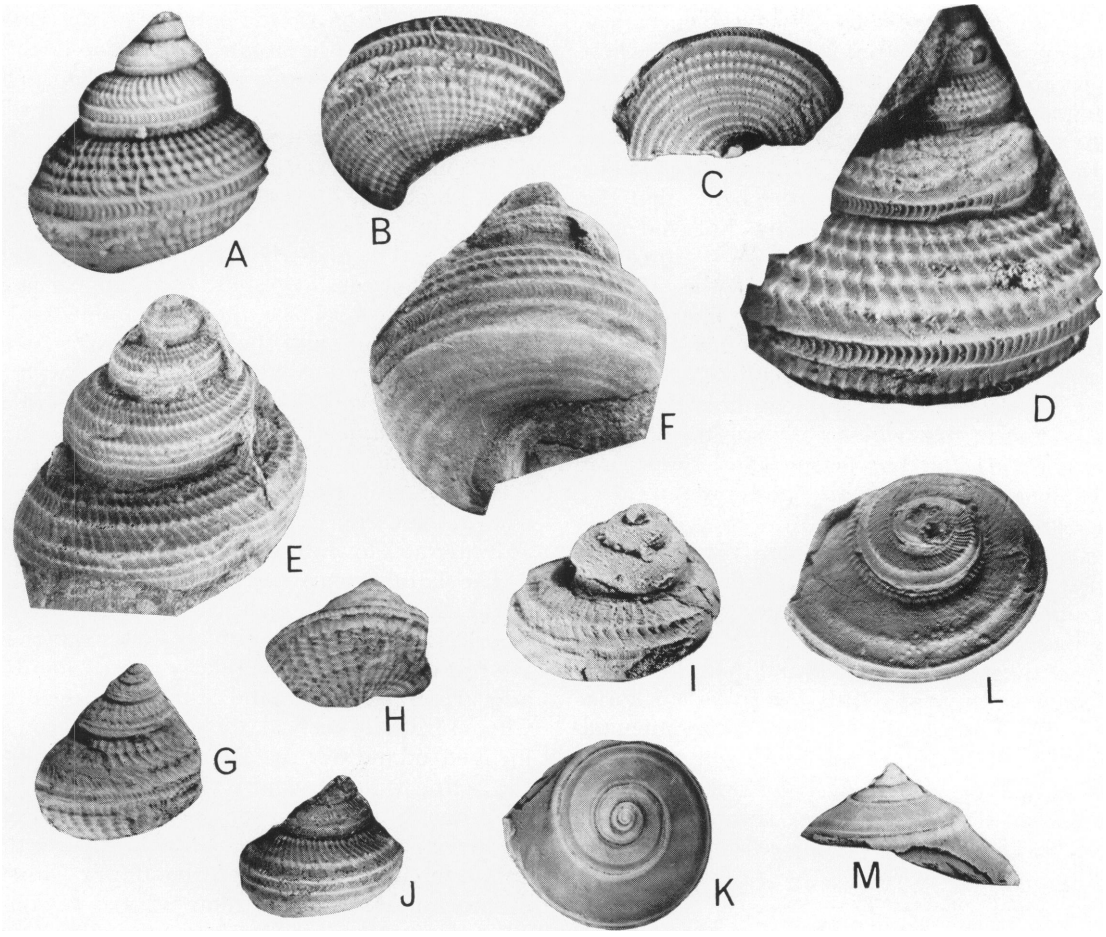


FIG. 10. A–F. *Glyptotomaria* (*Dictyotomaria*) *capillaria* (Conrad). A, B. From A.M.N.H. 3013, A.M.N.H. No. 28848. A. Side view of latex cast. ×12.5. B. Basal view. ×12.5. C. Basal view of latex cast showing ornament of mature specimens, from A.M.N.H. 3013, A.M.N.H. No. 28849. ×4.0. D. Lateral view of large individual, latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28850. ×5.0. E, F. One of Hall's figured specimens, from Hamilton Group, Madison County, New York, A.M.N.H. No. 4408 (746). E. Oblique lateral view. ×4.0. F. Oblique apertural view. ×4.0. G–I. *Bembexia adjutor* (Hall), from "Upper Helderberg limestone near Dublin, Ohio," A.M.N.H. No. 4232. G, H. Paralectotype. G. Side view. ×4.5. H. Basal view. ×4.5. I. Lectotype, side view. ×1.5. J–M. *Bembexia sulcomarginata* (Conrad), from A.M.N.H. 3013. J. Oblique side view of small specimen, latex cast, A.M.N.H. No. 28856. ×4.5. K. Large, sparsely ornamented individual, top view, A.M.N.H. No. 28857. ×1.0. L. Oblique top view; note ontogenetic change in ornament, A.M.N.H. No. 28858. ×2.0. M. Side view, A.M.N.H. No. 28857. ×1.0.

later whorls. The selenizone is often covered by the suture in later whorls, and collabral ornament is present only as faint growth lines throughout ontogeny.

On intermediate specimens (fig. 10L) found in both the calcareous gray shales and calcareous siltstones of the Solsville, a moderate carina develops and the selenizone remains uncovered. Prominent collabral lirae are developed in earlier whorls, but rapidly become obsolescent in later whorls.

The calcareous siltstones of the Solsville have produced many immature specimens of *B. sulcomarginata* (fig. 10J). Although the subsequent ontogeny of these specimens is unknown, the collabral ornament is very strong, and the carina of the upper whorl face is sufficiently heavy to form a gradate whorl shape. These specimens

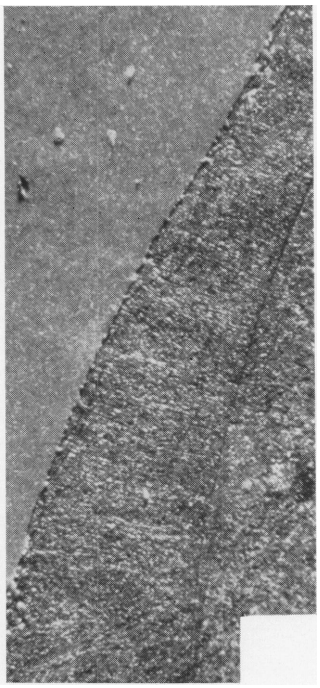

FIG. 11. *Bembexia sulcomarginata* (Conrad). Etched and stained longitudinal section showing fine prismatic shell structure, from A.M.N.H. 3013, A.M.N.H No. 28859. ×25.0.

are very similar to the early whorls of specimens found in higher units of the Skaneateles Formation (e.g. the Delphi Station and Pompey members); ornamentation remains strong in the later whorls of specimens from these higher units, and the selenizone is never covered by the suture.

*Bembexia sulcomarginata* is a common species throughout the Cazenovian of New York and the southern Appalachian states. It is also found in the Cazenovian Silver Creek limestone of southern Indiana and the Taghanic Tully limestone of New York. Hyde (1953, p. 53) has shown that *P. sulcomarginata* does not occur in the lower Mississippian Waverly group of Ohio, as reported by Herrick (1893). The full range of variation exhibited by the Solsville specimens is maintained on an interpopulational level throughout the Skaneateles Formation. Although interpopulational variation seems related to the nature of the sediments, the geographic and stratigraphic distributions of the variants is a complex problem warranting further study. Comparison of *B. sulcomarginata* with other species of *Bembexia* in the literature is difficult because of the highly variable nature of *B. sulcomarginata*.

According to Knight, Batten, and Yochelson (1960, p. I 206), *Bembexia* ranges from the Lower Devonian into the Mississippian. Early and Middle Devonian species form a closely knit complex centered around the type species, *B. larteti* (Munier-Chalmas) of the Lower Devonian of France. The most variable interspecific feature within this Devonian complex appears to be the position of the suture, which commonly lies directly below the spiral cord forming the ventral margin of the selenizone, as in *B. sulcomarginata* and *B. alta* (Drevermann), the latter from the Emsian of Germany. The suture may even overlap the selenizone in later stages of ontogeny. Other species, such as *B. larteti* and *B. adjutor* (Hall), from the Cazenovian Delaware limestone of Ohio, are more gradate, the suture occurring lower on the outer whorl face. All Devonian species possess a single carina approximately midway up the outer whorl face which generally forms a prominent ridge in early whorls and is commonly reduced and even lost in later whorls. A few secondary spiral cords appear in some species, but they are commonly restricted to the early whorls, and collabral ornament itself generally becomes subdued in later whorls, its expression commonly restricted to radially oriented nodal ridges near the suture and on the carina of the upper whorl face. In general, ornament seems more strongly developed in the more gradate species.

None of the Mississippian eotomarian species assigned to *Bembexia* agrees in these essential ornamental characters. Many Mississippian species assigned to *Bembexia* are more properly referred to *Glabrocingulum* (*Glabrocingulum*) Thomas. The whorl profile of *G.* (*Glabrocingulum*) is similar to that of *Bembexia*. If, in Mississippian species of *Glabrocingulum*, the spiral ornament is confined to but one or two threads, these are invariably positioned immediately subjacent to the suture. Such is the case, for example, in *G.* (*G.*) *stellaeformis* (Hyde) from the Waverly of Ohio and *G.* (*G.*) *binodosum* Sadlick and Nielsen from the Mississippian Chainman Formation of Utah. Other Mississippian species of *Glabrocingulum* develop more spiral cords lower down on the upper whorl face which may mask collabral ornament. Examples are *G.* (*G.*) *quadrigatum* Sadlick and Nielsen from the Chainman Formation of Utah and "*Bembexia*" *ellenae*

Conkin from the New Providence Formation of Kentucky. The spiral cords of the upper whorl face in Mississippian species of *Glabrocingulum* are usually heavily noded; in contrast to the radially oriented nodal ridges typical of Devonian species of *Bembexia*, the nodes on the spiral threads of *Glabrocingulum* are generally rounded tubercles.

Some of the Mississippian species that have been assigned to *Bembexia* are trochiform eotomarians that possess only collabral ornamentation on the upper whorl face. Many of these species will probably prove to belong to *Eucanospira* Ulrich and related genera.

Some Devonian eotomarians, e.g. *Dictyobembix bella* Tyler, develop heavy spiral ornamentation on the upper whorl face and appear to approach the general conformation typical of Mississippian *Glabrocingulum* species. However, since Devonian *Bembexia* species form a coherent complex readily distinguishable from any Mississippian eotomarian known to us, we believe that in light of present knowledge the generic name *Bembexia* should be used solely for those species within this Devonian complex.

*Bembexia sulcomarginata* is closely related to *B. adjutor* (Hall) from the Cazenovian Delaware limestone of Ohio. Hall's figured specimen (A.M.N.H. No. 4232, fig. 10 I) is a rather large individual which retains coarse collabral lirae, a strongly developed spiral carina on the upper whorl face, and a well-developed carina setting the base off from the outer whorl face. Ornament is preserved only on the last half of the final volution, but the specimen appears more gradate than typical *B. sulcomarginata*. On adult characters alone, *B. adjutor* might be considered a geographic variant of *B. sulcomarginata*.

However, there are important early ontogenetic differences between the two species. A small specimen included with Hall's figured specimen (see fig. 10G, H) is an undoubted *Bembexia* and assigned here to *B. adjutor*. It differs from *B. sulcomarginata* of comparable size by having the suture placed somewhat below the selenizone. It differs from the adult figured specimen, as well as comparably sized *sulcomarginata*, by having a second carina below the suture and a truly dictyate ornamental pattern over the base. Boucot and Yochelson (1966, p. A 8–A 9) have tentatively assigned four small specimens of *Bembexia* from the Eifelian Tomhegan Formation of Maine to *B. adjutor*, but their specimens do not show dictyate ornament over the base and seem more comparable with *B. sulcomarginata*.

Tyler (1965) recently erected the subgenus *B.* (*Genuspira*) based on *B.* (*Genuspira*) *nodosa* Tyler from the basal Tioughniogan Four Mile Dam limestone of eastern Michigan. According to Tyler (1965, p. 343), *Genuspira* is distinguishable from other subgenera of *Bembexia* by having "a narrower, immediately supraperipheral selenizone, deeper sutures, no collabral threads, and a more strongly developed angular shoulder." The great amount of variation in ornamentation within Solsville samples of *B. sulcomarginata* embraces the general pattern on which Tyler bases *Genuspira*. Indeed, one specimen of *sulcomarginata* from the lower gray shale A.M.N.H. 3013 (fig. 10L) appears virtually indistinguishable from a comparably sized paratype, United States National Museum, Smithsonian Institution, No. 144473, of *B.* (*G.*) *nodosa* (Tyler, 1965, pl. 48, fig. 9). In view of the variation exhibited by *sulcomarginata*, the subgenus *Genuspira* becomes unrecognizable. *Bembexia nodosa* may lose collabral ornament even earlier in ontogeny than the extremes discovered so far in *sulcomarginata*, and although very close to *sulcomarginata*, *B. nodosa* may profitably be considered a distinct species. It appears to be the sole North American Tioughniogan representative of *Bembexia* (see Cooper, 1957, p. 274).

Two poorly known species described by Hall (1879), "*Pleurotomaria*" *planidorsalis* from the "Hamilton" of New York, and "*P.*" *nitella* from the Onondaga limestone of New York, may also be referable to *Bembexia*. Although we have not examined Hall's material, on the basis of his descriptions and figures (1879, pp. 82–83, pl. XXI, figs. 21, 22), "*P.*" *planidorsalis* may be conspecific with *B. sulcomarginata*. "*Pleurotomaria*" *nitella* is a gradate species with strong collabral ornament; although indistinct in Hall's figures (1879, pl. XXX. fig. 19), Hall described (p. 85) a subdued carina on the upper whorl face. We tentatively refer this species to *Bembexia*, but the nature of its affinities cannot be clarified until additional material becomes available.

*Bembexia alta* (Drevermann) from the Emsian of Germany differs from *B. sulcomarginata* in having distinct lunulae on the selenizone and a concave adapical portion of the upper whorl face above a strong carina which shows little tendency towards obsolescence. Collabral threads traverse the base of *B. alta*, become obsolescent

midway, but then reappear as the columella is approached. When present, collabral elements are continuous over the base of *sulcomarginata*.

No specimens of the type species, *B. larteti*, were available for comparison with *sulcomarginata*. As seen in a small paratype of *larteti* figured by Knight (1941, pl. 34, fig. 2c, d), the suture is somewhat below the lower cord bounding the selenizone, giving *larteti* a more gradate form than typical *sulcomarginata*. Variation in ornament expression in *larteti* is too inadequately known to permit further comparison with *sulcomarginata*.

MATERIAL: *Bembexia sulcomarginata* is one of the most common elements of the Solsville fauna and was collected at all localities. More than 200 specimens were available for this study.

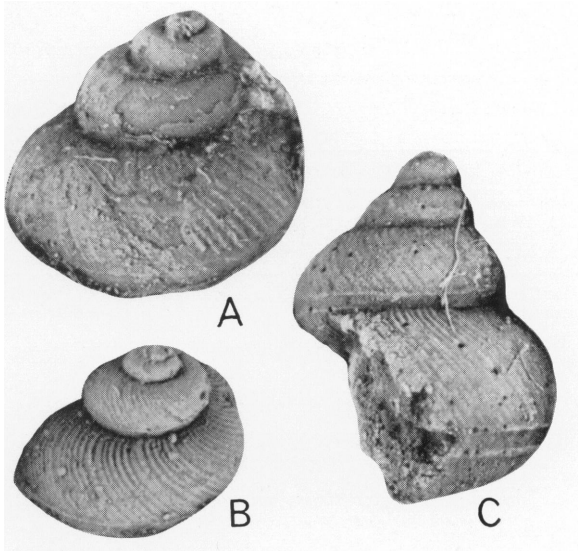


FIG. 12. *Mourlonia subzona*, new species, from A.M.N.H. 3013. A. Paratype, side view of latex cast, A.M.N.H. No. 28860. Approximately ×13.0. B. Small paratype, side view, latex cast; note smooth nuclear whorls. A.M.N.H. No. 28861. Approximately ×14.0. C. Holotype, side view showing position of selenizone, latex cast A.M.N.H. No. 28862. Approximately ×12.5.

## FAMILY **EOTOMARIIDAE** WENZ, 1938

## SUBFAMILY **EOTOMARIINAE** WENZ, 1938

## GENUS **MOURLONIA** DEKONINCK, 1883

TYPE SPECIES: *Helix carinatus* J. Sowerby, 1812.

### **Mourlonia subzona,** new species
Figure 12A–C

DIAGNOSIS: Low position of selenizone distinguishes *subzona* from all other species of *Mourlonia*, which have selenizone situated near mid-whorl, but variably placed in relation to whorl periphery. Detailed study of known species of *Mourlonia* may indicate that *M. subzona* represents a new subgenus of *Mourlonia*.

DESCRIPTION: This small species is moderately high-spired with a concave selenizone situated low on the whorl, well below the periphery. The tightly coiled nuclear whorls are unornamented and nearly discoidal. Distinct cords form the margins of the rather narrow selenizone. The lunulae of the selenizone are more closely spaced than the cords. The whorl profile is smoothly rounded and the periphery occurs at mid-whorl. Whorls are usually embraced below the periphery near the upper selenizone margin, but large individuals often display more open coiling in later whorls. Sutures are distinct to moderately impressed. Collabral ornament consists of sharp cords which, on the upper whorl surface, are orthocline for a short distance immediately below the suture, becoming strongly prosocline over the periphery to the upper selenizone margin, and are less strongly prosocline on the base of the whorl. The base is somewhat flattened and minutely phaneromphalous. Shell microstructure is unknown.

DISCUSSION: In terms of ornament, *M. subzona* resembles *Pleurotomaria plena* Hall, from the Onondaga limestone of New York State (Hall, 1876, pl. 17, figs. 11–13; 1879, p. 66, pl. 17, figs. 11–13). That species, however, has a narrow selenizone situated above the whorl periphery on the upper whorl surface and has recently been referred to the genus *Stenoloron* Oehlert (Boucot and Yochelson, 1966, p. A 9). As Hall's figures of *P. plena* show a selenizone just above mid-whorl, we doubt that that species should be assigned to *Stenoloron* and suggest that it falls within the currently accepted morphologic spectrum of *Mourlonia*.

*Catantostoma baylii* Oehlert and Davoust, from the Devonian of France, is apparently a species of *Mourlonia* and may be conspecific with *P. plena* Hall (Oehlert and Davoust, 1879, p. 713, pl. 15, fig. 4).

MATERIAL: Thirteen specimens from A.M.N.H. 3013.

TABLE 6
MEASUREMENTS (IN MILLIMETERS) OF *Mourlonia subzona*, NEW SPECIES

| | Total Height | Total Width | Selenizonal Width | SS[a] | Basal Whorl Height |
|---|---|---|---|---|---|
| A.M.N.H. No. 28860 paratype | 5.6 | 6.7 | 0.57 | 2.4 | 3.3 |
| A.M.N.H. No. 28862 holotype | 4.4 | 3.6 | 0.2 | 1.2 | 2.4 |
| A.M.N.H. No. 28863 paratype | 5.4 | 4.7 | 0.28 | 1.7 | 2.7 |
| A.M.N.H. No. 28864 | 3.6 | 3.3 | 0.2 | 1.2 | 2.2 |

[a]Distance between upper selenizonal margin and upper suture, as measured on basal whorl.

FAMILY **RAPHISTOMATIDAE** KOKEN, 1896

SUBFAMILY **LIOSPIRINAE** KNIGHT, 1956

GENUS **TREPOSPIRA** ULRICH AND SCOFIELD, 1897

TYPE SPECIES: *Pleurotomaria sphaerulata* Conrad, 1842.

SUBGENUS **TREPOSPIRA (ANGYOMPHALUS)** COSSMAN, 1916

TYPE SPECIES: *Euomphalus radians* deKoninck, 1843.

**Trepospira (?Angyomphalus) peneglabra,** new species
Figure 13D–G

DIAGNOSIS: Species based on two available specimens from A.M.N.H. 3013. The species is rare in the Solsville, and to our knowledge only two other species of *T.* (*Angyomphalus*) have been described from the Devonian of North America; *T.* (*A.*) *rotalia* (Hall), 1861, from Upper Skaneateles Formation, Pratts Falls, N.Y. (Hall, 1862, p. 46, pl. 5, fig. 11; 1879, p. 71, pl. 19,

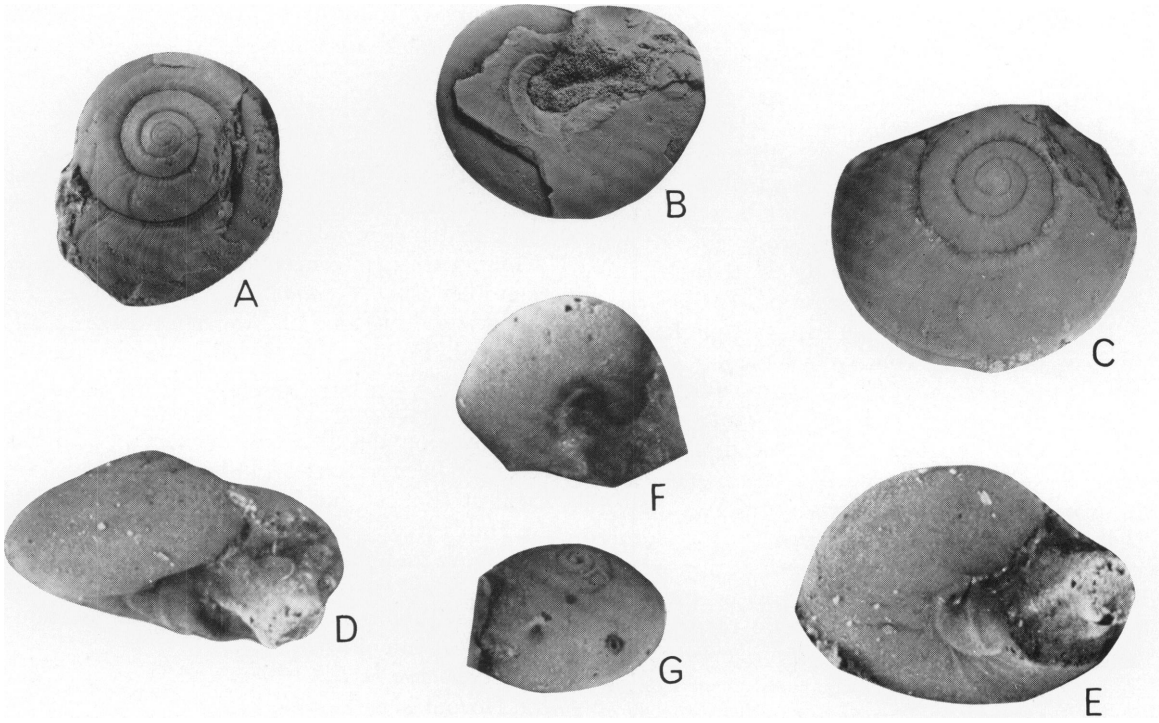


FIG. 13. A–C. *Trepospira* (*Angyomphalus*) *rotalia* (Hall), from Hamilton Group, near Pratts Falls, New York, A.M.N.H. No. 5415. A. Top view. ×3.0. B. Basal view. ×3.0. C. Another specimen in type lot, top view. ×6.0. D, E. *Trepospira* (*Angyomphalus*) ? *peneglabra*, new species, from A.M.N.H. 3013, A.M.N.H. No. 28878. D. Holotype, apertural view of latex cast; note flexured funicle. ×15.0. E. Basal view. ×15.0. F, G. Paratype from A.M.N.H. 3013, A.M.N.H. No. 28879. F. Basal view of latex cast. ×15.0. G. Oblique side view. ×15.5.

figs. 20–25), and *T.* (*A.*) *bella* Tyler, from Four Mile Dam Limestone of Michigan (Tyler, 1965, p. 342, pl. 47, figs. 22–24). *Trepospira* (*?A.*) *peneglabra* is distinguishable from *T.* (*A.*) *rotalia* in being smaller, in having a flexured circumumbilical funicle, and in lacking a subsutural spiral ornament. The type specimens of *T.* (*?A.*) *rotalia* (Hall) were examined, and since that species has a subsutural thread and subtle subsutural nodes on each post-nuclear whorl, the specimens of *T.* (*?A.*) *peneglabra* cannot be considered immature examples of Hall's species (see fig. 13A–C) *Trepospira* (*?A*) *peneglabra* lacks the subsutural and circumbilical nodes of *T.* (*A.*) *bella.*

DESCRIPTION: This species is very small and low-spired. The whorl profile is convex on both the upper and lower whorl surfaces with a rounded periphery situated at mid-whorl. The selenizone has not been observed but is presumed to be present and conformable to other species of *T.* (*Angyomphalus*)—that is, mid-whorl, immediately above the periphery. The base is gently rounded and hemiomphalous, with a flexured circumumbilical funicle. Ornament is collabral only, consisting of very obscure growth lines, more pronounced on the lower whorl surface and costate adjacent to the funicle. The shell structure is unknown.

DISCUSSION: Reports of *T.* (*Angyomphalus*) are notably rare in the Devonian and Lower Carboniferous of North America. To some extent, this might be explained by the tendency of *T.* (*Angyomphalus*) to possess an obscure selenizone, only discernible under careful scrutiny. Rollins [MS(a)] described a species of *T.* (*Angyomphalus*) based on an unusually large and well-preserved population from the Lower Mississippian Wassonville chert of southeast Iowa. Although nearly one-hundred individuals were available for that study, only one or two specimens displayed clear-cut evidence of the selenizone. The only other report of *T.* (*Angyomphalus*) from the Lower Carboniferous of North America is contained in Yochelson and Dutro (1960, p. 136, pl. 12, figs. 35, 36), where a single specimen from northern Alaska is questionably assigned to that subgenus.

Quite probably, such lenticular Lower Carboniferous forms as *Straparollus lens* Hall and *Straparollus northviewensis* Branson will prove to be species of *T.* (*Angyomphalus*).

Until a selenizone is observed in *T.* (*?A.*) *peneglabra*, an element of doubt exists regarding the generic assignment of that species. If a selenizone is not present, this species should be placed in the genus *Anomphalus* Meek and Worthen. Umbilical characters are of little taxonomic value in these genera. Not all species of *T.* (*Angyomphalus*) are hemiomphalous, with a funicle, and species of *Anomphalus* vary from cryptomphalous to phaneromphalous.

MATERIAL: Two specimens from A.M.N.H. 3013.

TABLE 7
MEASUREMENTS (IN MILLIMETERS) OF *Trepospira* (*?Angyomphalus*) *peneglabra*, NEW SPECIES

| | Total Width | Total Height |
|---|---|---|
| A.M.N.H. No. 28878 Holotype | 1.8 | 2.1 |
| A.M.N.H. No. 28879 Paratype | 1.8 | 3.3 |

## SUBORDER **MURCHISONIINA** COX AND KNIGHT, 1960

## SUPERFAMILY **MURCHISONIACEA** KOKEN, 1896

## FAMILY **MURCHISONIIDAE** KOKEN, 1896

### GENUS **MURCHISONIA** D'ARCHIAC AND VERNEUIL, 1841

TYPE SPECIES: *Muricites turbinatus* Schlotheim, 1820 [=*Murchisonia bilineata* (Dechen), 1832].

**Murchisonia** (**Murchisonia**) **micula** Hall, 1861
Figure 14A–E

*Murchisonia turricula* HALL, 1861, p. 22; 1862, p. 50, pl. 4, fig. 13.

*Murchisonia micula* HALL: MILLER, 1877, p. 244; HALL, 1879, p. 93, pl. 21, fig. 11.

DESCRIPTION: This small high-spired species possesses a subangular periphery which bears a selenizone bordered by well-developed revolving carinae. Both the upper and lower whorl faces are flattened to slightly concave. The whorl surface below the selenizone bears a faint spiral thread which, due to whorl overlap, is usually only visible on the basal whorl. The upper whorl surface immediately subjacent to the suture displays a variably developed crenulated ridge, apparently formed by the interference of rather well-developed growth lines and a faint spiral thread. The sutures are quite shallow and the

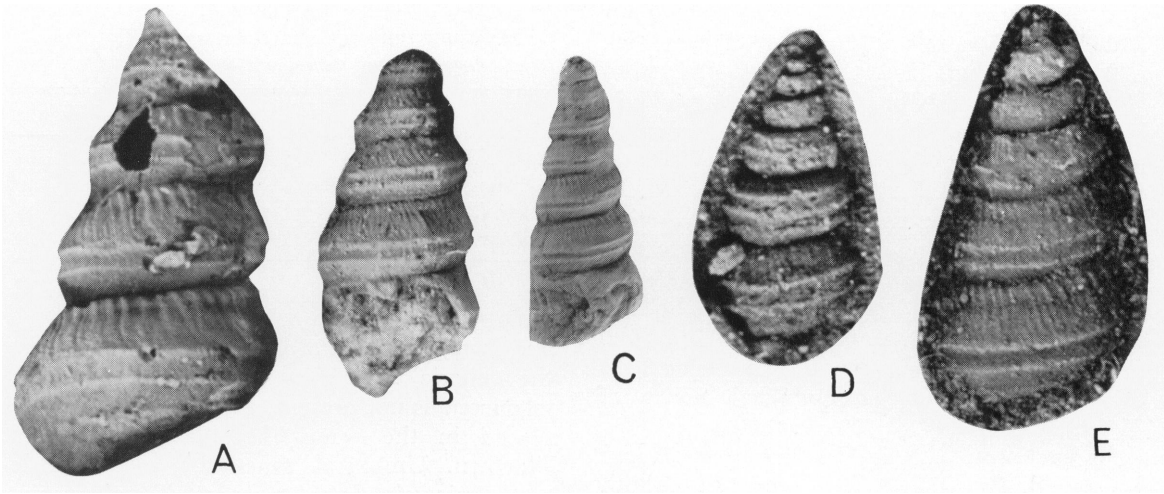


FIG. 14. *Murchisonia* (*Murchisonia*) *micula* Hall. A. Side view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28865. ×15.0. B. Side view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28866. ×10.0. C. Possibly one of Hall's figured specimens, side view, from Hamilton Group, Delphi Falls, Onondaga County, New York, A.M.N.H. No. 5426. ×6.0. D. Small specimen, latex cast, side view; note position and width of selenizone on early whorls, from A.M.N.H. 3013, A.M.N.H. No. 28867. ×21.0. E. Side view of latex cast; note early whorls, from A.M.N.H. 3016, A.M.N.H. No. 28868. ×15.0.

nuclear whorls are unknown. The base is strongly flattened, forming a sharp obtuse angle with the whorl surface immediately below the selenizone. This angle is usually the site of a faint spiral thread, visible on the basal whorl. Details of the aperture are poorly known. The umbilicus is either minute or lacking, and is covered by the reflexed columellar lip. The concave selenizone, bounded by two spiral lirae, is rather narrow with obscure lunulae. In earlier whorls, the selenizone is relatively wider and situated higher on the whorl. The outer lip of the aperture is unknown, but, based on the pattern of the growth lines, probably with a moderately shallow V-shaped sinus culminating in a notch that generates a selenizone on the whorl periphery.

DISCUSSION: *Murchisonia* (*M.*) *micula* Hall is distinguishable from most species of *Murchisonia* on the basis of its concave upper whorl surface, well-marked selenizone, and subsutural crenulated ornament pattern. The intensity of collabral ornament is very variable in this species. Some individuals possess strongly developed growth lines over the whole upper whorl surface, others have growth lines restricted to the subsutural region of the whorl. In every case, however, a subsutural lira is present.

The *M.* (*Murchisonia*) species illustrated by Boucot and Yochelson (1966, p. A 14, pl. 2, figs. 11, 12), although poorly preserved, possesses the whorl profile and carinated selenizone of *M.* (*M.*) *micula* Hall and is probably referable to that species.

*Murchisonia* (*M.*) *taltiensis* Tschernyschew (1893, p. 38, 163, pl. 3, figs. 13, 14) from the Lower Devonian of the Urals, resembles *M.* (*M.*) *micula* Hall but is distinguishable by its less deeply impressed sutures and weaker selenizone margins.

Linsley (1968) described several species of *Murchisonia* from the Middle Devonian Anderdon limestone of Michigan and Ontario. Although some of his species have similar placement of the selenizone, none possesses the combination of ornament and whorl profile characters of *M.* (*M.*) *micula* Hall.

MATERIAL: Twenty specimens were recovered from the Solsville: five from A.M.N.H. 3016 and 15 from A.M.N.H. 3013.

**Murchisonia (Murchisonia) sp.**

DISCUSSION: A single medium-sized specimen, unquestionably assignable to the subgenus *Murchisonia* (*Murchisonia*), was recovered from the Solsville, A.M.N.H. 3013. The specimen, A.M.N.H. No. 28870, is moderately well preserved and has the following measurements:

TABLE 8
MEASUREMENTS (IN MILLIMETERS) OF *Murchisonia* (*Murchisonia*) *micula*

| | Total Height | Total Width | Estimated Number of Whorls | Pleural Angle (degrees) |
|---|---|---|---|---|
| A.M.N.H. No. 28865 | 4.60 | 2.30 | 7 | 15 |
| A.M.N.H. No. 28866 | 5.06 | 2.07 | 7–8 | 18 |
| A.M.N.H. No. 28867 | 1.61 | 0.58 | 6 | 18 |
| A.M.N.H. No. 28868 | 2.99 | 1.61 | 6 | 16 |
| A.M.N.H. No. 28869 | 2.76 | 0.92 | 6–7 | — |
| A.M.N.H. No. 28869 | 4.60 | 2.30 | 6 | — |
| A.M.N.H. No. 28869 | 3.22 | 1.38 | 6 | ?9 |
| A.M.N.H. No. 28869 | 3.45 | 2.07 | 6 | — |

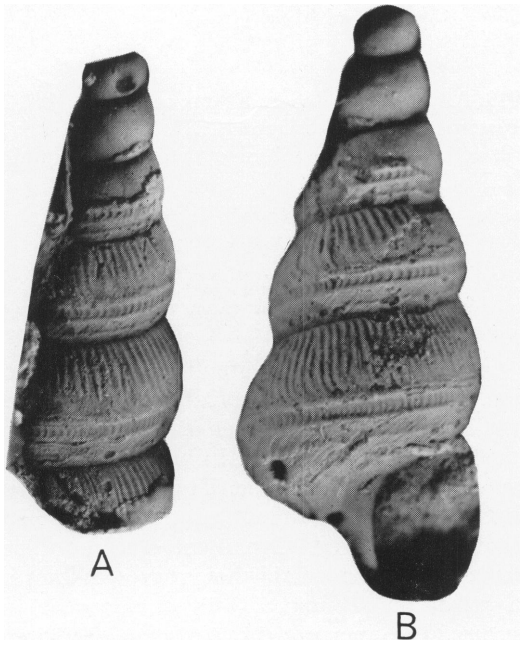


FIG. 15. *Murchisonia* (*Murchisonia*) species, from A.M.N.H. 3013, A.M.N.H. No. 28870. A. Back view of latex cast. ×8.0. B. Apertural view. ×8.0.

height, 8.97 mm.; width, 3.91 mm.; pleural angle, 26 degrees. The number of whorls is estimated at seven.

This species is easily distinguishable from *M.* (*M.*) *micula* Hall by its more rounded whorl profile, lack of a subsutural crenulated carina, and less strongly marginated selenizone. In both species, however, the whorl surface below the selenizone possesses a single spiral thread, visible on the basal whorl and also immediately above the suture on the earlier whorls. The ornament, other than the spiral thread mentioned above, is exclusively collabral, consisting of growth lines strongly developed on the upper whorl surface but faint on the whorl surface below the selenizone. The narrow concave selenizone, situated just below the whorl periphery, is well developed and lunulate. The sutures are quite shallow and nearly perpendicular to the columellar axis. Details of the aperture are unknown, and a thin parietal inductura obscures the umbilical region.

Although the specimen is fairly well preserved, we are not able to assign it to any described species and hesitate to erect a new species until more is known of the morphological variation. As many Devonian murchisoniid species are noted for their extreme morphological variability, it is unwise to attempt species description on a single specimen.

Of the described murchisoniid species, this specimen most closely resembles *M.* (*M.*) *subulata* Tyler, from the Middle Devonian Four Mile Dam Limestone of Michigan. *Murchisonia* (*M.*) *subulata* is considerably larger and lacks the spiral thread below the selenizone (Tyler, 1965, pl. 47, figs. 32, 33). *M.* (*M.*) *deludisubzona* Linsley, from the Middle Devonian Anderdon limestone of Michigan (Linsley, 1968, pl. 33, figs. 3a, b), also closely resembles the Solsville species but is larger, has more whorls and also lacks the spiral thread below the selenizone.

*Murchisonia* (*M.*) *demidoffi* Tschernyschew, from the Devonian of the Urals, generally resembles the Solsville specimen, but apparently has shallower sutures, more subdued collabral ornament, and lacks the subselenizonal spiral thread (Tschernyschew, 1893, pl. 2, figs. 5–8). *Murchisonia* (*M.*) *demidoffi* might be conspecific with *M.* (*M.*) *desiderata* Hall from the Middle Devonian Onondaga limestone.

It may be significant that several Devonian

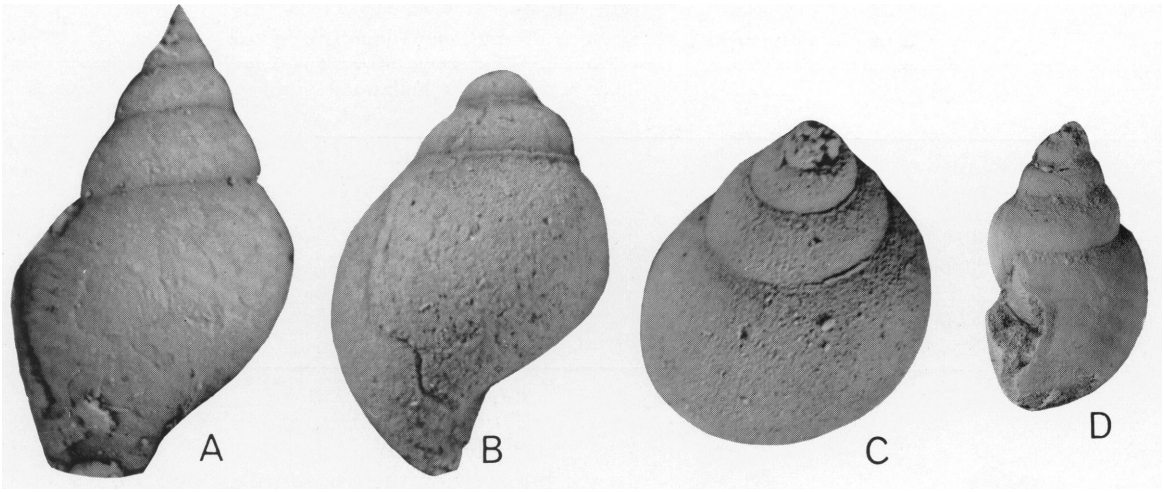


FIG. 16. ?*Holopea hebe* (Hall). A–C. From A.M.N.H. 3013. A. Abapertural view of latex cast, A.M.N.H. No. 28880. ×16.5. B. Back view of small individual, latex cast; note early whorl, A.M.N.H. No. 28881. ×7.0. C. Oblique top view of latex cast, A.M.N.H. No. 28882. ×9.0. D. Holotype?, side view, from "Hamilton Group, Hamilton and Pratts Falls, New York," A.M.N.H. No. 5401. ×1.5.

gastropod faunas display two basic morphological variations of murchisoniids (in contrast with the exotic forms from the Middle Devonian of Europe). One morphotype is characterized by subdued ornament, angular whorl profile, and strongly marginated selenizone—e.g. *M.* (*M.*) *micula* Hall. The other type is usually larger, with rounded whorls, uninterrupted collabral ornament (at least on the upper whorl surface), and weaker selenizone margins. In both types, the selenizone is peripheral or barely subperipheral.

These morphological types appear in the Devonian of the Moose River Synclinorium, of northern Maine (Boucot and Yochelson, 1966), the Middle Devonian Anderdon limestone of Michigan and Ontario (Linsley, 1968), the Lower Devonian of the Urals (Tschernyschew, 1893), and the Middle Devonian Solsville of New York.

## SUBORDER **TROCHINA** COX AND KNIGHT, 1960

## SUPERFAMILY **PLATYCERATACEA** HALL, 1859

## FAMILY **HOLOPEIDAE** WENZ, 1938

## SUBFAMILY **HOLOPEINAE** WENZ, 1938

## GENUS **HOLOPEA** HALL, 1847

TYPE SPECIES: *Holopea symmetrica* Hall, 1847.

### ?**Holopea hebe** (Hall), 1861

Figure 16A–D

*Macrocheilus hebe* HALL, 1861, p. 20; 1862, p. 48, pl. 4, fig. 1; 1876, pl. 12; 1879, pl. 12, figs. 4–7.

DESCRIPTION: This small fusiform species exhibits a very rapidly expanding basal whorl, the height of which is often greater than that of the entire spire. The total number of volutions varies from four to nine. The whorl profile is smoothly rounded and the sutures moderately to slightly impressed. Ornament consists of very faint, closely spaced opisthocyrt growth lines and a spiral thread immediately subjacent to the suture. The aperture is ovoid, elongate parallel to the columellar axis and extended anteriorly. The base is apparently anomphalous and the columellar lip slightly reflexed. Nuclear whorls and shell microstructure are unknown.

DISCUSSION: It is with some reluctance that we place *Macrocheilus hebe* Hall in the genus *Holopea* Hall. Species of *Holopea* are usually less fusiform and have open umbilici. *Macrocheilus hebe* superficially resembles *Elasmonema* Fischer but exhibits neither the funnel-like umbilicus nor the collabral cords that were considered by Knight, Batten, and Yochelson, (1960 p. I 243) characacteristic features of that genus.

Suppression of the genus *Macrocheilus* (=*Macrocheilina*) under the genus *Soleniscus* has possibly created a need for a new or resurrected genus that would include forms such as *Macrocheilus*

TABLE 9
MEASUREMENTS (IN MILLIMETERS) OF
*?Holopea hebe* (Hall)

| | Total Height | Total Width | Basal Whorl/ Spire Height |
|---|---|---|---|
| A.M.N.H. No. 28880 | 5.3 | 3.2 | 1.6 |
| A.M.N.H. No. 28881 | 5.0 | 3.4 | 2.9 |
| A.M.N.H. No. 28882 | 5.0 | 3.5 | 1.3 |
| A.M.N.H. No. 28883 | 5.3 | 3.5 | 1.8 |
| A.M.N.H. No. 28883 | 3.2 | 2.8 | 1.6 |
| A.M.N.H. No. 28883 | 2.5 | 2.1 | 1.4 |
| A.M.N.H. No. 28883 | 5.0 | 4.1 | 1.5 |
| A.M.N.H. No. 28883 | 3.5 | 2.3 | 0.9 |

*hebe* that have a *Soleniscus* shape, a rudimentary (at least) siphonal notch and no columellar folds.

*?Holopea hebe* exhibits considerable variability in height of spire and number of whorls. Yet, there is, among the Solsville specimens, a nearly complete intergradation between rapidly expanding individuals with few (4–5) whorls and those that are higher spired and many whorled (8–9). That Hall was aware of this variability can be seen by comparing his original description (1862, p. 48) of *Macrocheilus hebe* with a later description (Hall, 1879, p. 32). The original description ascribed nine whorls to the species, whereas, in the later work, he mentions five or six whorls.

The lower-spired specimens of *?H. hebe* (Hall) resemble *Macrocheilus hamiltoniae* Hall, but lack the rotund whorl shape and deeply incised sutures of the latter.

Fagerstrom (1961, p. 38, pl. 12, fig. 28) referred a form, from the Middle Devonian Formosa Reef, Ontario, to *Elasmonema bellatulum* (Hall). That species has ornament and whorl shape quite close to *?H. hebe* but lacks the subsutural threads of the latter.

MATERIAL: Fifteen specimens, all from A.M.N.H. 3013.

## SUBFAMILY **GYRONEMATINAE** KNIGHT, 1956

### GENUS **GYRONEMA** ULRICH, 1897

TYPE SPECIES: *Trochonema (Gyronema) pulchellum* Ulrich and Scofield, 1897.

**Gyronema lirata** (Hall), 1861
Figure 17A–D

*Cyclonema lirata* HALL, 1861, p. 19; 1862, p. 47, pl. 5, fig. 15; 1876, pl. 12; 1879, p. 35, pl. 12, fig. 27–29.

*Trochonema (Gyronema) liratum* (Hall): CLARKE AND SWARTZ, 1913, p. 674, pl. 68, fig. 13.

*non Gyronema liratum* ULRICH, 1897, p. 1056.

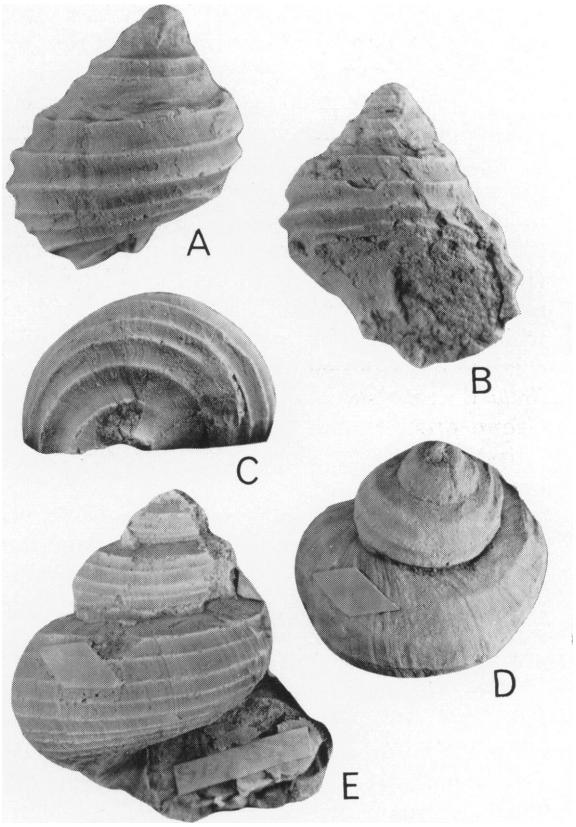


FIG. 17. *Gyronema lirata* (Hall). A–C. From A.M.N.H. 3013, A.M.N.H. No. 28893. A. Back view, ×2.0. B. Apertural view. ×2.0. C. Basal view. ×2.0. D. Lectotype?, from "Hamilton Group, Hamilton, New York," A.M.N.H. No. 5405. ×1.2. E. *Gyronema multilira* (Hall). Lectotype, "Hamilton Group, Hamilton, Madison County, New York," A.M.N.H. 5405. ×1.2.

DESCRIPTION: This medium-sized gastropod possesses strong spiral cords and a turreted spire. The whorl profile is basically rounded, but, as a result of coarse spiral cords, the upper whorl surface subjacent to the suture is the site of a moderately wide concave shelf which lends a turreted aspect to the shell. Collabral ornament consists only of weak growth lines which are prosocline on the upper whorl surface and orthocline below the first spiral cord. No apertural emargination is present. The base is rounded

and ornamented by about four spiral cords, more closely spaced and slightly weaker than the two cords on the exposed whorl surfaces. The columella is either anomphalous or minutely phaneromphalous. The aperture is oval with a slightly reflexed inner lip. The sutures are quite strongly indented. The shell is thick and its structure is unknown.

DISCUSSION: Only one specimen of *G. lirata* (Hall) was recovered from the Solsville. Fortunately, it is an excellently preserved individual which conforms in every respect to Hall's original description. All other specimens of *G. lirata* that we have observed in the Hamilton Group occur in the sandier lithologies of the Upper Skaneateles Formation (Pompey member).

*Gyronema lirata* (Hall) resembles *Cyclonema multilira* Hall, 1861 (see fig. 17E), also from the Hamilton Group of New York, but can be distinguished on the basis of its fewer and stronger spiral cords. *Cyclonema multilira* Hall is also probably referable to the genus *Gyronema*.

*Turbo bicostatus* F. A. Roemer, 1855, from the Devonian Iberger Kalk of Germany, also resembles *G. lirata*, but is slightly higher spired and apparently has more strongly developed collabral ornament.

Heretofore, the genus *Gyronema* has not been reported in rocks younger than of Silurian age. The Upper Paleozoic genus *Yunnania* Mansuy is morphologically similar to *Gyronema*. Knight, Batten, and Yochelson (1961, p. I 239) stated that *Yunnania* is anomphalous whereas *Gyronema* is narrowly phaneromphalous. Previously, Knight (1933, p. 38) had stated that the type species of *Yunnania*, *Y. termieri* Mansuy, had never been sectioned and that it is "sometimes almost impossible to discover a minute umbilicus in fossil species except by study of a section." Batten (1966, p. 54), in a description of the Lower Carboniferous species, *Yunnania semicancellata* (de Koninck), referred to an anomphalous to minutely phaneromphalous columellar area. It is not unusual to find anomphalous and minutely phaneromphalous species grouped in the same genus. Such minor differences in the columellar area are apparently of little taxonomic importance at the supraspecific level. The differences between *Yunnania* and *Gyronema* are thus reduced to features of ornament and over-all shell shapes. Species of *Yunnania* usually possess more spiral lirae or costae and are somewhat more higher spired (smaller pleural angle). It appears that the *Gyronema-Yunnania* lineage (Ordivician–Permian) is morphologically close-knit and conservative, and it will require study of species populations to make phylogenetic sense of the stock.

MATERIAL: One specimen from A.M.N.H. 3013.

## FAMILY **PLATYCERATIDAE** HALL, 1859

### GENUS **PLATYCERAS** CONRAD, 1840

#### SUBGENUS **PLATYCERAS** CONRAD, 1840

TYPE SPECIES: *Pileopsis vetusta* J. de C. Sowerby, 1829

**Platyceras (Platyceras) erectum** (Hall), 1843
Figure 18G–K

*Acroculia erecta* HALL, 1843, pp. 172, 174, fig. 6.

*Platyceras erectum* HALL, 1861, p. 4; 1862, p. 32; 1876, pl. 2; 1879, p. 5, pl. 2, figs. 4–11; CLARKE, 1903, p. 549; GRABAU AND SHIMER, 1909, p. 683, figs. 963a; PROSSER AND KINDLE, 1913, pp. 296–297, pl. 37, figs. 1–5.

DESCRIPTION: This small to medium-sized species has the first one and one-half to two whorls in contact but then undergoes a rapid whorl expansion concomitant with a variable degree of uncoiling. The ornament consists, in early growth stages, of fine, closely spaced regular growth lines which, in maturity, are more irregular, more distantly spaced, and often lamellose. Reentrant apertural sinuses are usually present, variable in number, and more pronounced in larger individuals. Coiling is nearly symmetrical, i.e. discoidal. Muscle scars and shell structure are unknown.

DISCUSSION: Nearly all of the platyceratids observed in the Solsville are assigned to *P.* (*P.*) *erectum* (Hall). Only larger, presumably mature, specimens, however, display the degree of uncoiling that is considered characteristic of the species. Although ontogenetic change in ornament and degree of coiling is striking in this

TABLE 10
MEASUREMENTS (IN MILLIMETERS) OF *Gyronema lirata* (Hall)

| | Total Height | Total Width | Pleural Angle (degrees) |
|---|---|---|---|
| A.M.N.H. No. 28893 | 17.5 | 15.8 | 75 |

species, we have observed a nearly complete gradational sequence and are quite confident that only one species is involved.

*Platyceras* (*P.*) *erectum* appears quite distinct from other Middle Devonian platyceratid species, but in view of the well-known morphological variation within platyceratid species there is a distinct possibility that *P.* (*P.*) *erectum* (Hall) represents a "catch-all" for several species.

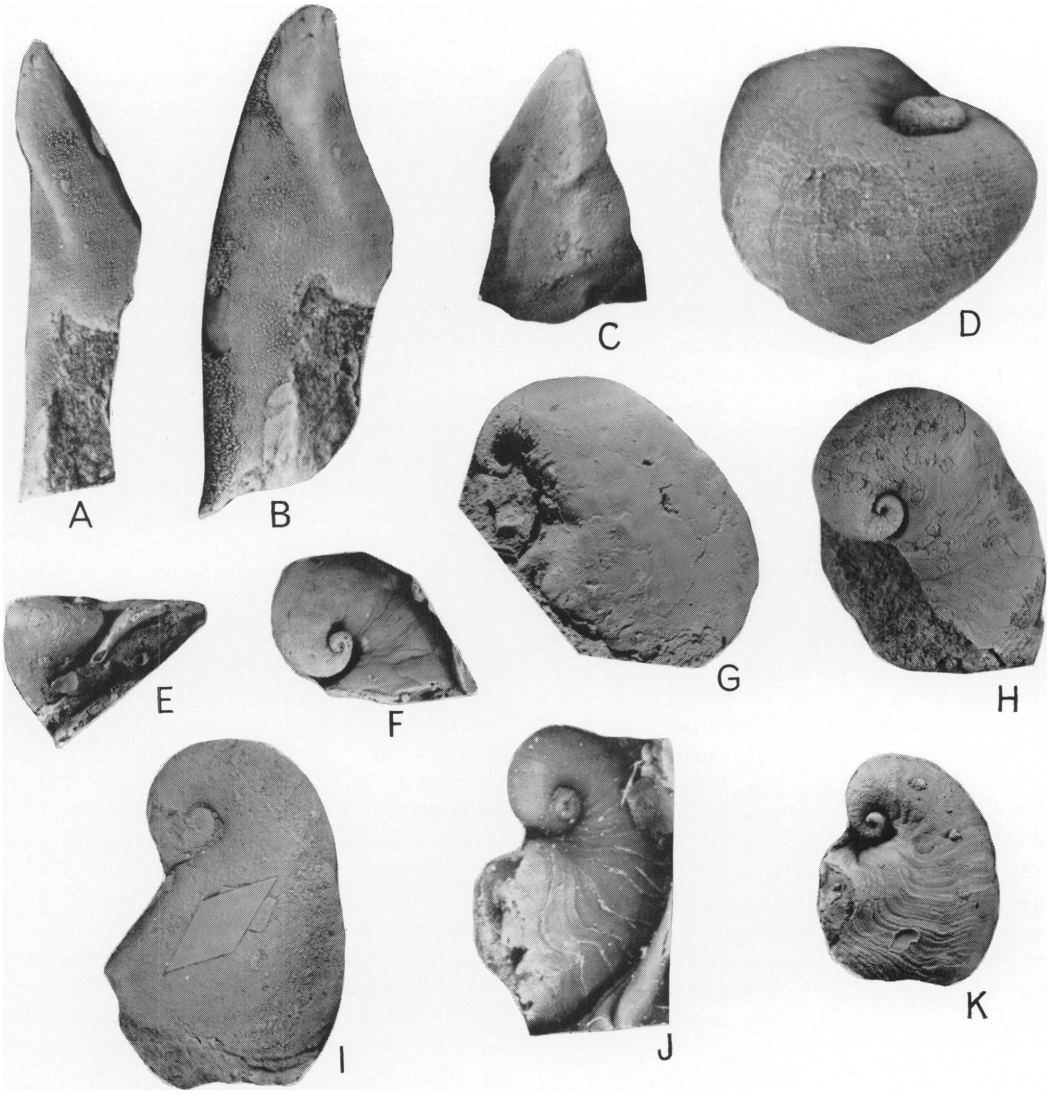


FIG. 18. A–C. *Platyceras* (*Orthonychia*) species, from A.M.N.H. 3013. A. Steinkern; note apical twist, A.M.N.H. No. 28886. ×7.5. B. Side view, A.M.N.H. No. 28886. ×7.5. C. Oblique side view of smaller steinkern, A.M.N.H. No. 28887. ×11.0. D. *Platyceras* (*Platyostoma*) species A, back view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28844. ×10.5. E, F. *Platyceras* (*Platyostoma*) sp. B, from A.M.N.H. 3013, A.M.N.H. No. 28888. E. Apertural view of latex cast. ×3.2. F. Top view. ×3.2. G–K. *Platyceras* (*Platyceras*) *erectum* (Hall). G. Steinkern, side view, from A.M.N.H. 3013, A.M.N.H. No. 28889. ×3.0. H–I. Two of Hall's specimens, from "Upper Helderberg, 5 miles east of Buffalo, New York," A.M.N.H. No. 4016. ×1.5. J. Lateral view of small specimen, latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28890. ×11.0. K. Lateral view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28891. ×2.5.

TABLE 11
MEASUREMENTS (IN MILLIMETERS) OF *Platyceras (Orthonychia)* SP.

| | Height |
|---|---|
| A.M.N.H. No. 28886 | 10.1 |

MATERIAL: Twenty-three specimens from A.M.N.H. 3013.

SUBGENUS **PLATYCERAS (ORTHONYCHIA)** HALL, 1843

TYPE SPECIES: *P. (Orthonychia) suberectum* Hall, 1859.

**Platyceras (Orthonychia)** sp.
Figure 18A–C

DISCUSSION: Two steinkerns were recovered from A.M.N.H. 3013 that are unquestionably assignable to the subgenus *P. (Orthonychia)*. The specimens are erect and elongate. The larger, presumably mature specimen is twisted apically, but does not complete an open coil. Its whorl profile is somewhat compressed in one plane, a feature that is most pronounced in the early growth stages where the whorl profile is both angular and sinuous. The adult portion of the shell expands quite rapidly and the aperture is apparently elongate patelliform. The ornament is unknown and muscle scars are not preserved.

This species most closely resembles *P. (O.) concavum* (Hall), from the Helderberg strata of New York and may be conspecific with that form. The Solsville specimens do not, however, complete a coil and thus differ from such species as *P. (O.) concavum* (Hall), *P. (O.) tortuosa* (Hall), and *P. (O.) dentalium* (Hall). Future study may determine whether, as Boucot and Yochelson suggested (1966, p. A 11), the twisted orthonychids might be profitably separated from the untwisted forms at the subgeneric level.

MATERIAL: Two steinkerns from A.M.N.H. 3013.

GENUS **PLATYCERAS** CONRAD, 1840

SUBGENUS **PLATYOSTOMA** CONRAD, 1842

TYPE SPECIES: *Platyostoma ventricosum* (Conrad), 1842.

**Platyceras (Platyostoma)** sp. A
Figure 18D

DISCUSSION: A single small specimen from A.M.N.H. 3013 is referable to the subgenus *Platyostoma* Conrad on the basis of its naticiform shape, several (at least three) whorls and lack of noticeable apertural reentrants. The spire, consisting of a nearly discoidal nucleus and first one and one half whorls, is slightly depressed below the very rapidly expanding basal whorl. The ornament consists of fine, irregular and densely spaced spiral threads transected at wide intervals by coarser collabral growth ridges. Details of the apertural lips are unknown, but the apertural shape is transversely elliptical, flaring above and below the earlier whorls. The umbilicus is probably phaneromphalous.

The specimen resembles some individuals of *P. (Platyostoma) lineata* Conrad, as figured by Hall (1879, pl. 10, figs. 1–21). Both Hall's and Conrad's conceptions of *P. (P.) lineata* were wide enough to include forms with variable coiling and ornament patterns (Conrad, 1842, p. 276; Hall, 1879, p. 21, 22). The described morphological latitude of *P. (P.) lineata* is so wide that it invites confusion with other described species, but apparently *P. (P.) lineata* can be differentiated on the basis of its delicate reticulated ornament pattern. The Solsville specimen, with its widely spaced, nearly rugose, collabral ornament and depressed spire seems well outside the morphological spectrum of *P. (P.) lineata.*

Boucot and Yochelson (1966, p. A 11–A 12) proposed the genus *Crossoceras* for distinctive platyceratid gastropods with flattened spire and an ornament combination of spiral threads and strongly developed collabral frills. The Solsville specimen is reminiscent of *Crossoceras belandi* Boucot and Yochelson, from the Glenerie limestone of New York and the Tarratine Formation of Northern Maine (Boucot and Yochelson, 1966). It is possible that the Solsville specimen is an immature representative of a species of *Crossoceras*. If the transverse ornament of the Solsville specimen were more strongly developed (frill-like), we would not hesitate to consider it a species of *Crossoceras*. However, in view of its general *Platyostoma* shape and the fact that *Crossoceras* has never been reported from strata of Hamilton age, we have followed a more conservative course with the Solsville specimen.

*Naticopsis elegantula* Oehlert and Davoust, from the Devonian of Sarthe, France, appears referable to the subgenus *Platyostoma* and, although it possesses both spiral and collabral ornament, is distinguishable from the Solsville species in lacking widely spaced transverse rugae

and a depressed spire (Oehlert and Davoust, 1879, p. 712, pl. 15, figs. 3a, b, c).

MATERIAL: One specimen from A.M.N.H. 3013.

**Platyceras (Platyostoma)** sp. B
Figure 18E–F

DISCUSSION: One other specimen, referable to the subgenus *Platyostoma*, was recovered from A.M.N.H. 3013. Although approximately the same size as the specimen discussed above, *P. (Platyostoma)* species A, this individual is ornamented very differently. The ornament is entirely collabral, consisting of growth lines, irregular over the upper whorl surface, but more regular and strongly prosocline on the outer and lower whorl surfaces. The whorls expand rapidly and only two whorls are completed. As in *P. (Platyostoma)* species A, the nucleus is discoidal and depressed below the basal whorl. The aperture is transversely elliptical and the umbilicus is unknown.

This specimen is distinguishable from *P. (Platyostoma) lineata* Conrad on the basis of its lack of spiral ornament.

MATERIAL: A single specimen, A.M.N.H. No. 28888, from A.M.N.H. 3013.

## SUBORDER **NERITOPSINA** COX AND KNIGHT, 1960

## SUPERFAMILY **NERITACEA** RAFINESQUE, 1815

## FAMILY **NERITOPSIDAE** GRAY, 1847

## SUBFAMILY **NATICOPSINAE** S. A. MILLER, 1889

## GENUS **NATICOPSIS** M'COY, 1844

## SUBGENUS **NATICOPSIS (NATICOPSIS)**

TYPE SPECIES: *Naticopsis phillipsii* M'Coy, 1844.

**Naticopsis (?Naticopsis)** sp.
Figure 19

DISCUSSION: Two incomplete and tiny specimens from A.M.N.H. 3013 are questionably assigned to the subgenus *N. (Naticopsis)* on the basis of a low spire and globular whorl shape. Apertural details are not preserved and thus it is impossible to substantiate the presence of a typical naticopsid parietal deposit. The ornament consists of strongly developed collabral threads, closely spaced, obliquely prosocline on the upper whorl surface, and more strongly prosocline on the outer whorl surface. On one specimen, the collabral threads suddenly change, adjacent to the aperture, into more widely spaced costae. Very faint spiral threads transect the dominant collabral elements. The whorl expansion rate is very rapid and only two postnuclear volutions are achieved.

TABLE 12
MEASUREMENTS (IN MILLIMETERS) OF *Platyceras (Platyostoma)* SP.A.

| | Total Height | Total Width |
|---|---|---|
| A.M.N.H. No. 28844 | 4.37 | 4.37 |

Morphological details of this form are too poorly known for adequate comparison with described species of *N. (Naticopsis)*. In fact, we are not certain of the generic affinity of this species. The two available specimens might prove referable to the genus *Isonema* Meek and Worthen. They resemble, in details of ornament, *Isonema corrugata* (Stauffer), from the Columbus limestone of Ohio (Stauffer, 1909, p. 194, pl. 16, fig. 10) and the Anderdon limestone of Michigan (Linsley, 1968, p. 411, pl. 36, figs. 5a, b). The rapid rate of whorl expansion perpendicular to the axis suggests affinities with *Naticopsis*.

MATERIAL: Two incomplete specimens from A.M.N.H. 3013.

## ORDER **CAENOGASTROPODA** COX, 1959

## SUPERFAMILY **LOXONEMATACEA** KOKEN, 1889

## FAMILY **PALAEOZYGOPLEURIDAE** HORNÝ, 1955

## SUBFAMILY **PALAEOZYGOPLEURINAE** HORNÝ, 1955

## GENUS **PALAEOZYGOPLEURA** HORNÝ, 1955

TYPE SPECIES: *Zygopleura alinae* Perner, 1907.

**Palaeozygopleura hamiltoniae** (Hall)
Figure 20A–G

*Loxonema nexilis*: HALL, 1843, p. 201; *non Loxonema nexilis* PHILLIPS, 1841, p. 99.

*Loxonema hamiltoniae* HALL, 1861, p. 25; 1862, p. 53, pl. 4, fig. 8; 1876, pl. 13; 1879, p. 45, pl. 13, figs. 15, 17.

DESCRIPTION: This moderately large species is elongate, high-spired, and multi-whorled. Ornament is collabral, consisting of variably developed symmetrically arcuate costae, which are apparently present on all post-protoconch

FIG. 19. *Naticopsis (Naticopsis)*? sp., side view of latex cast; note rapidly expanding whorl and change in ornament pattern, from A.M.N.H. 3013, A.M.N.H. No. 28884. × 18.0.

whorls. The costae are usually finer and more closely spaced on the earlier whorls. Sutures are rather shallow. The whorl profile is rounded over-all, but somewhat flattened on the upper whorl surface. The whorls are quite adpressed and the periphery occurs below mid-whorl. The outer lip, as suggested by growth lines, has a shallow to moderately deep U-shaped sinus which is situated at, or slightly above, mid-whorl. The aperture is ovoid, with a strongly reflexed columellar lip. The base is anomphalous and ornamented by weak collabral costae, or, sometimes, only growth lines.

DISCUSSION: A detailed study (R. M. Linsley and R. Marengo, oral commun., 1969) of numerous specimens of *Palaeozygopleura hamiltoniae* (Hall) from the Hamilton Group of New York State, coupled with examination of Hall's types, concluded that all post-protoconch whorls are ornamented and suggested placement of that species within the genus *Palaeozygopleura* Horný. Horný (1955, p. 154) noted that "*Loxonema*" *hamiltoniae* Hall probably belonged to the subfamily Palaeozogypleurinae, and Linsley (1968, p. 437) listed the species as "*Loxonema*" (*Palaeozygopleura?*) *hamiltoniae* Hall.

We figure in this paper (fig. 20A) a large unbroken specimen (A.M.N.H. No. 28871) from the Delphi Station member of the Skaneateles Formation, that shows the presence of collabral ornament on the neanic whorls.

TABLE 13
MEASUREMENTS (IN MILLIMETERS) OF *Naticopsis (?Naticopsis)* SP.

| | Total Height | Total Width |
|---|---|---|
| A.M.N.H. No. 28884 | 0.70 | 1.57 |
| A.M.N.H. No. 28885 | 0.57 | 0.85 |

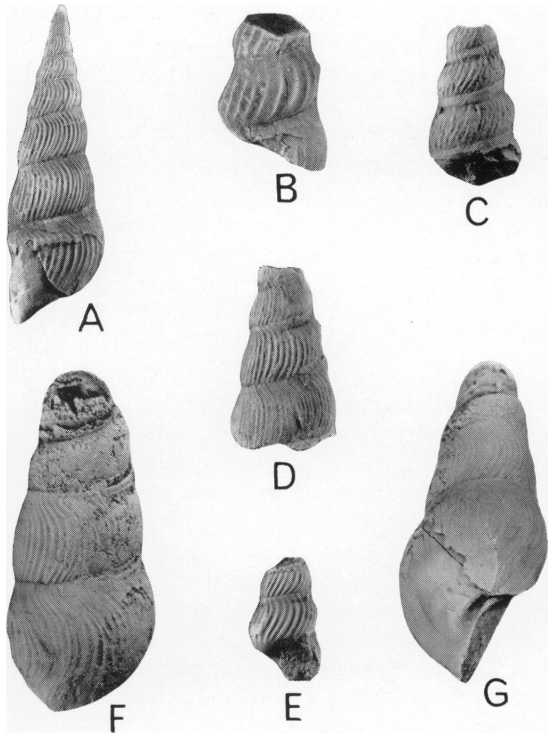


FIG. 20. *Palaeozygopleura hamiltoniae* (Hall). A. Side view of well-preserved specimen showing ornamented early whorls, Delphi Station member of Skaneateles Formation, from Delphi Falls, New York, A.M.N.H. No. 28871. × 1.5. B. Fragmented specimen with coarse costae, from A.M.N.H. 3017, A.M.N.H. No. 28872. × 1.5. C. Specimen with distinct sutural band, from A.M.N.H. 3017, A.M.N.H. No. 28873. × 1.5. D. Side view; note fine and closely spaced costae, from A.M.N.H. 3017, A.M.N.H. No. 28874. × 1.5. E. Apertural view of small specimen, from A.M.N.H. 3017, A.M.N.H. No. 28875. × 1.5. F, G. Very large individual, from A.M.N.H. 3014, A.M.N.H. No. 28876. F. Back view. × 1.1. G. Oblique basal view; note reflexed columellar lip. × 1.1.

Knight (MS), after an examination of the type specimens of *P. hamiltoniae* (Hall) and *P.? delphicola* (Hall), stated that these forms are conspecific. Hall (1862, p. 52–53) differentiated *P. delphicola* from *P. hamiltoniae* on the basis of straighter costae and "overlapping or banding of the upper margin of the volution at the sutureline." Many specimens of *P. hamiltoniae* from the Solsville show whorl adpression, and, where the shell is slightly weathered, a distinct sutural band (see fig. 20C). Moreover, the collabral costae vary from nearly orthocline to decidedly

arcuate. Only detailed population studies will determine whether *P. hamiltoniae* and *P. delphicola* are conspecific.

MATERIAL: *P. hamiltoniae* is one of the more persistent and abundant species in the Solsville, More than 100 specimens, from all localities, were collected.

## CLASS **MONOPLACOPHORA** WENZ, 1952

### SUBCLASS **CYCLOMYA** HORNÝ, 1965

### GENUS **CYRTONELLA** HALL, 1879

TYPE SPECIES: *Cyrtolites mitella* (Hall), 1862.

**Cyrtonella mitella** (Hall)
Figure 21A–E

*Cyrtolites? mitella* HALL, 1862, p. 61.
*Cyrtolites pileolus* HALL, 1862, p. 61.
*Cyrtolites (Cyrtonella) mitella* (HALL), 1879, p. 123, pl. 25, figs. 23–28.

DESCRIPTION: This medium-sized, horn-shaped species exhibits a rapid rate of whorl expansion and does not quite complete a volution. The whorl profile is gently rounded on both sides of a variably developed median dorsal angulation. The apex usually departs slightly from the predominantly planispiral mode of coiling. The aperture is devoid of any emargination or sinus. Ornament consists of distinct lamellose growth lines interspaced with fine spiral lirae. The spacing and strength of these two ornament components are variable, but usually result in a geometrically hexagonal reticulation. The aperture is subcircular. Muscle scars, as viewed on steinkerns, are symmetrically deployed around the axis of shell growth and consist of three pairs, dorsal, dorsal-lateral, and ventral. The dorsal muscle scars are discrete and elongate obliquely to the longitudinal shell axis.

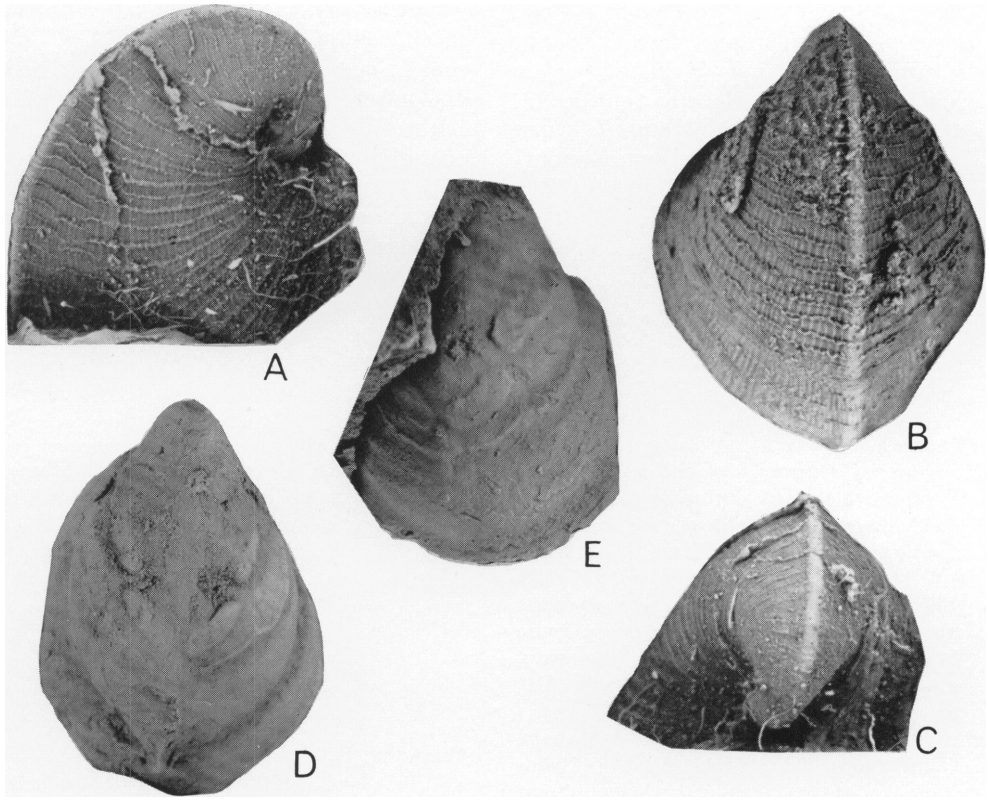


FIG. 21. *Cyrtonella mitella* (Hall). A. Oblique lateral view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28842. ×11.0. B. Dorsal view of latex cast, from A.M.N.H. 3013, A.M.N.H. No. 28841. ×10.0. C. Anterior view displaying asymmetry of coiling, A.M.N.H. No. 28842. ×11.0. D. Dorsal view of steinkern showing muscle scars, from A.M.N.H. 3013, A.M.N.H. No. 28843. ×3.0. E. Dorsal view of another steinkern with muscle scars, from A.M.N.H. 3014, A.M.N.H. No. 28845. ×3.0.

The dorso-lateral muscle scars are subcircular in outline but taper ventrally and may be fused with the narrow ventral muscle scars. The shell is moderately thick and its structure is unknown.

DISCUSSION: The taxonomic position of *C. mitella* (Hall) has been recently reassessed (Rollins, 1969) and it was suggested that the muscle scar pattern of that species supports assignment to the cyclomyan subfamily Cyrtolitinae.

Two steinkerns recovered from A.M.N.H. 3013 and 3014 excellently preserve the muscle scar patterns and invite some comment about what have been confusingly termed "shadow scars" in *C. mitella* (see fig. 21D, E). It appears that the "shadow scars" are in reality a continuous ridge on the inside of the shell, immediately adapertural (posterior) to the muscle field. This ridge may be a myostracal deposit adjacent to and connecting the adapertural margins of the muscle attachment pits (see Rollins, 1969).

The hexagonal ornament pattern of *C. mitella*, although distinctive, is not peculiar to that species. Several other monoplacophoran species, such as *Cyrtolites ornatus* Conrad and *Retipilina knighti* (Horný), and at least one bellerophontacean, *Salpingostoma sculptilis* Ulrich, exhibit identical ornament.

Specimens of *C. mitella* (Hall) are often encrusted by a species of bryozoan. Other cyclomyans, such as *Sinuitopsis acutilira* (Hall) and *Cyrtolites* spp. are often similarly encrusted by bryozoa, and, in multi-whorled forms, throughout ontogeny. This, in conjunction with the specialized muscle ring and rapid whorl expansion rate, would seem to represent strong evidence for a limpet-like benthic existence.

TABLE 14
MEASUREMENTS (IN MILLIMETERS) OF *Cyrtonella mitella* (HALL)

| | Total Length | Total Width |
|---|---|---|
| A.M.N.H. No. 28841 | 5.7 | 4.2 |
| A.M.N.H. No. 28842 | 7.5 | 5.7 |
| A.M.N.H. No. 28846 | 9.4 | 7.1 |

*Cyrtonella mitella* (Hall) is the most common monoplacophoran in the Hamilton Group and is rather long-ranging, persisting at least from the Upper Marcellus through Moscow.

*Cyrtonella pileolus* (Hall), 1861 is probably conspecific with *C. mitella*. Hall (1879, p. 125) stated that *C. pileolus* possessed a less angular dorsum and lower whorl expansion rate than *C. mitella*. Both of these characters are, it seems, variable enough in *C. mitella* to include Hall's conception of *C. pileolus*. Even Hall (1879, p. 125) admitted that the surface characters were virtually indistinguishable between the two species.

MATERIAL: Eight specimens from A.M.N.H. 3013.

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