SYSTEMATICS, ONTOGENY AND FUNCTIONAL MORPHOLOGY OF SILURIAN TRILOBED BELLEROPHONTACEAN GASTROPODS

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The status of the trilobed bellerophontacean genera *Bucanella, Plectonotus, Tritonophon* and *Nylanderina* is discussed; *Nylanderina* is considered to be a junior synonym of *Tritonophon*. The ontogeny of *Plectonotus* is described and a functional interpretation of the trilobed condition in the Bellerophontacea is presented. *Tritonophon trilobata* (Sowerby *in* Murchison, 1839) is redefined. The following new species are described: *Plectonotus boucoti, P. cherylae, Tritonophon kivitalonae.*

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Many species of Lower Ordovician – Middle Devonian bellerophontacean gastropods are characterised by the development of a trilobed dorsum. Typically a raised, median dorsal lobe is delimited from a pair of flanking lobes, one to each side, by two spiral grooves. Most of the species are poorly known and have been assigned to one or other of the two 'catch-all' taxa *Bellerophon trilobatus* Sowerby *in* Murchison, 1839 and *Planorbis trilobatus* Conrad, 1839. Both of these Silurian species have been generally accepted as bellerophontacean gastropods but uncertainty with regard to structure and taxonomic precedence has resulted in considerable confusion in earlier literature. Unfortunately, this uncertainty has grown to include all of the four genera which subsequent authors have proposed to accomodate some of the species showing this distincitive dorsal modification, namely *Bucanella* Meek, 1871; *Plectonotus* Clarke, 1899b, *Tritonophon* Öpik, 1953; and *Nylanderina* Boucot *in* Boucot, Cumming & Jaeger, 1967. The determinitive characters of all the genera have been questioned by various workers which in itself is suggestive of one of the major causes of much of the confusion – inadequate preservation of type materials.

The present paper aims to elucidate some of the problems currently associated with the systematics of trilobed bellerophontacean gastropods in the Silurian. A background for this discussion is provided by a large gastropod

fauna from the Siluro-Devonian Arisaig Group of Nova Scotia, in which trilobed bellerophontaceans are conspicuous, but comparative material from the Silurian of Sweden, the United Kingdom and Ireland is also incorporated. A necessary preliminary to the description of species is a clarification of the status of the four previously described genera of trilobed bellerophontaceans, and this is attempted insofar as available material allows. Recognition of ontogenetic variation in the degree of development of the trilobed dorsum has promoted a detailed description of the ontogeny of two new species of *Plectonotus* which is interpreted in relation to probable mode of life. The functional morphology of the trilobed condition in the Bellerophontacea is discussed in terms of the generally accepted hypothesis concerning the anatomical organisation of the group (Knight, 1952).

Trilobed bellerophontacean genera

The area of disagreement common to descriptions of *Bucanella* Meek, 1871, *Plectonotus* Clarke, 1899b, *Tritonophon* Öpik, 1953 and *Nylanderina* Boucot *in* Boucot, Cumming & Jaeger, 1967, and to most trilobed bellerophontacean species, is the nature of the dorsal emargination. Since this feature is employed as the basis for current classifications of the Bellerophontacea (Knight et al., 1960; Horný, 1963) the establishment of the presence of a dorsal sinus, or a true slit capable of generating a selenizone, is of considerable systematic importance.

Plectonotus and *Bucanella*

When introducing *Plectonotus*, with type species *P. derbyi* Clarke, 1899b, from the Middle Devonian of Brazil, Clarke (1899b) clearly stated that the genus was to be distinguished from *Bucanella* Meek, 1871 by the presence of a true dorsal slit generating a selenizone, Meek's genus being held to have only a sinus. McLearn (1924) followed Clarke's diagnosis and assigned to *Plectonotus* specimens from the Silurian of Arisaig, Nova Scotia, which carried a selenizone on the upper surface of the broad median lobe.

Knight (1941) redescribed the type material of *Plectonotus* noting 'a rather narrow, deep, V-shaped sinus in the anterior lip which does not culminate in a slit . . .' and subsequently placed the genus within the Sinuitidae as a subgenus of *Bucanella* (Knight et al., 1960).

Boucot & Saul (*in* Saul, Boucot & Finks, 1963) reinterpreted *Plectonotus* on the basis of specimens identified by them as *Plectonotus fraternus* (Reed, 1908) from the Devonian Accraian Series of Ghana, confirming the presence of a selenizone, as originally described by Clarke (1899b). In so

Fig. 1. *Bucanella nana* Meek, 1871, Lower Ordovician, Crater's Falls, Colorado, U.S.A. Oblique antero-dorsal view of lectotype showing growth lines (heavy lines) on lateral lobe and side of median lobe indicating the presence of a dorsal emargination, ×8 (after Knight, 1941, pl. 7, fig. 3b).
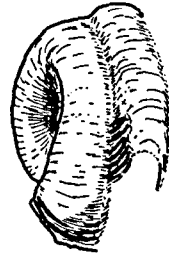
doing, they suggested that a fracture in the apertural margin of the lectotype of *Plectonotus derbyi*, the type species, had been misinterpreted by Knight (1941) and Knight et al. (1960) as an acutely V-shaped sinus. Accordingly, Horný (1963) transferred the genus to the subfamily Bucaniinae of the Bellerophontidae. During the discussion of a palaeozoic fauna from northern Maine, Boucot & Yochelson (1966) erected the subfamily Plectonotinae of the Bellerophontidae in which a redefined, slit-bearing *Plectonotus* was restricted to the Early and Middle Devonian.

Examination of the lectotype of *P. derbyi* (Pl. II, figs. 10, 14) confirms the presence of a true slit. In oblique light a median dorsal band with several deeply crescentic lunulae is visible on the otherwise coarsely preserved internal mould. Similarly, examination of the specimens referred to *P. fraternus* by Boucot & Saul (*in* Saul, Boucot & Finks, 1963) demonstrates that several of these are trilobed with true slits and are assignable to *Plectonotus*. It should be noted, however, that those specimens referred to *P. fraternus* and illustrated by Saul, Boucot & Finks (1963) as Pl. 138, figs. 3, 4 and 9 are not trilobed and do not possess true slits. Although distorted by crushing, gross form and the nature of the sinus are suggestive of *Sinuitopsis* Perner, 1903 ·which Rollins & Batten (1968) transferred to the Class Monoplacophora.

Bucanella nana Meek, 1871, the type species of *Bucanella* from the Lower Ordovician of Colorado, U.S.A., was described by Meek (1871) as showing no traces of a median dorsal band (selenizone) corresponding to a sinus in the apertural margin. Undoubtedly, the passage of seventy years before Knight (1941) illustrated this rare species for the first time severely hampered interpretation of the genus by later workers.

The type material of *Bucanella nana* Meek, 1871 indicates a trilobed bellerophontacean quite unlike *Plectonotus derbyi*. Whorl embracement and the rate of whorl expansion are slight, producing widely phaneromphalous umbilici in contrast to the narrow umbilici of *Plectonotus*. The lateral lobes carry strong transverse ribs which change suddenly to finer growth lines on the median lobe. Strong curvature of the growth lines on the sides of the

median lobe of the lectotype indicates the presence of a dorsal emargination (fig. 1) but examination has failed to demonstrate the nature of this.

Part of the small limestone slab containing the silicified type specimens of *Bucanella nana* (USNM 7858) was digested in dilute hydrochloric acid to provide additional material. One of the several poor specimens obtained in this way shows two strong spiral cords on the upper surface of the median dorsal lobe which are possibly suggestive of the margins of a selenizone. However, the precise form of the emargination could not be elucidated and must remain open to conjecture until better preserved material is forthcoming.

Reference is made to this slight but inconclusive evidence in support of the presence of a true slit merely to emphasize the importance of the correct determination of the feature in terms of accepted classification. *Bucanella* is the nominate genus of the subfamily Bucanellinae Koken & Perner, 1925 of the family Sinuitidae Dall *in* Zittel-Eastman, 1913, assignment to which family is currently conditional on the presence of a sinus (as distinct from slit) in the dorsal lip.

Although the systematic position of *Bucanella* is in doubt, it is clear that *Bucanella* and *Plectonotus* are unrelated forms which have independently acquired dorsal trilobation at different instants in geological time. The formation of the subfamily Plectonotinae by Boucot & Yochelson (1966) and separation of *Plectonotus* from *Bucanella* is consequently quite justified.

Tritonophon and *Nylanderina.*

Öpik (1953) described *Tritonophon* to include a strongly trilobed bellerophontacean with prominent spiral ornamentation from the Lower Silurian of Australia. The type species, *Tritonophon trimetra* Öpik, 1953, was held to be characterised by a 'short and wide U-shaped slit-notch' which generated a selenizone bordered by spiral lines. Öpik recognised the similarity of the dorsal trilobation to *Bucanella* and *Plectonotus* but followed Knight (1941) in considering both of these to be without a slit. Consequently, he placed *Tritonophon* as a subgenus of *Kokenospira* Bassler, 1915 which also has a well developed selenizone with spiral threads.

Rollins (*in* Rollins, Eldredge & Spiller, 1971) quoted a written communication from Ellis L. Yochelson (1968) stating that the type specimens of *T. trimetra* were lost by fire. In fact, the holotype (Commonwealth Palaeontological Collection No. 674) is preserved in the Bureau of Mineral Resources, Geology and Geophysics, Geological Section, Canberra, Australia, although some of the specimens in the collection were destroyed (J. M. Dickens, written communication, 1972). In view of the delicate nature of the specimen it has not been possible to borrow the holotype for study nor to prepare a latex

mould. However, judging from the illustrations of Öpik (1953, Pl. VII, figs. 52, 53) it is unlikely that the tiny, yet coarsely preserved specimen would provide further information. Although Öpik is emphatic in his description of a U-shaped slit-notch, it is not possible to conclusively demonstrate the nature of the emargination from the illustration. The paratype (Öpik, 1953, Pl. VII, fig. 54) undoubtedly has a dorsal band but such a band should not automatically be interpreted as a selenizone.

However, specimens which are morphologically close to *T. trimetra* are known from the Silurian and Devonian in many areas and the presence of a selenizone has been confirmed by several authors (Moberg & Grönwall, 1909; Straw, 1933; Rollins *in* Rollins, Eldredge & Spiller, 1971). Öpik (1953) suggested that in other cases, for example *Bucaniella trilobata* (Conrad) of Pitcher, 1939 from the Upper Llandovery of Shropshire, England, the selenizone might have been obscured by the prominent spiral lirae and a lack of discernible lunulae. This is the case with Pitcher's material where a recently prepared silicon rubber impression of GSM 56907, the original of Pitcher (1939, Pl. VII, fig. 1), shows a well developed selenizone. Additional specimens in the Yale Peabody Museum indicate that *Bucanella trilobata* (Conrad) of Swartz & Prouty (1923), from the Silurian Rochester and Rose Hill Formations of Maryland, U.S.A., also has a short slit and selenizone.

On the basis of these extra observations it would seem quite reasonable to accept the presence of a slit and selenizone in *Tritonophon* as originally described by Öpik (1953).

Boucot (*in* Boucot, Cumming & Jaeger, 1967) described *Nylanderina* from the Lower and Middle Devonian of Canada to include species that were morphologically similar to *Tritonophon* but differed in the reported presence of a V-shaped sinus. Following examination of the type collection of *Nylanderina goldringae* Boucot *in* Boucot, Cumming & Jaeger, 1967, the type species, it is not possible to maintain the distinction. Available evidence concerning the emargination of the abraded specimens is insufficient to warrant interpretation as a V-shaped sinus and is more suggestive of a U-shaped sinus of the type characteristic of *Tritonophon*. As a result, *Nylanderina* is considered to be a junior synonym of *Tritonophon*. Boucot assigned *Bellerophon rotalinea* Hall, 1879 to *Nylanderina* but Rollins (*in* Rollins, Eldredge & Spiller, 1971) considered this species to have a true selenizone and referred it to *Tritonophon*. Rollins has also inferred the presence of a selenizone in *N. goldringae* from Boucot's illustrations.

Plectonotus and *Tritonophon*

Knight et al. (1960) considered *Tritonophon* to be a junior subjective synonym of *Bucanella sensu stricto* in the family Sinuitidae. Although the pos-

sibility of *Bucanella* possessing a true slit and selenizone has briefly been outlined above, it is clear that any resemblance between the two genera is purely superficial, as is also the case between *Bucanella* and *Plectonotus*. Rollins (*in* Rollins, Eldredge & Spiller, 1971) allowed *Tritonophon* full generic status and placed it in the subfamily Bucaniinae of the slit-bearing Bellerophontidae. However, *Tritonophon* shows no obvious affinity to *Bucania* Hall, 1847 when details of the emargination are compared. With due regard to similarity in form, ornamentation and stratigraphical distribution it is currently considered most satisfactory to place *Tritonophon* alongside *Plectonotus* in the subfamily Plectonotinae Boucot & Yochelson, 1966.

Tritonophon is distinguished from *Plectonotus* by its more pronounced trilobation which produces a strongly vaulted median lobe. In *Tritonophon* the median lobe is narrow with the selenizone occupying the entire upper surface. In *Plectonotus* the median lobe is usually wide with the selenizone occupying only part of the width of the upper surface.

Ontogeny of *Plectonotus*

It has been widely recognised that the coiling of the gastropod shell approximates to a logarithmic spiral (Thompson, 1942). In his studies of coiling Raup (1961; 1966; 1967) developed four parameters which enabled him to quantify the form of a shell coiled in such a spiral. In a simplified model any particular shell form was considered to be an unvarying logarithmic spiral with the parameters retaining constant values throughout growth. As might be expected, however, many gastropod shells show significant departures from a single logarithmic spiral during growth – a familiar example is provided by the club-shaped shell of the present day land snail *Clausilia* Draparnaud, 1805 which initially increases and subsequently decreases the width of the spire during ontogeny. In such cases, some or all of Raup's parameters will also vary during ontogeny. However, such variation enhances rather than detracts from their value since a mechanism is provided for the quantification of the variation in shell form during ontogeny.

Raup's four basic parameters may be referred to as S, W, D and T (specific applications in *Plectonotus* are illustrated in fig. 2). S is a representation of the shape of the generating curve which is often equivalent to the outline of the growing edge of the shell. Such a curve is commonly complex and difficult to express mathematically but even a simple expression, such as the ratio of apertural width to apertural height, can provide a usable measure. A number of similar simple ratios can be included in more complex models (Gould, 1969). W is the rate of whorl expansion and is computed as the ratio of a linear measurement on one whorl to the same
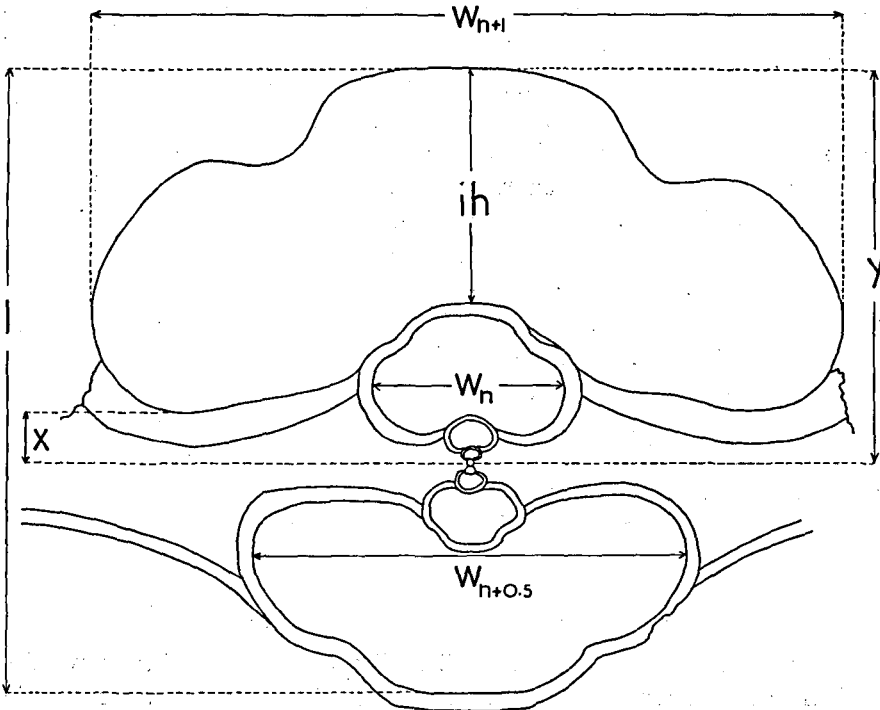
Fig. 2. *Plectonotus boucoti* sp. nov., GSC 3138, Doctors Brook Formation, Nova Scotia, camera lucida drawing of transverse section showing standard measurements employed in the determination of Raupian parameters. For the final whorl (W_{n+1}): $S = w_{n+1}/ih$; $D = x/y$; $W = w_{n+1}/w_n$; $V = w_{n+1}/w_{n+0.5}$

dimension one whorl previously. If the shell proportions change with growth, values of W computed from different sources, for example apertural height or apertural width, may themselves differ. In such cases it is often profitable to employ a rate of expansion measured at half whorl intervals, here called V, which approximates to the square root of W. D, the position of the generating curve relative to the axis of coiling may be measured as the ratio of the distance from the axis to the adaxial margin of the whorl, to the distance from the axis to the abaxial whorl margin. The rate of whorl translation, T, expresses the helicoid component of growth in the gastropod shell. In bellerophontacean gastropods, as in other planispirally coiled shells, T has a value of zero and need not be further considered.

The method of shell form analysis developed by Raup (1961; 1966; 1967) proves to be especially useful for elucidating the ontogeny of trilobed bellerophontaceans. From the study of population samples and transverse cross-sections of several Silurian and Devonian species it is clear that shell mor-

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phology in *Plectonotus* and *Tritonophon* varies considerably during ontogeny (figs. 4, 6, 12, 13). When considered in conjunction with the high degree of morphologic variability between individuals of some species (e.g. *Plectonotus cherylae* sp. nov., below, pl. I, figs. 1–13, 16), this ontogenetic variation necessitates full knowledge of the range in shell form of individual species before meaningful comparison with related species is attempted. This information can be most satisfactorily obtained by the examination of transverse cross-sections of well preserved specimens, cut so as to contain the axis of coiling and to be perpendicular to the plane of symmetry. Such sections provide transverse profiles of the early whorls of the bellerophontacean gastropod in a medium suitable for accurate measurement.

Well preserved material of sufficient quality is elusive. However, specimens of two new species of *Plectonotus* (described below) from the Siluro-Devonian Arisaig Group of Nova Scotia are described in detail. Similarly preserved specimens of *Tritonophon* were not available although some cross-sections are illustrated in the systematic section (figs. 12, 13).

Ontogeny of *Plectonotus boucoti* sp. nov.

A transverse section through the shell of *Plectonotus boucoti* sp. nov., described below, shows pronounced ontogenetic change in the whorl profile and in the nature of coiling (figs. 2–5). Departure from simple logarithmic increase is seen by plotting whorl width and overall length on logarithmic scale against successive half whorls of growth. Raup (1967) noted that an unvarying logarithmic spiral would plot as a straight line under such conditions. This is clearly not so in *P. boucoti* where width approaches and finally exceeds length instead of the two traces being parallel straight lines (fig. 3).

D, W, V and S show comparable variation during growth. In fig. 5 the parameters derived from a sample of six specimens are plotted against size which is defined as the sum of overall length and whorl width expressed in millimetres for a particular growth stage. If coiling showed unvarying logarithmic increase, and there were no changes in whorl profile during growth, all the traces would be linear and parallel to the horizontal axis.

Two stages may be recognised in the ontogeny of *Plectonotus boucoti*. In the earliest three whorls, up to a size of about 2.0, S, W and V diminish while D increases. The decrease in S is brought about by a fall in the rate of whorl expansion, shown by decreasing W and V, while widening of the umbilici produces an increase in D. The whorl profile of the three whorls of the first stage is transversely elliptical with the uniformly convex dorsum showing no signs of trilobation (figs. 4, 5). In the second stage, at sizes greater than about 2.0, the earlier trends are reversed. S increases, due to an increase in whorl width relative to internal and total height which also
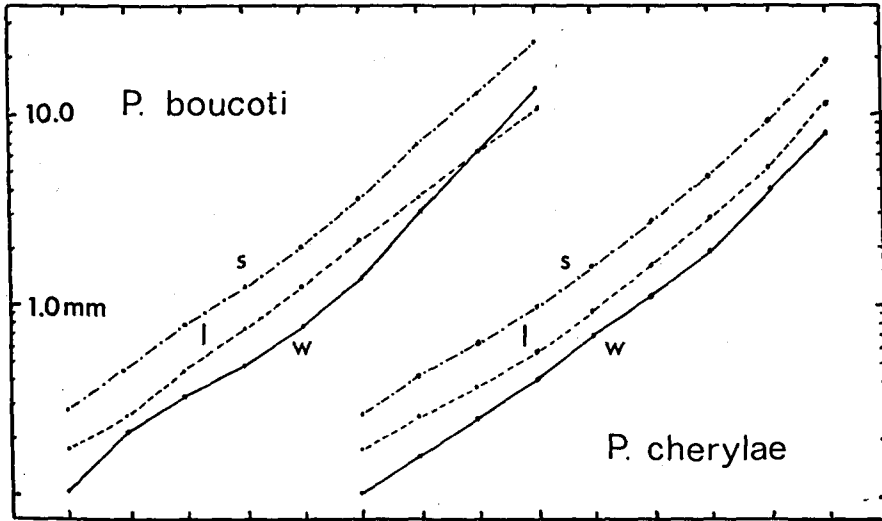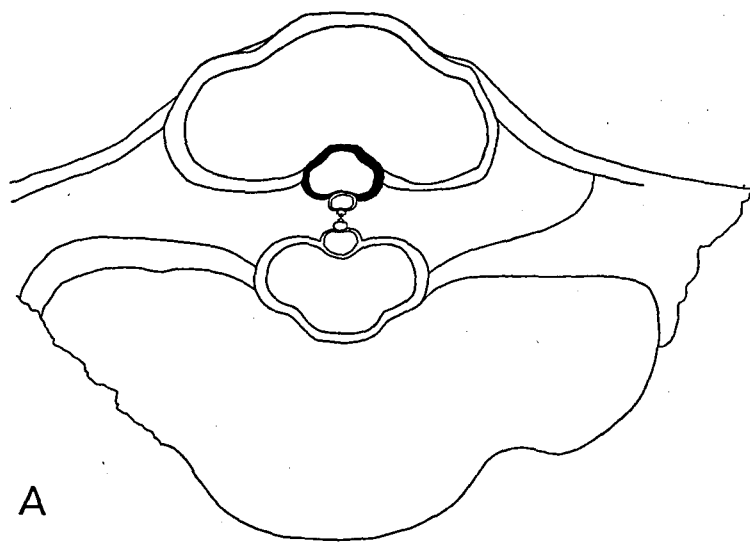
Fig. 3. Growth patterns in *Plectonotus*. Measurements of length (1), width (w) and size (s = 1+w) for *Plectonotus boucoti* sp. nov., USNM 169589, Doctors Brook Formation, Nova Scotia, and *P. cherylae* sp. nov., USNM 169581, Stonehouse Formation, Nova Scotia, at successive half whorl intervals during ontogeny. All measurements in mm on shell interior.

causes W and V to rise. D decreases sharply as a result of a relative narrowing of the umbilici. Finally, during the fifth whorl at sizes greater than 10.0, the rate of whorl expansion stabilises, or decreases slightly, although other parameters continue essentially unchanged.

The development of trilobation characteristic of the second growth stage is seen to commence with a slight median expansion of the dorsum after three whorls (fig. 4). Half a whorl later, size approximately 3.5, the flattened median dorsal surface passes with noticeable angularity onto concave dorso-lateral areas. These dorso-lateral areas become convex laterally, with the maximum width of the whorl at midwhorl height, and increase in curvature with passage into the umbilici. After four whorls, with size about 7.0, well marked shoulders are in evidence on the flanks of the median lobe. The upper surface of each flanking lobe slopes away from the median lobe towards the axis of coiling. In the succeeding whorl the flanking lobes become more strongly defined until, after five whorls and at a size of about 21.0, the upper surface of each lobe slopes in towards the median lobe. At this time maximum whorl width is at just above the angular umbilico-lateral shoulders, below midheight of the whorl.

With further increase in size definite channels separate the lateral lobes from the median dorsal lobe and the umbilical walls become increasingly
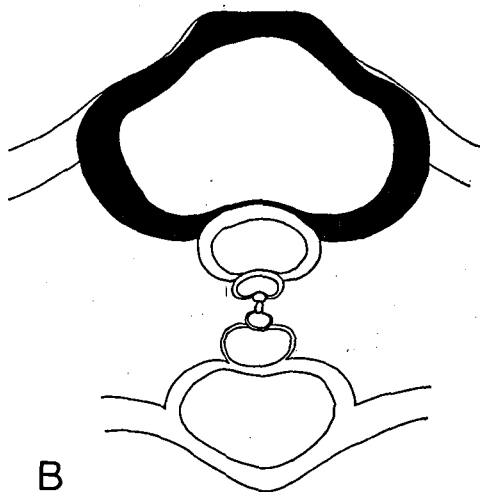
Fig. 4. Ontogenetic variation in *Plectonotus boucoti* sp. nov., USNM 169589, Doctors
Brook Formation, Nova Scotia. A, camera lucida drawing of transverse section
showing development of trilobation with increased growth and subsequent closure of
one umbilicus at a late growth stage, ×6.5; B, inner whorls of same, ×25.
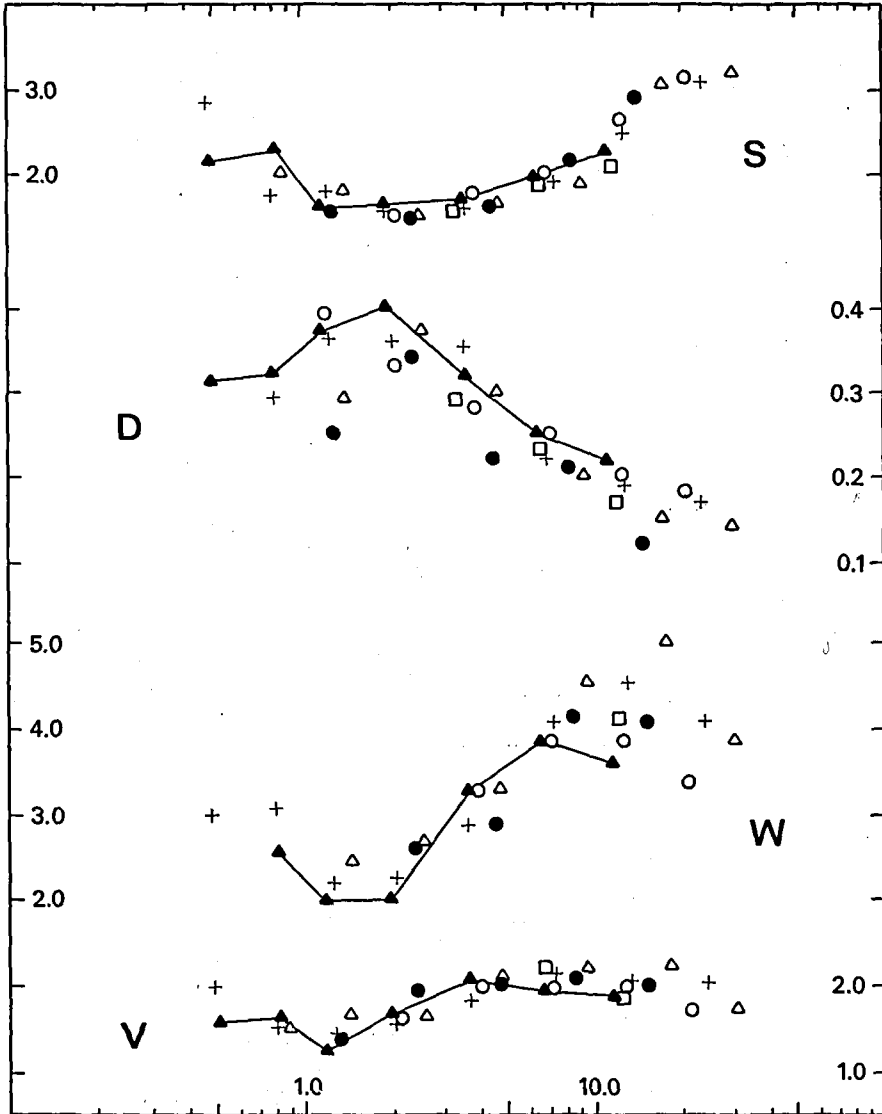
Fig. 5. Variation of Raupian parameters in *Plectonotus boucoti* sp. nov. during ontogeny. For explanation of S, D, W and V see fig. 2 and text. Horizontal axis is 'size' (length + width) on logarithmic scale. All measurements in mm on the shell interior. Open circle, USNM 169585; filled circle, USNM 188526; cross, USNM 169589; filled triangle, USNM 192123; open triangle, GSC 3138; square, USNM 169587. All specimens from Doctors Brook Formation, Nova Scotia.
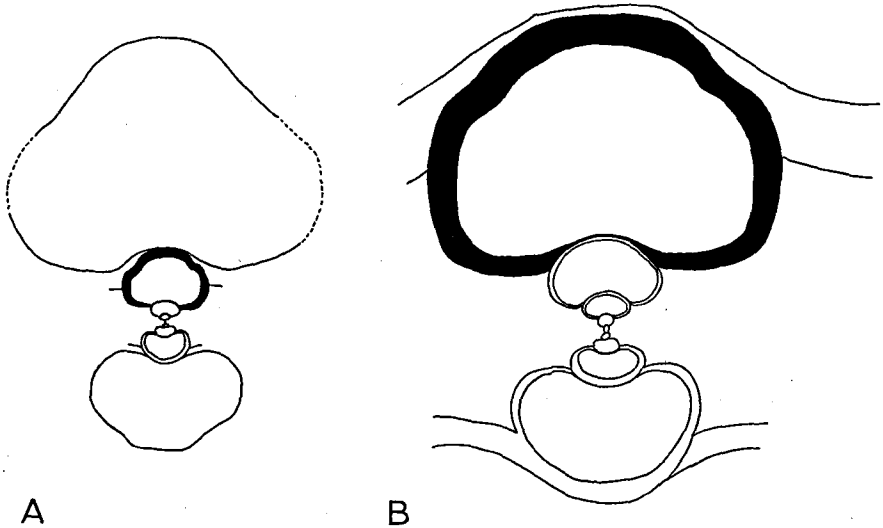
Fig. 6. Ontogenetic variation in *Plectonotus cherylae* sp. nov., USNM 169581, Stone-house Formation, Nova Scotia. A, camera lucida drawing of transverse thin section showing development of trilobation during ontogeny, ×5; B, inner whorls of same, ×20.

flattened. The largest individuals may develop a thickening of the umbilico-lateral wall a short distance back from the aperture which completely closes one umbilicus (fig. 4).

Ontogeny of *Plectonotus cherylae* sp. nov.

The increase of width over length characteristic of the development of *P. boucoti* is not seen within the size range of available specimens of *P. cherylae* (fig. 3). However, variation in Raupian parameters reflects comparable departure from unvarying logarithmic increase (fig. 7). In *P. cherylae* S increases to a peak of about 2.7 at a size of about 0.9 and subsequently decreases to about 1.6 at size 4.0, remaining constant thereafter. The initial increase and subsequent decrease in values of D typical of *P. boucoti* is also evident in *P. cherylae*. W increases throughout growth in contrast to the initial decrease and subsequent increase seen in *P. boucoti* (fig. 5). V also shows essentially linear increase although a slight tendency for decrease at sizes greater than 10.0 parallels the situation in *P. boucoti*.

It is clear that the few measurements on the earliest whorls of *P. cherylae* do not present such conclusive evidence of two growth stages as is seen in *P. boucoti*. However, it is apparent from the available measurements that the change in trend of S, D, W and V in *P. cherylae* occurs at a smaller size (0.9) than the corresponding change in *P. boucoti* (size 2.0).
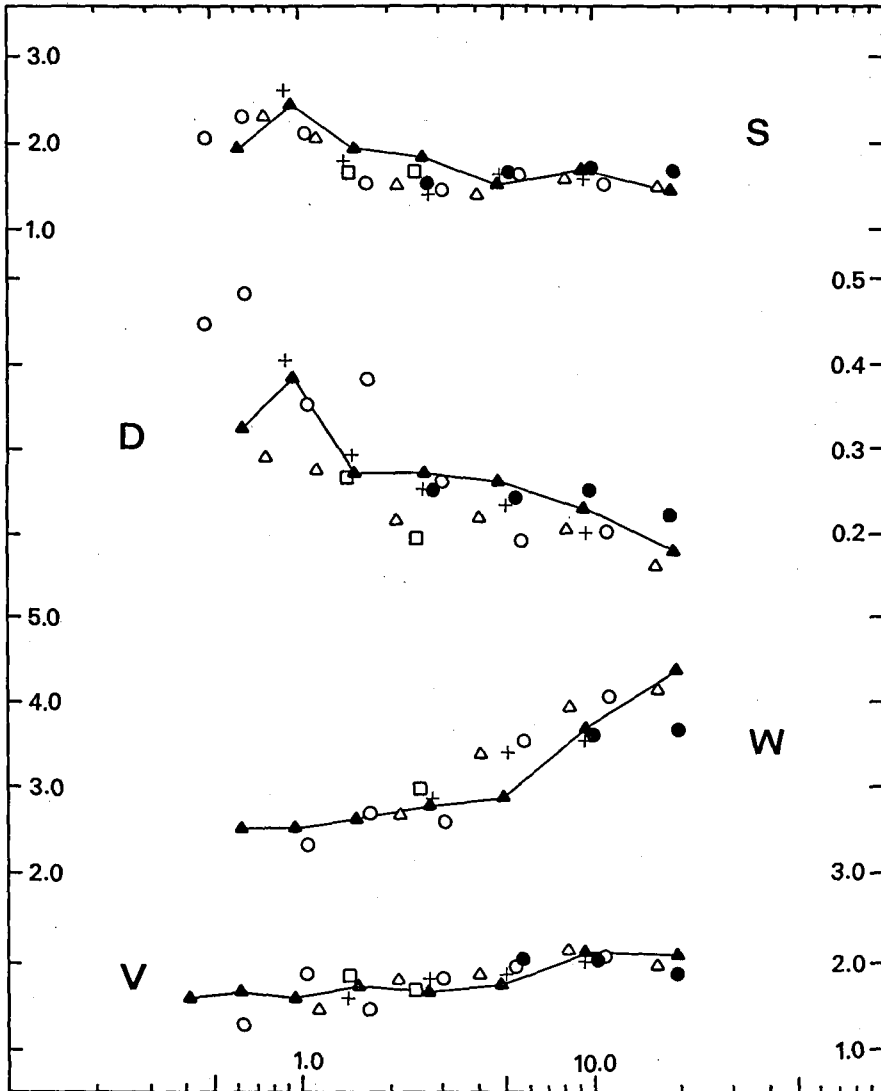
Fig. 7. Variation of Raupian parameters in *Plectonotus cherylae* sp. nov. during on-
togeny. For explanation of S, D, W and V see fig. 2 and text. Horizontal axis is
'size' (length + width) on logarithmic scale. All measurements in mm on the shell
interior. Open circle, GSC 33280; filled circle, GSC 33281; cross, USNM 188527;
filled triangle, USNM 169581; open triangle, USNM 169577; square, USNM 169576.
All specimens from Stonehouse Formation, Nova Scotia.

Below a size of 0.26 the whorl cross-section in *P. cherylae* is subcircular but at greater sizes the profile becomes transversely lenticular with the first indications of dorsal expansion commencing at about a size of 1.6 (fig. 6). It is not until the third whorl, size about 4, that dorsal trilobation is observed with the development of minor lateral shoulders. In some specimens the degree of trilobation hardly increases during the next two whorls but, more usually, the definition of the lateral shoulders is increased. The spiral grooves delimiting the three dorsal lobes are not well developed and are never deepened into the channels characteristic of *P. boucoti*.

Interpretation

The nett result of the ontogenetic changes in *Plectonotus boucoti* is the transformation of a laterally compressed juvenile shell with wide umbilici into a subsphaerical mature shell, with narrow or closed umbilici and a strongly trilobed dorsum. A comparable pattern is seen in *P. cherylae* although the subsphaerical form is not so well developed at maturity within the available material.

The two growth stages recognised in the ontogeny of *Plectonotus* may be regarded as the initial protoconch and the subsequent teleoconoch. The reduction in the rate of whorl expansion (W and V) in late growth stages is probably indicative of the attainment of maturity.

Vermeij (1971) has recently presented an analysis of the diversity of shell form in present day gastropods, demonstrating the relationship between shell morphology and mode of life. One of his many significant observations concerned the absence of the high spired form in recent members of the Archaeogastropoda where the typical shell form may be loosely referred to as 'trochiform'. Yonge (1947) suggested that most archaeogastropods are restricted to hard substrata in conditions of clear water by the structure of the aspidobranch ctenidia, which would be liable to be clogged by fine suspended sediment in turbid conditions. Vermeij (1971) concluded that the compact shell of archaeogastropods reflects the need for a gravitationally stabil shell form suited to life in the frequently higher energy conditions operative over hard substrata. Possible variation in shell morphology is consequently controlled by the nature of the habitat which is itself restricted by the structure of the ctenidia. High spired shells, being of low stability on a hard substratum, are therefore not found within living archaeogastropods, although this particular shell form is widely employed by mesogastropods and neogastropods. In these groups the more advanced ctenidia are better capable of dealing with suspended sediment in turbid waters, making life upon or within soft substrata possible. In such conditions there is little
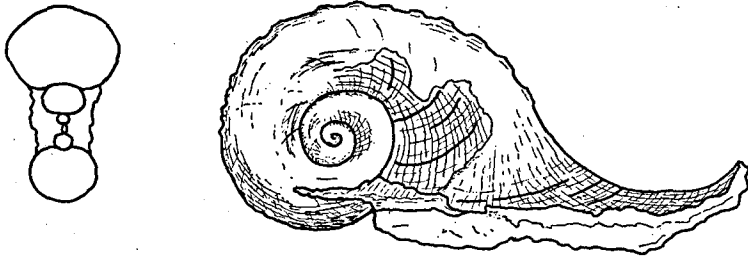
Fig. 8. *Boiotremus longitudinalis* (Lindström, 1884), Silurian, Visby, Gotland, Sweden. Transverse section and lateral view showing the low rate of whorl expansion, wide umbilici and widely expanded aperture of the final growth stage, ×0.67 (after Lindström, 1884, pl. IV, figs. 3,7).

need for a compact, gravitationally stabil shell and the development of the high spired shell form is not precluded by the operative energy regime.

As discussed more fully in the following section, it is widely accepted that bellerophontaceans possessed aspidobranch ctenidia in similar fashion to other archaeogastropods (Knight, 1952). It is consequently to be expected that restrictions in terms of habitat imposed on archaeogastropods by the structure of these ctenidia should also be experienced by bellerophontaceans, namely that bellerophontaceans should be generally restricted to hard substrata in clear water. In such a case, it is clear that the stability arguments advanced by Vermeij (1971) should also have some relevance to discussions of the range in bellerophontacean morphology. However, the bellerophontacean shell is planispiral and the question of degree of elevation of a helical spire, the environmentally limited criterion in archaeogastropods, is obviously inapplicable.

The main variables in bellerophontacean shell morphology are the rate of whorl expansion (W and V) and the position of the generating curve relative to the axis of coiling (D), the latter manifested in the width of the umbilici. The 'average' mature bellerophontacean has dimensions approximately intermediate between those described in *Plectonotus boucoti* and *P. cherylae* at maturity, with a rapidly expanding shell and narrow umbilici (Knight et al., 1960). Such a subsphaerical shell has a high degree of compactness and would appear to satisfy the stability requirements of life on a hard substratum.

However, bellerophontaceans exhibit considerable morphological variation, as is also the case with living archaeogastropods, and many species depart considerably from the average. One such morphological group of bellerophontaceans includes the genera *Salpingostoma* Roemer, 1876, *Tremanotus* Hall, 1865 and *Boiotremus* Horný, 1962 and is characterised by a low rate of whorl expansion and relatively wide umbilici (fig. 8). In this case, the

shell apparently has less stability than the more subsphaerical norm, when considered in life orientation with the axis of coiling parallel to the substratum and the plane of symmetry perpendicular to it.

Species of *Salpingostoma, Tremanotus* and *Boiotremus* often develop a widely expanded aperture (Peel, 1972) and the acquisition of this feature commonly appears to be an adaptation to life on a soft substratum. The expansion of the aperture probably reflects an expansion of the foot which may in turn serve to reduce the quantity of sediment raised into suspension by movement and to prevent partial submergence in the soft substratum. In such a low energy habitat a lower degree of stability is required than on a hard substratum and this is exemplified by the narrower, more widely umbilicate, less compact shells.

There is clear similarity in morphology between the early whorls of *Plectonotus* (figs. 4B, 6B) and the mature whorls of *Boiotremus longitudinalis* (Lindström, 1884; fig. 8) exclusive of the explanate final growth stage. In consequence, development of the two shells in response to similar stability and energy regime parameters is readily postulated. This does not imply, of course, that juveniles of *Plectonotus* lived in the areas of accumulation of fine sediment of the type which *Boiotremus longitudinalis* appears to favour in the Silurian of Gotland, nor that adult *Plectonotus* specimens subsequently migrated to firmer substrata. A pelagic mode of life may equally provide the energy conditions appropriate to the development of the juvenile shell, while subsequent settling onto a hard substratum would necessitate the production of the more compact, subsphaerical shell of the adult.

While a strictly morphological approach provides support for this interpretation of the significance of the change in coiling between the protoconch and the teleoconch in *Plectonotus*, it should be noted that, in terms of development or change in life habit, such disjunctions between protoconch and teleoconch in present day marine gastropods are poorly understood (Cox, 1960). In many opisthobranchs the change from the early hyperstorphic whorls to the normal coiling of the later shell does take place when the pelagic larva settles and starts to metamorphose. However, in other gastropods the change from pelagic to benthonic habit may produce no change in shell morphology, or ornamentation typical of the adult may be developed prior to settling (Cox, 1960).

Gould (1969) observed similar differences in coiling between the early and later whorls in a Pleistocene land snail from Bermuda. He attributed this 'nucleation effect' to the necessary departure of the first formed part of the protoconch from a logarithmic spiral. The mathematical spiral has its origin at a point whereas the earliest part of the protoconch is a small cap-shaped shell. Gould (1969) therefore argued that this atypical coiling of the early whorls was a result of accomodation of the initial departure within

the coiling pattern of the gastropod shell. It is clear that such an interpretation does not necessitate any correlation with changes in life pattern or development.

The development of trilobation in *Plectonotus boucoti* and *P. cherylae* accompanies the changes in values of Raupian parameters during the second growth stage (teleoconch) but there is little reason to suggest that the acquisition of a trilobed dorsum is the dominant force behind the evolution of the gross coiling of the shell. It should be noted that S, as employed in this context, does not directly reflect any change in the degree of trilobation. However, the general increase in W and V during the second growth stage (figs. 5, 7) could be seen as an attempt to compensate for the reduction in living space available to the gastropod produced by a deepening of the dorsal furrows. The gradual encroachment of the umbilical walls upon the axis of coiling, demonstrated by a decrease in D, might also be interpreted in this way. However, in *P. boucoti,* the area of cross-section of the whorl, the most convenient measure of available living space, shows a comparable rate of increase per half whorl to V, rendering such a direct interpretation inadequate.

Functional morphology of the trilobed condition in the Bellerophontacea

Following the classic studies of J. B. Knight (1947; 1952) it is commonly supposed that bellerophontaceans are primitive archaeogastropods showing the same general anatomical organisation as recent pleurotomariaceans, although some authors still propose a lack of torsion in the group (Termier & Termier, 1968). Knight (1947) described paired retractor muscle scars on finely preserved bellerophontacean internal moulds which he considered indicative of torsion having taken place. Similar scars have subsequently been described by Peel (1972) although the description of the coiled, sinus-bearing monoplacophoran *Sinuitopsis acutilira* (Hall, 1861) by Rollins & Batten (1968) serves to emphasize some of the problems which accompany systematic determination of the remaining bellerophontiform Mollusca.

Knight (1952) confidently stated his belief that bellerophontaceans were aspidobranch gastropods possessing a high degree of bilateral symmetry, namely symmetrically developed ctenidia, nephridea, osphradia and hypobranchial glands. To a large extent this opinion was based on analogy between the recent *Haliotis* Linné, 1758 and the bellerophontacean *Knightites (K.) multicornutus* Moore, 1941 from the Pennsylvanian of the U.S.A. Knight (1952) discussed the periodic paired extensions of the dorsal lip in *K. (K.) multicornutus* and concluded that the 'horns' were canals indicating the po-
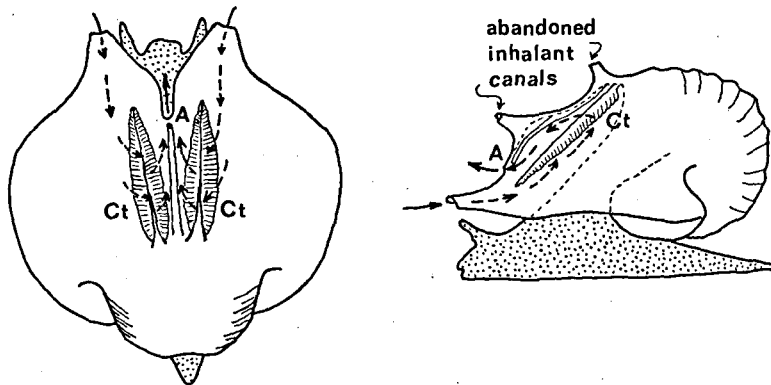
Fig. 9. *Knightites (K.) multicornutus* Moore, 1941, Pennsylvanian, Kansas, U.S.A., ×2. Reconstruction of mantle cavity after Knight (1952). Inferred water currents within the mantle cavity (finely broken line) are shown by heavy dashed lines. A, anus; Ct, ctenidium.

sition of inhalant currents. The mantle cavity housed a pair of aspidobranch ctenidia symmetrically disposed about the median anus (fig. 9), and water circulation patterns were considered comparable to those described in *Haliotis* (Crofts, 1937; Yonge, 1947).

The paired inhalant canals of *K. (K.) multicornutus* are unique within the Bellerophontacea where evidence of the position of the presumed inhalant currents is usually wanting. However, Horný (1963) noted emarginations on the lateral lobes of the strongly trilobed *Tritonophon* (?) *bohemica* (Perner, 1903) from the Upper Ordovician of Bohemia (fig. 10). Horný (1963) commented on the importance of the lateral emarginations but offered no explanation as to their function. Occasional specimens of *Tritonophon* (Pl. II fig. 23) and *Plectonotus* from the Arisaig Group of Nova Scotia show lateral emarginations of the type illustrated by Horný (1963) but the feature is variable, both in degree of development and occurrence.

It is suggested that the lateral emarginations of *Plectonotus* and *Tritonophon* indicate the position of the inhalant currents, in the same way as the paired extensions of the dorsal lip in *K. (K.) multicornutus*, and that the pair of ctennidia are located under the lateral lobes (fig. 11). Streams of oxygenated water enter the mantle cavity antero-laterally and pass over the laterally disposed ctenidia, prior to uniting medially and being expelled, together with the excretory products, through the dorsal slit.

Thus, trilobation of the dorsum may be interpreted as a modification of the shape of the mantle cavity designed to increase efficiency. The deepening of the grooves between the median and lateral lobes tends to produce partial

Fig. 10. *Tritonophon(?) bohemica* (Perner, 1903), Kosov
Beds, Upper Ordovician, Bohemia, showing lateral and
median emarginations, ×6 (after Horný, 1963).
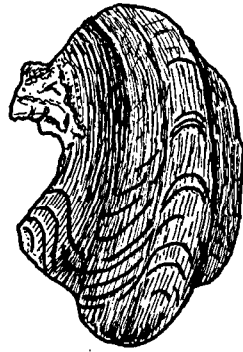
barriers separating the clean water of the inhalant streams from the fouled
and deoxygenated exhalant current.

An analogy may be drawn between the trilobed condition in the Belle-
rophontacea and the development of a median deflection in the anterior
commissure of many brachiopods. In the latter case, a fold and corresponding
sulcus are produced, giving a trilobed appearance to the folded valve. Rud-
wick (1970) has remarked that the median deflection of many fossil brachio-
pods may be so deepened as to effect a spatial separation of the exhalant
current from the inhalant currents. Water currents would enter the brachiopod
laterally and be expelled through the median deflection. In conditions of
quiet water, the risk of recirculation would consequently be greatly reduced.
In both bellerophontacean gastropods and brachiopods, trilobation is a simple
modification of the entrance to the mantle cavity capable of increasing the
efficiency of water circulation.

Such a functional interpretation of dorsal trilobation in the Bellerophon-
tacea readily explains the appearance of the trilobed dorsum in unrelated
stocks of bellerophontacean gastropods at different instants of geological
time. The adaptation is first observed in the rare, early Ordovician species
Bucanella nana (fig. 1) while, in the late Ordovician, trilobed species are
more common (*Tritonophon(?) bohemica*, fig. 10; Bretsky, 1970; Horný, 1963)
Some of the widespread Silurian species are described below and this abun-
dance continues into the Devonian (Clarke, 1899b; Boucot, Cumming &
Jaeger, 1967; Boucot & Yochelson, 1966; Horný, 1963; Rollins, Eldredge
& Spiller, 1971). Strongly trilobed bellerophontaceans are not known in
strata younger than the Devonian. However, several species from the Car-
boniferous and Permian exhibit an incipient trilobation of the dorsum which
may be interpreted in a similar fashion (Gemmellaro, 1889; Koninck, 1883).

To some degree the extreme trilobation of *Plectonotus boucoti* sp. nov.
may also reflect the pronounced ontogenetic change in morphology observ-
ed in that species (figs. 4, 5). As noted above, an explanation of the sub-
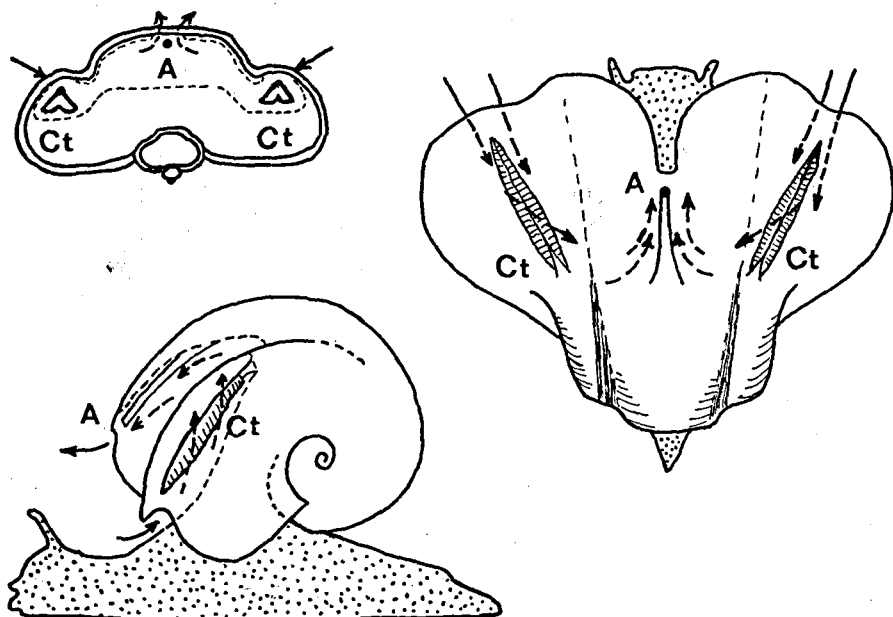
Fig. 11. Reconstruction of the mantle cavity in *Plectonotus boucoti* sp. nov. Water currents entering the shell laterally pass over the ctenidia prior to expulsion through the median dorsal slit. A, anus; Ct, ctenidium.

sphaerical form of the adult solely in terms of the development of trilobation is inadequate. On the other hand, it is clearly possible that the increased envelopment of earlier whorls by subsequent whorls in *P. boucoti* added impetus to the reorganisation of the mantle cavity concomitant with the development of trilobation. It is evident, however, that the high degree of whorl impression present in many other bellerophontacean gastropods throughout the Palaeozoic did not result in the acquisition of any semblance of trilobation (e.g. *Prosoptychus* Perner, 1903; *Pharkidonotus* Girty, 1912; *Bellerophon* Montfort, 1808).

Silurian trilobed bellerophontacean gastropods

Trilobed bellerophontaceans are often conspicuous in gastropod faunas from shallow water Silurian deposits (McLearn, 1924; Moberg & Grönwall, 1909; Öpik, 1953; Pitcher, 1939; Straw, 1933; Swartz & Prouty, 1923). In his general description of the fauna of the Siluro-Devonian Arisaig Group of Nova Scotia, McLearn (1924) referred all trilobed specimens to *Plectonotus trilobatus* (Sowerby *in* Murchison, 1839), although the presence of a narrow

variety in higher strata of the group was recognised. Recent examination of the gastropod fauna of the Arisaig Group, the background for the present study, has resulted in the distribution of the trilobed bellerophontaceans amongst five species.

In the Beechhill Cove, Ross Brook and French River Formations (Llandovery – Wenlock) of the Arisaig Group (Harper, 1973; Boucot, in press) trilobed bellerophontaceans are uncommon and poorly preserved. Consequently, the single species of *Tritonophon* has not been named and its relationships to material of similar age in England and Wales (Pitcher, 1939) and Maryland, U. S. A. (Swartz & Prouty, 1923) requires elucidation.

Plectonotus boucoti sp. nov. occurs in the succeeding Doctors Brook and McAdam Brook Formations (Wenlock – Ludlow) of the Arisaig Group and is known elsewhere from the Upper Llandovery of Ireland, the late Wenlock and Ludlow of Gotland (Lindström, 1884) and the Wenlock and Ludlow of the United Kingdom (Reed, 1920–21).

Tritonophon trilobata (Sowerby *in* Murchison, 1839), the species appellation previously applied to most trilobed bellerophontaceans throughout the Ordovician, Silurian and Devonian, is characteristic in late Ludlow and early Pridoli strata in Nova Scotia (Moydart Formation), Skåne (Moberg & Grönwall, 1909), the United Kingdom (Murchison, 1839; Straw, 1933) and southern Gotland.

In the part of the Stonehouse Formation of Pridoli age in Nova Scotia two trilobed species occur, *Plectonotus cherylae* sp. nov. and *Tritonophon kivitalonae* sp. nov. The former is not recorded elsewhere but *T. kivitalonae* occurs also in strata of similar age in New Brunswick. No gastropods have been seen from the Devonian part of the Stonehouse Formation (Harper, 1973; Boucot, in press) and species of trilobed bellerophontaceans from strata of this age from other localities have not been closely scrutinised.

Localities. – Full details of U.S. National Museum Collection localities are given by Harper (1973) and Boucot (in press). Field localities of Yale Peabody Museum Collection numbers are on file in the Division of Invertebrate Paleontology, Yale Peabody Museum. Some material with USNM Collection numbers is deposited in Yale Peabody Museum. Collections made by O. T. Jones from Arisaig shore, Nova Scotia, are localised on a section deposited with the Geological Survey of Canada.

Material with Schuchert Collection numbers is housed in the National Museum of Natural History, Washington, D. C. with generalised locality information. It should be noted that specimens in Schuchert Colln. 53 have been erroneously assigned to the Ross Brook Formation of the Arisaig Group. The gastropods and associated fauna clearly indicate derivation of the collec-

tion from the Stonehouse Formation of the Arisaig Group, Arisaig shore, Nova Scotia.

The following institutions are abbreviated in the text: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM); Geological Survey of Canada, Ottawa (GSC); Geological Museum of the Institute of Geological Sciences, London (GSM); Paleozoologiska avdeling of the Naturhistoriska Riksmuseet, Stockholm (Mo); Sedgwick Museum, Cambridge (SM); National Museum of Natural History, Washington D.C.(USNM); Yale Peabody Museum, New Haven, Conn., U.S.A (YPM).

Systematics

Family Bellerophontidae M'Coy, 1851.
Subfamily Plectonotinae Boucot & Yochelson, 1966

Diagnosis. – Slit bearing bellerophontaceans with a raised median lobe producing a spiral trilobation of the dorsum; the umbilici usually open and of moderate width.

Genus *Plectonotus* Clarke, 1899b.

Type species. – Plectonotus derbyi Clarke, 1899b.
Diagnosis. – Dorsal trilobation moderate, the median lobe low and relatively wide.

Discussion. - Tritonophon Öpik, 1953 is distinguished from *Plectonotus* by its more pronounced dorsal trilobation. In *Tritonophon* the median lobe is narrow with the selenizone occupying the entire upper surface. In *Plectonotus,* with the exception of *Plectonotus cherylae* sp. nov., below, the median lobe is wide with the selenizone occupying only part of the width of the upper surface. Boucot & Yochelson (1966) considered *Plectonotus,* as redefined by them, to be restricted to the Early and Middle Devonian. The description of the following species requires no material adjustment of their diagnosis but considerably extends the range of the genus.

Plectonotus boucoti sp. nov.
Pl. I, figs. 14, 15, 17–22; Pl. II, figs. 1–9, 11–13, 16, 17.

non. 1839. *Bellerophon trilobatus* Sowerby *in* Murchison, p. 604, Pl. 3, fig. 16.
        1884. *Bellerophon trilobatus:* Lindström, p. 80–81, Pl. IV, figs. 13–15.

1924. *Plectonotus trilobatus:* McLearn, (pars), p. 140–141, Pl. XX, fig. 18, *non* figs. 30–32.

Holotype. – USNM 169584 from USNM Colln. 10165, Doctors Brook Formation (Wenlock), Arisaig, Nova Scotia.

Other figured material. – Doctors Brook Formation, Arisaig, Nova Scotia, USNM 169583, USNM 169585, USNM 188526, USNM 169587–8, USNM 169591–2, USNM 192123 from USNM Colln. 10165; GSC 3138 from Arisaig, precise locality unknown; USNM 169589–90 from Schuchert Colln. 52D. Upper Llandovery of Tonlegee, Cong, Galway, Ireland, SM A39164–5. Hemse Beds (Ludlow), Petesvik, Hablingbo, Gotland, Sweden, Mo 26562–3; Mo 26567 probably from Halla Beds (upper Wenlock), Hörsne, Gotland.

Description. – Species of *Plectonotus* Clarke, 1899b with about five and a half whorls. Width greater than length in mature specimens. Dorsal surface trilobed at maturity with median lobe elevated above flanking lateral lobes and forming half of total width; earlier growth stages showing gradual development of the trilobed form (figs. 2–5). Upper surface of median lobe flattened, with selenizone forming about one third of total lobe width at maturity. Junction of lateral lobes with median lobe becoming progressively deepened and angular with increased ontogeny, culminating in the development of spiral channels in older individuals. Umbilical walls initially convex, becoming flat in later growth stages. Umbilici deep, decreasing in width relative to overall length with increased growth; largest specimens commonly with one umbilicus closed by considerable thickening of the umbilico-lateral shoulder (fig. 4). Whorl embracement near periphery of previous whorl; sutural indentation deep. Aperture poorly known; dorsal lip with a deep sinus passing into an apparently short slit. Selenizone obscure; ornamentation of fine spiral lirae and irregularly spaced lunulae. Shell ornamentation of numerous fine spiral lirae, which may be pustulose, crossed by obscure growth lines; greatest development on the lateral lobes, commonly lacking near the dorsal grooves. Shell of moderate thickness, structure unknown.

Discussion. – The tendency to develop deepened spiral grooves on the dorsum distinguishes *Plectonotus boucoti* from *P. derbyi* (Pl. II, figs. 10, 14); the latter species also has a less strongly differentiated median dorsal lobe. Clarke (1899a) described as *Bucanella trilobata* Conrad var. *viramundo* a species from the Silurian of Rio Trombetas, Brazil which appears to be a *Plectonotus* closely related to *P. boucoti.* The holotype has a greater rate of whorl expansion than *P. boucoti* but details of the emargination and ornamentation are not visible on the otherwise well preserved internal mould. Clarke (1899a) considered *Bellerophon trilobatus* Sowerby of Lindström (1884) from the Hemse Beds of Gotland to be precisely identical to the

South American species but the Gotland specimens are here referred to *P. boucoti* (Pl. I, figs. 17, 18, 20). *P. fraternus* (Reed, 1908) of Boucot & Saul (*in* Saul, Boucot & Finks, 1963) from the Devonian Accraian Series of Ghana has the selenizone bordered by spiral lirae, fewer spiral elements in the shell ornamentation and more pronounced growth lines.

The pustulose nature of the spiral ornamentation is well seen in USNM 169583 (Pl. II, fig. 8) and USNM 169588 (Pl. II, Fig. 11). In the former, the individual pustules are subcircular in plan but in the latter they tend to be elongate with a preferred orientation. On either side of the selenizone on the median dorsal lobe, the long axes of the pustules are oriented approximately perpendicular to the growth lines and trend obliquely forwards from the spiral grooves in towards the selenizone. Within the selenizone the long axes converge upon the median dorsal line to produce a V-shaped pattern closing towards the rear. It is difficult to relate the shape of the individual pustules to the intersection of successive growing edges with the spiral lirae as the long axes do not follow the growth lines, as might be expected if this were so. The preferred orientation might be a reflection of shell structure but general preservation of the recrystallised shell is not conducive to the determination of this.

P. boucoti occurs in the Doctors Brook Formation (Wenlock), where it may be locally abundant, and in the McAdam Brook Formation (Ludlow) at Arisaig, Nova Scotia. In Gotland the species is rare. With the exception of the two examples figured by Lindström (1884) from the Hemse Beds of Ludlow age (Pl. I, figs. 17, 18, 20), only two poor internal moulds from probable Halla Beds (upper Wenlock) at Hörsne have been seen, one of which is figured here (Pl. I, fig. 14). The species is common in several decalcified blocks from the Upper Llandovery of Tonlegee, Cong, Galway, Ireland, which are preserved in the Sedgwick Museum, Cambridge (Pl. II, figs. 12, 13, 16, 17). *P. boucoti* is seemingly present in the Wenlock and Ludlow of the United Kingdom (Reed, 1920–21) but these occurrences have not been closely scrutinised.

Plectonotus cherylae sp. nov.
Pl. I, figs. 1–13, 16.

non 1839. *Bellerophon trilobatus* Sowerby *in* Murchison, p. 604, Pl. 3, fig. 16.
    1924. *Plectonotus trilobatus:* McLearn, (pars), p. 140–141, Pl. XX, figs. 30, 31, non figs. 18, 32.

Holotype. – USNM 169582 from Schuchert Colln. 53, Stonehouse Formation (Pridoli), Arisaig, Nova Scotia.

Other figured material. – Stonehouse Formation, Arisaig, Nova Scotia, USNM 169573 from USNM Colln. 10206; USNM 169468, USNM 169471, USNM 169576–81, USNM 188527 from Schuchert Colln. 53; GSC 3138g from Arisaig; YPM 479 from Spring-ville, Nova Scotia.

Description. – Species of *Plectonotus* Clarke, 1899b with about five whorls. Shell moderately compressed laterally such that length:width is about 4:3. Dorsum trilobed at maturity with median lobe elevated above flanking lateral lobes. Early growth stages showing gradual development of trilobation (figs. 3, 6, 7). At maturity, median lobe with flattened upper surface commonly bearing an angular relationship to the slightly convex sides of the lobe. Dorsal grooves delimiting the lobes of the dorsum commonly indistinct; lateral lobes merely shoulders flanking the median lobe. Lateral areas of whorl convex; rapidly increasing in curvature with passage into the open umbilici. Umbilical walls convex. Whorl embracement at, or just above, periphery of previous whorl; sutural indentation deep. Aperture poorly known; dorsal lip with deep sinus occupying the full width of the median lobe and passing into a short slit. Selenizone extending over the full width of the upper surface of the median lobe; margins obscure or bounded by spiral lirae; ornamentation of fine spiral lirae and concave lunulae. Shell ornamentation of fine lirae and obscure growth lines. Shell thin; structure unknown.

Discussion. – *Plectonotus cherylae* resembles *P. boucoti* in the degree of fineness of the spiral ornamentation but is distinguished from that species by its less severe trilobation and greater lateral compression. The narrow-ness of *P. cherylae* is further illustrated by the way in which the selenizone occupies the entire width of the upper surface of the median lobe whereas the selenizone covers only half the upper surface of the wider median lobe in *P. boucoti*. In this character *P. cherylae* is similar to *Tritonophon* Öpik, 1953 but the latter genus is readily delimited by its more extreme trilobation producing a strongly vaulted median lobe. The species described by Clarke (1899b) as *Bucaniella reissi* from the Devonian of Brazil has a similar profile to *P. cherylae* but details of ornamentation and the emargination are not known in the South American species.

There is quite considerable variation in the degree of tumidity of the whorl profile within the available sample of *P. cherylae*. Rarely, the profile may be so globose as to lack all but a trace of spiral trilobation (USNM 169468, Pl. I, fig. 7). At the other extreme, the degree of lateral compression may be great with accentuated trilobation (USNM 169573, Pl. I, figs. 10–12; YPM 479, Pl. I, figs. 1, 2, the specimen figured by McLearn, 1924, Pl. XX, figs. 30, 31). *Plectonotus cherylae* is currently known only from the Stonehouse Formation (Pridoli) of Nova Scotia.

Genus *Tritonophon* Öpik, 1953

Type species. – *Kokenospira (Tritonophon) trimetra* Öpik, 1953.

> 1953. *Tritonophon* Öpik, p. 20.
> 1967. *Nylanderina* Boucot *in* Boucot, Cumming & Jaeger, p. 8.

Diagnosis. – Dorsum trilobed with the selenizone occupying the full width of the upper surface of the strongly vaulted median lobe.

Discussion. – *Tritonophon* is distinguished from *Plectonotus* Clarke, 1899b by its more pronounced trilobation producing a narrow and strongly vaulted median lobe. In *Plectonotus* the median lobe is usually wide with the selenizone forming only part of the upper surface while in *Tritonophon* the selenizone occupies the entire upper surface of the narrower median lobe. In *Plectonotus cherylae* sp. nov., above, an unusually narrow species of *Plectonotus*, the selenizone also occupies the full width of the upper surface of the median lobe but the degree of trilobation of the dorsum is less extreme than in *Tritonophon*.

Tritonophon trilobata (Sowerby *in* Murchison, 1839)
Pl. II, figs. 15, 18–22, 24, 25; Pl. III, figs. 1–9, 14.

> 1839. *Bellerophon trilobatus* Sowerby *in* Murchison, p. 604, Pl. 3, fig. 16.
> 1909. *Bellerophon trilobatus:* Moberg & Grönwall, p. 43–44, Pl. III, figs. 13, 14.
> non 1924. *Plectonotus trilobatus:* McLearn, p. 140–141, Pl. XX, figs. 18, 30–32.
> 1933. *Plectonotus trilobatus:* Straw, p. 125, Pl. IX, figs. 26, 27.

Figured material. – Upper Ludlow, Felindre, Radnorshire, Wales, GSM Geol. Soc. Coll. 4384; BM PG 5002–4 from a loose, decalcified lense at waterfall 245 m. southwest of Stone House, Felindre (National Grid Reference SO 175802). Borehole at Little Missenden, Buckinghamshire, England, into Pridoli strata, GSM 51860D–E, GSM 51861C, GSM 51879. Green Member of Moydart Formation (Ludlow), Arisaig, Nova Scotia, USNM 169593–4 from Schuchert Colln. 52B; GSC 33276 from Jones Colln. Ar Mo 4800; YPM 28347 in USNM Colln. 10853 from Sutherland River, Pictou County, Nova Scotia.

Description. – Species of *Tritonophon* Öpik, 1953 with about four slowly expanding whorls. Early whorls imperfectly known but with uniformly convex dorsum (fig. 12). Later whorls showing gradual development of dorsal trilobation with strongly vaulted median dorsal lobe. Upper surface of median lobe flattened, passing onto shallowly convex but steeply inclined sides. Upper surface of flanking lobes convex, sloping away from median lobe. Lateral areas of whorl strongly convex with maximum whorl width at or just below midwhorl height. Umbilici widely phaneromphalous with flattened umbilical walls. Whorl embracement at midheight of previous whorl produc-

Fig. 12. *Tritonophon trilobata* (Sowerby *in* Murchison, 1839), USNM 169593, Moydart Formation, Nova Scotia, camera lucida drawing of transverse section, ×6.25.
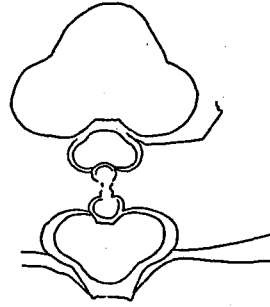
ing deep sutural indentation. Aperture poorly known; growth lines on dorsal surface sweeping obliquely backwards on sides of median lobe before passing into a short slit. Selenizone bordered by fine spiral striae or threads and occupying full width of upper surface of median lobe; ornamentation of numerous concave lunulae and spiral lirae. Shell ornamentation of closely spaced spiral lirae and fine transverse growth lines. Shell of moderate thickness, structure unknown.

Discussion. – Sowerby (*in* Murchison, 1839) described *Bellerophon trilobatus* from the uppermost Ludlow of Felindre, Radnorshire, Wales. The type series has not been recognised in the Geological Society of London Collection of the Institute of Geological Sciences, London, which houses most of Sowerby's types, and is presumed lost. Two isolated internal moulds of *B. trilobatus* from Felindre are present in the collection but are not the specimens figured by Sowerby (*in* Murchison, 1839, Pl. 3, fig. 16), the illustration being of a small block containing several specimens. One of these two internal moulds, GSM Geol. Soc. Coll. 4384, is illustrated here (Pl. III, figs. 6, 7) but the other, GSM Geol. Soc. Coll. 4383, is too badly abraded. Following his studies of the stratigraphy of the area around Felindre (Earp, 1938; 1940) Dr. J. R. Earp (written communication, 1972) kindly pointed out the original locality of Murchison at Felindre. Several visits to this exposure produced one fallen block containing many decalcified specimens of *B. trilobatus*, associated with the other gastropods noted by Sowerby from Felindre, which form the basis for the redescription of *B. trilobatus*, although characters of ornamentation are partly described from better preserved specimens from the borehole at Little Missenden, Buckinghamshire, England (Straw, 1933).

Pitcher (1939) stated that Sowerby's description of *B. trilobatus* was published in Murchison's '*Silurian System*' in January 1839 and this date is also given by Sherborn (1922). Pitcher further commented that in February of the same year Conrad (1839) described *Planorbis trilobatus* from the Llandovery Medina Group of New York State although this date has not

been confirmed. Conrad's species is poorly known and the existence of
type materials has not been established. Similarly, specimens figured by Hall
(1843; 1852) from the Medina Group and respectively assigned to *Bellero-
phon trilobatus* (Conrad) and *Bucania trilobatus* (Conrad) have not been
traced. The precise nature of *Planorbis trilobatus* is consequently unknown
although the illustrations of Hall (1843; 1852) show a strongly trilobed belle-
rophontacean readily assignable to *Tritonophon*.

Specimens referred to Conrad's species have been described from the Rose
Hill and Rochester Formations (Llandovery-Wenlock) of Maryland, U.S.A.
by Swartz & Prouty (1923). The Maryland species seems to have a greater
rate of whorl expansion than is here associated with *Tritonophon trilobata*
(Sowerby *in* Murchison, 1839) but most specimens are crushed in shale mak-
ing comparison difficult. Specimens from the Upper Ross Brook and French
River Formations of Arisaig, Nova Scotia also show this increased rate of
expansion and it is possible that this character might be a criterion for the
delimitation of a Llandovery-Wenlock species from the Upper Ludlow and
Pridoli species of Sowerby. Should this prove to be so, it will be necessary to
formulate a new specific name for *T. trilobata* (Conrad, February (?) 1839)
due to pre-occupation of the name by *T. trilobata* (Sowerby *in* Murchison,
January 1839).

T. trimetra Öpik, 1953, from the Lower Silurian of Australia, is poorly
known but seemingly has a wider median lobe. *T. rotalinea* (Hall, 1879)
of Rollins (*in* Rollins, Eldredge & Spiller, 1971), from the Devonian of New
York State, has less well defined flanking lobes and fewer, more prominent
spiral lirae, as does *T. goldringae* (Boucot *in* Boucot, Cumming & Jaeger,
1967). *Tritonophon* (?) *bohemica* (Perner, 1903) of Horný (1963), from the
Upper Ordovician of Bohemia, has much finer spiral ornamentation and
the sides of the U-shaped emargination in the only specimen showing details
of the shell exterior are not quite parallel, thereby failing to generate a true
selenizone (fig. 10).

T. trilobata is common in the Green Member of the Moydart Formation
(Ludlow) at Arisaig, Nova Scotia, at an equivalent horizon to the Felindre
occurrence. In the borehole at Little Missenden, Buckinghamshire, England
the species is present in Pridoli strata. *T. trilobata* is also known from the
Öved-Ramsåsa Series of Skåne, Sweden although Moberg & Grönwall (1909)
did not consider the specimens described by themselves to be completely
identical with Sowerby's original specimens. A few specimens are present
in the Naturhistoriska Riksmuseet, Stockholm, from the higher Ludlow beds
at Burgsvik in southern Gotland (Mo 26564–5).
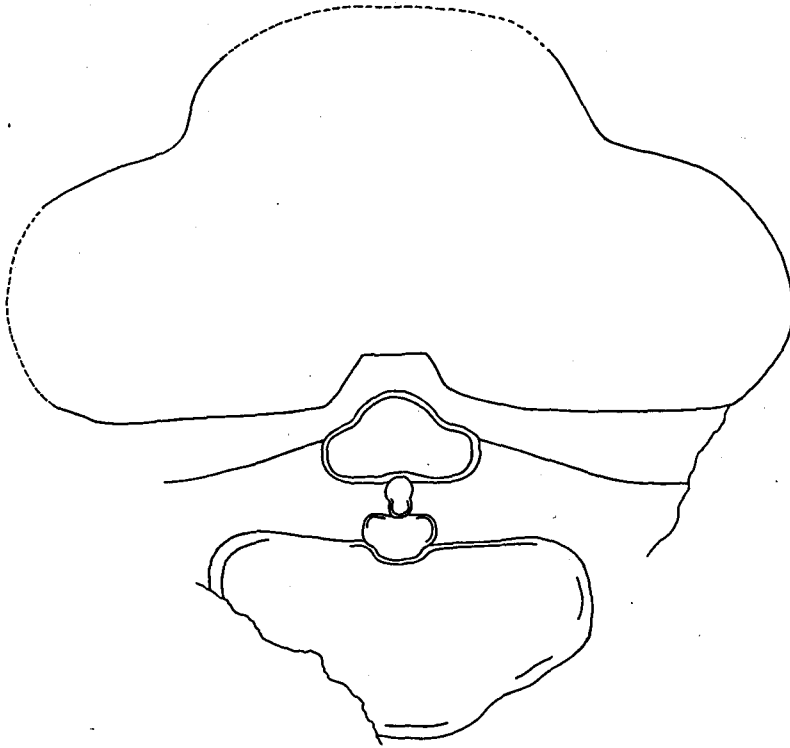
Tritonophon kivitalonae sp. nov.
Pl. III, figs. 10–13, 15–22.

Fig. 13. *Tritonophon kivitalonae* sp. nov., GSC 3138a, Stonehouse Formation, Nova Scotia, camera lucida drawing of transverse section, ×6.25.

non 1839. *Bellerophon trilobatus* Sowerby *in* Murchison, p. 604, Pl. 3, fig. 16.
   1924. *Plectonotus trilobatus:* McLearn, (pars), p. 140–141, Pl. XX, fig. 32, *non*
   figs. 18, 30, 31.

Holotype. – GSC 33275 from Jones Colln. Ar S 7820, Stonehouse Formation (Pridoli), Arisaig, Nova Scotia.

Other figured material. – Stonehouse Formation, Arisaig, Nova Scotia, GSC 3138a, GSC 3138m, GSC 5649, GSC 32782; GSC 33279 from Jones Colln. Ar S 7820.

Description. – Species of *Tritonopho*n Öpik, 1953 with about four rapidly expanding whorls. Early whorls poorly known but with uniformly convex dorsum. Later whorls showing gradual development of dorsal trilobation with median lobe raised above wide lateral lobes (fig. 13). Upper surface of median lobe commonly flattened. Upper surface of flanking lobes initially convex, sloping away from median lobe, but becoming flattened in later growth stages with slight channeling of the angulation between the median

and lateral lobes. Lateral areas of whorl strongly convex with maximum whorl width at just below midwhorl height. Umbilical walls flat. Umbilici open, of moderate width, becoming narrower in final whorl due to thickening of umbilical walls. Whorl embracement at above midheight of previous whorl producing deep sutural indentation. Aperture poorly known; transverse growth lines on upper surface of lateral lobes curving strongly backwards across the sides of the median lobe and culminating in a slit of unknown depth. Selenizone bordered by fine spiral lirae and occupying the full width of the upper surface of the median lobe; selenizonal ornamentation of shallowly concave lunulae and closely spaced spiral lirae, the latter being equally developed all over the dorsal surface. Shell thin but with thickened umbilicolateral walls in final whorl; structure unknown.

Discussion. – *Tritonophon kivitalonae* is distinguished from *T. trilobata* (Sowerby *in* Murchison, 1839) by its greater rate of whorl expansion. In the latter, the shell is laterally compressed with length greater than width while in *T. kivitalonae* width exceeds length after a length of about 5 mm. has been attained. *T. kivitalonae* resembles *Plectonotus boucoti* sp. nov., above, in terms of its increased width and tendency in some specimens to develop channels between the dorsal lobes. However, it is readily distinguished from *P. boucoti* by its narrower median lobe with the selenizone occupying the full width of the upper surface, the selenizone covering only half of the width of the upper surface of the median lobe in *P. boucoti.*

   T. kivitalonae occurs in the higher beds of the Stonehouse Formation exposed along the coast at Arisaig, Nova Scotia but a single specimen has been kindly supplied by Mr. Andrew Porter from the equivalent Jones Creek Formation of New Brunswick (University of New Brunswick, Saint John, Department of Geology No. S1–97).

Tritonophon sp.
Pl. II, figs. 23, 26–28.

Figured material. – Beechhill Cove Formation (Lower Llandovery), GSC 33277 from Jones Colln. Ar B. Cove loc. 4, Arisaig, Nova Scotia. Upper Ross Brook Formation (late Llandovery), YPM 75 from YPM Colln. A3592; YPM 28350 from YPM Colln. A3760, Arisaig, Nova Scotia. French River Formation (Wenlock), YPM 28343 from YPM Colln. A3775, French River, Pictou County, Nova Scotia.

Discussion. – Several crushed and poorly preserved specimens of *Tritonophon* from the lower part of the Arisaig Group cannot be referred to *T. trilobata* or *T. kivitalonae,* both of which occur in the upper beds of the Arisaig Group. The short slit, selenizone and widely spaced spiral lirae of the dorsum are

well seen in specimens from the Upper Ross Brook Formation (Pl. II, figs. 27, 28). *T. trilobata* has a lower rate of whorl expansion producing narrower whorls whereas *T. kivitalonae* has a similar rate of whorl expansion but more closely spaced spiral lirae. The Arisaig specimens are close to specimens of equivalent age from Maryland, U.S.A. described by Swartz & Prouty (1923) as *Bucanella trilobata* (Conrad, 1839). However, as noted above, Conrad's species is imperfectly known and cannot be identified with confidence from the descriptions of later authors. It is probably a species of *Tritonophon,* and a junior homonym of *T. trilobata* (Sowerby *in* Murchison, 1839).

Dansk sammendrag

Den systematiske stilling af de fire trilobate bellerophontide snegleslægter *Bucanella, Plectonotus, Tritonophon* og *Nylanderina* diskuteres, og det konkluderes at *Nylanderina* er junior synonym for *Tritonophon.* Den ontogenetiske udvikling af de to arter af *Plectonotus* gennemgås, og på basis heraf præsenteres en generel tolkning af den trilobate tilstands funktion og betydning i bellerophontide snegle. *Tritonophon trilobata* (Sowerby *in* Murchison, 1839) redefineres, og følgende nye arter opstilles: *Plectonotus boucoti, P. cherylae* samt *Tritonophon kivitalonae.*

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Plate 1

Plectonotus cherylae sp. nov., figs. 1–13, 16, Stonehouse Formation, Nova Scotia. Figs. 1,2: YPM 479, ×2.25; 2, oblique dorsal view showing selenizone. Figs. 3,4: USNM 169582, holotype; 4, posterior view showing fragment of selenizone margin. Fig. 5: USNM 169578. Fig. 6: USNM 169580. Fig. 7: USNM 169468, unusually globose individual. Fig. 8: GSC 3138g. Fig. 9: USNM 169471, juvenile, ×3.5. Figs. 10–12: USNM 169573, unusually narrow specimen; 10, posterior view showing selenizone, ×3. Figs. 13, 16: USNM 169579; 16, oblique lateral view showing growth lines. All magnifications ×1.5 unless otherwise stated.

Plectonotus boucoti sp. nov., figs. 14, 15, 17–22. Fig. 14: Mo 26567, Halla Beds? Gotland, Sweden, ×0.75. Fig. 15: USNM 169589. Figs. 17, 18: Mo 26562, Hemse Beds, Gotland, Sweden. Figs. 19, 22: USNM 169590. Fig. 20: Mo 26563, Hemse Beds, Gotland, Sweden. Fig. 21: GSC 3138, dorsal view showing slit. Figs. 15, 19, 21, 22 from Doctors Brook Formation, Nova Scotia. All magnifications ×1.5 unless otherwise stated.
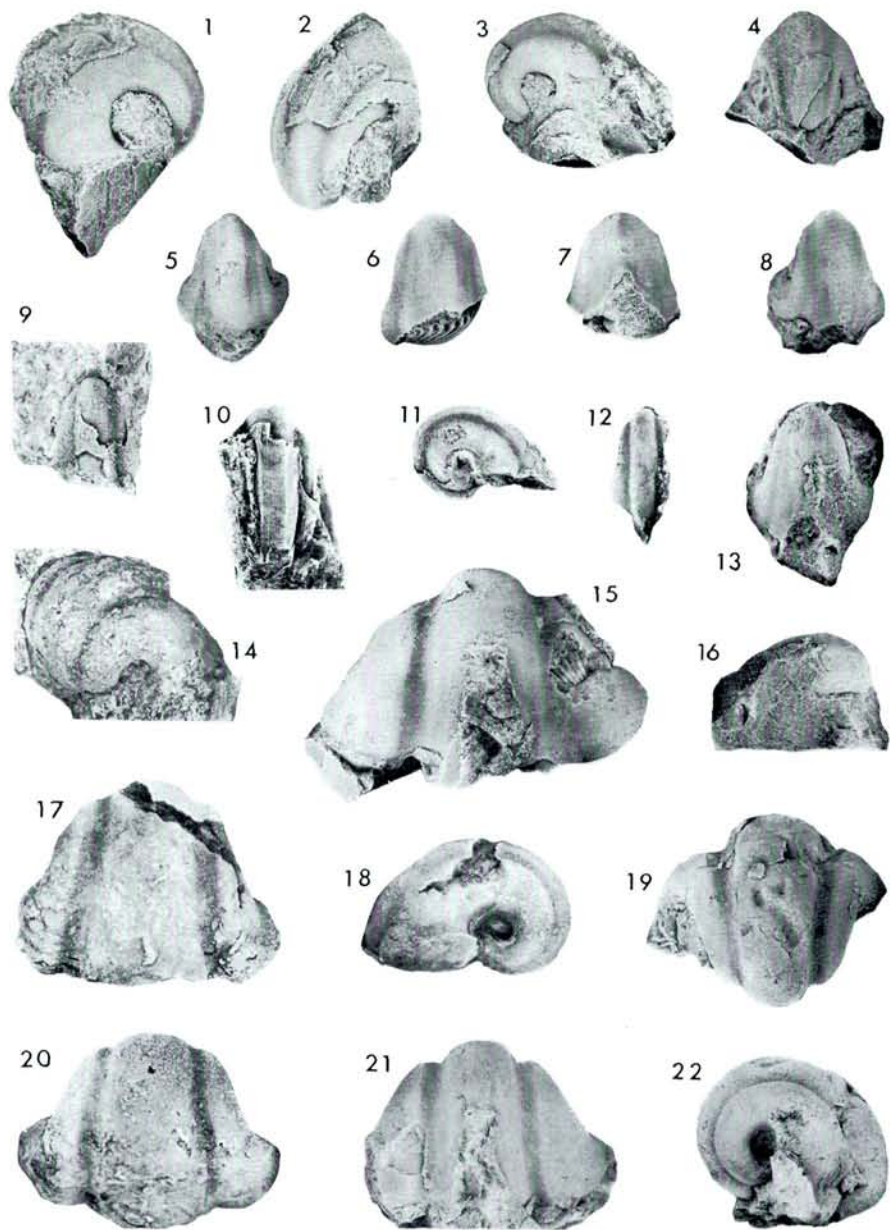
Plate 2

Plectonotus boucoti sp. nov., figs. 1–9, 11–13, 16,17. Figs. 1–4: USNM 169584, holo-
type; 1, dorsal view; 2, oblique dorsal view; 3, lateral view; 4, selenizone ×3. Figs.
5,6: USNM 169592, juvenile. Figs. 7,9: USNM 169591. Fig. 8: USNM 169583, dorsal
view showing selenizone and pustulose ornamentation, ×3.5. Fig. 11: USNM 169588,
dorsal view showing V-shaped trend of pustules within selenizone, ×4.5. Figs. 12, 13:
SM A39164. Figs. 16,17: SM A39165. Figs. 1–9, 11 from Doctors Brook Formation,
Nova Scotia; figs. 12, 13, 16, 17 from Upper Llandovery of Tonlegee, Cong, Ireland.
Magnifications ×1.5 unless otherwise stated.

Plectonotus derbyi Clarke, 1899b, figs. 10,14. Lectotype, Devonian, Rio Maecurú,
Pará, Brazil, dorsal views showing median band with obscure lunulae, ×0.75.

Tritonophon trilobata (Sowerby *in* Murchison, 1839), figs. 15, 18–22, 24, 25. Figs.
15, 18: GSM 51879. Fig. 19: GSC 33276. Fig. 20: YPM 28347, ×3. Figs. 21, 22:
USNM 169594. Fig. 24: GSM 51860E, ×1.5. Fig. 25: USNM 169593. Figs. 15, 18,
24 from Little Missenden borehole, Bucks., England; figs. 19–22, 25 from Moydart
Formation, Nova Scotia. All magnifications ×2.25 unless otherwise stated.

Tritonophon sp., figs. 23, 26–28. Fig. 23: YPM 28343, French River Formation, Nova
Scotia, ×0.75. Fig. 26: GSC 33277, Beechhill Cove Formation, Nova Scotia. Fig. 27:
YPM 28350, Upper Ross Brook Formation, Nova Scotia, showing selenizone. Fig.
28: YPM 75, Upper Ross Brook Formation, Nova Scotia, showing selenizone and
slit. All magnifications ×2.25 unless otherwise stated.
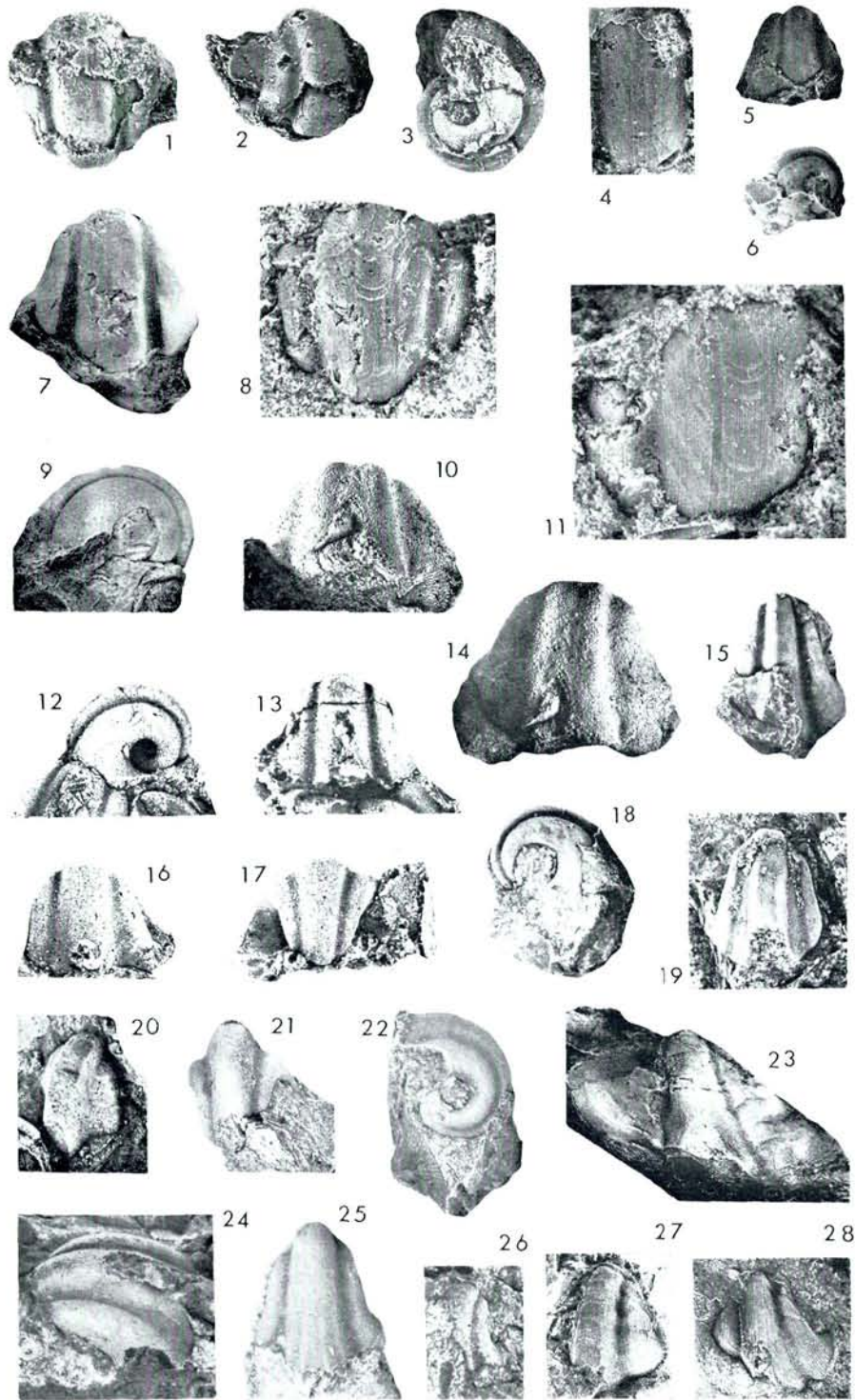
Plate 2

Plate 3

Tritonophon trilobata (Sowerby *in* Murchison, 1839), figs. 1–9, 14. Figs. 1, 2: BM PG5002. Figs. 3, 4: BM PG5004. Fig. 5: GSM 51860D, showing selenizone, ×3. Figs. 6, 7: GSM Geol. Soc. Coll. 4384, slightly crushed individual. Figs. 8, 14: BM PG5003, silicon rubber impression showing selenizone, ×3. Fig. 9: GSM 51861C, ×3. Figs. 1–4, 6–8, 14 from Upper Ludlow at Felindre, Radnorshire, Wales; figs. 5, 9 from Little Missenden borehole, Bucks., England. All magnifications ×2.25 unless otherwise stated.

Tritonophon kivitalonae sp. nov., figs. 10–13, 15–22, Stonehouse Formation, Nova Scotia. Figs. 10–13: GSC 3138m; 10, 11, apertural views of juvenile showing selenizone, ×3.5; 12, 13, ×2.25. Figs. 15, 16, 19: GSC 32782, ×2.25. Figs. 17, 18, 21: GSC 33275, holotype, ×2.25. Fig. 20: GSC 3138a, ×1.5. Fig. 22: GSC 5649, crushed in shale, showing selenizone, ×1.5.