OBSERVATIONS ON SOME LOWER PALAEOZOIC TREMANOTIFORM BELLEROPHONTACEA (GASTROPODA) FROM NORTH AMERICA

by JOHN S. PEEL

ABSTRACT. Muscle scars are described in *Salpingostoma buelli* (Whitfield 1878) and *Tremanotus alpheus* Hall 1865 with reference to finely preserved specimens of *Bellerophon* spp. The taxon Salpingostomatidae Koken 1925 is abandoned with transferal of *Salpingostoma* Roemer 1876 to the subfamily Bucaniinae of the Bellerophontidae. A new subfamily of the Sinuitidae, the Tremanotinae, is proposed to accommodate *Tremanotus* Hall 1865 and *Boiotremus* Horný 1962. Brief discussion is given of described species of the three genera from the Silurian of North America.

IT is over a hundred years since F. B. Meek (1866) discussed the affinity of the family Bellerophontidae M'Coy 1851 and gave '. . . as nearly a positive demonstration of . . . the affinities of the *Bellerophon*-group, as we can probably ever expect in such a case'. In so doing, he ended much of the controversy that had developed regarding the systematic position of this extinct molluscan group since von Hupsch first noted their existence in 1781. By reference to *Tremanotus chicagoensis* (McChesney 1859), Meek reiterated de Koninck's (1842–1844) interpretation of the bellerophontaceans as prosobranchiate gastropods. The presence of tremata was held to indicate that *Tremanotus* '. . . bears exactly the same relations to *Bucania*, that *Polytremaria* does to *Pleurotomaria*, and *Rimula* to *Emarginula*'.

Since that time there have been considerable advances in our knowledge concerning the bellerophontiform molluscs. A notable contribution was the demonstration by Wenz (1940) of the tryblidiid affinity of the coiled *Cyrtonella mitella* (Hall 1862) which, of necessity, cast doubt upon the status of the remaining members of the group. Wenz (1940) presumed that all bellerophontaceans possessed similar musculature indicating a lack of torsion and placed the superfamily alongside the Tryblidiacea in the subclass Amphigastropoda. However, the description by Knight (1947) of muscle scars, suggestive of torsion having taken place, in *Bellerophon gibsoni* White 1882 and *Sinuites cancellatus corrugatus* (Hall 1847) clearly indicated that the Amphigastropoda of Wenz (1940) was not a homogeneous unit. Furthermore, the Bellerophontacea of then current usage could itself no longer be maintained as a single entity.

The distinction between the coiled Cyclomya (Monoplacophora) and the Bellerophontacea (Gastropoda) is now well recognized, principally through the works of Horný (1962, 1963*a*, 1963*b*, 1965*a*, 1965*b*, 1966). Recent summaries are given by Yochelson (1967), Rollins (1969), and Starobogatov (1970). Muscle scars are known in an increasing number of bellerophontiform molluscs, though the description by Rollins and Batten (1968) of the sinus-bearing monoplacophoran *Sinuitopsis acutilira* (Hall 1861) serves to emphasize some of the problems accompanying systematic determination of the many remaining taxa.

The intention of this paper is to describe structures of the shell interior in the Ordo-

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vician *Salpingostoma buelli* (Whitfield 1878) and a specimen of *Tremanotus alpheus* Hall 1865 from the Niagaran (Silurian) dolomites of Illinois. Owing to the coarseness of preservation, interpretation of these structures is attempted with reference to well-preserved specimens of *Bellerophon* spp. of Carboniferous age. It is of historical interest that the conclusions reached by Meek (1866) after examination of one member of this group of dorsally perforate molluscs receive further support, the described internal structures being interpreted as muscle scars of gastropod type. On the basis of general morphology the suprageneric classification of *Tremanotus*, *Salpingostoma*, and *Boiotremus* Horný 1962 is revised and a brief discussion given of the described species of those genera from the Silurian of North America.

Repositories. The following Institutions are denoted by abbreviations in the text: USNM, U.S. National Museum, Washington D.C.; AMNH, American Museum of Natural History, New York; GPM, Greene Paleontology Museum, Univ. of Wisconsin at Milwaukee; YPM, Yale Peabody Museum, New Haven, Conn.; OUM, Oxford University Museum.

MUSCLE SCARS IN *BELLEROPHON*

The most readily observed indication of the position of supposed rectractor muscles of the type described by Knight (1947) is a fine spiral ridge on each umbilical shoulder of natural internal moulds of the shell. Under exceptional conditions of preservation a series of fine crescentic striae can be seen on the mould at the adapertural extremity of each ridge. The crescents are convex adaperturally and coalesce dorsally at the spiral ridge. Each spiral ridge was interpreted by Knight (1947) as forming the dorsal margin of a muscle attachment scar, with successive positions of the adapertural scar margin producing the crescentic striae. In some cases a groove on the mould may replace the spiral ridge while a number of minor structures are commonly developed in association with the general muscle attachment area. The latter include local swellings of the mould, corresponding to slight hollows on the shell interior, and changes in the degree of angularity of the umbilical shoulders.

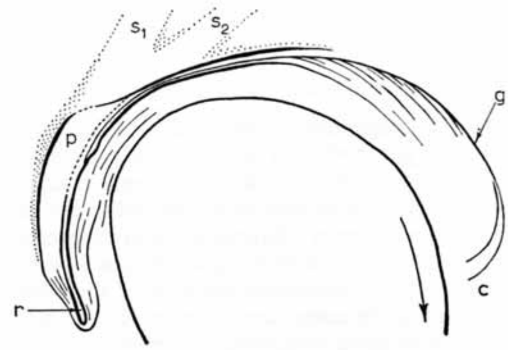
Two internal moulds assigned to *Bellerophon* show well-preserved muscle scars. The larger specimen (USNM 169475), apparently from the Pennsylvanian of the U.S.A. and hereafter referred to as *Bellerophon* specimen *A*, lacks the apertural margin, though the last preserved growth stage is almost certainly less than one tenth of a whorl back from the true aperture (Pl. 79, fig. 1). Three whorls are present, the nuclear whorls having been lost. Although the shell infilling is rather coarse the surface of the mould is smooth and polished.

A well-marked spiral ridge is observed on each umbilical shoulder with crescentic scars developed at the adapertural extremity of the ridges. The crescentic scars lie half a whorl back from the final preserved growth stage. Both spiral ridges terminate abruptly one half whorl back from their anterior extremities. In detail, the nature of the spiral ridges is seen to vary over the half whorl extension. Abaperturally, each spiral ridge has greater relief and is overturned towards the dorsum. As a consequence, a narrow well-defined channel exists between the acute overturned crest of the spiral ridge and the dorso-lateral surface of the mould. In terms of the shell interior, this channel equates with a low-angled projection of shell towards the umbilical shoulder.

Proceeding adaperturally, the relief of each ridge decreases, the crest becomes less acute and the channel is lost. However, the general form of a gently convex slope on the umbilical side of the ridge and a steep surface on the dorsal side, is retained. A series of grooves occupies the crest of each spiral ridge, the various grooves being continuous with the several crescentic scars.

A broad, elongate swelling is seen on the dorsal side of each spiral ridge. This structure, representing a hollow in the inner side of the shell, is subparallel to the ridges but commences at a slightly earlier growth stage. Proceeding towards the aperture, the swelling and spiral ridge diverge. It is not possible to trace the swelling beyond the midpoint of the spiral ridge on either shoulder.

The second internal mould, *Bellerophon* specimen *B*, is from the Carboniferous Limestone of Armagh, Northern Ireland (OUM E2214). The apertural margin is not preserved and the left side is obscured by coarsely recrystallized calcite [*left* and *right* are used in the sense of Knight (1947). In lateral view with the aperture facing to the left, the side visible is the left side]. The muscle scar on the right side is visible (Pl. 79, fig. 2) and is of particular interest in that the abapertural margin of the muscle attachment area can be observed. In addition, the scar shows notable morphologic differences from the form seen in *Bellerophon* specimen *A*.



TEXT-FIG. 1. Lateral view of the right muscle scar of *Bellerophon* specimen *B* (OUM E2214). The arrow indicates the direction of growth. For explanation see text (×6).

The spiral ridge (text-fig. 1; *r*) is symmetrical with a convex upper surface in contrast to the ad-dorsally overturned acute ridges of the previously described specimen. The abapertural termination is sudden and a faint scar passing around the extremity indicates the margin of the muscle attachment area. The umbilical margin of the scar is visible for about one-third of the length of the spiral ridge and encloses a spirally striated muscle attachment area. Dorsally, the scar margin is continued as the acute dorsal edge of a flat topped swelling (*p*) which parallels the abapertural third of the spiral ridge. The swelling has a concave slope passing from this dorsal edge to the normal surface level of the dorsum and fades away suddenly when the dorsal edge converges with, and meets, the spiral ridge. Two obscure swellings (s_1; s_2) diverge from the spiral ridge at this point at approximate angles of 30° and 45° and pass obliquely across the dorsum, almost to the median plane. Approach of the spiral ridge towards the umbilical shoulder causes an increase in the angularity of the mould shoulder which reaches a maximum at the point of divergence of the oblique transdorsal swellings.

Proceeding adaperturally, the spiral ridge increases in relief but loses the initial strong delimitation from the dorsal surface by the acquisition of more gently sloping sides. The upper surface is marked with a prominent median groove (*g*) from which adumbilically concave striae diverge in the direction of the umbilical shoulder. After a total length of half a whorl, the spiral ridge gradually disappears and obscure crescentic striae (*c*) are developed with the median groove forming their dorsal margin.

The muscle scars in *Bellerophon* specimen *A* are essentially identical to those described by Knight (1947, pl. 42, figs. 2, 3*a*, *b*) in *B. gibsoni* White 1882. The scar in *Bellerophon* specimen *B* retains the over-all form but differs with regard to expression of the detail. In the absence of variation studies of bellerophontacean muscle scars it would be unwise to attempt any assessment of the importance of the differences.

The spiral ridges were interpreted by Knight (1947) as the dorsal margins of muscle attachment scars, the crescentic grooves marking successive ontogenetic positions of the adapertural margin of the scars. Although not observing the umbilical and abapertural margins of the muscle attachment areas, Knight (1947, p. 266) considered the length of the spiral ridges to approximate to the length of attachment of the retractor muscles. While the abrupt abapertural termination of the spiral ridges in many observed specimens of *Bellerophon* tends to support this view, the evidence available from *Bellerophon* specimen *B*, above, adds direct confirmation.

However, this would not appear to be the case in all bellerophontaceans and, as a general rule, the spiral ridges are best regarded as the locus of the muscle attachment scars unless detail of the scar margins permits additional qualification.

Both of the described specimens of *Bellerophon* have swellings variously associated with the spiral ridges, though the equivalence of these structures is uncertain. The prominent flat-topped swelling seen in specimen *B* is closely related to the ridge itself, and lies within the muscle attachment area. The swellings on specimen *A* lack this specific association with the spiral ridges and the embedded nature of the dorsal margin of the retractor muscles, indicated by the overturned spiral ridges, suggests that the swellings were outside the muscle attachment areas. It is more probable that the oblique transdorsal swellings which diverge from the spiral ridge in specimen *B* are comparable to the structures seen in the North American example. While the location of the various swellings on the moulds demonstrates some connection with the musculature, the nature and purpose of the structures is quite unknown.

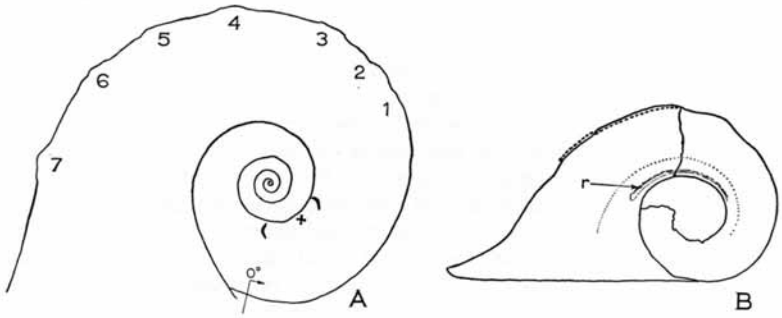
MUSCLE SCARS IN *SALPINGOSTOMA BUELLI* (WHITFIELD 1878)

A full description of this species is given by Ulrich and Scofield (1897, pp. 900–901). The two specimens discussed here are internal moulds from the Middle Ordovician (Black River) Plattville Fm. at Beloit, Wisconsin. The more complete (USNM 15641) shows the bell-shaped final growth stage and explanate aperture characteristic of the genus (Pl. 79, figs. 3, 6, 8) but in the other (USNM 169472) the explanate stage is not preserved. The median dorsal slit is represented by a raised spiral ridge on each specimen.

Circumbilical spiral ridges have been observed in both specimens but crescentic scars of the type noted above have not been seen (Pl. 79, figs. 3–5). In view of the relative coarseness of the matrix, it is unlikely that such delicate structures would be preserved. Specimen USNM 15641 shows the right and left spiral ridges but the former is rather obscure. Each ridge is located on the umbilical wall about halfway between the whorl periphery and the suture with the previous whorl. The adapertural extremity of each ridge lies vertically above the plane of the aperture, high on the side of the bell-shaped final growth stage. A low callosity is developed on the floor of the whorl at this point. It is difficult to ascertain the length of the spiral ridges but it would appear that the left ridge (text-fig. 2B, *r*) extends over at least half a whorl.

In USNM 169472 only the right spiral ridge is seen, the left umbilical wall being damaged. The ridge is essentially identical with those visible in the more complete specimen but is only observable over about one quarter of a whorl.

The spiral ridges in *Salpingostoma buelli* differ from those in *Bellerophon* specimens *A* and *B* with regard to position, relief, and relationship to the slit. In *S. buelli* the ridges are located on the umbilical walls, well within the umbilicus, while in specimens *A* and *B* of *Bellerophon* the ridges are situated on the umbilical shoulders, essentially at the maximum width of the whorl. The positional differences can be partly accounted for by change in whorl profile. The latter specimens have whorls which are reniform in cross-section with relatively high impression of the earlier whorl and a deep, narrow umbilicus.



TEXT-FIG. 2A. Lateral view (×1) of *Tremanotus alpheus* Hall 1865 (GPM 21123) showing the position of the left swelling. The cross indicates the point of maximum relief of the structure. Numbers around the periphery mark the location of the tremata though an earlier probably incomplete trema noted in text-fig. 3 is omitted. The origin of the radial scale employed in text-fig. 3 is shown.

B, lateral view (×1) of *Salpingostoma buelli* (Whitfield 1878) (USNM 15641) illustrating the left spiral ridge (*r*). The extent of the open dorsal slit which is partly infilled with matrix is denoted by the dashed line. The fine dotted line indicates maximum whorl width.

S. buelli is evolute with minor impression of the previous whorl and a lenticular whorl profile. The relatively acute nature of the junction between the dorso-lateral and umbilical surfaces in *S. buelli* possibly affords a less suitable site for muscle attachment than the corresponding more convex site in *Bellerophon* Specimens *A* and *B*.

It is difficult to assess the effects of acquisition of the bell-shaped late growth stage

EXPLANATION OF PLATE 79

Fig. 1. *Bellerophon* specimen *A* (USNM 169475), Pennsylvanian, U.S.A. (*non loc.*); lateral view of internal mould showing right muscle scar, the arrow indicates the obscure anterior margin crescentic scar, ×1.

Fig. 2. *Bellerophon* specimen *B* (OUM E2214), Armagh, N. Ireland; lateral view of internal mould showing right muscle scar, ×1.

Figs. 3–6, 8. *Salpingostoma buelli* (Whitfield 1878), Beloit, Wisconsin, U.S.A. 3, 6, 8 (USNM 15641); 3, oblique umbilical view showing circumbilical ridge, ×1; 6, dorsal view, ×0·75; 8, posterior view, ×0·75; 4, 5 (USNM 169472); oblique views illustrating the circumbilical spiral ridge, ×1.

Figs. 7, 9–11. *Tremanotus alpheus* Hall 1865 (GPM 21123), Hawthorne, Illinois, U.S.A. 7, oblique lateral view showing ridge on ad-dorsal margin of swelling, ×0·75; 9, posterior view showing swellings, ×0·75; 10, lateral view, ×0·75; 11, dorsal view illustrating the dorsal tremata, ×0·75.

upon the musculatory requirements of the individual. It is probable that the more central position of the retractor muscles in *S. buelli* enabled better control of the body mass than muscles situated peripherally. The relationship between the presently observed musculature and that prior to attainment of the bell-shaped shell is unknown.

The spiral ridges in *S. buelli* are much broader than those in *Bellerophon* specimens *A* and *B* and lack the strong delimitation from the normal steinkern surface typical of their development in the Carboniferous examples.

Although the adapertural extremities of the ridges are comparable distances back from the aperture, there is variation with respect to position relative to the dorsal emargination. In *Bellerophon* specimen *A* the slit is very short, the deepest portion being half a whorl forward from the ends of the spiral ridges. In *S. buelli* the deepest part of the long slit lies one quarter of a whorl back from the apertural termination of the ridges. The importance of this dissimilarity is unknown since studies into the nature, particularly depth, of the bellerophontacean or pleurotomariacean slit have not been made. Anatomical differences are presumably involved but, at present, there is no way of resolving these. Indeed, neither is it possible to make analogies concerning the slits for there is no reason to presume that the respective anal openings bore similar relationships within those structures.

MUSCLE SCARS IN *TREMANOTUS ALPHEUS* HALL 1865

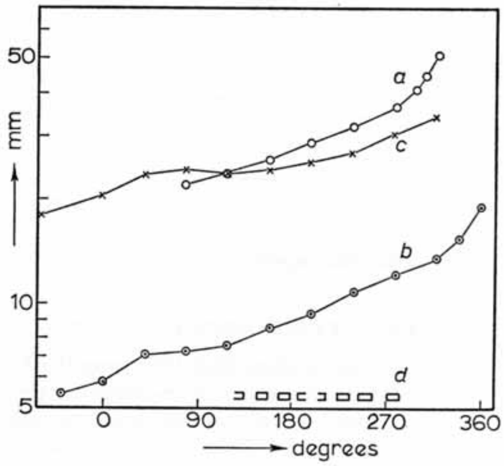
An internal mould of *Tremanotus alpheus* Hall 1865 from the Niagaran dolomites at Hawthorne, Illinois (GPM 21123) shows paired swellings on the umbilical shoulders (Pl. 79, figs. 7, 9–11). The specimen differs from the holotype and materials described by Clarke and Ruedemann (1903) and Knight (1941) in its lack of a well-developed flared aperture. However, measurement of gradients of growth (text-fig. 3; *a*, *b*) indicates the characteristic rapid expansion of the later portions of the whorl and, since the development of the feature is cyclic, it is probable that the specimen represents a growth stage intermediate between successive flared stages. The form of the tremata (text-fig. 3; *d*) is in close agreement with the holotype and other specimens in the large sample available at Milwaukee do have flared apertures preserved.

The structures take the form of a discrete swelling on each umbilical shoulder producing a slight increase in the total whorl width (text-fig. 3; *c*). The increase commences suddenly at the beginning of the final whorl (text-fig. 2A) and the internal mould has returned to normal width by the appearance of the first trema, a fifth of a whorl later. An increment of 2 mm is added to the width by the swellings. Similar swellings are apparently present at approximately one quarter of a whorl earlier.

The left side is slightly damaged, but on the right side a crude spiral marking forms the dorsal limit of the swelling (Pl. 79, fig. 7). The specimen has no structures comparable to the fine spiral ridges and crescentic scars which characterize the muscle attachment areas in the described specimens of *Bellerophon* but the nature of the matrix precludes preservation of these. However, equivalence can be suggested between the undamaged right swelling in the specimen of *T. alpheus* and the similar swelling located on the abapertural portion of the right spiral ridge in *Bellerophon* specimen *B*. The strong dorsal margin to the swelling in *T. alpheus* favours comparison with the latter-mentioned structure rather than with the more subdued paired swellings of *Bellerophon* specimen *A*.

Wing (unpublished Ph.D. thesis, 1923, The Silurian Gastropoda of northeastern

Illinois, University of Chicago) in his description of *Tremanotus umbonus nom. nud.*, commented on intermittent expansion of the final whorl causing development of distinct shoulders. The description and the illustration do not permit precise comparison with the swellings observed here, but Wing's comment that three expansions appear on the last half whorl must surely cast doubt on any interpretation as muscle scars. As noted in the final section of this paper, the holotype is too poorly preserved to warrant description.



TEXT-FIG. 3. Growth gradients in *Tremanotus alpheus* Hall 1865 (GPM 21123).

a, Radial vector from axis of coiling to periphery of final whorl showing increased rate of expansion in latest growth stage.
b, Radial vector from axis of coiling to suture between final and penultimate whorls. The discrepancy in time of commencement of the increased rates of expansion in *a* and *b* is an apparent effect produced by the radial method of measurement. Since the lines of growth are opisthocline, a point on the whorl periphery lies on a different radius than an ontogenetically equivalent point on the suture.
c, Increase in whorl width during the final whorl illustrating the paired swellings.
d, Location of the dorsal tremata. The tremata are represented in diagrammatic form at their *true* width (not scale width). Incomplete rectangles denote damaged tremata.

The vertical scale is logarithmic. The horizontal scale is an angular measure of growth stage from an arbitrarily selected point on the final whorl (text-fig. 2A).

SUPRAGENERIC CLASSIFICATION OF *TREMANOTUS*, *BOIOTREMUS*, AND *SALPINGOSTOMA*

Horný (1962) elevated the subfamily Salpingostomatinae Koken 1925 to familial status, placing his new genus *Boiotremus* therein. In a later discussion (Horný 1963) he considered the family containing *Salpingostoma* Roemer 1876, *Tremanotus* Hall 1865, and *Boiotremus* to lie close to the Sinuitidae but to have certain connections with the Bellerophontidae.

In discussing *Tremanotus* Horný (1963*a*, p. 97) noted that the genus developed tremata only in the later growth stages and that early growth stages had no such openings or sign of them ever having been present. The tremata were considered to be related to the periodic development in late ontogenetic stages of the flared aperture and did not occur prior to the acquisition of this feature. *Boiotremus* was erected by Horný (1962) to include those species previously assigned to *Tremanotus* which developed tremata and an associated flaring aperture throughout ontogeny.

The type species of *Salpingostoma* is the poorly known *S. megalostoma* (Eichwald 1840) from the Ordovician of Esthonia. Following the generally accepted interpretation of the genus by Ulrich and Scofield (1897), *Salpingostoma* is characterized by the possession of a slit in all stages of growth but the very latest. The slit is deep and narrow and generates a true selenizone. An open slit is not present in the latest portions of the bell-shaped expansion typical of the genus, or in the explanate part of the aperture.

In terms of the characters of the emargination, *Tremanotus* prior to the development of the flared aperture and its associated tremata has affinity with the Sinuitidae in its possession of a V-shaped sinus. As Ulrich and Scofield (1897) have observed, prior to attainment of the flared aperture, *Salpingostoma* agrees in all aspects with *Bucania* Hall 1847. The two forms are comparable only in the development of a flared aperture which produces a closing of the emargination. In *Salpingostoma* the apertural portion of the true slit is closed while in *Tremanotus* the deepest part of the sinus is left as an open trema at the commencement of apertural expansion. *Boiotremus* is closely related to *Tremanotus*, differing in its production of tremata and flared aperture throughout ontogeny.

Accepting the differences in the nature of the emargination it is not possible to uphold the family Salpingostomatidae and relocation of the three genera previously placed there is necessary. A new subfamily—Tremanotinae—of the family Sinuitidae is proposed to contain *Tremanotus* and *Boiotremus*. *Salpingostoma* is transferred to the subfamily Bucaniinae of the family Bellerophontidae.

Class GASTROPODA
Subclass PROSOBRANCHIA Milne-Edwards 1848
Order ARCHAEOGASTROPODA Thiele 1925
Suborder BELLEROPHONTINA Ulrich and Scofield 1897
Superfamily BELLEROPHONTACEA M'Coy 1851
Family SINUITIDAE Dall *in* Zittel–Eastman 1913
Subfamily TREMANOTINAE nov.

Diagnosis. Essentially sinuitid bellerophontaceans developing dorsal tremata in association with a widely expanded aperture.

Discussion. This taxon is proposed to accommodate *Tremanotus* Hall 1865 and *Boiotremus* Horný 1962. The latter genus represents the endpoint of a sequence more clearly seen in *Tremanotus* whereby dorsal tremata are developed in relation to rapid expansion of the shell aperture. In *Tremanotus* the periodic expansions are commenced only in later ontogenetic stages, while in *Boiotremus* they occur throughout ontogeny. It is presumed that the successive flared apertures are resorbed with continuation in growth.

SILURIAN SPECIES OF *TREMANOTUS*, *BOIOTREMUS*, AND *SALPINGOSTOMA* FROM NORTH AMERICA

Bassler (1915) recorded the following described species of *Tremanotus*, all of Silurian age:

- *T. alpheus* Hall 1865
- *T. angustata* (Hall 1852)
- *T. chicagoensis* (McChesney 1859)
- *T. crassolare* (McChesney 1861)
- *T. pervoluta* (McChesney 1861)
- *T.? trigonostoma* Hall and Whitfield 1875

to which may be added:

T. longitudinalis Lindström 1884 of Northrop 1939	*T. minutus* Northrop 1939.

T. alpheus is well known from the works of Clarke and Ruedemann (1903) and Knight (1941) and need not be further discussed. The holotype of *T. angustata* (AMNH 2235) is a rather poorly preserved internal mould from the Guelph Formation of Ontario. Although the general form is moderately well displayed, there is no indication of the nature of the dorsal emargination. This is possibly the reason for some of the confusion that has arisen concerning the relationship of this form to *T. alpheus* (see Whiteaves 1895, pp. 70–71). Comparison of the two holotypes shows that *T. angustata* is more laterally compressed, with a much wider umbilicus. A specimen in the U.S. National Museum (USNM 67088), referred with confidence to *T. angustata*, has the dorsal tremata clearly preserved. Much of the expanded portion of the shell is missing but there are at least ten open tremata borne on a raised median ridge on the mould. External shell characters remain unknown but the tremata justify transferal to *Boiotremus*. The genus is typified by abundant, short, and closely spaced tremata, while in *Tremanotus* the dorsal openings are numerically fewer, elongate, and more widely spaced.

The type of *T. chicagoensis* is lost, but a plastercast in the U.S. National Museum (USNM 67594), purporting to be of that specimen, agrees exactly with McChesney's (1867, pl. 8, fig. 5) illustration. The very slowly expanding whorl profile prior to the bell-shaped final growth stage seems to be characteristic. Details of the dorsal emargination are not visible, but internal moulds from Huntington, Indiana (USNM 67128) show elongate, widely spaced tremata of *Tremanotus*-type, carried on a dorsal ridge. A fragmental external mould has some suggestion of the distinctive tremanotinid ornament of prominent spiral cords and posteriorly directed growth lines.

McChesney's *Bucania crassolare* and *Bucania pervoluta* are imperfectly known. The original descriptions (McChesney 1861) are unaccompanied by illustrations and provide no definite criteria for delimitation from co-existent species. In the absence of type specimens, it is not possible to make any reliable determination. Wing (1923 MS.) referred forms with a broad whorl profile to *T. crassolare* but failed to recognize *Bucania pervoluta*. *T.* ?*trigonostoma* is similarly in need of reinvestigation.

One of the major problems in determination of the Niagaran species of *Tremanotus* is a lack of knowledge concerning variation. This would appear to be considerable in terms of whorl tumidity and apertural shape. As a consequence, determination of such poorly defined forms as the three previously mentioned species must at best be delayed and might prove to be undesirable.

Horný (1963) considered *T. longitudinalis* Lindström 1884 to be a typical *Boiotremus*. Although the specimen assigned to that species by Northrop (1939) has not been examined, an example from the Gascons Formation of the Port Daniel area, Quebec (USNM 169474) would appear comparable to Lindström's species. The dorsum is partly damaged but shows at least eleven tremata of *Boiotremus* aspect.

Northrop (1939) mentioned the presence of tremata in *T. minutus*, but his descriptions and illustrations do not demonstrate the form of the openings sufficiently to permit assignment to either *Tremanotus* or *Boiotremus*.

In an unpublished thesis Wing (see above) described a new species of *Tremanotus* from the Niagaran of Illinois under the name *T. umbonus* (above). The name was included in the published abstract of that thesis (Wing 1925) without description, illustration, or reference to the earlier manuscript description and is consequently a *nomen nudum*. The specimen, in the collections of the University of Chicago at the Field Museum, Chicago, is in a thoroughly fragmented state and is not considered worthy of description. Gross form suggests *T. chicagoensis*.

Four recorded species of *Salpingostoma* from the Silurian of North America have been noted:

S. boreale Whiteaves 1904	*S. inornatum* Northrop 1939
S. dilatus (Sowerby 1839) of Northrop 1939	*S. orientalis* Twenhofel 1928

S. boreale is a diminutive form unusual in its subcircular whorl profile. Type material in the collections of the Geological Survey of Canada, Ottawa indicates a selenizone of *Salpingostoma*-type. In the specimen examined, the expanded apertural portion has no slit while earlier growth stages show a narrow selenizone with lunulae. Damage has removed the portion of the dorsum where the open emargination might be expected to occur. The depth of the slit must be considerably less than that seen in *S. buelli*.

The two species recorded by Northrop (1939) from Gaspé are each known only from a single specimen. *S. dilatatum* (Sowerby 1839) of Northrop 1939 cannot be placed in Sowerby's species if it is a true *Salpingostoma*. In his description of the holotype Reed (1921, p. 82) commented on the distinct traces of foramina (tremata) which are indicative of *Tremanotus* or *Boiotremus* rather than *Salpingostoma*. The specimen, in the Yale Peabody Museum, is a fragment of the aperture rather too poor for comparison.

The holotype of *S. inornatum* (YPM 13314) is of particular interest because of Northrop's (1939, p. 207) claim of 'two curious bodies, probably opercula . . .' which occupy the aperture. Examination of the specimen reveals that the bodies are respectively a trilobite cephalon and a bivalve of *Paracyclas*-type. The holotype is badly abraded, comparison at generic and specific levels being hardly possible. However, the aperture can be examined and a median dorsal groove is present for a short distance just within the edge of the smooth lip. The structure was apparently interpreted as a selenizone by Northrop (1939). Specimens of *Salpingostoma*, *Tremanotus*, and *Boiotremus* often show a raised dorsal band on the mould, the tremata being situated upon it in the last two named forms. Such a ridge would correspond to a groove on the inside of the shell of the type seen here. There is some suggestion of tremata on the dorsum but the evidence is inconclusive.

The type of *S. orientalis* from Anticosti Is. has not been examined but referal to *Salpingostoma* would seem justified, on the basis of Twenhofel's (1928) description and illustrations.

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J. S. PEEL
Department of Geology
University of Leicester
Leicester LE1 7RH

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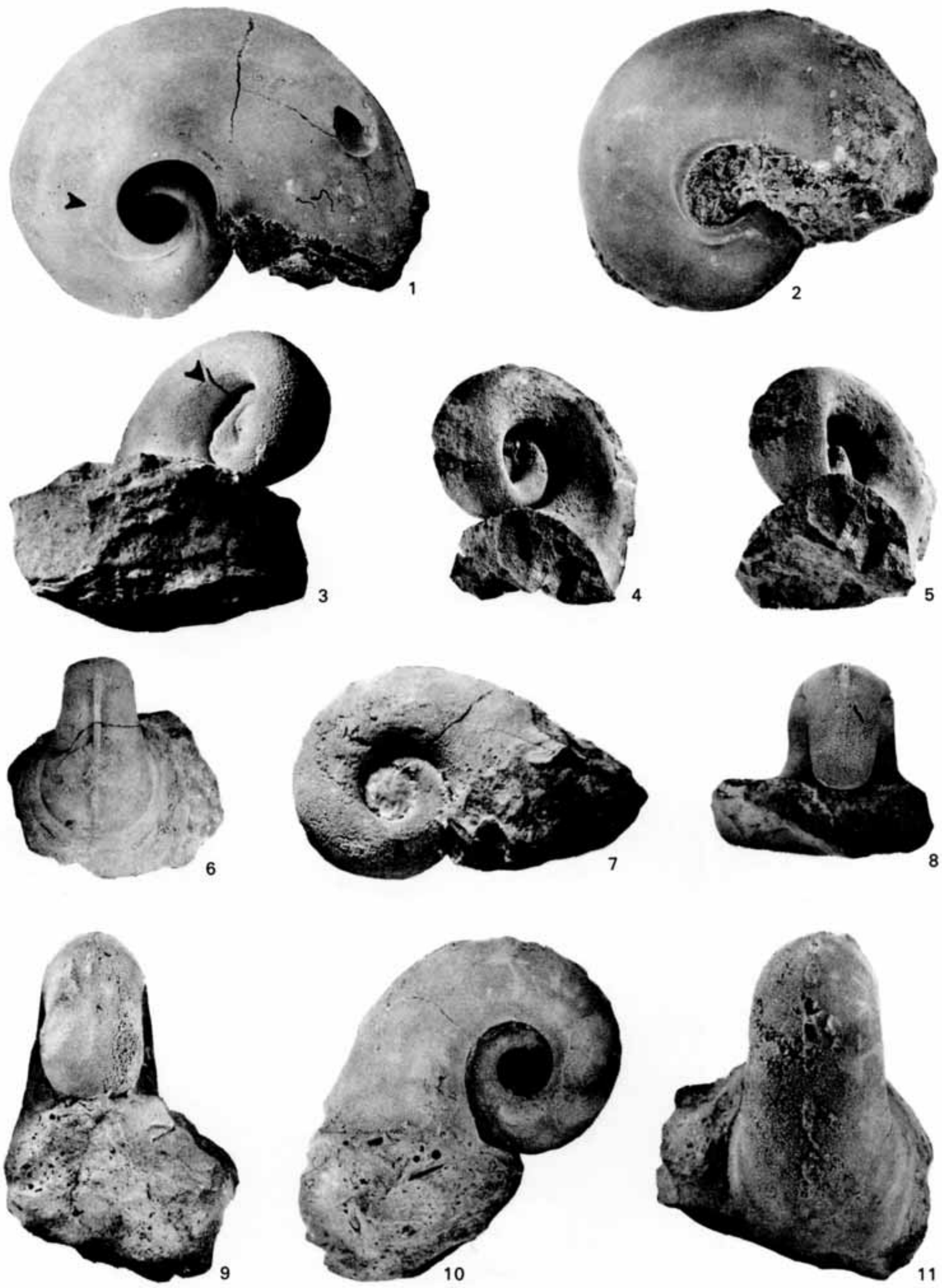

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