

Arjalle



Evolutionary and Ecologic Studies of Palaeozoic Gastropods

*A*

*SILURIAN*

*GASTROPOD FAUNA*

*FROM THE*

*ARISAIG GROUP*

*OF NOVA SCOTIA*

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Thesis submitted for the degree of Doctor of Philosophy

University of Leicester

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TO  
THOSE OF MY FELLOW COUNTRYMEN  
AMONG THE WORKING CLASSES  
WHO WISELY EMPLOY THEIR LEISURE HOURS  
IN THE  
PURSUIT OF USEFUL AND ELEVATING KNOWLEDGE  
WITH THE HOPE THAT OTHERS AMONG THEIR RANKS  
MAY BE INDUCED TO  
FORSAKE THE PATHS OF PROFITLESS AND DEGRADING  
DISSIPATION,  
THIS VOLUME  
IS  
WITH EVERY GOOD WISH  
DEDICATED...

(from Rimmer, R. 1880. Land and Freshwater Shells of the  
British Isles. Allen & Co., London)

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## Introduction

Arisaig is a small village on the Northeastern shore of Nova Scotia (text-fig. 1) adjacent to one of the best exposed and most complete Silurian sections in the Appalachian Mountain System. Some four thousand feet of sediments form a continuous record from the lower Llandovery through Wenlock, Ludlow and Pridoli into the lower Gedinnian (Devonian) (text-fig. 2). Overlying red beds contain lower Devonian fish remains (Dineley, 1967).

The Arisaig Group has attracted the attention of geologists for over a hundred years and a full account of the history of exploration is given by McLearn (1924) and Boucot et al (in press). McLearn (1924) provided full descriptions of more than two hundred species from the Arisaig Group and his study remains the most comprehensive survey of the general fauna to date.

A.J. Boucot, with several associates and students, commenced a mapping programme of the Arisaig region in 1958. Unlike most previous workers, Boucot and his coworkers gave particular attention to inland exposures in the deeply incised valleys of the streams flowing North into Northumberland Strait. A series of large scale maps were prepared as part of a memoir upon the area (Boucot et al, in press) and these maps form the basis of text-fig. 3. Boucot et al (in press) recognised seven formations within the Arisaig Group with the McAdam Formation of McLearn (1924) and earlier workers divided into three (text-fig. 2). Strata described by Maehl (1960s; 1961) in Pictou County, to the West of Arisaig, were also integrated into this sequence (text-figs. 1, 2).

Comparison with faunas from European type sections established that the Arisaig Group extended beyond the Ludlow into the Pridoli (Berry and Boucot, 1970) while brachiopods from inland exposures of the highest beds were considered to be of lower Gedinnian age by Boucot et al (in press).

R.K. Bambach (1969ms) continued the association of Yale Peabody Museum with Arisaig, previously expressed by Schuchert, Twenhofel (1909) and McLearn (1924), with a study of the palaeoecology of the bivalve fauna of the Arisaig Group. He followed Boucot et al (in press) in recognising seven formations but divided the Stonehouse Formation into an Upper, and a Lower, Member. This division is accepted here (text-fig. 2). The sequence of stratum numbers used by Bambach (1969ms; text-fig. 2) is discussed in the Appendix.

The gastropod fauna of the Arisaig Group has not previously received individual attention. Hall (1860) included three new species in his description of the fauna. McLearn (1924) described six new species and one new variety in a total of eighteen recorded species of gastropods, about a third of the present total (Table 1) which includes thirteen new species and two new genera.

No specimens have been seen from the inland exposures which Berry and Boucot (1970) and Boucot et al (in press) referred to the lower Gedinian (Devonian). Consequently, the described gastropod fauna is entirely of Silurian (Llandovery - Pridoli) age.

Unfortunately, it was not possible to collect personally from the Arisaig Group, all specimens for the present study being obtained from the collections of previous workers (see Appendix). Details of the geology of the area are taken almost exclusively from the, as yet, unpublished studies of Bambach (1969ms) and Boucot et al (in press). These authors generously supplied copies of their papers for study.

A systematic description of the gastropod fauna is followed, in the present paper, by a discussion of the palaeoecology of the Class in the Arisaig Group. The latter section is intended to partially compliment the analysis of trophic group associations carried out by

TEXT-FIG. 1

Silurian localities in Nova Scotia.

(adapted from Boucot et al, in press)

TEXT-FIG. 2

Stratigraphic divisions and correlation of the Arisaig Group.

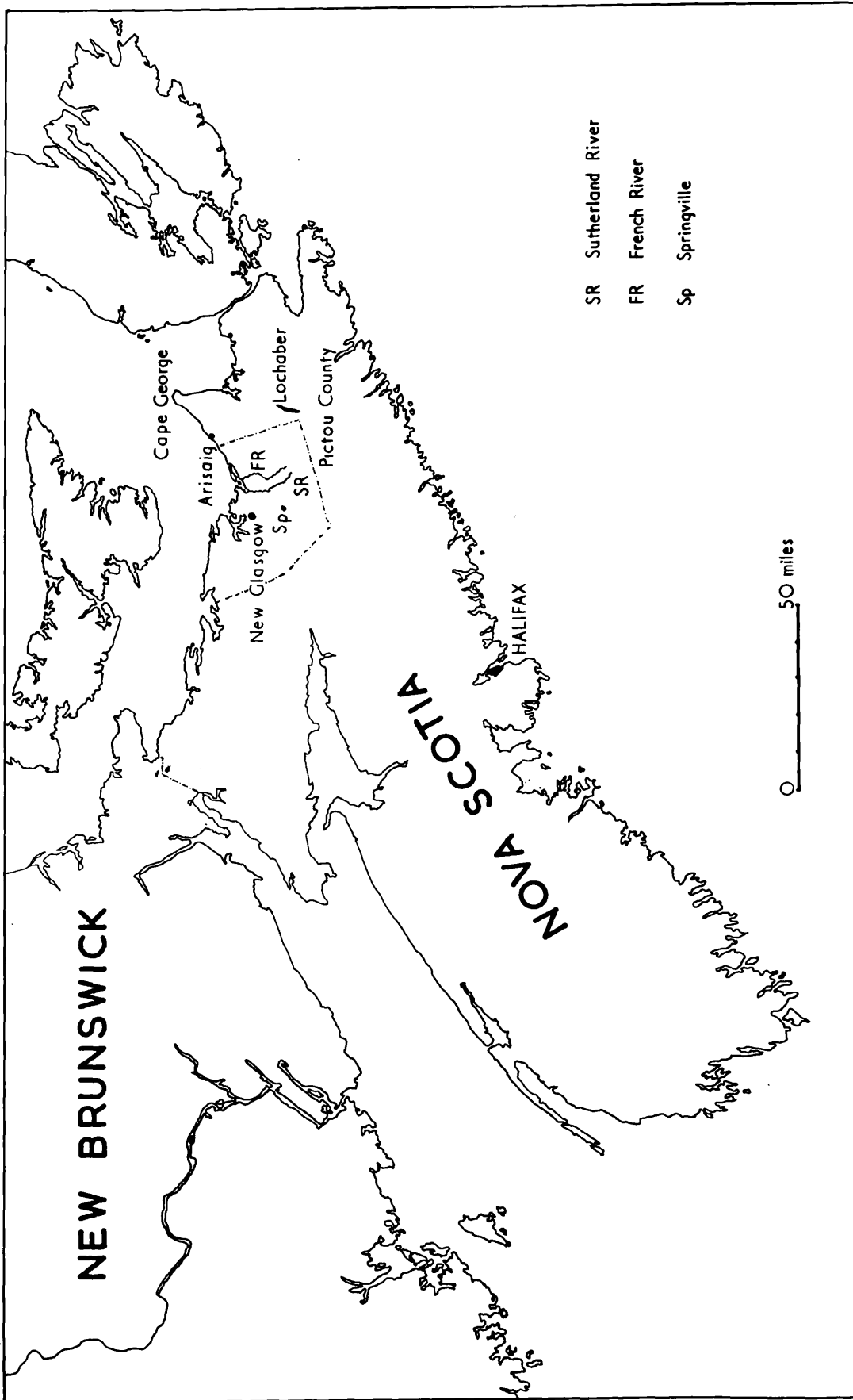
(adapted from Boucot et al, in press)

TEXT-FIG. 3

Geography and Geology of the Arisaig area.

(adapted from Boucot et al, in press)

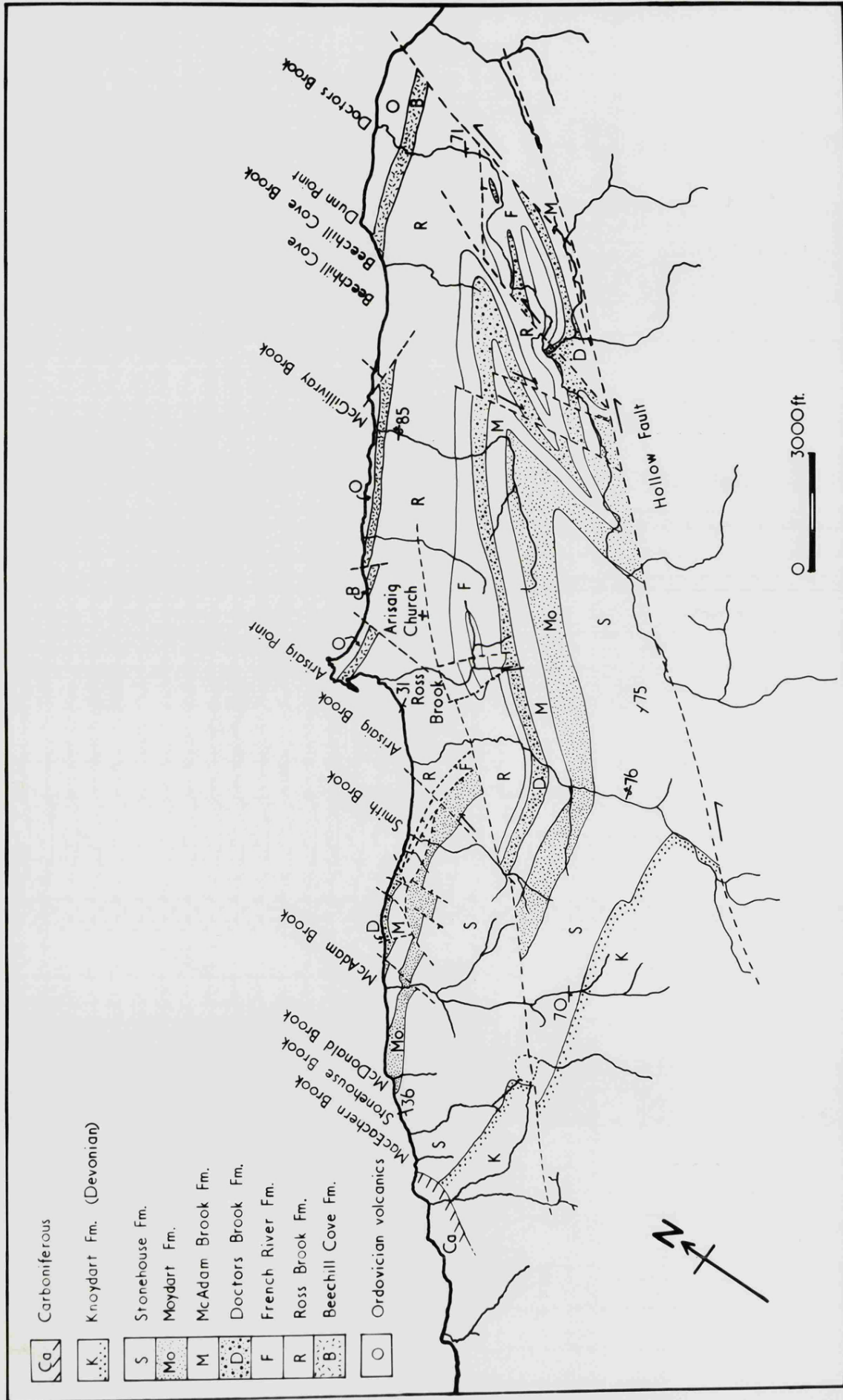
Text-fig. 1



Text-fig. 2

STANDARD SERIES	ARISAIG REGION, NOVA SCOTIA									
	SOUTH PICTOU Co.	NORTH PICTOU Co. + ARISAIG	McLEARN (1924)	STRATUM No. of BAMBACH						
L. GEDINNIAN  PRIDOLI	STONEHOUSE FORMATION			d	342-509					
				c						
				b						
				a		316 - 341				
LUDLOW	K E R R O W G A R E  F M.	RED MEMBER ----- MOYDART FM.		b	-					
		GREEN MEMBER		a	291-315					
McADAM		UPPER	McADAM	c	273-290					
----- BROOK		FM.		c	179-272					
----- DOCTORS		BROOK	FM.	b	122-178					
----- BROOK						FM.				
WENLOCK		FRENCH	RIVER	FM.	a	108-121				
							----- FRENCH	RIVER	FM.	
LLANDOVERY		ROSS	BROOK	FM.	e	32-107				
							UPPER	ROSS	d	
	MIDDLE						BROOK	FM.	c	11-31
	LOWER						----- BROOK	FM.	a	-
GLENCOE	BEECHHILL	BEECHHILL	1-10							
BROOK	COVE	FM.								
FM.	FM.	FM.								

Text-fig. 3



Bambach (1969ms) on the bivalve fauna -- the most abundant element of the Arisaig fauna.

In both the systematic and palaeoecological sections particular attention is given to the structure and faunal position of trilobed bellerophontaceans of the subfamily Plectonotinae. Members of this distinctive group are frequently conspicuous in collections from Arisaig and form part of an association typical of shallow water deposits. The stratigraphic distribution of this, and other gastropod associations is discussed in relation to the sedimentary history of the Arisaig Group and reflects the repeated advance of barrier and back-barrier conditions into the shallow marine environment of the Arisaig area during the Silurian.

#### Specimens and Collections

More than a thousand specimens in the collections of a number of institutions have been examined during the present study and their respective styles of delimiting specimens, collections, localities and stratigraphic horizons are varied and sometimes complicated. Individual collections, and their associated problems, are discussed in the Appendix.

Preservation of specimens is poor to mediocre. As a result, measurements of specimens are not usually given, sufficient information regarding size being obtainable from the illustrations.

#### Specimen numbers:

The following abbreviations are employed in the text:

AMNH: American Museum of Natural History, New York; BM: British Museum (Nat. Hist), London; GSC: Geological Survey of Canada, Ottawa; GSM: Institute of Geological Sciences, London; GSM Geol. Soc. Coll.:

Geological Society of London Collection of the Institute of Geological Science, London; Mo: Paleozoologiska sektionen, Naturhistoriska Riksmuseet, Stockholm; SM: Sedgwick Museum, Cambridge; USNM: U.S. National Museum of Natural History, Washington, D.C.; YPM: Yale Peabody Museum, New Haven, Connecticut.

Photography.

The majority of specimens were painted with a thin coat of water soluble, black photographic opaque and covered with Ammonium Chloride sublimate from a hot tube prior to photographing.

TABLE 1. Stratigraphic distribution of gastropod species.

	Beechhill Cove Fm. Ross Brook Fm., Lwr. Mid. Upp.	French River Fm. Doctors Brook Fm.	McAdam Brook Fm., Lwr. Upp.	Moydart Fm., (Green). (Red).	Stonehouse Fm., Lwr. Upp.
<i>Pharetrolites bambachi</i>			○		
<i>Ph. purchisoni</i>				○	○
<i>Plectonotus boucoti</i>		○	○	○	
<i>P. cherylae</i>					○
<i>Tritonophon trilobata</i>				○	
<i>T. kivitalonae</i>					○
<i>T. sp.</i>	○	○	○		
<i>Anapetopsis raclearni</i>					○
<i>A. lalajae</i>					○
<i>Eucanopsis sp.</i>	○	○	○		
<i>Phragmosphaera sp.</i>				○	
<i>Cymbularia carinata</i>				○	
<i>C. sp.</i>			○		
<i>Tropidodiscus (?) sp.</i>			○		
Undet. bellerophontacean sp. A	○				
Undet. bellerophontacean sp. B	○				
Undet. bellerophontacean sp. C		○			
Undet. bellerophontacean sp. D					○
' <i>Holopea</i> ' <i>reversa</i>					○
<i>Mimospira abbae</i>			○	○	

TABLE 1 (cont.).

	Beechhill Cove Fm. Ross Brook Fm., Lwr. Mid. Upp.	French River Fm. Doctors Brook Fm.	McAdam Brook Fm., Lwr. Upp.	Moydart Fm., (Green). (Red).	Stonehouse Fm., Lwr. Upp.
<i>Umbospira</i> sp.					○
<i>Liospira marklandensis</i>					○
<i>L.</i> cf. <i>L. affinis</i>	○				
<i>Eotomaria</i> sp.	○		○		
<i>Loxoplocus</i> ( <i>Lophospira</i> ) <i>sedgwickii</i>	○				
<i>L.</i> ( <i>Lo.</i> ) sp. A	○				
<i>L.</i> ( <i>Lo.</i> ) sp. B	○				
<i>Longstaffia centervillensis</i>	○		○		
<i>Lon.</i> sp.	○				
<i>Arjamannia cancellatula</i>	○				
<i>A. woodlandi</i>	○				
<i>A. aulangonensis</i>			○		
<i>Phanerotrema</i> affin. <i>Ph. jugosum</i>	○				
<i>Brachytomaria</i> sp.					○
<i>Platyconus</i> (?) sp.					○
Undet. trochonematid gen. and sp.					○
<i>Holopea</i> sp.			○		
Undet. holopeid gen. and sp.			○		
<i>Haplospira sibelieuxeni</i>					○
<i>Gyronema haliburtoni</i>			○		
Undet. gyronematinid gen. and sp.				○	

TABLE 1 (cont.).

	Beechhill Cove Fm. Ross Brook Fm., Lwr. Mid. Upp.	French River Fm. Doctors Brook Fm.	McAdam Brook Fm., Lwr. Upp.	Moydart Fm., (Green). (Red).	Stonehouse Fm., Lwr. Upp.
<i>Naticonema kauffmani</i>	○				
<i>Cyclonema</i> (Cy.) <i>parvimedium</i>	○				
Cy. (Cy.) <i>lydiamariarum</i>					○
<i>Platyceras</i> ( <i>Platyostoma</i> ) cf. <i>P.(P.) humilis</i>		○			○
<i>P.</i> ( <i>Platyostoma</i> ) <i>cornutum</i>	○	○	○	○	○
Undet. trochinid gen. and sp.	○				
<i>Naticopsis trevorpatriciorum</i>				○	
<i>Murchisonia</i> (M.) <i>aciculata</i>					○
M. (M.) <i>amii</i>					○
M. (? <i>Hormotoma</i> ) <i>arisaigensis</i>					○
M. (H.) sp. A		○			
M. (H.) sp. B				○	
Undet. <i>murchisoni</i> id gen. and sp.				○	
<i>Seelya moydartensis</i>				○	
<i>Loxonema sinuosum</i>					○
Lox. sp. A				○	
Lox. sp. B		○			
<i>Morania</i> (?) <i>boltoni</i>					○
<i>Morania</i> (?) sp.			○		
<i>Auriptygma</i> sp.					○
Undet. high spired gastropod species	○	○	○	○	○
Undet. gastropod species	○	?	○	○	○

## SYSTEMATICS

But as for stones found like Sea-fish, though in this Mediterranean County, I have met with many, and of many sorts; but chiefly resembling Shell-fish of the testaceous kinds, both univalves and bivalves; and of the former of these, some not turbinated, and others again of the turbinated kind. Of the first sort whereof, viz. Stones representing univalves not turbinated, I had two bestowed on me by the curious Observer the Worshipfull Walter Chetwynd of Ingestre Esq; so altogether unlike any of the living Shell-fish, that alone they are sufficient to convince any unprejudiced person, that all these formed stones cannot be shaped in Animal molds.

(Robert Plot. 1686. The Natural History of Staffordshire)

Class GASTROPODA Cuvier, 1797

Subclass PROSOBRANCHIATA 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 TEMNODISCINAE Horny, 1962

Genus PHARETROLITES Wenz, 1943

Type species. Cyrtolites pharetra Lindström, 1884 (= Temnodiscus pharetra; Wenz, 1938; Pharetrolites pharetra; Wenz, 1943).

Diagnosis. Loosely, or open coiled with the dorso-lateral lip initially curving forwards (adaperturally) from the floor of the whorl prior to curving backwards into the median dorsal sinus.

Discussion. Wenz (1938, p. 97) considered Temnodiscus Koken, 1896 to have a more or less distinct selenizone, as noted by Ulrich and Scofield (1897) in their earlier description of Cyrtolitina Ulrich and Scofield, 1897, a junior objective synonym of Temnodiscus. Pharetrolites Wenz, 1943 was subsequently proposed for forms of similar shape to Temnodiscus but without a true slit (Wenz, 1943, p. 1491). Horny (1963) reiterated Koken (1897) in his belief that a selenizone was not present in Temnodiscus but that the sides of the emargination merely approached parallelism. As a consequence, the criterion employed by Wenz (1938; 1943) for the delimitation of the two genera, namely the presence or absence of a true slit, was removed and the status of Pharetrolites cast in doubt.

Both genera are recognised during the present study but the

criterion used to distinguish between them is the shape of the dorso-lateral lip and consequent growth ornamentation in lateral view. In Pharetrolites the lip curves forwards after leaving the floor of the whorl and gradually curves backwards into the median dorsal sinus (text-fig. 4A). In Temnodiscus the shallowly convex lip is directed obliquely backwards from the floor of the whorl towards the dorsum and has no forwards curvature (text-fig. 4B). In both genera the shell may be loosely, or open coiled.

The shape of the inner, median portion of the sinus in some species of Temnodiscus and Pharetrolites is partly dependent on the degree of development of a strong dorsal keel. A keel with vertical sides and flat upper surface tends to produce an inner sinus with subparallel sides and a concave termination. When the keel is subdued or lacking, the subparallelism is reduced and the termination of the sinus may be more acute. Since there is considerable ontogenetic and individual variation in the degree of development of a dorsal keel, the inner portion of the emargination will likewise vary greatly within the population.

In the holotype of Pharetrolites bambachi sp. nov., below, there is no keel and the deepening of the inner portion of the dorsal sinus is greater than would normally be expected in deepening related only to the presence of such a keel.

Pharetrolites bambachi sp. nov.

(Pl. I, figs. 21, 24)

Holotype. Lower McAdam Brook Fm., YPM 28328 from Bambach Colln. A3822(199).

TEXT-FIG. 4

A. Pharetrolites pharetra (Lindström, 1884).

Lateral view showing growth ornamentation curving slightly forwards from the floor of the whorl prior to curving backwards into the median dorsal sinus (after Lindström, 1884, Pl. VI, fig. 39), x6.

B. Temnodiscus lamellifer (Lindström, 1884).

View of right side showing growth ornamentation curving obliquely backwards from floor of whorl across lateral surface and into median dorsal sinus (after Knight, 1941, Pl. 10, fig. 3a), x2.

C. Pharetrolites murchisoni (d'Orbigny in Ferussac and d'Orbigny, 1840).

Lateral view of internal mould showing diagnostic forward curvature of growth ornamentation (drawn from photograph of USNM 169461), x2.5.

D. Cymbularia carinata (Sowerby in Murchison, 1839), USNM 169575.

Camera lucida drawing of transverse polished section showing median dorsal keel on inner whorl and closed umbilici, x6.25.

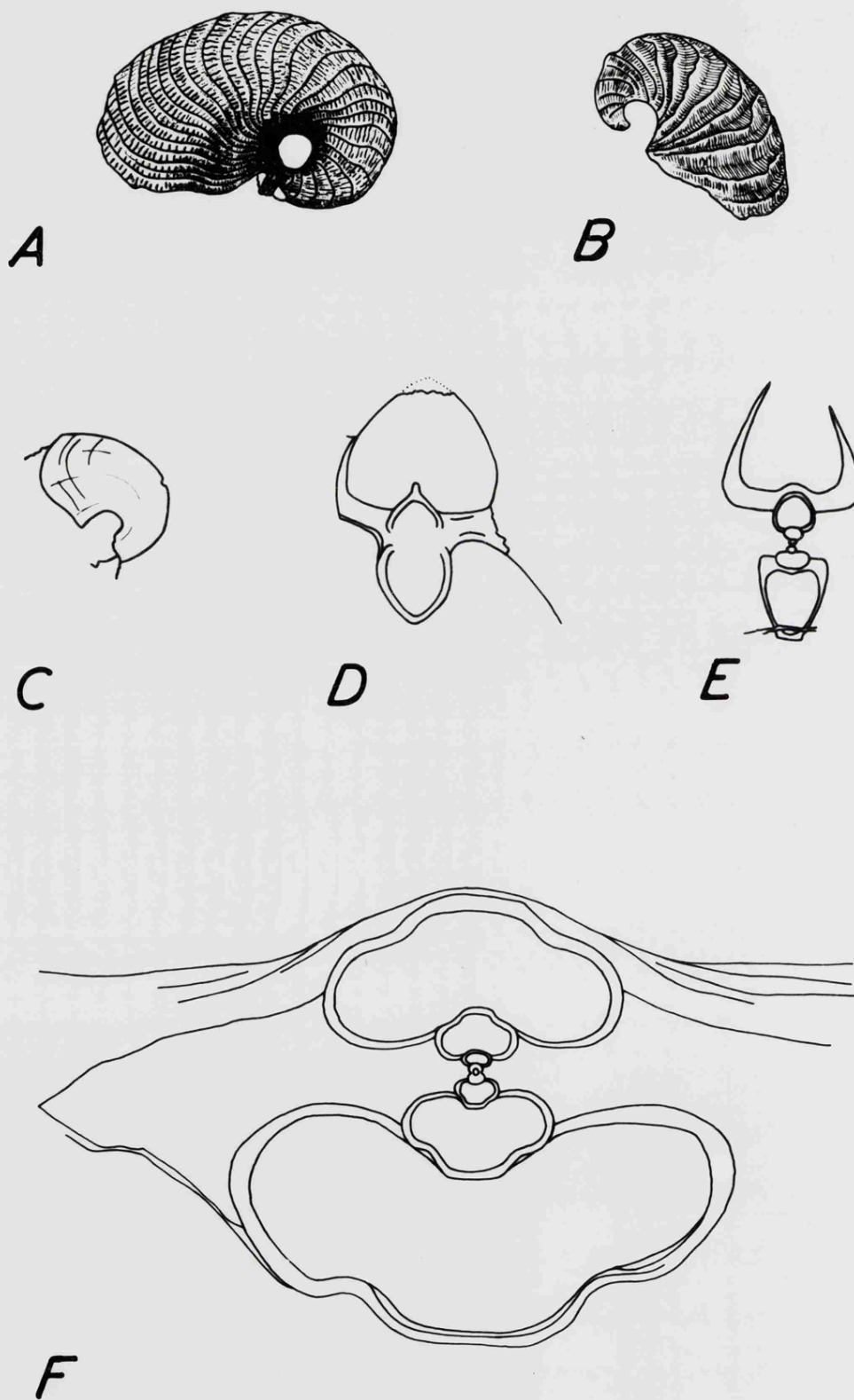
E. Tropidodiscus (?) sp., USNM 169586.

Camera lucida drawing of transverse thin section showing ontogenetic variation in whorl profile, x25.

F. Plectonotus boucoti sp. nov., USNM 169585.

Camera lucida drawing of transverse thin section showing thickening of umbilical walls a half whorl back from aperture and closure of the umbilicus (left side of illustration), x6.25.

*Text-fig. 4*



Additional material. Lower McAdam Brook Fm., Bambach collections  
A3620(209), A3637(232), A3822(199), A3836(240), A3844(251).

Description. Species of Pharetrolites Wenz, 1943 with one or more whorls. Earliest growth stages and umbilici unknown. Dorsum of final whorl seemingly uniformly convex, increasing in curvature with lateral passage into the umbilici; umbilical walls with spiral folds. Aperture poorly known; growth lines indicating a wide median sinus deepening angularly into a narrow V-shaped inner notch. Margins of dorsal apertural lips crenulate producing apparent polygonal ornamentation. Umbilical folds with narrow emarginations, the umbilical areas lacking the crenulations of the dorso-lateral margins. Ornamentation of crenulate growth lines with transverse undulations in later growth stages. Shell thickness and structure unknown.

Discussion. Pharetrolites bambachi is distinctive with respect to the shape of the dorsal emargination and the nature of the ornamentation. The apertural margin is thrown into a series of crenulations, perpendicular to the margin, which combine to form apparent polygonal ornamentation as successive growth stages are added. Similar ornamentation is known in Bucania Hall, 1847 and possibly Pharetrolites pharetra (Lindström, 1884, Pl VI, fig. 39-51) but the significance of the crenulation is not understood. The deepened inner portion of the emargination in P. bambachi has no equivalent in P. pharetra but is reminiscent of Temnodiscus lamellifer (Lindström, 1884). As previously noted, the degree of emphasis of such an inner emargination is partly dependent on the presence or absence of a strong dorsal keel. In T. lamellifer a dorsal keel is commonly present and tends to produce a U-shaped median notch with subparallel sides. In specimens without the keel the culmination of the sinus is less noticeably deepened and

lacks the U-shaped form. The degree of deepening of the inner part of the emargination in P. bambachi is greater than that normally associated with the presence of a keel, the development of which would appear to be infrequent.

The spiral folds (Pl. I, fig. 24) are poorly known but similar structures seem to be developed in P. pharetra (Lindström, 1884, Pl. VI, fig. 39).

All the Arisaig specimens are crushed in shale, to a greater or lesser extent. As a consequence, the dorsal profile is not well known although the visible characters are considered sufficiently distinctive to merit determination as a new species.

Pharetrolites murchisoni (d'Orbigny in Férussac and  
d'Orbigny, 1840)

(Pl. I. figs. 16-19, 22, 25, 27; Pl. II, figs. 1, 3, 5)

Bellerophon striatus Sowerby in Murchison, 1839, p. 604,  
Pl. 3, fig. 12e, non Bronn, 1835.

Bellerophon murchisoni d'Orbigny in Férussac and d'Orbigny,  
1840, p. 210, Pl. VII, figs. 1-3.

Temnodiscus murchisoni; Reed, 1921, p. 49-51, Pl. IX, figs.  
8, 9.

Bellerophon sp.; McLearn, 1924, p. 141, Pl. XX, figs. 28, 29.  
non Bellerophon murchisoni; d'Archiac and de Verneuil, 1842,  
p. 353, Pl. XXVIII, figs. 7, 8.

Figured material. Moydart Fm., Green Member, USNM 169461, USNM  
169462 from Schuchert Colln. 52B. Stonehouse Fm., YPM 28327 from  
Twenhofel Colln. 19j/3032; YPM 462 from coastal section; GSC 33268  
from Jones Colln. Ar S 7820.

Additional material. Moydart Fm., Green Member, Schuchert Colln. 52B.

Stonehouse Fm., Jones Colln. Ar S 7820. (3 specimens).

Description. Species of Pharetrolites Wenz, 1943 with about two loosely coiled whorls. Early whorl profile unknown. At intermediate stages, whorl profile dorso-ventrally subelliptical with greatest width at just below midheight of whorl. Later growth stages with trigonal whorl profile; dorso-lateral surfaces gently convex and increasing in curvature prior to passing subperipherally onto flat umbilical walls. Umbilici phaneromphalous. Whorl impression seemingly slight producing deep sutural indentation in later growth stages. Dorsum sinuate; growth lines on dorso-lateral areas curving forwards from the suture (text-fig. 4C) prior to curving backwards into the deep, wide sinus; sides of inner portion of sinus approaching parallelism at the culmination on the median dorsal keel. Ornamentation of sharply defined, somewhat lamellose growth elements with crenulate margins which produce fine, discontinuous spiral lirae. Upper surface of keel with fine spiral striae. Shell thin; structure unknown.

Discussion. Pharetrolites evolvens (Perner, 1903) from the Ashgillian of Bohemia is similar in profile and ornamentation to individuals of P. murchisoni of comparable size but differs in having a deeper median sinus. Plaster casts in the U.S. National Museum of P. cristatus (Perner, 1903) from the Silurian Liten Beds of Bohemia indicate a shell with more widely spaced growth elements and a wider, deeper sinus.

Sowerby in Murchison (1839) stated that Bellerophon murchisoni occurs at Felindre, Radnorshire. Reed (1921) commented that the holotype (GSM Geol. Soc. Coll. 6669) is labelled 'Upper Ludlow, Horeb Chapel' while the accompanying plate description states that the

specimen is from Felindre. It would appear that the specimen was originally located on a slab from Horeb Chapel and has subsequently been isolated. However, the species is certainly present at Felindre also.

All the available specimens of P. murchisoni from the Green Member of the Moydart Fm. are small internal moulds but features of the ornamentation are preserved on the internal moulds due to the somewhat plicate ornamentation of the thin shell. The greater tumidity of specimens from the Stonehouse Fm. reflects their increased size.

#### Family BELLEROPHONTIDAE M'Coy, 1851

##### Subfamily PLECTONOTINAE Boucot and 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.

Discussion. Considerable uncertainty exists concerning the nature and systematic position of the various lower Ordovician to middle Devonian bellerophontacean species which exhibit spiral trilobation of the dorsum. Most are imperfectly known and have been assigned to one or other of the two 'catch-all' species Bellerophon trilobatus Sowerby in Murchison, 1839 or Planorbis trilobatus Conrad, 1839. However, four genera have been proposed to accommodate some of the species showing this distinctive dorsal modification: Bucanella Meek, 1871; Plectonotus Clarke, 1899b; Tritonophon Opik, 1953 and Nylanderina Boucot in Boucot, Cumming and Jaeger, 1967. The determinative characters of all the genera have been questioned by various authors which in itself suggests one of the major causes of the confusion - inadequate preservation of the type materials.

The area of disagreement common to all four genera and to most described species is the nature of the dorsal emargination. Is there a true slit producing a selenizone or does the emargination take the form of a sinus without parallel sides which consequently fails to generate a selenizone? Since the nature of the emargination has been widely recognised as a character of major importance in the classification of the Bellerophontacea (Knight et al, 1960; Horný, 1963), the determination of the feature assumes critical taxonomic importance.

When introducing Plectonotus, Clarke (1899b) clearly stated that the genus was to be distinguished from Bucanella Meek, 1871 by the presence of a true slit generating a selenizone, Meek's genus being held to have only a sinus. McLearn (1924) assigned to Plectonotus specimens from Arisaig which carried a selenizone on the upper surface of the broad median lobe and Straw (1933) made similar use of the taxon for strongly trilobed specimens from the borehole at Little Missenden, Bucks. into Downtonian strata.

Knight (1941) redescribed 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 and Saul in Saul, Boucot and 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 original description of Clarke (1899b) and the presence of a selenizone. In so 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, following an assurance from Yochelson that a selenizone was present in Plectonotus. During the discussion of a lower Palaeozoic fauna from northern Maine, Boucot and 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 (AMNH 10335/2; Pl. VI, figs. 11, 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 and Saul in Boucot, Saul and 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 and 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 and Batten (1968) transferred to the Class Monoplacophora.

Bucanella nana Meek, 1871, the type species of Bucanella from the lower Ordovician of Colorado, was described by Meek (1871) as showing no traces of a median dorsal band corresponding to a sinus in the apertural margin. Undoubtedly, the passage of seventy years before Knight (1941) illustrated the 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 P. derbyi. Whorl embracement and the rate of whorl expansion are slight with widely phaneromphalous umbilici being formed 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 a dorsal emargination but examination has failed to demonstrate the form of this.

Part of the small limestone slab containing the silicified type specimens (USNM 7858) was digested in acid to provide additional material. One of the specimens obtained in this way showed a pair of strong spiral cords on the upper surface of the median dorsal lobe, possibly suggestive of the margins of a selenizone. However, the nature of the emargination could not be conclusively demonstrated and must remain open to conjecture until better material is forthcoming.

Regardless of the outcome of such investigation, it is clear that Plectonotus and Bucanella are unrelated forms which have independently acquired dorsal trilobation at different instances in geologic time. The formation of the subfamily Plectonotinae by Boucot and Yochelson (1966) and separation of Plectonotus from Bucanella is, consequently, quite justified.

Öpik (1953) described Tritonophon to include a 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 profile 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 and Spiller (1971) quoted Yochelson (written communication, 1968) in saying 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 or 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 and Grönwall, 1909; Straw, 1933; Rollins, Eldredge and Spiller, 1971). Öpik (1953) suggested that in other cases, for example Bucaniella trilobata (Conrad) of Pitcher, 1939 from the upper Llandovery of Shropshire, the selenizone might have been obscured by the 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 and Prouty (1923), from the Silurian Rochester and Rose Hill Formations of Maryland, 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 and 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 and 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 also assigned Bellerophon rotalina Hall, 1879 to Nylanderina but Rollins in Rollins, Eldredge and Spiller (1971) considered this species to have a true selenizone and referred it to Tritonophon. Rollins also inferred the presence of a selenizone in N. goldringae from Boucot's illustrations.

Knight et al (1960) regarded Tritonophon as a junior subjective synonym of Bucanella (Bucanella) in the family Sinuitidae but the assignment is clearly not tenable since Tritonophon is believed to have a well developed selenizone. Rollins in Rollins, Eldredge and Spiller (1971) allowed Tritonophon full generic status and placed it in the Bucaniinae of the Bellerophontidae. However, Tritonophon has no obvious close affinity to Bucania Hall, 1847 and, with due regard for similarity in form and ornamentation, it is here considered most satisfactory to place the genus alongside Plectonotus in the Plectonotinae.

To summarise: Bucanella Meek, 1871, Plectonotus Clarke, 1899b, and Tritonophon <sup>ii</sup>Öpik, 1953 are recognised here. Bucanella needs to be redescribed but is clearly not closely related to Plectonotus and Tritonophon. Tritonophon, of which Nylanderina Boucot in Boucot, Cumming and Jaeger, 1967 is a junior subjective synonym, is placed

alongside Plectonotus in the subfamily Plectonotinae Boucot and Yochelson, 1966.

Trilobed bellerophontaceans are a widely distributed and common element in the gastropod fauna of the Arisaig Group. McLearn (1924) noted specimens from the Doctors Brook, McAdam Brook and Upper Stonehouse Formations but referred all the material to Plectonotus trilobatus (Sowerby in Murchison, 1839), though he did recognise an additional, more laterally compressed variety in the Upper Stonehouse Fm. During the present study specimens have been observed in collections from all formations and have been assigned to two species of Plectonotus and three of Tritonophon.

A discussion of the palaeoecology and functional morphology of the Plectonotinae is given in a later section.

Genus PLECTONOTUS Clarke, 1899b

Type species. Plectonotus derbyi Clarke, 1899b.

Diagnosis. Dorsal trilobation moderate, the median lobe usually being low and relatively wide.

Discussion. Tritonophon <sup>"</sup>Opik, 1953 is distinguished from Plectonotus by its more pronounced trilobation producing a highly vaulted median lobe. 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 usually wide with the selenizone occupying only part of the width of the upper surface.

Boucot and Yochelson (1966) considered Plectonotus, as redefined by them, to be restricted to the early and middle Devonian. The

description of the Silurian species from Arisaig requires no material adjustment of their diagnosis but considerably extends the stratigraphic range of the genus.

Plectonotus boucoti sp. nov.

(Pl. V, figs. 14, 15, 17-22; Pl. VI, figs. 1-10, 12, 13,  
15, 17, 18)

Bellerophon trilobatus; Lindström<sup>"</sup>, 1884, p. 80-81, Pl. IV,  
figs. 13-15.

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

non Bellerophon trilobatus Sowerby in Murchison, 1839,  
p. 604, Pl. 3, fig. 16.

Holotype. Doctors Brook Fm., USNM 169584 from USNM Colln. 10165(141).

Other figured material. Doctors Brook Fm., USNM 169583, USNM 169585, USNM 188526, USNM 169587, USNM 169588, USNM 169591, USNM 169592, USNM 192123 from USNM Colln. 10165(141); GSC 3138 from Arisaig, locality unknown; USNM 169589, USNM 169590 from Schuchert Colln. 52D. SM A39164, SM A39165 from upper Llandoverly of Tonlegee, Cong, Galway, Ireland. Mo 26562, Mo 26563 from Hemse Beds, Petesvik, Hablingbo, Gotland; Mo 26567 probably from Slite Beds, Hørsne<sup>"</sup>, Gotland.

Additional material. Doctors Brook Fm., USNM Colln. 10165(141), abundant. Lower McAdam Brook Fm., Bambach Collections A3633(256), A3635(228), A3640(263), A3844(251); Twenhofel Colln. 117/3032(258). Upper McAdam Brook Fm., Bambach Collections A3645(282), A3646(278), (about 130 specimens in all).

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. 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. 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, the latter species also having 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. V, figs. 17, 18, 20). P. fraternus (Reed, 1908) of Boucot and Saul in Saul, Boucot and 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.

P. boucoti occurs in the Doctors Brook Fm., where it is abundant in USNM Colln. 10165(141), and the McAdam Brook Fm. at Arisaig. In Gotland the species is rare. Apart from the two figured examples of Lindström (1884) from the Ludlovian Hemse Beds (Pl. V, figs. 17, 18, 20) there are two poorly preserved internal moulds from the upper Slite beds of Hørsne, one of which is figured here (Pl. V, fig. 14). In the Sedgwick Museum there are several decalcified blocks from the upper Llandoverly of Tonlegee, Cong, Galway, Ireland which contain many sharp internal moulds of P. boucoti (Pl. VI, figs. 13, 15, 17, 18).

The pustulose nature of the spiral ornamentation is well seen in USNM 169583 (Pl. VI, fig. 7) and USNM 169588 (Pl. VI, fig. 12). 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 point 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 trend 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 immediately conducive to the determination of this.

Ontogeny. It has been widely recognised (Thompson, 1942) that the coiling of the gastropod shell approximates to a logarithmic spiral. 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 vary but such variation enhances rather than detracts from their value since a mechanism is provided for the quantification of the variation in shell form during growth.

Raup's four basic parameters may be referred to as S, W, D and T and their specific applications (S, Z, W, V and D) in P. boucoti are illustrated in text-fig. 5A. 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 of shape. Two ratios, S and Z, are employed in this

TEXT-FIG. 5

A. Camera lucida drawing of transverse polished section of Plectonotus boucoti sp. nov., GSC 3138, showing standard measurements employed in determination of the current applications of Raupian parameters, (for explanation see text).

S, Z: representations of the shape of the generating curve, S (whorl profile).

D: a measure of the position of the generating curve relative to the axis of coiling, D.

W, V: measures of the rate of whorl expansion, W, calculated at whole whorl and half whorl intervals, respectively.

All illustrated values of Raupian parameters relate to the largest half whorl present, ( $w_{\rho+1}$ ).

B. Growth patterns in Plectonotus.

Measurements of length (l), width (w) and size (l+w) for Plectonotus boucoti, USNM 169589, and Plectonotus cherylae, USNM 169581, at successive half whorl intervals during growth.

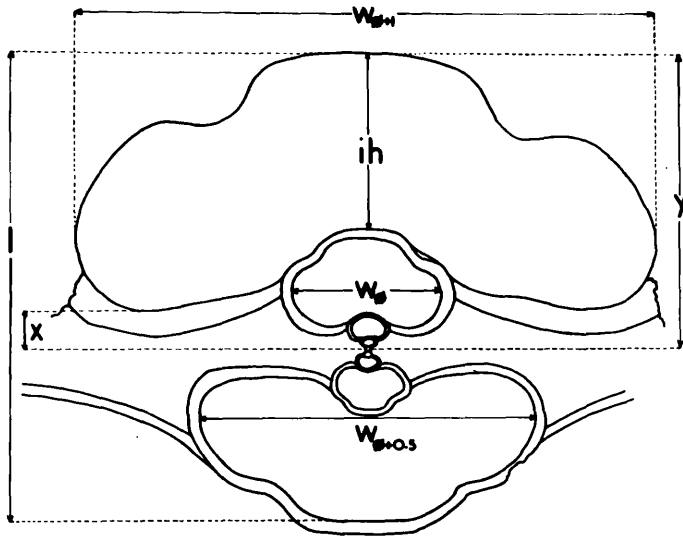
The curvature of the growth traces indicates departure from simple, unvarying logarithmic increase (see text).

The allometric increase of w relative to l in P. boucoti is not seen in P. cherylae within the size range of available specimens. In view of the allometry, all subsequent measurements of increased growth in Plectonotus or Tritonophon are given in terms of 'size' (length+width) rather than as a single linear parameter.

All measurements are made in millimetres on the more sharply defined shell interior (internal mould).

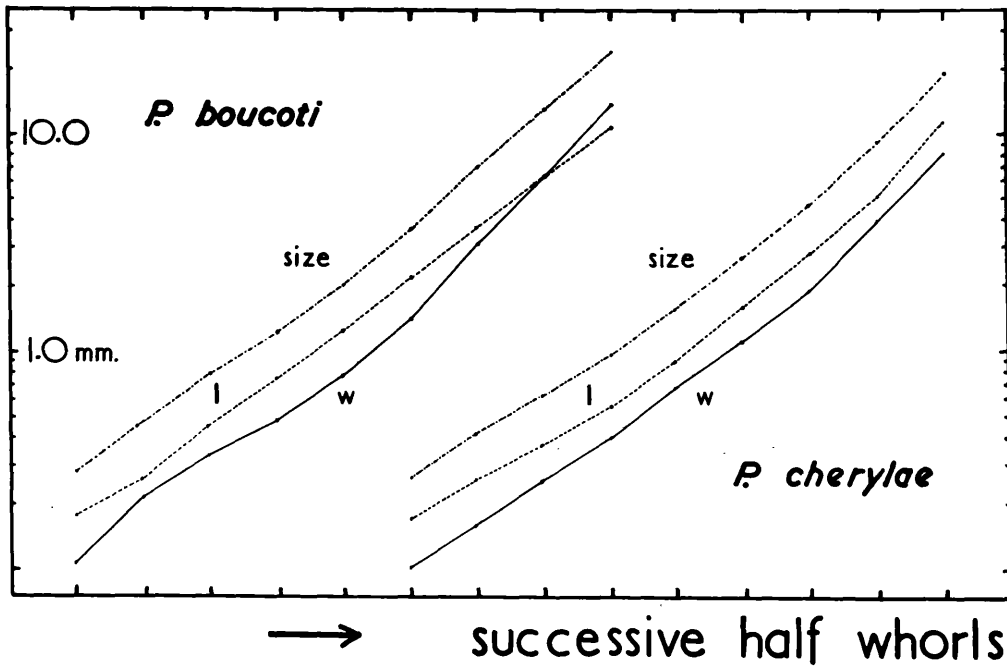
Text-fig. 5

A



$$Z = \frac{W_{B+1}}{y-x} \quad S = \frac{W_{B+1}}{ih} \quad D = \frac{x}{y} \quad W = \frac{W_{B+1}}{W_B} \quad V = \frac{W_{B+1}}{W_{B+0.5}}$$

B



context but a number of similar ratios can be included in more complex models (Gould, 1969).  $\underline{W}$  is the rate of whorl expansion and is computed as the ratio of a linear measurement on one whorl to the same dimension one whorl previously. If the shell proportions change with growth values of  $\underline{W}$  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  $\underline{V}$ , which approximates to the square root of  $\underline{W}$ . In the present context  $\underline{W}$  and  $\underline{V}$  are computed from measurements of whorl width at whole whorl and half whorl intervals, respectively.  $\underline{D}$ , the position of the generating curve relative to the axis of coiling, is here measured as the ratio,  $\underline{D}$ , 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,  $\underline{T}$ , expresses the helicoid component of growth in the gastropod shell. In *P. boucoti*, as in other planispirally coiled shells,  $\underline{T}$  has a value of zero and need not be further considered.

Raup's approach proves to be especially useful in studying the growth of *P. boucoti*. A transverse section through the shell, cut so as to contain the axis of coiling and to be perpendicular to the plane of symmetry, shows pronounced ontogenetic change in the whorl profile and in the nature of coiling (text-figs. 4F, 5A, 6A, 6B). 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 (text-fig. 5B).

$\underline{D}$ ,  $\underline{W}$ ,  $\underline{V}$ ,  $\underline{S}$  and  $\underline{Z}$  show comparable variation during growth. In text-fig. 7, 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 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.

Although the growth changes in P. boucoti are essentially continuous rather than discrete, the sequence can be reduced to two stages for purposes of discussion. In the earliest three whorls, up to a size of about 2.0, S, Z, W and V diminish while D increases. The decrease in S and Z 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 (text-fig. 6A, 6B).

In the second stage, at sizes greater than 2.0, the earlier trends are reversed. S and Z increase due to an increase in whorl width relative to internal and total height which also 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 (text-fig. 6A, 6B). 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

TEXT-FIG. 6

Ontogenetic variation in Plectonotus Clarke, 1899b.

A, B. Plectonotus boucoti sp. nov., USNM 169589. A, camera lucida drawing of transverse polished section showing development of trilobation with increased growth and closure of one umbilicus at a late growth stage (right side of illustration), x6.25; B, inner whorls of same, x25.

C, D. Plectonotus cherylae sp. nov., USNM 169581. C, camera lucida drawing of transverse thin section showing development of trilobation during ontogeny, x6.25; D, inner whorls of same, x25.

TEXT-FIG. 7

Variation in Raupian parameters with growth in Plectonotus boucoti sp. nov.

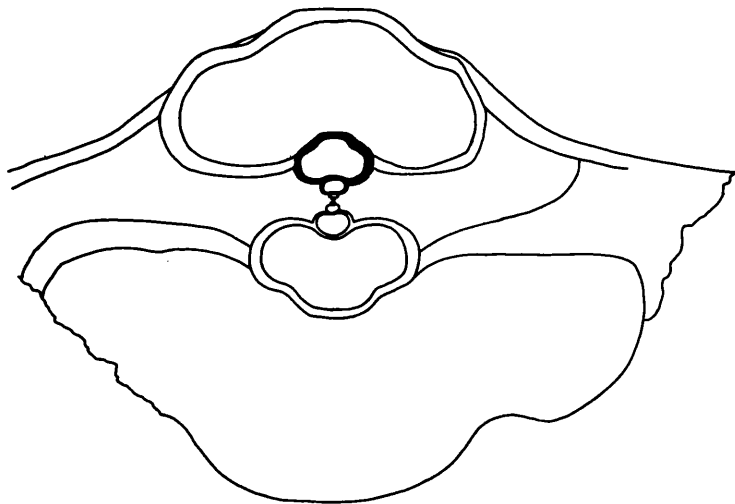
For explanation of Z, S, D, W and V see text and text-fig. 5A.

Horizontal axis is 'size' (length+width) on logarithmic scale.

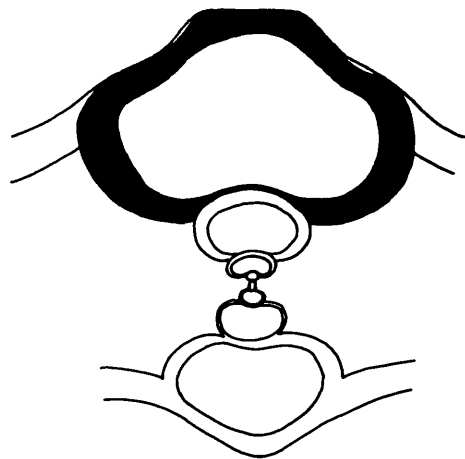
All measurements are made in millimetres on the more sharply defined shell interior (internal mould) of transverse thin or polished sections.

- |                |                |
|----------------|----------------|
| 1. USNM 169585 | 4. USNM 192123 |
| 2. USNM 188526 | 5. USNM 169587 |
| 3. USNM 169589 | 6. GSC 3138    |

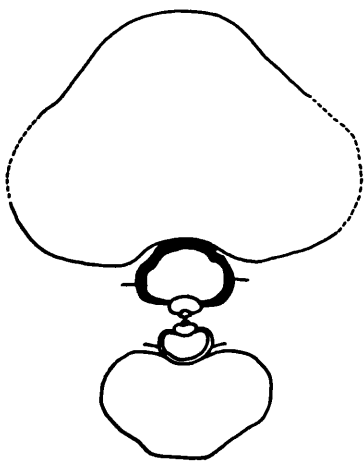
*Text-fig. 6*



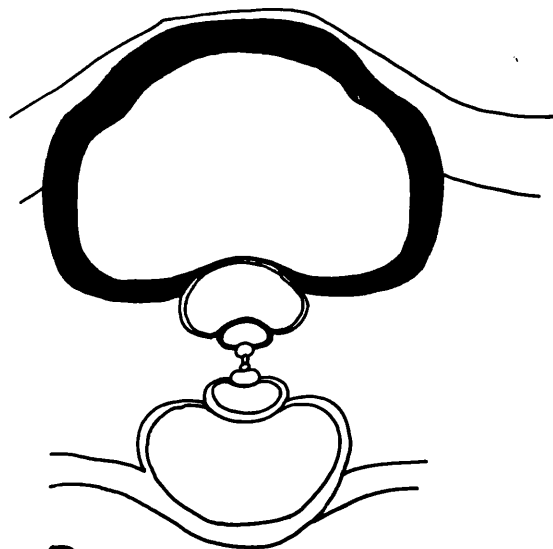
*A*



*B*

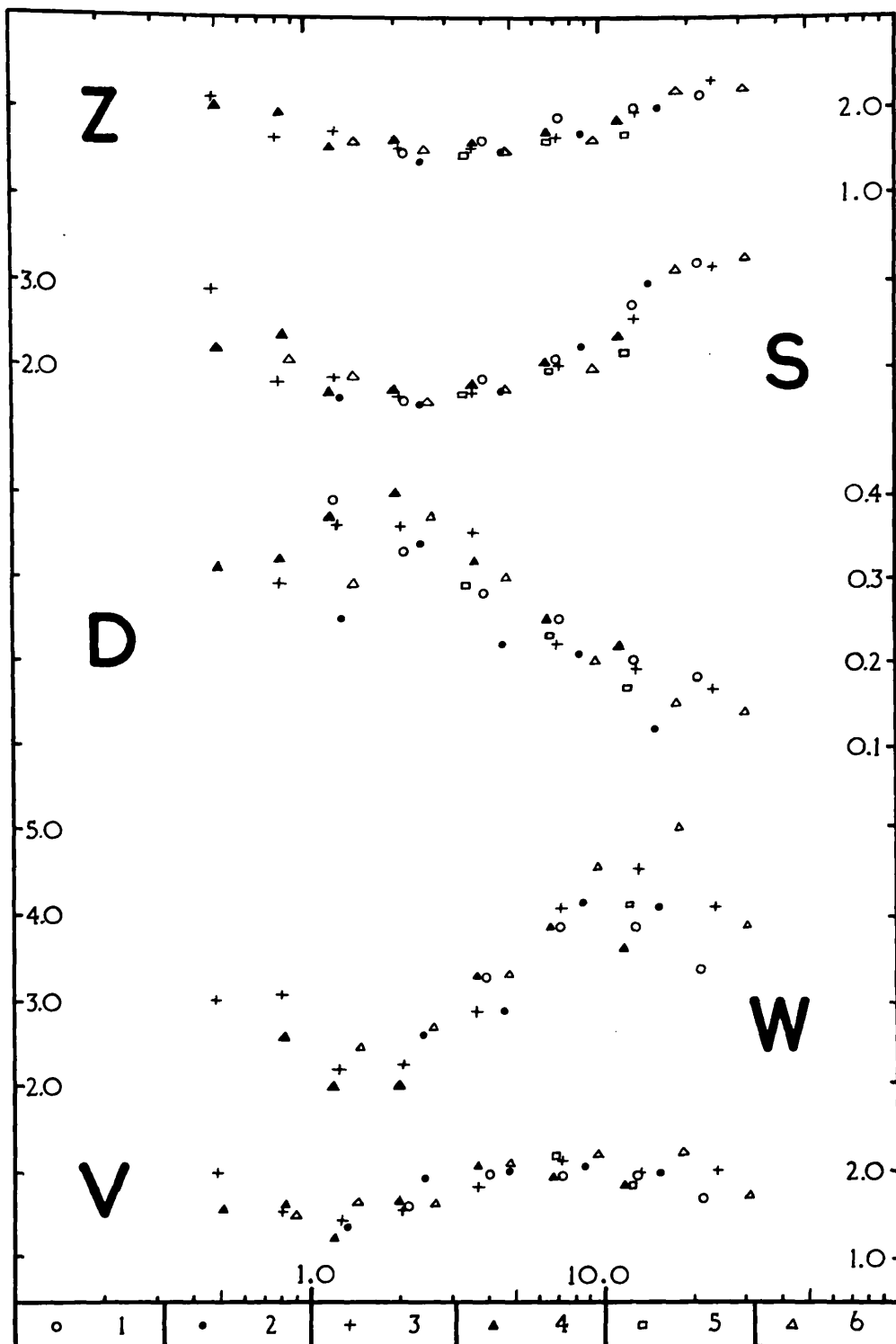


*C*



*D*

Text-fig. 7



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 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 (text-figs. 4F, 6A).

The two growth stages may be regarded as the initial protoconch and the subsequent teleoconch but little developmental or ecological significance can be attached to the recognition of this division. Cox (1960) has noted that the earliest whorls of a gastropod may be strongly differentiated from the later growth stages in the nature of coiling and ornamentation. However, in terms of development or change in life habit, such disjunctions between protoconch and teleoconch in marine gastropods are not well understood. In many opisthobranchs the change from the early hyperstrophic whorls to the normal coiling of the later shell takes place when the pelagic larva settles and starts to metamorphose. 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.

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) argued that this atypical coiling of the early whorls was a result of accommodation of the initial departure within the coiling pattern of the gastropod shell. It is clear that such an interpretation need not necessitate any correlation with changes in life pattern or development.

Although the development of trilobation in P. boucoti accompanies the changes in the values of Raup's parameters during the second growth stage, it is difficult to suggest that the acquisition of a trilobed dorsum is the dominant force behind the evolution of the coiling of the shell. The general increase in W and V could be seen as an attempt to compensate for the reduction in living space available to the snail produced by a deepening of the dorsal furrows. The gradual encroachment of the umbilical walls upon the axis of coiling, demonstrated by the decrease in D, might also be interpreted in this way. However, the area of cross-section of the whorl, the only convenient measure of available living space, shows a comparable rate of increase per half whorl to V, making such a direct interpretation inadequate.

Regardless of cause, the nett result of the ontogenetic changes is a subspherical shell with narrow or closed umbilici and a strongly trilobed dorsum which would appear to offer an increased degree of compactness over the widely phaneromphalous, more laterally compressed juvenile form.

Plectonotus cherylae sp. nov.

(Pl. V, figs. 1-13, 16)

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

Holotype. Stonehouse Fm., USNM 169582 from Schuchert Colln. 53.

Other figured material. Stonehouse Fm., USNM 169573 from USNM Colln. 10206(501); USNM 169468, USNM 169471, USNM 169576, USNM 169577, USNM 169578, USNM 169579, USNM 169580, USNM 169581, USNM 188527 from Schuchert Colln. 53; GSC 3138g from Arisaig; YPM 479 from Springville, Nova Scotia.

Additional material. Stonehouse Fm., USNM Colln. 10206(501); USNM Colln. 10910(496); Twenhofel Collections 19a<sup>8</sup>/3032(422), 19a<sup>13</sup>/3032(427), 19a<sup>14</sup>/3032(432) and 19a<sup>16</sup>/3032(462); Schuchert Collections 49A and 53; Jones Collections Ar S 7380 and Ar S 7820 (about 55 specimens). Poorly preserved specimens assignable either to P. cherylae or Tritonophon kivitalonae sp. nov., described below, have been observed in the following collections from the Stonehouse Fm., USNM Colln. 10843(505) from Cape George; Bambach Collections A3659(459), A3671(443), A3689(495), A3703(472) and A3888(490).

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. 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 narrowness 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 <sup>"</sup>Opik, 1953 but the latter genus is 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.

Ontogeny. The increase of width over length characteristic of the development of P. boucoti is not seen in P. cherylae, within the available size range of specimens (text-fig. 5B), but variation in Raup's parameters (text-fig. 8) reflects comparable departure from unvarying logarithmic increase. W and V increase throughout growth in contrast to the initial decrease and subsequent increase seen in P. boucoti (text-fig. 7). There is slight stabilisation of V values in the largest sizes but this is not so pronounced as in P. boucoti. In P. cherylae S increases to a peak of about 2.7 at a size of 1.0 and subsequently decreases to about 1.6 at a size of 4.0, remaining constant thereafter. A comparable trend is seen in Z but at lower absolute values. This early peak is not present in P. boucoti where S and Z also increase in larger sizes. In contrast, the initial increase and later decrease in values of D typical of P. boucoti is not seen in P. cherylae where D decreases throughout growth.

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 (text-fig. 6C, 6D). 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.

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. V. fig. 7). At the other extreme,

TEXT-FIG. 8

Variation in Raupian parameters with growth in Plectonotus cherylae sp. nov.

For explanation of Z, S, D, W and V see text and text-fig. 5A.

Horizontal axis is 'size' (length+width) on logarithmic scale.

All measurements are made in millimetres on the more sharply defined shell interior (internal mould) of transverse thin or polished sections.

- |                |                |
|----------------|----------------|
| 1. GSC 33280   | 4. USNM 169581 |
| 2. GSC 33281   | 5. USNM 169576 |
| 3. USNM 188527 | 6. USNM 169577 |

TEXT-FIG. 9

Transverse sections of Tritonophon<sup>"</sup> Opik, 1953

A. Tritonophon trilobata (Sowerby in Murchison, 1839), USNM 169593.

Camera lucida drawing of transverse polished section showing lower rate of whorl expansion than in B and C, below, x6.25.

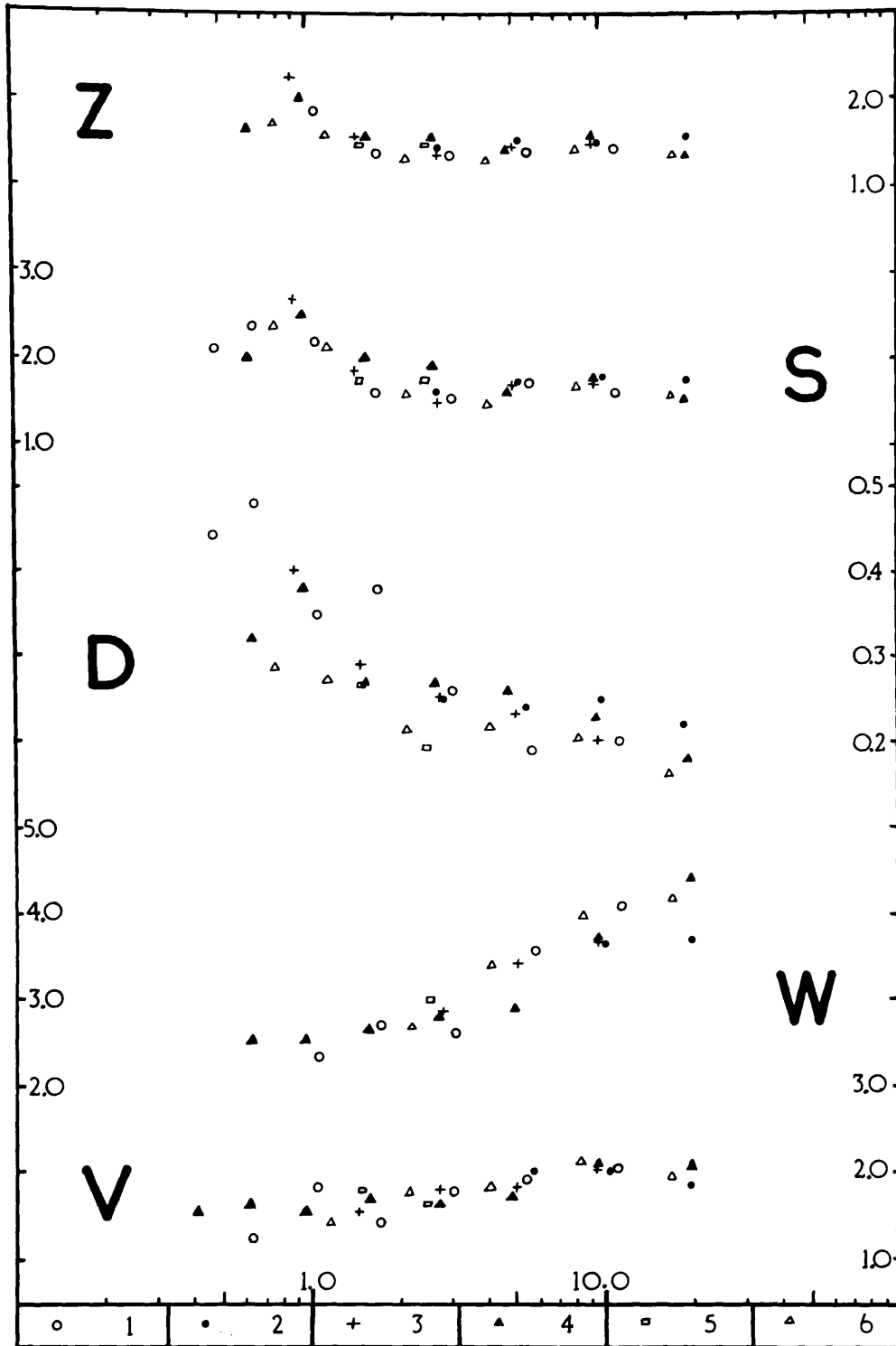
B. Tritonophon kivialonae sp. nov., GSC 3138a.

Camera lucida drawing of transverse polished section, x6.25.

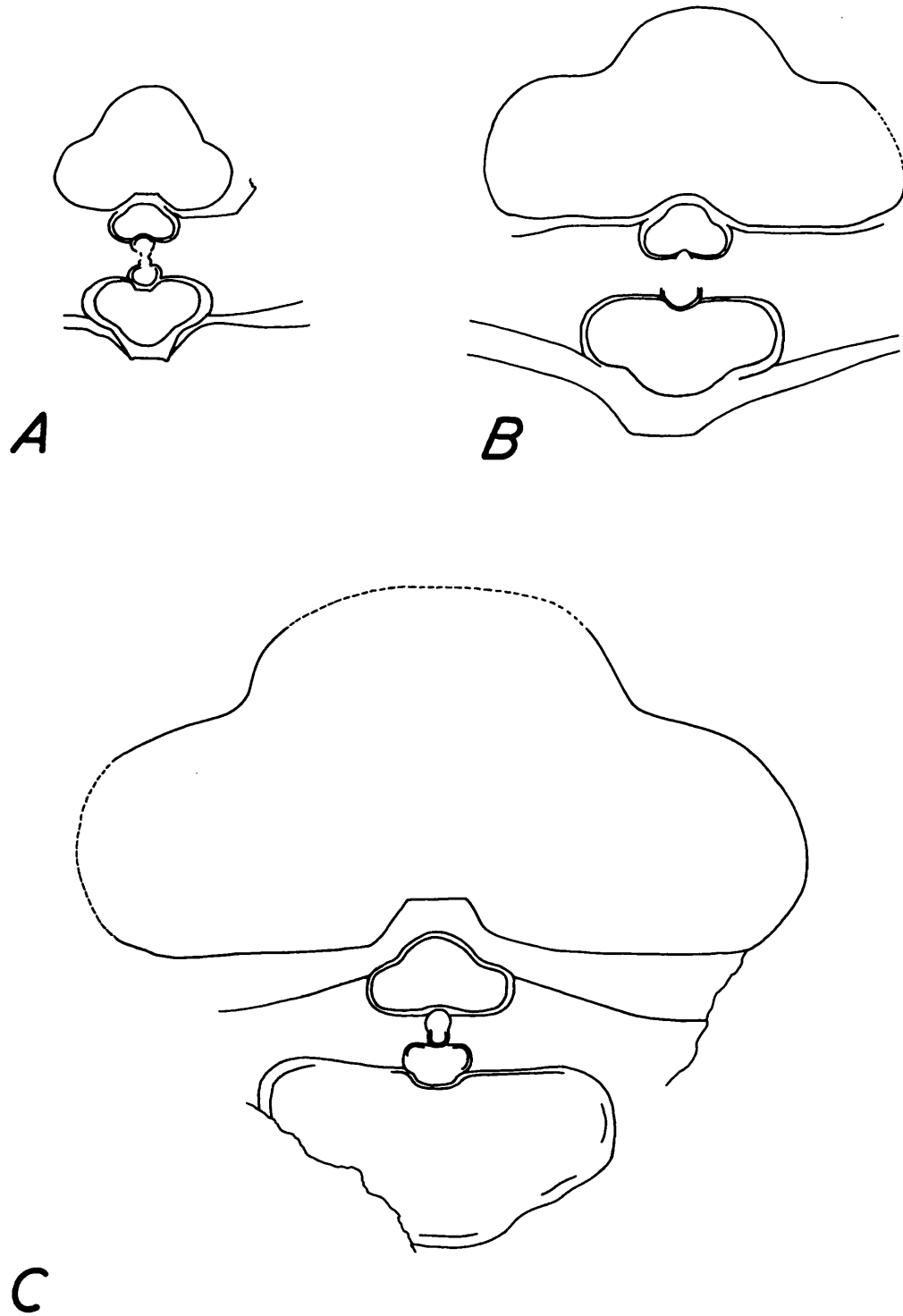
C. Tritonophon kivialonae sp. nov., GSC 33279.

Camera lucida drawing of transverse polished section, x6.25.

Text-fig. 8



*Text-fig. 9*



the degree of lateral compression may be great with accentuated trilobation (USNM 169573, Pl. V, figs. 10-12; YPM 479, Pl. V, figs. 1, 2, the specimen figured by McLearn, 1924, Pl. XX, figs. 30, 31 from Springville, N.S.).

Genus TRITONOPHON<sup>"</sup> Opik, 1953

Type species. Kokenospira (Tritonophon) trimetra<sup>"</sup> Opik, 1953.

Tritonophon<sup>"</sup> Opik, 1953, p. 20.

Nylanderina Boucot in Boucot, Cumming and Jaeger, 1967, 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. 111, figs. 13-21; Pl. IV, figs. 1-9, 14)

Bellerophon trilobatus Sowerby in Murchison, 1839, p. 604,

Pl. 3, fig. 16.

do. ; Moberg and Grönwall, 1909, p. 43-44,

Pl. III, figs. 13, 14.

Plectonotus trilobatus; Straw, 1933, p. 125, Pl. IX, figs.

26, 27.

non Plectonotus trilobatus; McLearn, 1924, p. 140-141, Pl.

XX, figs. 18, 30-32.

Figured material. GSM Geol. Soc. Coll. 4384 from the upper Ludlow of Felindre, Radnorshire; BM PG5002, BM PG5003, BM PG5004 from a loose block of upper Ludlow rottenstone at waterfall 270 yds. SW of Stone House, Felindre, Radnorshire (Grid Ref. SO 175802). GSM 51860D, GSM 51860E, GSM 51861C, GSM 51879 in Downtonian strata from the borehole at Little Missenden, Bucks. Arisaig, Green Member of Moydart Fm., USNM 169593, USNM 169594 from Schuchert Colln. 52B; YPM 28347 in USNM Colln. 10853(292) from Sutherland River, Pictou Co.; GSC 33276 from Jones Colln. Ar Mo 4800.

Additional material. Moydart Fm., Green Member, Common in Schuchert Colln. 52B.

Description. Species of Tritonophon Opik, 1953 with about four slowly expanding whorls. Early whorls imperfectly known but with uniformly convex dorsum. 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 producing 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. The type series has not been recognised in the Geological Society of London Collection of the Institute of Geological Sciences, 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. IV, figs. 6, 7) but the other, GSM Geol. Soc. Coll. 4383, is too badly abraded. Following his studies of the stratigraphy of the area (Earp, 1938; 1940), Dr. J.R. Earp (written communication, 1972) kindly pointed out that the original locality of Murchison at Felindre was located 270 yards Southwest of Stone House, Felindre, by a small waterfall, Grid Reference SO 175802. Several visits to this exposure produced

one fallen block containing many specimens of B. trilobatus associated with the other gastropods noted by Sowerby from Felindre.

All the available specimens from Felindre are preserved as internal and external moulds in a friable decalcified lense but details of the shell exterior can usually be ascertained. The recently collected material forms the basis for the redescription of the species although characters of the ornamentation are described from the better preserved specimens from the borehole at Little Missenden, Bucks.

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. 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 Bellerophon 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 bellerophontacean readily assignable to Tritonophon.

Specimens referred to Conrad's species have been described from the Llandovery-Wenlock Rose Hill and Rochester Formations of Maryland by Swartz and Prouty (1923). The species occurring in Maryland 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 making comparison difficult. Specimens from the Upper Ross Brook and French River Formations of Arisaig 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 Downtonian species of Sowerby in Murchison. 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 taxon by T. trilobata (Sowerby in Murchison, January 1839).

T. trimetra Opik, 1953, from the lower Silurian of Australia, is poorly known but seemingly has a wider median lobe. T. rotalina (Hall, 1879) of Rollins in Rollins, Eldredge and 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 and 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.

The specimens from Felindre (Pl. IV, figs. 1-4, 6-8, 14) show some of the considerable variation typical of most populations of trilobed bellerophontaceans. As with Plectonotus cherylae sp. nov. (Pl. V, figs. 1-13, 16) the main variable is the depth of the spiral dorsal grooves and the consequent degree of development of trilobation.

Preservation does not allow detailed study of the development of T. trilobata but in one example, USNM 169593 from the Moydart Fm., text-fig. 9A, trilobation is seen to be developed from early whorls with an initially convex dorsum, with a decrease from 0.25 to 0.18 in Raupian D over the last whorl and a half. Decrease in S (1.9 to 1.7) and Z (1.7 to 1.4) shows the increased vaulting of the median lobe while V also shows a slight fall (for explanation see text-fig. 5A).

T. trilobata is common in the Green Member of the Moydart Fm. at Arisaig at an equivalent horizon to the Felindre occurrence. In the borehole at Little Missenden, Bucks. the species occurs in association with Murchisonia (Murchisonia) amii (McLearn, 1924) in Downtonian strata but has not been found at such a high level at Arisaig. In the Upper Stonehouse Fm. at Arisaig it is T. kivitalonae sp. nov. which occurs in association with M. (M.) amii. T. trilobata is also present in the "Öved-Ramsåsa Series of Scania, Sweden although Moberg and Grönwall (1909) did not consider the specimens described by themselves to be identical to Sowerby's species.

Tritonophon kivitalonae sp. nov.

(Pl. IV, figs. 10-13, 15-22)

Plectonotus trilobatus; McLearn, 1924, (pars), p. 140-141,  
Pl. XX, fig. 32, non figs. 18, 30, 31.

Holotype. Upper Stonehouse Fm., GSC 33275 from Jones Colln.  
Ar S 7820.

Other figured material. Upper Stonehouse Fm., GSC 3138a, GSC 3138m, GSC 5649 from Arisaig; GSC 32782 from GSC loc. 1302, Arisaig; GSC 33279 from Jones Colln. Ar S 7820.

Additional material. Upper Stonehouse Fm., GSC 32781, a block from GSC loc. 1302, Arisaig with illustrated specimens of Anapetopsis lalajae gen. et sp. nov. and A. maclearni gen. et sp.

nov.; Jones Colln. Ar S 7820. Poorly preserved specimens assignable to Plectonotus cherylae sp. nov., above, or T. kivitalonae have been observed in the following Stonehouse Fm. collections: USNM Colln. 10843(505) from Cape George; Bambach Collections A3659(459), A3671(443), A3689(495), A3703(472) and A3888(490). Jones Creek Fm., Univ. of New Brunswick in Saint John, Dept. of Geology No. S1-97, a single specimen collected 0.9 miles West of Highway 102 on the North side of the road to Brown's Corner, New Brunswick.

Description. Species of Tritonophon <sup>"</sup>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. 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; selenizone 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 umbilico-lateral 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 in sizes greater than about 10.0. 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. It is 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.

Changes in coiling and whorl profile during ontogeny are not well known in T. kivitalonae. Trilobation appears during the last two whorls and is generally accompanied by a narrowing of the umbilici as in the other trilobed bellerophontaceans from Arisaig. Combined measurements on GSC 3138a (Pl. IV, fig. 20; text-fig. 9B) and GSC 33279 (text-fig. 9C) indicate decrease in Raupian D from 0.38 to 0.18 with other parameters showing little variation in the comparatively small size interval of 4.5 to 32.5 ( $S = 2.2$ ;  $Z = 1.9$ ;  $V = 2.3$ ;  $W = 5.3$ . For explanation see text-fig. 5A).

T. kivitalonae occurs in the higher beds of the Upper Stonehouse Fm. exposed along the coast at Arisaig but a single specimen, collected by Mr. Andrew Porter, University of New Brunswick in Saint John, is known from the equivalent Jones Creek Fm. of New Brunswick.

Tritonophon sp.

(Pl. III, figs. 6, 8, 9, 12)

Figured material. Beechhill Cove Fm., GSC 33277 from Jones Colln. Ar B. Cove loc. 4. Upper Ross Brook Fm., YPM 75 from Bambach Colln. A3592(95); YPM 28350 from Bambach Colln. A3760(80). French River Fm., YPM 28343 from Bambach Colln. A3775(113), French River, Pictou Co.

Additional material. Upper Ross Brook Fm., Twenhofel Colln. 179b/3032(61). French River Fm., USNM Colln. 11247 from Pictou Co.; Bambach Colln. A3775(113), French River, Pictou Co.

Discussion. Several crushed and poorly preserved specimens of Tritonophon from the lower part of the Arisaig succession cannot be referred to T. trilobata (Sowerby in Murchison, 1839) from the Moydart Fm. or T. kivitalonae sp. nov. from the Upper Stonehouse Fm. The short slit, selenizone and widely spaced spiral lirae of the dorsum are well seen in specimens from the Upper Ross Brook Fm. (Pl. III, figs. 6, 12). 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 described by Swartz and Prouty (1923) as Bucanella trilobata (Conrad, 1839). However, as noted in the discussion of T. trilobata (Sowerby in Murchison, 1839), above, Conrad's species is imperfectly known and cannot be confidently identified from the descriptions of later authors. It is probably a species of Tritonophon and, as such, would be a junior homonym of T. trilobata

(Sowerby in Murchison, 1839).

Subfamily BUCANIINAE Ulrich and Scofield, 1897

Genus ANAPETOPSIS gen. nov.

Derivation of name. From anapetes (Gr.) = widely expanded + -opsis (Gr.) = relating to appearance, referring to the widely expanded appearance. Feminine.

Type species. Anapetopsis maclearni gen. et sp. nov.

Diagnosis. Phaneromphalous, rapidly expanding bellerophontacean characterised by the development of transverse and lateral thickening of the shell interior in the explanate late growth stage. High rate of whorl expansion increasing with ontogeny to produce a widely expanded aperture with explanate margins after about four whorls, the extreme margin of the aperture extending posteriorly beyond the earlier coiled whorls. Dorsal slit short. Ornamentation of spiral lirae and intercalated threads crossed by transverse growth lines.

Discussion. Anapetopsis is homeomorphic with Patellilabia Knight, 1945 from the upper Palaeozoic but may be distinguished by the diagnostic tendency to produce transverse and lateral thickening of the shell interior at maturity. In addition, the spiral ornamentation of Patellilabia consists of flat topped, closely spaced lirae in contrast to the more widely spaced, cord-like lirae of Anapetopsis. Phragmosphaera Knight, 1945, from the Silurian and Devonian, differs in the production of a plate-like extension

of the inductura into the aperture and the early whorls are less strongly elevated above the plane of the apertural margins.

Anapetopsis maclearni sp. nov.

(Pl. II, figs. 2, 4, 6-12, 14, 15; Pl. III, fig. 3)

Bucanopsis sp.; McLearn, 1924, p. 141, Pl. XX, fig. 17.

Holotype. Stonehouse Fm., GSC 3140a from Arisaig shore, collected by Weston in 1869.

Paratypes. GSC 3140b, GSC 3140c. Paper labels accompanying all the type specimens give the horizon as E2, 3 and 6 (presumably of Fletcher, 1887) which embraces the entire coastal section with the exception of the Beechhill Cove Fm. It would appear that these labels have been added at some considerable time after collection. The nature of the preservation and the red stained matrix suggest derivation from the Stonehouse Fm.

Other figured material. A poor specimen (GSC 32781A) on a slab from the Upper Stonehouse Fm. at GSC loc. 1302, Arisaig.

Description. Type species of Anapetopsis gen. nov. with about four whorls. Profile of early whorls rounded, with slight median expansion, becoming elliptical in later growth stages with whorl width about twice whorl height. Dorsum gently convex at maturity, with maximum width of whorl at below midwhorl height; umbilical walls flattened. Late growth stage widely expanded with explanate apertural margin, probably subcircular in plan, extending posteriorly

beyond the earlier coiled whorls. Interior of aperture of late growth stage with pronounced transverse thickening of the shell just prior to the widely expanded stage; two similar thickened areas occurring laterally, anterior to the transverse constriction and perpendicular to it. Umbilici phaneromphalous, of moderate width; whorl embracement at about two thirds of the height of the impressed whorl, producing deep sutural indentation. Growth lines indicating a wide sinus passing into a short slit which generates a slightly raised selenizone with a flat upper surface. Selenizone ornamentation of fine spiral striae and a median spiral lira crossed by many fine lunulae. Shell ornamentation of widely spaced, cord-like spiral lirae and intercalated threads with fine transverse growth lines; spiral lirae obscure on explanate margins. Shell generally thin but with thickening of the umbilical walls, development of an apertural boss and acquisition of the diagnostic transverse and lateral thickened areas in later growth stages; structure unknown.

Discussion. Although the thickening of the shell interior is well displayed on internal moulds, there is little or no indication of their presence on the shell exterior. Consequently, it is not possible to assign to the genus with certainty material which has been crushed in shale, as is the case with several specimens from the Stonehouse Fm. Superficially similar explanate bellerophontaceans have been observed in a number of collections from the Silurian of Britain. Several undescribed species appear to be present but the generally poor preservation makes comparison with Anapetopsis impossible.

The single available transverse section of A. maclearni (GSC 3140c; text-figs. 10A, 10C, 11C) indicates a progressive

TEXT-FIG. 10

A. Anapetopsis maclearni gen. et sp. nov., GSC 3140c.

Camera lucida drawing of transverse polished section showing apertural boss, x6.5.

B. Anapetopsis lalajae gen. et sp. nov., USNM 169596.

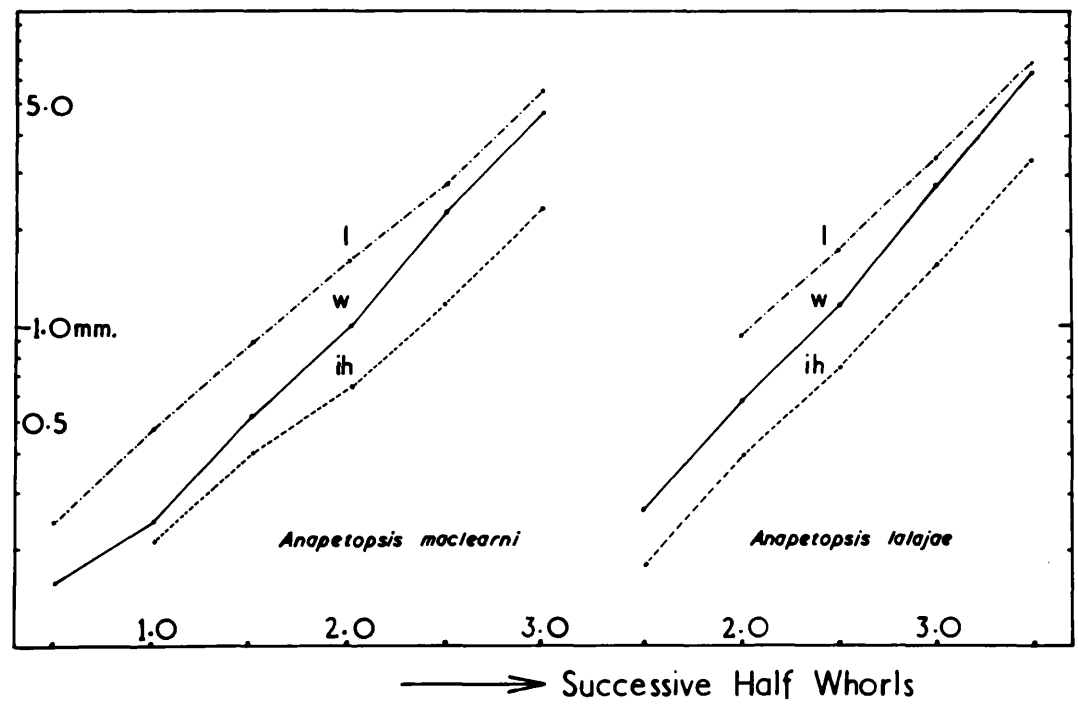
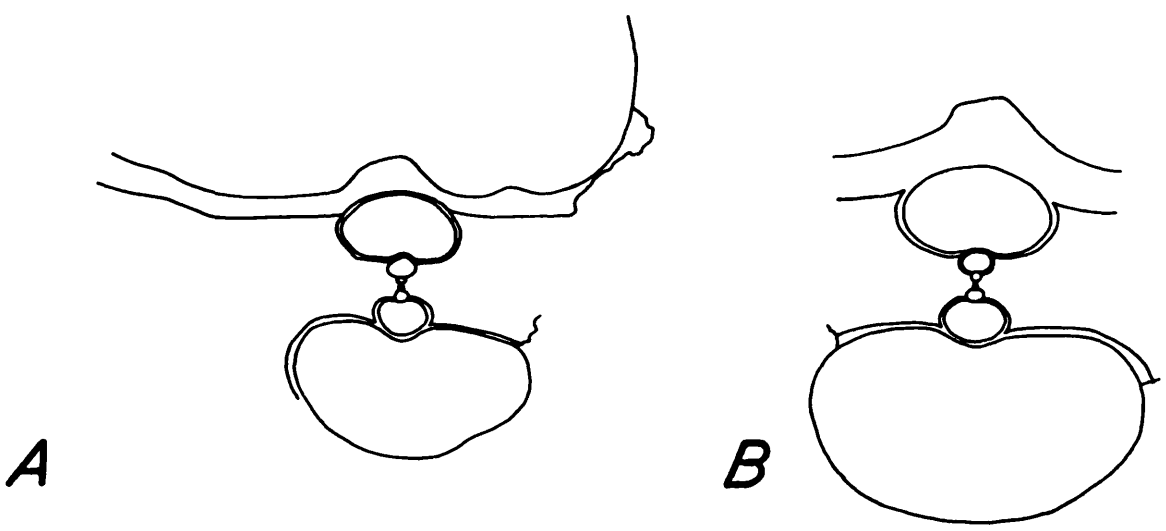
Camera lucida drawing of transverse polished section showing apertural boss, x6.5.

C. Allometry in Anapetopsis gen. nov.

Plots of length (l), whorl width (w) and height of whorl along the median plane of symmetry (ih) against growth measured as successive half whorls in Anapetopsis maclearni gen. et sp. nov. and Anapetopsis lalajae gen. et sp. nov. The change in whorl profile is shown by the divergence of w and ih with increased growth.

Measurements were made in millimetres on the shell interior of the specimens illustrated in A and B, above, and do not include the imperfectly preserved, widely expanded late growth stage. The numbers applied to the successive half whorls of the horizontal axis are arbitrary and their equivalence from one species to the other is not precise.

Text-fig. 10



**C**

ontogenetic increase in whorl width relative to total length (Raupian S, Z and W increasing with growth) and an accompanying slight relative narrowing of the umbilici (Raupian D decreasing), prior to the widely expanded final growth stage (for explanation of Raupian parameters see text-fig. 5A).

Anapetopsis lalajae sp. nov.

(Pl. II, figs. 13, 16, 17; Pl. III, figs. 1, 4, 7, 10, 11)

Bucanopsis sp.; McLearn, 1924, p. 141, Pl. XX, fig. 20.

Holotype. Stonehouse Fm., USNM 169595 from Schuchert Colln. 53

Paratypes. Stonehouse Fm., USNM 169596 from Schuchert Colln. 53; GSC 3140 from Arisaig shore, figured by McLearn (1924).

Other figured material. Two specimens from the Stonehouse Fm. tentatively assigned here: USNM 169467 from Schuchert Colln. 49A; GSC 32781B on a slab from GSC locality 1302, Arisaig.

Additional material. Poorly preserved specimens from the Stonehouse Fm., Bambach collections A3700(488), A3724(415); Schuchert Colln. 49D.

Description. Species of Anapetopsis gen. nov. with four or five whorls. Early whorls rounded. Intermediate growth stages initially with uniformly convex dorsum passing angularly at midwhorl height onto flattened, adumbilically sloping umbilico-lateral walls. Whorl profile becoming subelliptical at about three whorls. Late

growth stage widely expanded, with explanate margins probably subcircular in plan and extending posteriorly beyond the earlier coiled whorls. Interior of aperture with prominent transverse thickening at commencement of the widely expanded stage. Umbilici phaneromphalous, of moderate width; whorl embracement at about two thirds of the height of the impressed whorl, with deep sutural indentation. Dorsum sinuate, a deep wide sinus passing into a short slit. Nature of selenizone unknown. Ornamentation of wrinkled spiral lirae and fine growth elements, the latter dominating on the explanate margins. Shell thin but with thickening of the umbilical walls and formation of an apertural boss in later growth stages; shell structure unknown.

Discussion. Anapetopsis lalajae differs from the type species, A. maclearni, in having a wider whorl profile and deeper sinus. Internal moulds of the latter species show an apparently more abrupt transition from the earlier whorls to the later widely expanded stage than is seen in A. lalajae due to the more pronounced transverse and lateral thickening of the shell interior. In GSC 3140 (Pl. II, figs. 13, 16) a deep V-shaped channel is present on the internal mould immediately posterior to the transverse thickening and a similar, but less well developed, structure is seen in the holotype (Pl. II, fig. 17). No equivalent structure has been observed in A. maclearni. In USNM 169596 (Pl. III, figs. 4, 10) two pairs of depressions on the dorsal surface of the internal mould, produced by increased deposition on the inside of the shell, likewise find no equivalent in A. maclearni.

The significance of the constrictive shell thickenings in A. maclearni and A. lalajae is not known. Horný (1963) observed the occurrence of similar transverse elements in Strangulites

TEXT-FIG. 11

A. Ontogenetic variation in Raupian parameters in Anapetopsis gen. nov., (for explanation of W, D, S and Z see text-fig. 5A and discussion in text following description of Plectonotus boucoti sp. nov., above).

Measurements were made in millimetres on the shell interior of the specimens illustrated in text-fig. 10A, 10B and do not include the imperfectly preserved, widely expanded late growth stage.

B. Phragmosphaera sp., USNM 169600.

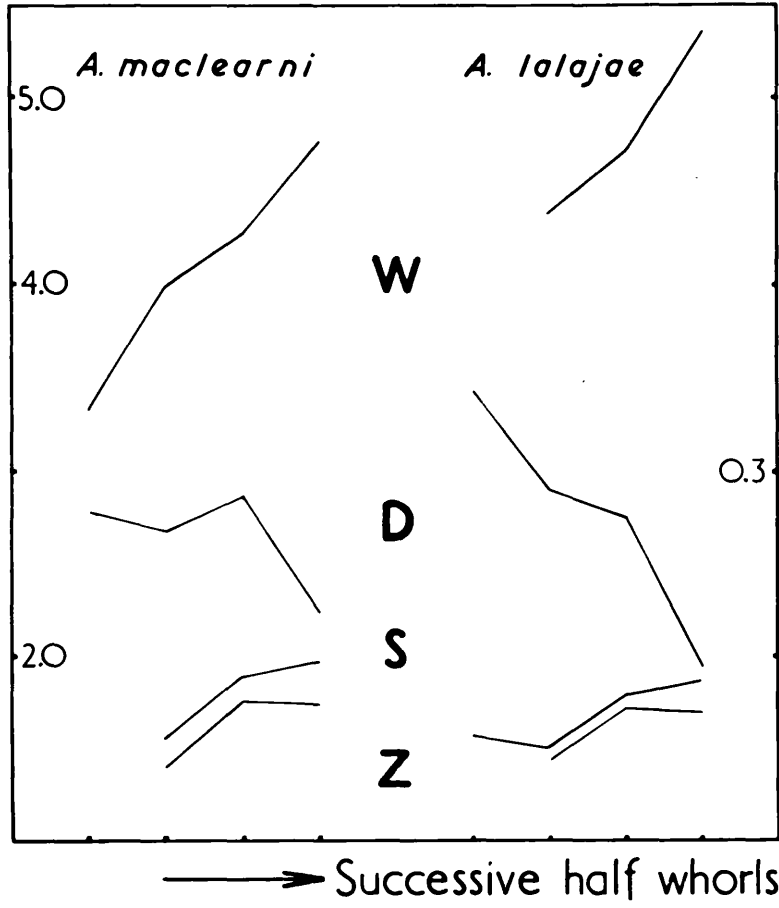
Camera lucida drawing of median polished section showing the parietal deposit within the aperture, x6.25.

C. Phragmosphaera sp., USNM 169597.

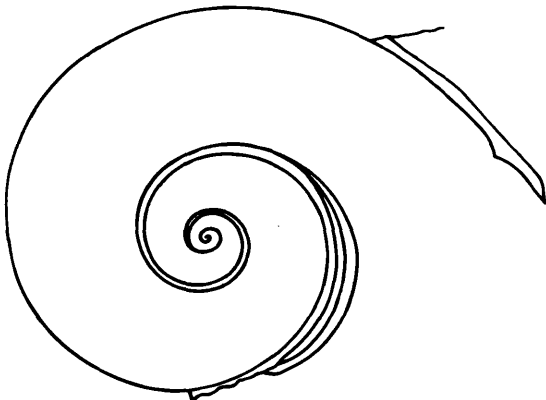
Reconstruction of transverse section from obliquely polished specimen, x6.25.

Text-fig. 11

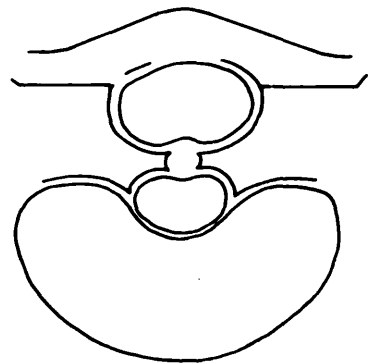
A



B



C



strangulatus (Perner, 1903) from the lower Ashgill Králuv Dvur Beds of Bohemia but thought it unlikely that they were of any taxonomic significance.

The only available transverse section of A. lalajae, USNM 169596, indicates a slight increase in whorl width relative to total length (Raupian S, Z and W increasing), prior to the final expanded stage, and a more pronounced relative narrowing of the umbilici (Raupian D decreasing), in similar fashion to A. maclearni (text-figs. 10B, 10C, 11A).

There are several crushed specimens in shale from the Stonehouse Fm. which are tentatively assigned to A. lalajae. One specimen, USNM 169467, Pl. III, Fig. 11, has the aperture preserved and shows a deep sinus passing into a short slit. There is a shallow posterior emargination and a small scar on the floor of the whorl is reminiscent of the better developed structure characteristic of Ptomatis patulus (Hall, 1843) of Rollins (1966, figs. 1-3) and Knight (1941, Pl. 7, figs. 1d, e).

Subfamily CARINAROPSINAE Ulrich and Scofield, 1897

Genus BUCANOPSIS Ulrich in Ulrich and Scofield, 1897

Type species. Bucanopsis carinifera Ulrich and Scofield, 1897.

Bucanopsis sp.

(Pl. I, figs. 15, 20, 23)

Figured material. Doctors Brook Fm., USNM 169465, USNM 169466 from USNM Colln. 10919.

Additional material. Beechhill Cove Fm., USNM Colln. 10115; USNM Colln. 10819 from Wallace Brook, Pictou Co. Upper Ross Brook Fm., Bambach Colln. A3592(95). Doctors Brook Fm., USNM Colln. 10919. Lower McAdam Brook Fm., Bambach Collections A3604(181), A3606(187), A3607(180), A3608(183), A3616(197), A3620(209), A3811/A3815(198), A3820(196), A3826(226).

Discussion. Several internal moulds from the Beechhill Cove and Doctors Brook Formations are characterised by subglobose shell form and narrow, open umbilici. A groove on the floor of the internal mould indicates a carina on the floor of the whorl. One specimen (USNM 169466; Pl. I, figs. 20, 23) illustrates the gently convex dorsal lip with a narrow sinus passing into a short slit. A larger example has the dorsal band consisting of a slight depression between two spiral cords (USNM 169465; Pl. I, fig. 15). Ornamentation and characters of the shell are unknown.

Fragments of shale from the Upper Ross Brook and Lower McAdam Brook Formations show many crushed examples of the same genus. The selenizone varies from depressed to slightly raised and reticulate ornamentation is prominent.

As Horný (1963) has observed, Bucanopsis is a poorly understood genus although the name has been widely used for species with reticulate or spiral ornamentation throughout the Palaeozoic. Devonian-Permian species formerly referred to the genus are now generally considered to belong to Retispira Knight, 1945 which lacks the carina on the floor of the whorl. The type species, Bucanopsis carinifera, is from the middle Ordovician of Kentucky but the status of many Ordovician and Silurian <sup>species</sup> is in great need of reinvestigation.

Genus PHRAGMOSPHAERA Knight, 1945

Type species. Phragmosphaera miranda Knight, 1945.

Discussion. Rollins in Rollins, Eldredge and Spiller (1971) transferred Phragmosphaera from the Carinaropsinae to the Knightitinae, as a subgenus of Patellilabia Knight, 1945. He considered the plate-like extension of the inductura into the aperture to be closely related to the tooth-like apertural boss of Patellilabia and unlike the so called apertural diaphragm of the Carinaropsinae. In spite of Rollins' elucidation of the structure of the inductura developed on the parietal wall of Phragmosphaera, it is not thought that the genus is better placed within the Knightitinae and retention within the Carinaropsinae, as proposed by Knight et al (1960), is preferred.

Phragmosphaera sp.

(Pl. I, figs. 1-3, 6, 7, 11, 12)

Figured material. Moydart Fm., Green Member, USNM 169597, USNM 169598, USNM 169599, USNM 169600, USNM 192113 from Schuchert Colln. 52B.

Additional material. Moydart Fm., Green Member, Schuchert Colln. 52B; Jones Colln. Ar Mo 4820. (15 specimens).

Description. Species of Phragmosphaera Knight, 1945 with about three and a half whorls. Early whorls poorly known; seemingly well rounded with slight arching of the median dorsal area. Later whorls becoming subreniform with whorl width almost twice whorl height;

maximum width at one third of whorl height. Dorso-lateral surfaces uniformly shallowly convex increasing suddenly in curvature with passage into the deep umbilici. Whorl embracement is just above point of maximum width of previous whorl producing deep sutural indentation (text-fig. 11C). Latest growth stage with rapid lateral and posterior expansion of aperture; possible anterior expansion unknown. Aperture poorly known; dorsum with a wide deep sinus passing into a slit of unknown depth. Late growth stage with shell thickenings within the aperture which produce a pair of transverse channels on the dorsum of the internal mould. At commencement of expanded stage an obliquely transverse thickening of the shell interior, with steep apertural edge and more shallow abapertural edge, converges on the median dorsal area from each lateral margin of the whorl; parietal inductura thickened to form apertural boss (text-fig. 11B), the lateral areas of which form a plate-like extension into the aperture. Selenizone wide, slightly raised; upper surface concave between spiral cords. Ornamentation of spiral lirae and transverse growth lines. Shell thin; structure unknown.

Discussion. This species differs from Phragmosphaera lyra (Hall, 1861) of Rollins in Rollins, Eldredge and Spiller (1971) from the Devonian of New York State in having a deeper dorsal sinus and less prominent spiral ornamentation. An internal mould described by Sowerby in Murchison (1839 Pl. 3, Fig. 15), from the Ludlovian of the Welsh Borderlands as Bellerophon globatus, has similar proportions to the Arisaig species and exhibits transverse channels on the dorsum comparable to those described in the Arisaig specimens. M'Coy in Sedgwick and M'Coy (1855) thought that there could be 'not the slightest doubt of the propriety of uniting' B. globatus with B. expansus Sowerby in Murchison, 1839, the former being a

juvenile of the latter. Reed (1921) commented that the type of B. globatus was not to be found in the Geological Society Collection (in the Institute of Geological Sciences) which contains most of the types of Sowerby in Murchison (1839), so its relationship with B. expansus could not be established. Until such time as a revision of Sowerby's two species is attempted, further comparison with the specimens from the Moydart Fm. is not possible.

Subfamily CYMBULARIINAE Horný, 1963

Genus CYMBULARIA Koken, 1896

Type species. Cymbularia galeata Koken, 1896.

Cymbularia carinata (Sowerby in Murchison, 1839)

(Pl. III, figs. 2, 5)

Bellerophon carinatus Sowerby in Murchison, 1839, p. 604,

pl. 3, figs. 4, 1d.

Cymbularia carinata; Reed, 1921, p. 64-66, Pl. X, fig. 12.

Bellerophon lenticularis Grönwall, 1897, p. 237, (nom. nud.).

B. lenticularis Moberg & Grönwall, 1909, p. 43, Pl. III,

fig. 12a, b.

Figured material. Moydart Fm., Green Member, USNM 169574, USNM

169575 from Schuchert Colln. 52B.

Additional material. Moydart Fm., Green Member, Schuchert Colln. 52B;

Jones Colln. Ar Mo 4820. (4 specimens).

Description. Species of Cymbularia Koken, 1896 with about four whorls. Early whorls poorly known but seemingly sublanceolate with dorso-latero-umbilical areas uniformly convex, becoming concave immediately adjacent to base of dorsal keel. Whorl profile of later whorls subtrigonal with prominent dorsal keel; dorso-lateral areas shallowly convex, becoming parallel to axis of symmetry and forming maximum whorl width at about one third of whorl height, just above the prominent umbilical shoulders. Umbilical walls flattened at this stage. Whorl embracement great with much of the previous whorl and the strong dorsal keel projecting into the body chamber of the following whorl. Umbilici cryptomphalous; a thick inductural deposit filling the umbilici and extending onto the lower lateral whorl surfaces; pseudo-umbilici narrow, may be deep. Dorsum sinuate, the deep sinus apparently culminating in a narrow slit of unknown depth; selenizone forming the flat upper surface of the keel. Ornamentation poorly known, seemingly of growth lines. Shell of moderate thickness but with strong thickening of the umbilical area by the inductural deposits; shell structure unknown.

Discussion. The type of Cymbularia carinata (Sowerby in Murchison, 1839) from the Ludlovian of Britain is an internal mould, in the Geological Society of London Collection of the Institute of Geological Sciences, which provides little information concerning the shell exterior. In contrast, the material described as Bellerophon lenticularis by Moberg and Grönwall (1909) from the "Öved-Ramsåsa series of Scania, Sweden is finely preserved. The Arisaig material, although poorly preserved, may provide a link between the two in terms of shell morphology since it would appear that specimens referred to B. lenticularis are juveniles of C. carinata. Increase in ontogeny produces a relative increase in

whorl width which obscures the lenticular form of earlier growth stages. Reed (1921) noted the existence of such a 'narrow lenticular much compressed form with ... very acute angular dorsum, very small umbilicus and large outer whorl' associated with C. carinata but thought that these specimens might prove to be distinct from the latter. Moberg and Grönwall (1909) stated their awareness of the similarity between the two species, and also of the difficulties involved in making comparison between different modes of preservation, but were of the opinion that they could detect differences in apertural shape and coiling between their specimens and Sowerby's illustrations. B. lenticularis is here considered to be a junior synonym of C. carinata. If the separate identity of B. lenticularis is recognised it should be noted, after Reed (1921), that the name Cymbularia lenticularis is preoccupied by a species of Koken (1897).

Of other species, C. carinata is similar to Joleaudella mansuyi Patte, 1929 from the Silurian or Devonian Schistes de Ban Hom, Région de Van Yen, Tonkin. Knight et al (1960) considered Joleaudella to be a junior subjective synonym of Tropidodiscus Meek and Worthen, 1866 but Patte's genus is readily distinguished from Tropidodiscus by its narrow umbilici and cymbularioid emargination. In contrast with Joleaudella, C. carinata has closed umbilici, is less compressed laterally and lacks the crenulated lamellose ornamentation.

As with other material from the Green Member of the Moydart Fm., the specimens of C. carinata are preserved as internal moulds in thinly bedded limestones. Features of the emargination and ornamentation are consequently obscure although a narrow median band on the dorsum indicates the location of the selenizone. The closed umbilici and dorsal keel are best seen in transverse section (text-fig. 4D).

Cymbularia sp.

(Pl. I, figs. 10, 13, 14)

Figured material. Doctors Brook Fm., USNM 169464 from USNM Colln.

10919. Lower McAdam Brook Fm., YPM 28329 from Bambach Colln.

A3623(223).

Additional material. Two specimens from each of the above collections.

Discussion. Fragmentary internal moulds from the Doctors Brook Fm. show the typical cymbularioid configuration of a wide dorsal emargination, with a deepened inner portion, passing into a narrow median slit. The dorsal profile is asymmetric and angulated at the selenizone; the aperture is about twice as wide as high, while the umbilici are narrow. Specimens crushed in shale from the Lower McAdam Brook Fm. show essentially the same form but lack ornamentation, with the exception of four spiral threads on the selenizone of one example.

Subfamily TROPIDODISCINAE Knight, 1956

Genus TROPIDODISCUS Meek and Worthen, 1886

Type species. Bellerophon curvilineatus Conrad, 1842.

Tropidodiscus (?) sp.

(text-fig. 4E)

Figured material. Doctors Brook Fm., USNM 169586 on a transverse thin-section associated with Plectonotus boucoti from USNM Colln. 10165(141).

Additional material. BM PG5009, a small internal mould (not illustrated) from a limestone band in the basal Wenlock of Brinkmarsh Quarry, Tortworth Inlier, Gloucestershire, collected by Mr. David J. Siveter. Doctors Brook Fm., a further specimen on the same thin-section as the illustrated specimen and three specimens on a transverse polished section associated with P. boucoti, USNM 188526 from USNM Colln. 10165(141).

Discussion. In the course of preparation of cross-sections of Plectonotus boucoti sp. nov. from the Doctors Brook Fm., a number of minute bellerophontaceans were observed on polished surfaces and in thin section. While juveniles of P. boucoti were readily distinguished, several specimens clearly belonged to a laterally compressed form which has not otherwise been recognised. A maximum of four whorls has been seen, of which the earliest two and a half are transversely lenticular with whorl width greater than whorl height. The third and fourth whorls show pronounced dorsal expansion to produce a highly vaulted profile, whorl height exceeding whorl width. At this latter stage, the umbilical walls become flattened and considerably thickened while the median dorsal area is flat and bears a strongly angular relationship to the dorso-lateral areas, suggesting the presence of a selenizone.

The species is also present in samples from the basal Wenlock of Brinkmarsh Quarry, Tortworth, Gloucestershire which were collected and prepared in search of ostracodes by Mr. David Siveter, University of Leicester. The gastropods are preserved as phosphatised

moulds and form part of the residue left after acid treatment of samples.

Microceras Hall, 1845 was proposed for a morphologically similar species which may be locally abundant in rocks of Ordovician to Devonian age. The type species, M. inornatum Hall, 1845, was described from the upper Ordovician of Cincinnati. Ulrich and Scofield (1897) considered many of the specimens examined by themselves to be adults of small bellerophontacean species but Knight (1941) expressed conviction that all Hall's specimens of the type species from Cincinnati were embryos. In an attempt to remove the taxonomic uncertainty, Knight (1941) selected as lectotype of M. inornatum a specimen which he considered to be 'almost certainly a young Cyrtolites so that Hall's name may rest comfortably in the synonymy of Conrad's earlier name...'

The small size of the specimens from Arisaig and Tortworth (length less than 2mm.) might be considered as support for an interpretation as the nuclear whorls of some macrogastropod. However, the well marked ontogenetic change between the second and third whorls suggests that the specimens are mature individuals of some species of microgastropod. The profile of the last one and a half whorls is not one that would be expected in the nucleus of a bellerophontacean, which more usually resembles the earliest whorls of the present species.

It is clearly not possible to refer the described specimens to Microceras. The widely phaneromphalous umbilici and lenticular form suggest the macromorphic Tropidodiscus Meek and Worthen, 1886, to which tentative assignment is made while recognising the discrepancy in size.

## Undetermined bellerophontacean genera and species

(Pl. I, figs. 4, 5, 8, 9, 26)

Described and figured material. Undetermined bellerophontacean genus and sp. A, USNM 188525 associated with figured specimens of Arjamannia cancellatula and Longstaffia centervillensis in a small slab from USNM Colln. 10115, Beechhill Cove Fm. Undetermined bellerophontacean genus and sp. B, USNM 169488 associated with a figured specimen of Longstaffia sp., USNM Colln. 10115 from the Beechhill Cove Fm. Undetermined bellerophontacean genus and sp. C, YPM 28348 from Bambach Colln. A3777(118), French River Fm. in Pictou Co. Undetermined bellerophontacean genus and sp. D, GSC 6216 from Stonehouse Fm. at Arisaig. Undetermined bellerophontacean genus and sp. E, GSC 3139a, Arisaig, locality unknown.

Discussion. Several specimens discussed here are too imperfectly known to merit more formal description. Species A, not figured, is a single fragmentary internal mould with rapidly expanding whorls and narrow umbilici. Ornamentation, other than strong growth lines in the latest stages, is not known but the floor of the whorl bears a deep groove presumably corresponding to a flat topped carina on the previous whorl. An obscure band apparently represents the same structure on the final whorl.

Species B, not figured, is a large laterally compressed form with a rounded dorsum. The umbilici are narrow but the groove on the floor characteristic of the previous species is not present.

Species C, Pl. I, fig. 26, has a rapidly expanding shell with many fine spiral lirae. The crushed specimen shows a shallow median sinus culminating in a slit which generates a selenizone.

Species D, Pl. I, figs. 4, 5, was referred by McLearn (1924, p. 141, Pl. XX, figs. 13, 14) to Bucania Hall, 1847. The dorsum is flattened with whorl height about half of whorl width. The degree of whorl impression is relatively great while the umbilici are closed, precluding retention in the widely phaneromphalous Bucania. Details of the emargination and the ornamentation are unknown.

Species E, Pl. I, figs. 8, 9, is a poor internal mould supposedly collected at Arisaig by Honeyman. Its preservation in a buff, coarsely crystalline limestone is unlike any other examined specimen from Arisaig and, in view of the imprecise locality information, its occurrence should be noted with caution. The dorsum is arched medially and the aperture a little expanded just prior to the anterior breakage.

Suborder MACLURITINA Cox and Knight, 1960

Superfamily MACLURITACEA Fischer, 1885

Family ONYCHOCHILIDAE Koken and Perner, 1925

Subfamily and Genus undetermined

'Holoepa' reversa Hall, 1860

(Pl. VI, figs. 16, 20)

Holoepa reversa Hall, 1860, p. 154, fig. 14.

do. ; Dawson, 1868, p. 605, fig. 211

do. ; McLearn, 1924, p. 148.

Holotype. Stonehouse Fm., AMNH 1648 from Arisaig, labelled "Clinton Group".

Discussion. The holotype and only known example of this species is a partially embedded sinistral internal mould showing about three whorls, probably referable to the Onychochilidae. However, without evidence concerning the shell ornamentation, more precise placement is not possible. Mimospira abbae, below, is higher spired with more whorls and possesses strong opisthocline costae. No such costae can be discerned at this time in the cross-section of the thick shell visible around the margins of the internal mould in 'H'. reversa. There is some indication, from the impression of the shell margin, that the outer lip in 'H'.reversa is convex immediately adjacent to the suture with the previous whorl, in contrast to the opisthocline condition in M. abbae. Versispira contraria Perner, 1903 from the Bohemian Ordovician has comparable shell proportions and possibly a similar outer lip but the ornamentation is also unknown in this species. The Middle Devonian Hyperstrophomena devonicans Horný, 1964 is comparable in gross form but has prominent spiral ornamentation.

Superfamily CLISOSPIRACEA Miller, 1889

Family CLISOSPIRIDAE Miller, 1889

Subfamily CLISOSPIRINAE Miller, 1889

Genus MIMOSPIRA Koken and Perner, 1925

Type species. Onychochilus helmhackeri Perner, 1900.

Discussion. On the basis of undescribed specimens in the U.S. National Museum from the upper Ordovician of Sweden, the genus Mimospira is interpreted as a hyperstrophically coiled gastropod. The Swedish specimens compare well with Perner's (1900) illustrations

and show the essential characters of the basal spire, the concave umbilical surface and the prominent transverse costae. There is apparently no 'frill-like lamella' projecting from the whorl periphery as in Clisospira Billings, 1865 or Ferroggyra Horný, 1964.

Mimospira abbae sp. nov.

(Pl. VI, figs. 19, 21-23)

Holotype. McAdam Brook Fm., USNM 169489 from USNM Colln. 11183 at Molson's Brook, Lochaber, Antigonish Co.

Other figured material. Moydart Fm., USNM 169571 from USNM Colln. 10183(315).

Description. Species of Mimospira Koken and Perrier, 1925 with three whorls. Nature of umbilicus and umbilical surface unknown. Protoconch consisting of initial half whorl; seemingly bulbous at first, thereafter laterally compressed with coiling axis almost perpendicular to teleoconch axis. Teleoconch with uniformly convex whorl face between successive sutures; whorl embracement at periphery of previous whorl with moderate sutural indentation. Shape of aperture poorly known; obscure growth lines paralleling ornamentation indicate an opisthocline outer lip. Ornamentation of obscure growth elements on the protoconch which appear oblique to the strong costae of later growth stages due to the change in coiling direction. Teleoconch with opisthocline costae which take half a whorl to traverse the whorl face between successive sutures; costae sharp, with concave sides; ornamentation relatively most strongly developed on penultimate whorl. Shell thickness and

structure unknown.

Discussion. Mimospira abbae is distinguished from M. helmhackeri (Perner, 1900) from the Ordovician of the Baltic by its lower basal spire and fewer, more widely spaced costae. M. turrita Koken and Perner, 1925 is a higher spired trochoidal form probably more closely related to Trochoclisia Horný, 1964. A fragment in the U.S. National Museum from the lower Silurian Brassfield Fm. of Tennessee indicates a lower spired shell with more abundant, finer costae.

The holotype of M. abbae is of interest in that the heterostrophic protoconch is preserved. Perner (1900, text-fig. 2) illustrated similar coiling in the type species, whilst reference to the previously mentioned Ordovician specimens from Sweden adds further confirmation. The protoconch is an open coiled half whorl which, by way of a perpendicular change in direction of the axis of coiling, assumes the hyperstrophic form of the teleoconch.

In conjunction with the Brassfield Fm. specimen, M. abbae represents the first Silurian record of Mimospira.

Suborder PLEUROTOMARIINA Cox and Knight, 1960

Superfamily PLEUROTOMARIACEA Swainson, 1840

Family SINUOPEIDAE Wenz, 1938

Subfamily PLATYSCHISMATINAE Knight, 1956

Genus UMBOSPIRA Perner, 1903

Type species. Umbospira nigrans Perner, 1903.

Umbospira sp.

(Pl. VIII, fig. 5)

Figured material. Upper Ross Brook Fm., YPM 28330 from Bambach Colln. A3582(86).

Additional material. Five other specimens in the same collection.

Discussion. Although crushed in shale, the upper surface of the whorl of this species appears more convex than one would expect for Liospira Ulrich and Scofield, 1897, where McLearn (1924, p. 144) seems to have placed similar specimens. Several examples show a distinct crack parallel to the suture due to crushing which, in the absence of growth lines, might be misinterpreted as the upper margin of a selenizone of the type seen in Liospira. In only one specimen (YPM 28330; Pl. VIII, fig.5) is the apertural margin preserved and here the lip sweeps forwards slightly before curving into the deep, narrow sinus. The emargination is located above the whorl periphery and the crack parallel to the suture approximately corresponds to its upper edge.

Family RAPHISTOMATIDAE Koken. 1896

Subfamily LIOSPIRINAE Knight, 1956

Genus LIOSPIRA Ulrich and Scofield, 1897

Type species. Pleurotomaria micula Hall, 1862.

Liospira marklandensis McLearn, 1924

(Pl. VII, figs. 1-4)

Liospira marklandensis McLearn, 1924, p. 144, Pl. XX,  
figs. 23, 24.

Holotype. Stonehouse Fm., GSC 5654 collected at Arisaig by  
Honeyman.

Other figured material. Stonehouse Fm., USNM 169572 from  
USNM Colln. 10206(501); USNM 192114 from Schuchert Colln. 53.

Additional material. Stonehouse Fm., USNM Collections  
10206(501), 10910(496); Bambach Collections A3703(472),  
A3708(458), A3657(457); Twenhofel Collections 12-17/3032(482),  
14/3032(477), 15/3032(474), 19a<sup>4</sup>/3032(411), 19a<sup>5</sup>/3032(412),  
19a<sup>8</sup>/3032(423), 19a<sup>12</sup>/3032(426), 19a<sup>13</sup>/3032(427),  
19a<sup>14</sup>/3032(432), 20c/3032(395), 24a/3032(380), 24i/3032(371);  
Schuchert Colln. 53, (total of 45 specimens).

Description. Species of Liospira Ulrich and Scofield, 1897  
with about five adpressed whorls. Whorl profile subrhomboid  
with peripheral angulation at midwhorl height separating  
flattened upper whorl surface from uniformly convex base;

umbilical walls convex with marked angular relationship to base in later growth stages. Upper whorl surface relatively more convex in early growth stages, becoming flattened with increase in ontogeny such that commonly slightly concave in large individuals. Umbilicus closed to varying degrees by a thick callus; funicle may be developed on umbilical shoulder. Embracement of previous whorl at, or just above, whorl periphery producing very shallow sutural indentation; deep indentation of internal suture within umbilicus. Inner lip unknown; outer lip with deep emargination. Growth lines curving forwards with forward convexity until, at two fifths of the distance to the periphery, commence to curve back to form the sinus which is one eighth of the final whorl circumference in depth. Sinus passing into a peripheral slit of unknown depth. Selenizone obscure, with fine bordering threads; ornamentation of fine spiral striae and obscure concave lunulae. Shell ornamentation of fine growth lines and spiral striae. Shell thin with thickening of inner lip to form funicle and of sutural area due to the adpressed whorls. Shell structure unknown.

Discussion. The prosoclyt growth lines on the upper whorl surface are characteristic of this species and serve to distinguish it from Liospira affinis (Foerste, 1885) or any of the species described by Lindström (1884), Longstaff (1924) or Pitcher (1939). In these species, the growth lines are prosocline, curving obliquely backwards below the suture without any forward projection.

The degree of closure of the umbilicus would seem to be variable. In USNM 169572 the umbilicus appears to be completely closed by a callus deposit which also produces great thickening of the columellar lip (text-fig. 12A). A

TEXT-FIG. 12

A. Liospira marklandensis McLearn, 1924, USNM 169572.

Camera lucida drawing of transverse polished section showing the closed umbilicus, x6.25.

B. Platyceras (Platystoma) cornutum (Hisinger, 1837), GSC 33271.

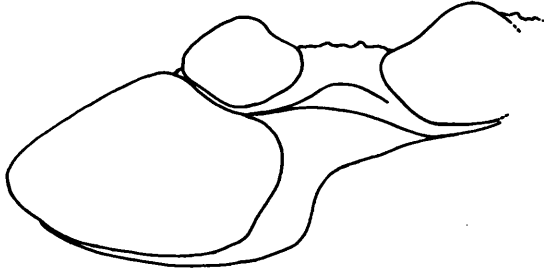
Sketch of lateral view showing irregular growth lines of outer whorl surface. The minor emarginations probably correspond to the shape of the echinoderm calyx to which the gastropod clung, x2.5.

C. Murchisonia (?Hormotoma) arisaigensis (Hall, 1860), USNM 192122.

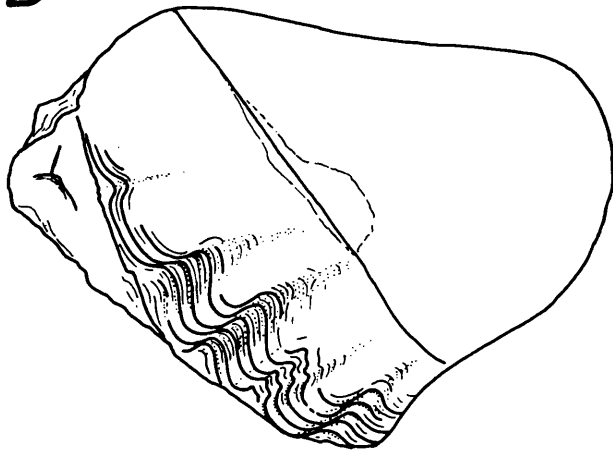
Camera lucida drawing (oblique lateral view) of internal mould showing crescentic striations of muscle attachment scar, x6.25.

*Text-fig. 12*

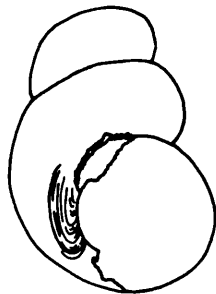
**A**



**B**



**C**



slight swelling corresponds to the funicle seen in larger specimens. In other specimens the umbilicus is phaneromphalous with just local thickening of the columellar lip.

Liospira cf. L. affinis (Foerste, 1885)

(Pl. VII, figs. 10, 11, 14)

Liospira cf. affinis; McLearn, 1924, p. 144, Pl. XX,  
figs. 26, 27.

Figured material. Beechhill Cove Fm., YPM 480A, YPM 480 B on a small slab from Rory McDonald's Brook of McLearn (1924) and earlier authors ( McGillivray Brook of Boucot et al, in press, and current usage (text-fig. 3).

Additional material. Beechhill Cove Fm., USNM Collections 10114(1), 10115, (15 specimens).

Description. Species of Liospira Ulrich and Scofield, 1897 with about four whorls. Whorl profile rhomboid with a peripheral angulation at midwhorl height forming the junction of the flattened inclined upper whorl surface and the seemingly convex base. Upper whorl surface becoming slightly concave near periphery in latest growth stages. Whorls adpressed with linear sutures producing a conical spire. Umbilical characters unknown. Aperture poorly known; outer lip seemingly with a deep sinus passing into a slit which generates an obscure selenizone on the upper surface of the peripheral angulation; growth lines below the periphery initially curving strongly forwards. Ornamentation poorly known, seemingly of fine growth lines. Shell thin, structure

unknown.

Discussion. Liospira cf. L. affinis (Foerste, 1885) differs from L. marklandensis McLearn, 1924 from the Stonehouse Fm. in having a more perfectly conical spire which is relatively more elevated. In the latter, the incremental angle approaches one hundred and fifty degrees whereas in L. cf. L. affinis the angle is some thirty degrees less. The shape of the lip above the selenizone is not known in the Arisaig specimens but type materials of Foerste's species from Ohio show a prosocline lip as distinct to the prosocyrt condition in L. marklandensis. L. cornovica Pitcher, 1939, from the upper Llandovery of Shropshire seems to have a less strongly convex base with the periphery being consequently lower on the whorl.

The specimen figured by McLearn (1924), YPM 480A (Pl. VII, fig. 10), is a poor internal mould. Preparation of another specimen on the same slab, YPM 480B (Pl. VII, figs. 11, 14), produced an almost complete external mould showing the conical spire and supraproperipheral band.

Family EOTOMARIIDAE Wenz, 1938

Subfamily EOTOMARIINAE Wenz, 1938

Tribe EOTOMARIIDES Wenz, 1938

Genus EOTOMARIA Ulrich and Scofield, 1897

Type species. Eotomaria canalifera Ulrich in Ulrich and Scofield, 1897.

Eotomaria sp.

(Pl. VII, figs. 5, 6, 8)

Figured material. Glencoe Brook Fm., USNM 169463 from USNM Colln. 11267, NE of Kerrowgare, Pictou Co. Middle Ross Brook Fm., YPM 76 from Bambach Colln. A3731(11).

Discussion. The two poorly preserved specimens placed here lack the apical and apertural portions but each shows parts of two whorls. The subrhomboid whorl profile has a slightly concave upper whorl surface passing, by way of a pronounced peripheral angulation at midwhorl height, onto a uniformly convex base. Whorl embracement is subperipheral producing deep sutural indentation. Umbilical characters are unknown. Apertural details are obscure but prosocline growth lines on the base indicate a deep sinus probably passing into a slit at the peripheral angulation. Other ornamental characters are unknown. There is some degree of similarity with the species described by Foerste (1923) as Lophospira ehlersi from shales of lower Llandovery age below the Brassfield limestone of Centerville, Ohio. However, the latter is higher spired and has an obscure angulation on the base below the peripheral selenizone.

Family LOPHOSPIRIDAE Wenz, 1938

Subfamily LOPHOSPIRINAE Wenz, 1938

Genus LOXOPLOCUS Fischer, 1885

Type species. Murchisonia tropidophora Whiteaves, 1886

Subgenus LOXOPLOCUS (LOPHOSPIRA) Whitfield, 1886

Type species. Murchisonia bicincta Hall, 1847.

Loxoplocus (Lophospira) sedgwickii (Donald, 1906)

(Pl. VII, fig. 19)

Lophospira Sedgwickii Donald, 1906, p. 562, Pl. XLIII,  
figs. 11, 12.

Figured material. Beechhill Cove Fm., USNM 169481 from USNM Colln. 10819 at Wallace Brook, Pictou Co.

Additional material. A further specimen from the same collection.

Description. Relatively high spired species of Loxoplocus (Lophospira) Whitfield, 1886 with about six whorls. Nature of umbilicus and nuclear whorls not known. Whorl profile with a flange at just above midwhorl height of the final whorl, slightly below the middle of the exposed face of earlier whorls; upper edge of flange forming periphery of whorl. Upper whorl surface concave with a spiral cord immediately below the suture. Below periphery, flat outer surface of flange sloping down and inwards, towards base of whorl prior to passing by way of obtusely angled lower edge onto concave outer whorl surface; a prominent angulation developing at junction between outer whorl face and convex base. Whorl embracement at the angulation between the base and outer whorl surface, producing little or no sutural indentation. Shape of aperture and nature of outer lip unknown; outer surface of flange possibly the locus of a selenizone or pseudoselenizone. Ornamentation, structure and thickness of shell unknown.

Discussion. The Arisaig specimens agree closely with the description of Donald (1906) except in the presence of the flat outer surface of the flange of which she makes no mention. Donald (1906) recorded the species from Mulloch Hill,

Ayrshire in strata also of lower Llandovery age.

Loxoplocus (Lophospira) sp. A

(Pl. VII, fig. 15)

Figured material. Beechhill Cove Fm., USNM 169482 from USNM Colln. 10115.

Description. Species of Loxoplocus (Lophospira) Whitfield, 1886 with about four whorls. Early whorls unknown. Later whorls with prominent flange the peripheral upper edge of which is at three fifths of height of final whorl, at middle of exposed face of earlier whorls. Upper whorl surface concave, becoming convex immediately below suture with previous whorl to produce, in detail, narrow but deep sutural indentation. Upper surface of flange flat, sloping out and downwards towards the shell periphery; outer surface of flange shallowly concave between acute peripheral edge, above, and obtusely angular junction with outer whorl surface, below. Outer whorl surface concave and passing by way of pronounced angulation onto uniformly convex base. Whorl embracement just below angular junction of outer whorl surface and base. Aperture poorly known; inner lip seemingly thickened and reflexed over minute umbilical perforation; obscure growth lines on upper whorl surface indicating deep sinus, possibly with a slit on the outer surface of the flange. Ornamentation poorly known, seemingly of growth lines. Shell thickness and structure unknown.

Discussion. This species differs from Loxoplocus (Lophospira) sedgwickii (. Donald, 1906), above, in being lower spired

and having a more strongly defined flange. In addition, in the latter the periphery is lower on the whorl face.

Loxoplocus (Lophospira) sp. B

(Pl. VII, fig. 7)

Figured material. Beechhill Cove Fm., USNM 169485 from USNM Colln. 10114 (1).

Discussion. This species is known only from an external mould of part of the final whorl. The upper whorl surface is inclined but becomes horizontal on forming the upper surface of the peripheral flange. The inclination of the upper whorl surface is much less than that seen in Loxoplocus (Lophospira) sedgwickii (Donald, 1906), above. The outer surface of the flange slopes down, and in towards the base and has a spiral cord at its upper and lower edges. Immediately below the flange, the whorl surface is excavated but becomes convex with passage onto the anomphalous base. In L. (Lo.) sedgwickii and L. (Lo.) sp. A, this subperipheral excavated band is better differentiated and forms a well marked outer whorl surface with a prominent angular junction with the base. The aperture is poorly known, growth lines on the base seemingly indicate a deep sinus at the periphery. Preserved ornamentation is confined to the base and consists of growth lines and obscure spiral striae.

Subfamily RUEDEM/NNIINAE Knight, 1956

Genus LONGSTAFFIA Cossman, 1908

Type species. Pleurotomaria tubulosa Lindström, 1884.

Discussion. Knight et al (1960) referred Longstaffia to the Subfamily Lophospirinae Wenz, 1938. The relatively well developed selenizone and the acquisition of spiral ornamentation on the base seem more characteristic of the ruedemanniinid Lophospiridae and the genus is accordingly transferred to this subfamily.

Longstaffia centervillensis (Foerste, 1923)

(Pl. VII, figs. 9, 16, 20)

Lophospira (Ruedemannia?) centervillensis Foerste, 1923,  
p. 84-86, Pl. XIV, fig. 18.

Figured material. Beechhill Cove Fm., USNM 188524 from USNM Colln. 10115. Middle Ross Brook Fm., YPM 28349 from Banbach Colln. A3731(11).

Additional material. Beechhill Cove Fm., an additional specimen on the same slab as the figured specimen.

Description. Species of Longstaffia Cossman, 1908 with an incremental angle of about ninety degrees and at least four whorls. Early whorls and umbilical characters unknown. Upper surface of later whorls flattened, inclined; divided into three spiral concave areas by two prominent spiral carinae, the lowermost of which is the locus of a narrow selenizone. Below the selenizone the lowest concave area is steeply inclined and has its basal margin delimited by the first of a series of closely spaced spiral cords which occupy

the base, the highest of these cords forming the whorl periphery. Whorl embracement at just below the third basal cord, producing a gradate profile with deep sutural indentation. Latest growth stage with reduction in emphasis of the spiral carinae and introduction of intercalated striae. Aperture poorly known; growth lines sweeping strongly backwards from the suture to the selenizone; selenizone narrow, seemingly convex between spiral threads; growth lines curving forwards between selenizone and first basal cord, unknown on base. Shell thickness and structure unknown.

Discussion. Foerste (1923) described Longstaffia centervillensis from shales below the Brassfield Fm. at Centerville, Ohio which appear to be equivalent to the lower Llandovery Belfast Member and, hence, of comparable age to the Beechhill Cove Fm. Longstaffia tubulosa (Lindström, 1884), the type species from the Hemse Beds of Gotland, has a smaller incremental angle and only three spiral elements below the selenizone compared to the nine or ten of L. centervillensis. Pitcher (1939) referred specimens from the upper Llandovery of Shropshire to Gyronema octavium (d'Orbigny) var. multicarinata (Lindström, 1884) while noting the presence of a 'band'. GSM 56878, the original of Pitcher (1939, Pl. V, fig. 1) has a profile reminiscent of Longstaffia and there is some suggestion of an emargination in the rather poorly preserved specimen. This specimen is quite unlike that illustrated as Pitcher (1939, Pl. V, fig. 3) which would appear to be a true Gyronema Ulrich in Ulrich and Scofield, 1897 with no selenizone.

Longstaffia sp.

(Pl. VII, figs. 17, 18)

Figured material. Beechhill Cove Fm., USNM 169487 from USNM Colln. 10115.

Additional material. Beechhill Cove Fm., fragment on same slab as Arjanannia cancellatula, USNM 188523, from USNM Colln. 10115.

Description. Species of Longstaffia Cossman, 1908 in which the nature of the umbilicus and the early whorls is unknown. Final whorl grossly convex but modified by pronounced spiral ornamentation; embracing penultimate whorl below the periphery such that sutural indentation deep, overall, but shallow in detail due to the spiral carinae. Shape of aperture poorly known; outer lip with a narrow sinus passing into a slit which generates a convex selenizone at four fifths of the whorl height on the outer edge of a strong carina; selenizone bordered above and below by fine threads. Spiral ornamentation pronounced; a strong carina below the suture having an acute crest and concave sides, the upper concavity extending to the suture to produce the detailed shallow indentation, the lower concavity extending to the selenizone-bearing carina which is the most conspicuous ornamental feature. At least twelve spiral elements below the selenizone grade uniformly from carinae to cords towards the base with concave areas between spiral elements in proportion to their width; first carina below selenizone forming shell periphery. Thickness and structure of shell unknown.

Discussion. Longstaffia sp. is distinguished from the contemporaneous L. centervillensis (Foerste, 1923) by its narrower incremental angle of seventy degrees. In the latter species, which also has a more gradate profile, the

incremental angle is near ninety degrees.

Genus ARJAMANNIA gen. nov.

Derivation of name. An arbitrary combination of letters in the style of the name of the closely related Ruedemannia Foerste, 1914. Feminine.

Type species. Murchisonia cancellatula M<sup>c</sup>Coy in Sedgwick and M<sup>c</sup>Coy, 1852.

Diagnosis. Ruedemanniinid gastropods with reticulate ornamentation and a tendency to develop a conical or subconical spire.

Discussion. This genus includes members of that group of upper Ordovician and Silurian species, characterised by well developed spiral ornamentation, which have previously been referred to Lophospira Whitfield, 1886, (for example, Longstaff, 1924; Pitcher, 1939). The shell is turbiniform, commonly with a conical spire and adpressed whorls. The base is convex and globose such that the apertural height in many species may constitute more than half of the total height, though in the type species it is rather less. There is no umbilicus but the curvature of the base may produce a shallow pseudo-umbilicus. A true slit is present generating a convex selenizone which typically carries a strong median cord. Ornamentation is reticulate with many sharply defined, closely spaced, spiral lirae and transverse growth lines. A prominent spiral cord is commonly developed on the upper whorl surface. The shell is usually thick, its structure is not known.

In addition to Arjammania cancellatula (M'Coy in Sedgwick and M'Coy, 1852), A. woodlandi (Longstaff, 1924) and A. aulangonensis sp. nov., described below, Pleurotomaria inexpectans Hall and Whitfield, 1875 from the upper Llandoverly Brassfield limestone of Ohio is referred to this genus. Foerste (1923, p. 96-99) gave a full description of this species but the only published illustration is the inadequate original figure of Hall and Whitfield (1875, Pl. 5, fig. 12). The figure and accompanying description were based on two specimens in the collection of U. P. James of Cincinnati. Dr. K. E. Caster (Univ. of Cincinnati; written communication, 1970) believes that this collection was probably donated to the Cincinnati Society of Natural History, whose collections are now located at the University of Cincinnati. However, the specimens have not yet been found in the relevant collection and it is feared that they may no longer exist.

In view of the lack of a suitable illustration, advantage is taken of this opportunity to figure a well preserved specimen of A. inexpectans (Pl. VIII, figs. 2, 3, 6, 7). The specimen (USNM 85063) was collected from the Brassfield limestone at Whippoorwill Church, Northeast of West Union, Ohio, and is labelled 'typical' in Foerste's hand.

Arjammania cancellatula (M'Coy in Sedgwick and M'Coy, 1852)

(Pl. VIII, figs. 1, 4, 8, 10-12)

Murchisonia cancellatula M'Coy in Sedgwick and M'Coy, 1852,

p. 292-293, Pl. 1L, figs. 20, 20a.

Lophospira cancellatula; Longstaff, 1924, p. 419-420,

Pl. XXXIII, figs. 1, 2.

Holotype. SM A34829, Mulloch Sandstone, lower Llandoverly, Mulloch Quarry, Dalquorhan, Girvan, Ayrshire.

Other figured material. Beechhill Cove Fm., USNM 169484 from USNM Colln. 10114(1); USNM 169480, USNM 169483, USNM 188523 from USNM Colln. 10115. SM A34830, Mulloch Sandstone, lower Llandoverly, Mulloch Quarry, Dalquorhan, Girvan.

Additional material. Beechhill Cove Fm., USNM Collections 10114(1), 10115. Jones Colln. Ar B. Cove loc. 4. (10 specimens). BM G25427, from the same locality as the holotype.

Description. Type species of Arjamannia gen. nov. with about five whorls. Spire conical with adpressed whorls; whorl embracement at periphery of previous whorl, commonly covering the peripheral selenizone. Peripheral angulation at midwhorl dividing whorl profile into upper whorl surface, above, and convex base, below. Upper whorl surface steeply inclined; divided into two shallowly concave surfaces in early growth stages by a prominent spiral cord halfway between selenizone and suture; reduction in relief of cord in later growth stages producing a flattening of the surface as a whole. Whorl initially vertical below selenizone but increasing in curvature to form inflated base; pseudo-umbilicus shallow. Aperture subquadrate; growth lines prosocline on upper whorl surface at about sixty degrees to the suture before curving backwards into the slit of unknown depth; growth lines curving forwards on vertical whorl surface below selenizone prior to passing radially, with slight forward concavity, across base and into pseudo-umbilicus. Selenizone convex between bordering cords; ornamentation of numerous concave lunulae crossed by a median spiral cord. Shell

ornamentation of spiral lirae and growth elements of equal size intersecting to form a fine reticulation with small nodes at the intersections; a prominent spiral cord is commonly present on the upper whorl surface. Shell seemingly thick; structure unknown.

Discussion. Arjamannia inexpectans (Hall and Whitfield, 1875) from the upper Llandoverly Brassfield limestone of Ohio is to be distinguished from A. cancellatula by its lower spire and more inflated base. In USNM 85063, the illustrated specimen of A. inexpectans (Pl. VIII, figs. 2, 3, 6, 7), the incremental angle is about eighty degrees compared with sixty degrees in A. cancellatula. The holotype of A. cancellatula is a rather poor steinkern with parts of four whorls preserved. The earlier whorls have a rounded profile but a strong peripheral angulation at midheight of the final whorl delimits the convex base from the flat, inclined, upper whorl surface. A paratype, SM A34830, preserves the reticulate ornamentation. No stronger spiral element is seen on this final whorl but at least one stronger cord is present on the upper surface of the penultimate whorl.

One of the major sources of variation in A. cancellatula is the exact position of whorl embracement. This may vary from below the whorl periphery, as in BM G25427, a topotype figured by Longstaff (1924), to just above the periphery. In the former case the perfection of the conical spire is lost but all details of the selenizone in early whorls may be seen. In the latter, linear sutures are produced and the selenizone may be partly or completely covered by the following whorl.

Arjamannia woodlandi (Longstaff, 1924)

(Pl. VIII, figs. 18, 19)

Lophospira woodlandi Longstaff, 1924, p. 418, Pl. XXXIII,  
figs. 7a, 7b.

do. ; Pitcher, 1939, p. 88-89, Pl. II,  
figs. 1-4.

Figured material. Beechhill Cove Fm., USNM 188521 from USNM  
Colln. 10819, Wallace Brook, Pictou Co.

Description. Somewhat gradate species of Arjamannia gen. nov.  
with about four whorls. Early whorls unknown. Whorl profile  
with peripheral angulation at just above midwhorl height, a  
little below the middle of the exposed whorl face of earlier  
whorls. Upper whorl surface flattened, gently inclined, with  
a prominent subsutural cord producing a slight shouldering  
of the whorl and dividing the upper whorl surface into two  
shallowly concave surfaces. Below periphery, outer whorl  
surface flattened, sloping down and inwards towards the base  
prior to passing rapidly onto the relatively shallowly  
convex base. Anomphalous. Whorl embracement at junction  
between outer whorl surface and base; sutural indentation  
deep for the genus. Inner lip thickened; basal lip  
seemingly convex anteriorly; outer lip deeply sinuate  
with strongly prosocline growth lines on upper whorl  
surface passing into a slit which generates a selenizone  
on the peripheral angulation. Ornamentation of sharply  
delimited, regularly spaced growth lines and spiral lirae  
with a prominent subsutural cord and a more subdued suprasutural  
spiral element. Shell thickness and structure unknown.

Discussion. Arjamannia woodlandi is distinguished from A. cancellatula, A. inexpectans, above, and A. aulangonensis sp. nov., below, by its greater sutural indentation and lack of adpressed whorls. In this respect, there is similarity in form with many species of Loxoplocus (Lophospira) Whitfield, 1886 but the true slit and reticulate ornamentation seem to justify placement within Arjamannia. The Arisaig specimen has a more shallowly inclined upper surface than the specimens illustrated by Pitcher (1939) from the upper Llandoverly of Shropshire and is a little taller than wide. The Shropshire specimens, and the original specimens of Longstaff (1924) from the middle Llandoverly of Girvan, are reportedly slightly wider than tall. Ornamentation is poorly preserved in the single example from Arisaig, the specimen apparently having been abraded.

Arjamannia aulangonensis sp. nov.

(Pl. VIII, figs. 13, 14)

Holotype. Doctors Brook Fm., USNM 169469 from USNM Colln. 10919.

Additional material. Three fragments in the same collection.

Description. Species of Arjamannia gen. nov. with at least four whorls. Spire conical with adpressed whorls covering the peripheral selenizone of earlier whorls and the lower margin of the selenizone of the penultimate whorl. Upper whorl surface steeply inclined with strong spiral cord at just above midheight. Lower whorl surface uniformly convex, external features unknown. Aperture subquadrate; inner and

basal lips unknown; growth lines prosocline on upper whorl surface before curving backwards into a slit of unknown depth. Selenizone relatively wide, shallowly convex between two bordering threads; ornamentation of regularly spaced concave lunulae crossed by a median groove, the edges of which are marked by fine spiral striae. Shell ornamentation, a reticulation of equally developed spiral lirae and growth elements with small nodes at intersections. Shell seemingly thin but thickened at the sutures due to the whorl adpression; structure unknown.

Discussion. Arjamannia culangonensis is distinguished from A. cancellatula and A. inexpectans by its wider selenizone with a median groove. In the latter two species, from the Llandoveryan, the selenizone is narrow with a strong spiral cord. A. woodlandi, another Llandovery species, has a more gradate profile with well developed sutural indentation in contrast to the conical form and flat sutural indentation of the other species. The subsutural thickening of the shell associated with the adpressed whorls in A. culangonensis is well illustrated by comparing the silicon rubber impression of the external mould of the holotype (Pl. VIII, fig. 13) with the natural internal mould of the same specimen (Pl. VIII, fig. 14).

Family PHANEROTREMATIDAE Knight, 1956

Genus PHANEROTREMA Fischer, 1885

Type species. Pleurotomaria labrosa Hall, 1860.

Phanerotrema Fischer, 1885, p. 851.

Pseudoscalites Boucot and Johnson in Boucot et al., 1966,

Discussion. Boucot and Johnson in Boucot et al (1966)

erected Pseudoscalites with type species Pleurotomaria labrosa Lindström, 1884 non Hall, 1860, renamed by them Pseudoscalites lindstroemi. There are a number of similar species known from the Silurian and Devonian and, following examination of some of these, it is suggested that Pseudoscalites falls within the limits of the rather variable genus Phanerotrema of Fischer, into the synonymy of which it is placed.

Phanerotrema affin. Ph. jugosum Pitcher, 1939

(Pl. VII, figs. 12, 13)

Figured material. Beechhill Cove Fm., USNM 188520, USNM 169478 from USNM Colln. 10116.

Additional material. About 30 specimens from the same collection.

Description. Species of Phanerotrema Fischer, 1885 probably with four whorls. Shell gradate with flattened upper whorl surface passing via peripheral angulation at two thirds of whorl height onto strongly convex base. Final whorl embracing penultimate whorl below periphery such that exposed whorl face of penultimate whorl overhangs the final whorl; sutural indentation deep. Umbilicus narrowly phaneromphalous, about one twentieth of total width. Aperture poorly known; basal lip rounded; slightly discontinuous growth lines on upper whorl surface indicate strongly prosocline lip passing into a slit of unknown depth which generates a selenizone on the upper outer edge of the angular periphery; prosocyrte growth lines on base. Selenizone varying from flush with

surface to raised; surface flat, sloping down and outwards from the base; bordered by spiral lirae; ornamentation of numerous shallowly crescentic lunulae and a submedian spiral groove. Ornamentation of upper whorl surface consisting of about five spiral cords and lirae; at least twelve spiral elements on the base; intersections with growth lines nodose. Shell thin, structure unknown.

Discussion. This species is close to Phanerotrema jugosum Pitcher, 1939 from the upper Llandovery of Shropshire but is distinguished by having about five spiral cords on the ramp. Ph. jugosum has two or three strong spiral cords, the American Silurian species Ph. occidentis (Hall, 1867) has about nine, and Ph. lindstroemi (Boucot and Johnson in Boucot et al., 1966) has a smooth upper whorl surface. The development of the flange carrying the selenizone would seem to be a feature of maturity since it is commonly lacking in smaller specimens.

Genus BRACHYTOMARIA Koken and Perner, 1925

Type species. Pleurotomaria baltica de Verneuil, 1845.

Brachytomaria sp.

(Pl. VIII, fig. 15)

Figured material. Upper Stonehouse Fm., YPM 28326 from Twenhofel Colln. 19e/3032.

Discussion. The only known specimen, crushed in shale, is apparently turbiniform with a gradate profile. Umbilical

characters are unknown. The peripheral selenizone is located on the upper edge of the angulation between the upper whorl surface and the base and is raised, with the surface concave between bordering spiral lirae. Circularly concave lunulae are numerous. Two prominent spiral cords occur above the selenizone and are crossed by sharply defined ornamentation paralleling growth. This growth ornamentation is prosocline immediately below the suture but, after crossing the subsutural cord, curves forward and is thereafter prosoclyt. A minor emargination, in addition to the slit, is consequently present high on the upper whorl surface. Bifurcation of the growth ornament and intercalation of equally prominent secondary ribs takes place at the deepest point of this second emargination. The nature of the unusual ornamentation paralleling growth is close to that seen in specimens in the U.S. National Museum which are attributed to the type species. However, Brachytomaria baltica (de Verneuil, 1845), which is apparently the only documented species, is restricted to the Middle Ordovician of the Baltic.

Family UNCERTAIN

Genus PLATYCONUS Perner, 1907

Type species. Pleurotomaria (Platyconus) incumbens Perner, 1907.

Platyconus(?) sp.

(Pl. X, fig. 21)

Figured material. Upper Stonehouse Fm., GSC 32783 from GSC locality 39089.

Discussion. This large, poorly preserved specimen has the low spire and convex whorls displayed by Platyconus carinatus (Sowerby in Murchison, 1839) from the Ludlovian of the Welsh Borderlands. The characteristic ornamentation of spiral cords crossed by prominent growth elements is not preserved. But a ramp on the lower part of the final whorl is suggestive of the raised selenizone found in Sowerby's species and in the type species from the Budnanium of Bohemia. Prosolarium scalatum Northrop, 1939, one of three species described and referred to Prosolarium by Northrop (1939) on the basis of poorly preserved material from the Ludlovian of Gaspé, has a similar profile to the Arisaig specimen - rather too high spired, with more convex whorls and deeper sutural indentation than seems usual for Prosolarium.

Superfamily TROCHONEMATACEA Zittel, 1895

Family TROCHONEMATIDAE Zittel, 1895

Undetermined trochonematid genus and species.

(Pl. IX, fig. 24)

Figured material. Stonehouse Fm., USNM 192115 from Schuchert Colln. 53.

Additional material. One other specimen in the same collection.

Discussion. The illustrated, larger example of this turbiniform species is an internal mould of four whorls with adhering shell fragments. The final whorl is convex with a peripheral flat band suggestive of a selenizone or

pseudoselenizone. A subsutural cord is present and it would appear that the ornamentation is formed of spiral lirae and intervening concave areas crossed by fine growth lines. The previous whorl, equivalent in growth stage to the final whorl of the other specimen, lacks the convexity of the final whorl and has a tendency to develop a trochonematiform profile of flattened whorl surfaces bearing an angular relationship to each other. There is some similarity to Proturritella gracilis Koken, 1889 from the middle Ordovician of the Baltic in whorl profile and ornamentation but the imperfect preservation of the Arisaig specimens hinders further comparison.

Suborder TROCHINA Cox and Knight, 1960

Superfamily PLATYCERATACEA Hall, 1859

Family HOLOPEIDAE Wenz, 1938

Subfamily HOLOPEINAE Wenz, 1938

Genus HOLOPEA Hall, 1847

Type species. Holopea symmetrica Hall, 1847.

Holopea sp.

(Pl. IX, figs. 18, 21)

Figured material. Upper Ross Brook Fm., YPM 28333 from Bambach Colln. A3592(95); YPM 28334 from Bambach Colln. A3759(84).

Additional material. Upper Ross Brook Fm., abundant in Bambach Colln. A3592(95) but also Bambach Collections A3583(72),

A3586(78), A3759(84), A3760(80); Twenhofel Colln. 175/3032(70);  
USNM Colln. 10129(100). Lower McAdam Brook Fm., Bambach  
Collections A3604(181), A3606(187), A3611(194).

Description. Species of Holopea Hall, 1847 with at least  
four whorls. Nuclear whorls unknown. Later whorls with  
circular profile. Whorl embracement at well below the  
periphery of the previous whorl producing deep sutural  
indentation. Umbilical characters unknown. Aperture poorly  
known, seemingly simple; growth lines indicating orthocline  
outer lip. Ornamentation of growth lines only. Shell  
seemingly thin, structure unknown.

Discussion. This species differs from the type species,  
Holopea symmetrica Hall, 1847 from the Ordovician of  
New York State, in having a slightly greater rate of whorl  
expansion as shown by the relatively larger final whorl.  
Holopea striatella (Sowerby in Murchison, 1839) from the  
upper Ordovician of Shropshire has similar proportions to  
the Arisaig examples and Sowerby (in Murchison, 1839, p. 642)  
comments on the presence of 'fine longitudinal lines of  
growth', such as are present here.

Undetermined holopeid genus and species

(Pl. IX, figs. 19, 20)

Figured material. Middle Ross Brook Fm., YPM 28336 from  
Bambach Colln. A3556(16).

Additional material. One other specimen in the same  
collection.

Discussion. A turbiniform, minutely phaneromphalous species from the Middle Ross Brook Fm. is characterised by strong spiral lirae which are located mainly below the periphery of the rather globose whorls. Whorl embracement is low on the previous whorl producing deep sutural indentation. The aperture is imperfectly known but growth lines indicate a nearly orthocline outer lip. The figured specimen shows parts of two whorls with about fifteen spiral lirae and intervening spiral concavities on the base of the final whorl. In addition, the penultimate whorl has less well pronounced and more widely spaced lirae on the outer whorl surface. Threavia gulosa Lamont, 1946 from the Ashgillian of the Girvan district is distinguished by only having a single spiral lira on the lower part of the whorl. In Gyronema Ulrich in Ulrich and Scofield, 1897 fewer, and relatively more coarse spiral lirae are distributed over all the whorl surface.

Genus HAPLOSPIRA Koken, 1897

Type species. Haplospira variabilis Koken, 1897.

Discussion. Knight et al (1960) considered Haplospira to be a junior subjective synonym of Holopea Hall, 1847. The characteristic feature of Koken's genus is a prominent subsutural carina which is here considered to be sufficiently distinctive to merit full generic recognition.

Haplospira sibelixeni sp. nov.

(Pl. IX, figs. 14, 15)

Holotype. Upper Stonehouse Fm., USNM 192116 from USNM Colln. 10206(501).

Additional material. A specimen located on a small slab with the holotype of 'Holopea'reversa Hall, 1860, AMNH 1648, also from the Stonehouse Fm.

Description. Species of Haplospira Koken, 1897 with about four whorls. Nuclear whorls unknown. Later whorl profile convex, with slight flattening of the upper whorl surface; periphery at midwhorl. Whorl embracement at periphery of previous whorl; sutural indentation shallow but somewhat emphasised by the subsutural carina. Aperture poorly known; growth lines indicating a slightly prosocline, almost orthocline, outer lip. Ornamentation of growth lines with a strong subsutural carina producing a slight shouldered effect on the final whorl. Shell thick, structure unknown.

Discussion. The type materials of Haplospira variabilis in the collections of the Naturhistoriska Riksmuseet, Stockholm have more convex whorls and deeper sutural indentation, with the subsutural carina lower on the whorl face. 'Turbo pengellii' Whidborne (1891, Pl. XVII, fig. 14; 1892, Pl. XXVII, fig. 7) from the Devonian of Southwestern England has grossly similar form but is too poorly known for detailed comparison to be made. 'Cyclonema' zonatum Lindström, 1884 from the Ludlovian Hemse Beds of Gotland resembles H. sibelixeni closely in terms of profile but is

distinguished by its spiral ornamentation. The generic position of Lindström's species is uncertain although it is certainly not a Cyclonema Hall, 1852.

Subfamily GYRONEMATINAE Knight, 1956

Genus GYRONEMA Ulrich in Ulrich and Scofield, 1897

Type species. Trochonema (Gyronema) pulchellum Ulrich and  
Scofield, 1897.

Gyronema haliburtoni (McLearn, 1924)

(Pl. IX, fig. 25)

Cyclonema haliburtoni McLearn, 1924, p. 147, Pl. XXI, fig. 3

Holotype. Ross Brook Fm., YPM 462B from the coastal section,  
Arisaig.

Additional material. Common in the lower part of the Upper  
Ross Brook Fm., Bambach Collections A3565(51), A3566(50),  
A3567(49), A3570(38), A3577(59), A3578(60), A3739(47a),  
A3742(48), A3743(56), A3744(57), A3885(53); Twenhofel  
Collections 179/3032(62), 179b/3032(61), 180/3032(54);  
Jones Colln. Ar 1900.

Description. Species of Gyronema Ulrich in Ulrich and  
Scofield, 1897 with about five whorls. Nuclear whorls  
unknown. Profile of later whorls seemingly uniformly convex  
with periphery at midwhorl height. Whorl embracement low on  
previous whorl producing deep sutural indentation. Umbilicus

poorly known, seemingly minutely phaneromphalous. Growth lines indicating slightly prosocline outer lip; basal and inner lips unknown. Ornamentation of growth lines crossing regularly spaced spiral lirae and concave interstices, with obscure spiral striae between the lirae. Shell thickness and structure unknown.

Discussion. Gyronema haliburtoni differs from most of the varieties of Gyronema octavia (d'Orbigny, 1850) illustrated by Lindström (1884) and Donald (1905) by virtue of its more convex whorls and deeper sutural indentation. The holotype most closely agrees with Lindström's (1884, Pl. XVIII, fig. 31, 32) variety multicarinata from the Mulde Beds of Gotland in terms of profile but this form is said to have more abundant spiral ornamentation. Pitcher (1939) referred an upper Llandovery species to G. octavia var. multicarinata and one of the specimens illustrated by him (Pitcher, 1939, Pl. V, fig. 3) appears to have the more circular profile characteristic of G. haliburtoni. As previously noted, GSM 56878, the original of Pitcher (1939, Pl. V, fig. 1) is probably better placed within Longstaffia sp., described above. Specimens in Yale Peabody Museum from the Silurian near Cumberland, Maryland, U.S.A. are also assigned here. The holotype has parts of three whorls preserved, the final one showing seven lirae with possibly three more not exposed.

Undetermined gyronematinid genus and species

(Pl. IX, fig. 10)

Figured material. Moydart Fm., YPM 28346 from USNM Colln. 10853(292), Sutherland River, Pictou Co.

Discussion. This single external mould has three preserved whorls indicating an overall subtrochoid form. Below the suture the whorl profile is concave but soon becomes convex prior to passing rapidly onto the convex base. Maximum whorl width is below midwhorl height. Whorl embracement is just below the periphery of the previous whorl producing shallow sutural indentation. The aperture is unknown but growth lines show the prosocline nature of the outer lip. Ornamentation is of spiral lirae and intervening concave areas, becoming finer away from the preceding suture. The final whorl has about twelve lirae above the periphery. Although assigned to the Gyronematinae, the generic position of this species is uncertain. The adpressed subsutural area and the spiral ornamentation find no close equivalent in other members of the subfamily but the material is insufficient to delimit a new genus.

Family PLATYCERATIDAE Hall, 1859

Genus NATICONEMA Perner, 1903

Type species. Naticonema similare Perner, 1903.

Naticonema kauffmani sp. nov.

(Pl. IX, figs. 12, 13, 16, 17)

Holopea? sp.; McLearn, 1924, p. 148, Pl. XXI, fig. 2.

Holotype. Beechhill Cove Fm., YEM 462A from West Point, Beechhill Cove, Arisaig.

Other figured material. Beechhill Cove Fm., USNM 169479, a small slab and counterpart with Phanerotrema affin. Ph. jugosum Pitcher, 1939 from USNM Colln. 10116.

Description. Species of Naticonema Perner, 1903 with about three rapidly expanding whorls. Nuclear whorls unknown. Whorl profile globose, naticiform, with incised sutures; whorl embracement at periphery of previous whorl. Anomphalous. Aperture ovate, slightly taller than wide; columellar lip thickened with a deep median groove delimiting the acute peristomial margin from a massive columella; outer lip irregular, with deep emarginations. Ornamentation of cord-like growth lines. Shell thin, structure unknown.

Discussion. This species is distinctive with regard to the structure of the columellar lip. The massive columella is longitudinally excavated on its axial side so as to be separated from the acute peristomial margin by a deep groove. The groove narrows and disappears on approaching the parietal and basal terminations of the lip. Immediately behind the margin of the peristome, a wide channel parallels the arcuate edge of the lip from the parietal extremity to the base, falsely suggesting the presence of an umbilicus.

Naticonema similare Perner, 1903, as illustrated by Knight (1941, Pl. 89, figs. 1a-d), has a plate-like columellar lip which is also excavated medially. However, the columella is not so massively developed, relative to the peristomial margin, and the unusual channel behind the arcuate margin of the lip is not present. N. similare has prominent spiral ornamentation but Knight (1941, p. 205) commented on the extreme variability of this and other characters in the sample available to him. In Strophostylus Hall, 1859 the outer lip

is characteristically strongly prosocline. S. andrewsi Hall, 1860, the type species from the Devonian of Maryland, has a spiral plate-like extension of the columella into the shell interior quite unlike the thickened columellar lip of N. kauffmani. S. cyclostomus Hall, 1863 from the Waldron Shale of Indiana has a medially excavated columellar lip not unlike that seen in the Arisaig species but also develops a thick parietal deposit on the base of the previous whorl. No equivalent deposit has been observed in N. kauffmani.

The holotype of N. kauffmani, YPM 462A (Pl. IX, figs. 13, 17) retains traces of the prominent growth ornamentation which indicate two emarginations in the outer lip, one above and one below the periphery. In USNM 169479 (Pl. IX, figs. 12, 16) there is a single wide emargination occupying much of the outer surface of the whorl. Such variation in the form of the aperture is well known within the Platyceratidae due to the adaptation of many species to a sedentary life on crinoid and cystoid calices. The conformity between the apertural margin of the gastropod and the variable surface of the echinoderm calyx produces many irregularities in the shape of the aperture of the former, few of which are of any taxonomic importance.

Genus CYCLONEMA Hall, 1852

Type species. Pleurotomaria bilix Conrad, 1842.

Subgenus CYCLONEMA (CYCLONEMA)

Cyclonema (Cyclonema) parvimedius McLearn, 1924

(Pl. X, figs. 1-4)

Cyclonema parvimedius McLearn, 1924, p. 146, pl. XXI,  
figs. 13, 14.

Holotype. Beechhill Cove Fm., GSC 5655 from Arisaig.

Other figured material. Beechhill Cove Fm., USNM 169475,  
USNM 169476, USNM 169477 from USNM Colln. 10114(1).

Additional material. Beechhill Cove Fm., about twenty five  
specimens from USNM Collections 10114(1), 10115. Jones  
Colln. Ar B. Cove loc. 4; SM A32391 from Gasworks Mudstone  
lower Llandovery, Pembrokeshire.

Description. Subtrochiform species of Cyclonema (Cyclonema)  
Hall, 1852 with about four rapidly expanding whorls. Nuclear  
whorls unknown. Final whorl with narrow, rounded shoulder  
passing onto slightly convex, inclined outer whorl surface  
which becomes vertical immediately prior to curving sharply  
onto the flat base. Whorl embracement at periphery of previous  
whorl; sutural indentation shallow. Aperture subtrigonal;  
inner lip thickened, with longitudinal opercular groove;  
basal lip simple, rounded; outer lip strongly prosocline.  
Base of previous whorl covered by thick parietal deposit  
entirely within the aperture of the following whorl.  
Ornamentation of alternating spiral cords and threads crossed  
by strongly prosocline growth lines and undulations. Shell  
thick; structure unknown.

Discussion. Cyclonema (Cyclonema) daytonense Foerste, 1899  
from the Llandovery Brassfield Fm. of Ohio, Illinois and  
Missouri is very similar to C. (C) parvimedius in terms of  
ornamentation although large individuals of the former may

develop stronger spiral cords. In C. (C) daytonense the rate of whorl expansion is less, producing a relatively smaller final whorl, while the relative width is also greater. The increased convexity of the whorls in Foerste's species gives rise to wider, more deeply indented sutures. C. (C) crebistria (M'Coy) var. rugatum Pitcher, 1939 from the upper Llandovery of Shropshire has similar ornamentation but is characterised by the lower, more vertically compressed form of C. (C.) daytonense. C. (C.) bellulum Billings, 1866, as figured by Twenhofel (1928, Pl. XLIII, figs. 9, 10) and Bolton (1972, Pl. XI, figs. 5, 6) from the lower Silurian of Anticosti Is., has a similar rate of whorl expansion but differs in its more convex profile. C.(C.) varians Billings, 1859 of Twenhofel (1928), another Anticosti Is. species, is delimited by its turbinate form.

The single specimen in the Sedgwick Museum from the Gasworks Mudstone of Pembrokeshire referred to this species has the subtrochiform spire and alternation of coarse and fine spiral elements in the ornamentation well displayed.

Cyclonema (Cyclonema) lydiamariarum sp. nov.

(Pl. IX, figs. 5, 9, 11; Pl. X, fig. 20)

Holotype. BM PG5000, upper Ludlow, loose block by waterfall, 270 yds. SW of Stone House, Felindre, Radnorshire (GR 175802).

Other figured material. Upper Stonehouse Fm., Arisaig, YEM 28335 from Bambach Colln. A3717(437). BM PG5001 from the same block as the holotype.

Description. Small, relatively gradate species of

Cyclonema (Cyclonema) Hall, 1852 with about three and a half whorls. Whorl profile with narrow subsutural shoulder; convex outer whorl surface increasing in curvature with passage onto the convex base; periphery of whorl below midwhorl height. Whorl embracement at periphery of previous whorl; sutural indentation deep. Nature of base and umbilicus unknown. Aperture poorly known; growth lines indicating strongly prosocline outer lip. Ornamentation of numerous spiral cords and intercalated threads crossed by fine growth lines. Shell thickness and structure unknown.

Discussion. Cyclonema (Cyclonema) lydiamariarum is distinguished from C. (C.) parvimedium McLearn, 1924 from the Beechhill Cove Fm. by its smaller size, more convex whorls and base and greater sutural indentation. Both species have similar ornamentation of alternating spiral cords and threads crossed by fine growth lines. C. (C.) daytonense Foerste, 1899 and C. (C.) crebistria (M'Coy) var. rugatum Pitcher, 1939 from the Llandovery of the Mid West and Shropshire, respectively, have less rounded whorls with more open sutures.

Only one crushed specimen is known from Arisaig but there seems little doubt that this is identical with the better preserved specimens from Radnorshire.

Genus PLATYCERAS Conrad, 1840

Type species. Pileopsis vetusta J. de C. Sowerby, 1829.

Subgenus PLATYCERAS (PLATYOSTOMA) Conrad, 1842

Type species. Platyostoma ventricosum Conrad, 1842.

Platyceras (Platyostoma) cf. P. (Pl.) humilis (Billings, 1866)

(Pl. X, fig. 23)

Figured material. Middle Ross Brook Fm., USNM 169490 from USNM Colln. 11291, Pictou Co.

Additional material. Middle Ross Brook Fm., USNM Colln. 11224, Pictou Co.; Bambach Colln. A3732(13).

Discussion. Poor specimens from the Middle Ross Brook Fm. show the rapidly expanding turbinate form characteristic of Billings's (1866) species from Anticosti Is. Ornamentation consists of somewhat irregularly spaced and slightly rippled spiral striae, with flat intervening areas, crossed by prosocline growth lines. Similar ornamentation is seen in specimens in the Foerste Collection of the U.S. National Museum from the Brassfield Fm. of Ohio, referred to Platyceras (Platyostoma) clintonensis (Foerste, 1923).

Platyceras (Platyostoma) cornutum (Hisinger, 1837)

(Pl. X, figs. 5, 7-12, 14)

Pileopsis cornuta Hisinger, 1837, Pl. 12, fig. 11.

Platyceras cornutum; Lindström, 1884, p. 63, Pl. 2, figs. 29-51; Pl. 3, figs. 6-9, 19-26.

Diaphorostoma cornutum var. arisaigensis McLearn, 1924, p. 148, Pl. XXI, figs. 8-10.

Holopea caecistriata McLearn, 1924, p. 147, Pl. XXI, fig. 1.

Figured material. French River Fm., USNM 188522 from

USNM Colln. 10158, the iron ore mine NE of Arisaig Brook. Moydart Fm., USNM 192117 from USNM Colln. 10175; GSC 33271, GSC 33272 from Jones Colln. Ar Mo 5500; GSC 33273 from Jones Colln. Ar Mo 4980. Stonehouse Fm., GSC 5656, GSC 5657 from Arisaig shore.

Additional material. Glencoe Brook Fm., USNM Colln. 11262 from Pictou Co. French River Fm., USNM Colln. 10153. Doctors Brook Fm., USNM Colln. 10164(123). McAdam Brook Fm., USNM Colln. 11217 from Pictou Co. Moydart Fm., USNM Collections 10174, 10175, 10181, 10183(315); Twenhofel Colln. 102/3032; Schuchert Colln. 52B; Jones Collections Ar Mo 4700, Ar Mo 5300, Ar Mo 5420, Ar Mo 5450, Ar Mo 5500. Stonehouse Fm., USNM Collections 10211, 10910(496); USNM Colln. 11214 from Cape George, N. S.; Schuchert Collections 49D, 53.

Discussion. The concept applied to this species is essentially that employed by Lindström (1884, p. 62) due to the "...almost incredible variation in its shape and growth." As such, a varied and stratigraphically widely distributed group of fossils are included. The shell is naticiform, reflecting the rapid rate of whorl expansion, with the spire commonly sunk below the level of top of the final whorl at the aperture. The whorl profile is strongly convex and usually smooth although specimens from the Moydart Fm. commonly develop spiral plications. Whorl embracement is high on the whorl profile with the strong adapical convexity of the upper surface of the embracing whorl producing deep, channel-like sutural indentation. Apertural shape varies considerably but growth lines indicate a grossly prosocline outer lip with many irregular emarginations (text-fig. 12B). The inner lip may be thickened but apparently not so as to

close the minutely phaneromphalous umbilicus. Ornamentation is of growth lines and irregular varices, sometimes with well marked spiral threads in earlier growth stages only. The shell is of variable thickness, its structure is unknown.

USNM 192117, an internal mould from the Moydart Fm., shows a single, large muscle scar on the final whorl about one quarter of a whorl back from the aperture (Pl. X, fig. 5).

Of the many different shell forms illustrated by Lindström (1884) from the Silurian of Gotland, those shown as figs. 31-33 on Plate II most closely approach the Arisaig specimens. The holotype of Holopea caecistriata McLearn, 1924 is merely a juvenile form with well developed spiral ornamentation.

#### Undetermined trochinid genus and species

(Pl. VIII, fig. 9)

Figured material. Beechhill Cove Fm., USNM 169486 from USNM Colln. 10115.

Discussion. This single fragmentary external mould preserves the impression of parts of two whorls. The shell seems to be subtrochiform with a convex base and moderately elevated spire. The upper whorl surface is convex, becoming vertical prior to passage into a deep spiral channel at about two fifths of the whorl height. A strong peripheral carina is located immediately below this channel at the junction between the upper whorl surface and the base. A fine reticulate ornament of spiral lirae and growth lines is seen on the base. The specimen is quite unlike any known Palaeozoic species but would appear at least superficially similar to

certain members of the Mesozoic subfamily Proconulinae of the Trochidae. However, in the Arisaig specimen the growth lines on the lower part of the whorl are orthocline as distinct from the strongly prosocline condition characteristic of many trochids.

Suborder NERITOPSINA Cox and Knight, 1960

Superfamily NERITACEA Rafinesque, 1815

Family NERITOPSIDAE Gray, 1847

Subfamily NATICOPSINAE S.A. Miller, 1889

Genus NATICOPSIS M'Coy, 1844

Type species. Naticopsis phillipsii M'Coy, 1844.

Naticopsis trevorpatriciorum sp. nov.

(Pl. IX, figs. 1-4, 6-8; Pl. X, fig. 18)

Natica glaucinoides; J. de C. Sowerby in Murchison,  
1839, p. 603, Pl. 3, fig. 14.

Naticopsis? glaucinoides; M'Coy in Sedgwick and M'Coy,  
1852, p. 302, Pl. 1K, fig. 35.

non Natica glaucinoides J. Sowerby, 1812, p. 19-20,  
Tab. V, fig. 1.

Holotype. Green Member, Moydart Fm., YPM 28332 from  
Twenhofel Colln. 103a/3032(291).

Other figured material. SM A37091, Kirkby Moor Flags  
sensu lato, Benson Knot, Westmoreland (seemingly Whitcliffian-  
Downtonian Kirkby Moor Flags sensu stricto and Scout Hill

Flags of Shaw, 1971). BM PG5005, BM PG5006, BM PG5007, BM PG5008, from upper Ludlow, 270 yds. SW of Stone House, Felindre, Radnorshire, (Grid Ref. SO 175802).

Additional material. Moydart Fm., Green Member, Schuchert Colln. 52B; Jones Colln. Ar Mo 5450 (4 specimens). Upper Ludlow of Felindre, Radnorshire, GSM Geol. Soc. Coll. 6694, the figured specimen of Sowerby in Murchison (1839).

Description. Species of Naticopsis M'Coy, 1844 with about five rapidly expanding whorls; apertural height about two thirds of total. Whorl profile uniformly convex, globose, commonly with subsutural shoulder. Whorl embracement at periphery of previous whorl producing deep, wide sutural indentation. Anomphalous. Aperture imperfectly known; columellar lip thickened, seemingly smooth; growth lines indicating slightly prosocyrta, almost orthocline, outer lip. Ornamentation of fine growth lines which may become rugose in later growth stages. Shell thick, structure unknown.

Discussion. Natica glaucinoides was described by J. Sowerby (1812) from the Tertiary London Clay. The misidentification of this species in the upper Ludlow strata of Felindre, Radnorshire by J. de C. Sowerby in Murchison (1839) was noted by M'Coy in Sedgwick and M'Coy (1852) when he tentatively transferred the Silurian species to Naticopsis. However, M'Coy retained the species-group name and acknowledged J. de C. Sowerby in Murchison (1839) as the author. Application of Article 49 of the ICZN Code (1961, revised 1964) prevents retention of the species-group name, following J. de C. Sowerby's misidentification, even after the transfer to another genus. It is therefore necessary to propose a new species name,

Naticopsis trevorpatriciorum sp. nov., to include the materials of J. de C. Sowerby and M'Coy.

The species described by Lindström (1884) as Holopea transversa from the lower Wenlock Högklint Beds of Gotland differs from N. trevorpatriciorum in having less rapidly expanding whorls with the apertural height being only about half of the total height. Holopea niagarensis Winchell and Marcy, 1865, from the Niagaran of Illinois, U.S.A., would appear to resemble N. trevorpatriciorum in general form. However, Winchell and Marcy (1865, p. 99) note deeply impressed sutures and the apparent presence of an umbilicus in contrast to the peripheral embracement of previous whorls and anomphalous base seen in N. trevorpatriciorum. The incremental angle of about ninety degrees in N. trevorpatriciorum is considerably greater than the fifty eight degrees noted by Winchell and Marcy (1865) for H. niagarensis.

SM A37091, the original of M'Coy in Sedgwick and M'Coy (1852, pl. 1K, fig. 35), differs from the holotype of N. trevorpatriciorum in having rugose growth ornamentation on the last half whorl but this is probably just an ontogenetic difference. At equivalent size to the holotype, the rugose character of the growth lines is much reduced. M'Coy's specimen also has some suggestion of a slight anterior siphonal notch (Pl. IX, fig. 8) but the presence of this feature has not been confirmed in other available material.

The specimen figured from Felindre by J. de C. Sowerby in Murchison (1839) is a poor internal mould, GSM Geol. Soc. Coll. 6694. Additional specimens from Felindre (Pl. IX, figs. 1-4, 7) are generally larger than the Arisaig specimens and commonly lack the same degree of shouldering of the whorls. Ornamentation is poorly preserved but the rugose growth elements seen in M'Coy's specimen are not conspicuous.

Suborder MURCHISONIINA Cox and Knight, 1960

Superfamily MURCHISONIACEA Koken, 1896

Family MURCHISONIIDAE Koken, 1896

Genus MURCHISONIA d'Archiac and de Verneuil, 1841

Type species. Turritella bilineata Dechen, 1832.

Subgenus MURCHISONIA (MURCHISONIA)

Murchisonia (Murchisonia) aciculata Hall, 1860

(Pl. XI, figs. 1-3)

Murchisonia aciculata Hall, 1860, p. 154.

do. ; Dawson, 1868, p. 605

Goniostropha aciculata; McLearn, 1924, p. 142, Pl. XXI,  
figs. 21, 25.

Holotype. Stonehouse Fm., AMNH 1649 labelled "Clinton Group,  
Arisaig, N.S."

Other figured material. Stonehouse Fm., GSC 5650, GSC 5651,  
the figured specimens of McLearn (1924).

Additional material. Stonehouse Fm., USNM Colln. 10206(501);  
Bambach Collections A3654(476), A3684(416), A3689(495),  
A3699(466), A3703(472), A3730(390), A3871(396); Twenhofel  
Collections 14/3032(477), 19a<sup>12</sup>/3032(426), 19a<sup>13</sup>/3032(427),  
21a/3032(386), 21h/3032(384); Schuchert Colln. 49D; Jones  
Colln. Ar S 7815, (about 20 specimens in all).

Description. Species of Murchisonia (Murchisonia) d'Archiac and de Verneuil, 1841 with numerous whorls. Early whorls and nature of umbilicus unknown. Whorl profile of later growth stages slightly angulated at the peripheral selenizone which is at midheight of the exposed whorl surface. Whorl surface subhorizontal immediately below the suture with the previous whorl, forming a narrow shoulder; upper whorl surface flattened or shallowly concave but steeply inclined; lower whorl surface gently convex, increasing in curvature with passage onto the uniformly convex base. Whorl embracement slight; sutural indentation deep, narrow. Aperture oval; inner lip smooth, thickened; basal lip unknown; growth lines indicating steeply prosocline lip on upper whorl surface curving rapidly into the slit of unknown depth; below selenizone, growth lines oblique and shallowly convex adaperturally. Selenizone concave between strong bordering lirae; a fine groove on the crest of each lira indicating the margins; selenizone ornamentation of numerous shallowly concave lunulae. Shell ornamentation of growth lines and obscure spiral striae; outer edge of subsutural shoulder commonly slightly elevated to form a spiral cord. Shell of moderate thickness, structure unknown.

Discussion. Murchisonia (Murchisonia) cambria (Donald, 1905) from the Ludlovian of Wales resembles M. (M.) aciculata in general form of the spire and whorl profile but the selenizone is a little lower on the whorl face. Unfortunately, the shell ornamentation is unknown in Donald's species. In M. (M.) elegans Sollas, 1879, from the Wenlockian of South Wales, the upper whorl surface is concave and there is no subsutural shoulder.

The holotype is a poorly preserved internal mould showing none of the ornamental features. However, the specimens

figured by McLearn (1924) agree exactly with the diagnosis of Hall (1860) which cannot be satisfactorily applied to other contemporaneous species. McLearn (1924) recorded M. (M.) aciculata from the Lower Stonehouse Fm. but no specimens have been seen from this unit during the present study.

Murchisonia (Murchisonia) amii (McLearn, 1924)

(Pl. XI, figs. 4, 5, 11)

Hormotoma amii McLearn, 1924, p. 143, Pl. XX, fig. 22.

Hormotoma cf. articulata; Straw, 1933, p. 124, Pl. IX,  
fig. 23-24.

non Pleurotoma articulatum Sowerby in Murchison, 1839,  
p. 612, Pl. 5, fig. 25.

Holotype. Stonehouse Fm., GSC 5652 from Arisaig.

Other figured material. Stonehouse Fm., YPM 28337B, a small slab from USNM Colln. 10206(501) which also carries the illustrated specimen of Loxonema sinuosum (Sowerby in Murchison, 1839); USNM 192121 from Schuchert Colln. 53.

Additional material. Stonehouse Fm., USNM Colln. 10206(501); Schuchert Collections 49D, 53. (6 specimens).

Description. Species of Murchisonia (Murchisonia) d'Archiac and de Verneuil, 1841 with many whorls. Earliest whorls unknown. Whorl surface horizontal, immediately below suture, producing a subsutural shoulder which may develop an obscure spiral cord on its outer margin; upper whorl surface steeply

inclined, flattened or slightly concave between the shoulder and the peripheral selenizone; upper edge of selenizone at just below middle of exposed whorl face, at midheight of final whorl; whorl surface below selenizone shallowly convex, inclined towards suture with following whorl and increasing in curvature with passage onto the convex base. Sutural indentation narrow, deep. Aperture subquadrate; growth lines indicating steeply prosocline, almost orthocline, margin of lip between suture and upper edge of the short slit; growth lines below selenizone running obliquely across exposed lower whorl face. Upper and lower edges of selenizone delimited by obscure spiral grooves; selenizone ornamentation of two spiral cords with intervening concavity crossed by fine crescentic lunulae. Shell ornamentation of growth lines and spiral striae. Shell thick; structure unknown but a thin outer layer carrying the spiral cords on the selenizone is readily lost.

Discussion. Murchisonia (Murchisonia) amii differs from M. (M.) dudleyensis Donald, 1902 and M. (M.) cambria (Donald, 1905) from the Wenlockian and Ludlovian of Britain, respectively, in having a less angular whorl profile with shouldered whorls. M. (M.) cava Lindström, 1884 from the Slite Beds of Gotland has a similar profile but lacks the deep sutural indentation and the spiral cords on the selenizone. M. (M.) amii is distinguished from the contemporaneous M. (M.) aciculata in having a more quadrate whorl profile with the selenizone lower on the exposed whorl face. In addition, the two spiral cords in M. (M.) amii lie completely inside the margins of the selenizone while in M. (M.) aciculata the selenizone margins are indicated by grooves along the crests of the two cords.

Specimens described by Straw (1933) from the marine Downtonian of the Little Missenden Borehole, Buckinghamshire as Hormotoma cf. articulata (Sowerby in Murchison, 1839) are referred to M. (M.) amii. GSM 51876, the original of Straw (1933, Pl. IX, fig. 23), shows well the shouldered whorl profile, the near orthocline growth lines above the selenizone and the characteristic two spiral cords entirely within the margins of the selenizone. The holotype of Sowerby's species, as illustrated by Donald (1899, Pl. XXII, fig. 7) has more open sutures and greater inclination of the growth lines above the selenizone.

The holotype of M. (M.) amii is well preserved in that parts of five whorls with growth ornamentation are present. However, a thin outer shell layer bearing the cords of the selenizone has been lost on all but the very earliest whorl preserved. Presumably, it was the apparent absence of these strong spiral elements which promoted McLearn (1924) to refer the then only known member of the species to Hormotoma.

Subgenus MURCHISONIA (HORMOTOMA) Salter, 1859

Type species. Murchisonia gracilis Hall, 1847.

Murchisonia (?Hormotoma) arisaigensis (Hall, 1860)

(Pl. XI, figs. 6, 7, 10, 16)

Murchisonia arisaigensis Hall, 1860, p. 154.

do. ; Dawson, 1868, p. 604

Goniostropha? arisaigensis; McLearn, 1924, p. 143.

Lectotype. Here designated as the larger of two specimens

bearing the number AMNH 1650 from the Stonehouse Fm. but labelled "Clinton Group. Arisaig, Nova Scotia." (Pl. XI, fig. 7).

Paralectotype. The smaller of the two specimens in the same collection, (Pl. XI, fig. 10).

Other figured material. Stonehouse Fm., USNM 192118, USNM 192119, USNM 188527 from Schuchert Colln. 53.

Additional material. Stonehouse Fm., USNM Collections 10205(500), 10206(501); Schuchert Colln. 53. (17 specimens).

Description. Seemingly a species of Murchisonia (Hormotoma) Salter, 1859 with eleven whorls. Whorl profile strongly convex with a slight angulation at the middle of the exposed whorl face, a little above midheight of the final whorl. Degree of whorl embracement slight; sutural indentation deep. Aperture tear-shaped, with height a little greater than width; inner lip thickened, curving back over the minutely phaneromphalous umbilicus; outer lip with steeply prosocline growth lines on upper whorl surface curving into a slit of unknown depth; growth lines strongly oblique below selenizone. Selenizone bounded by fine threads; surface ornamentation unknown. Shell ornamentation of fine growth lines. Shell thick, structure unknown.

Discussion. Murchisonia (?Hormotoma) arisaigensis is readily distinguished from the accompanying M. (Murchisonia) aciculata and M. (M.) amii by its greater incremental angle of about twenty five degrees compared to the fifteen degrees of the two latter species. Hall's type specimens, not figured by McLearn (1924), are internal moulds without any indication

of external characters other than a band at the periphery suggestive of a selenizone. Of the other specimens placed here, all except USNM 192118 (Pl. XI, fig. 16) lack any preserved shell. The latter is a partially exfoliated juvenile in which details of the upper surface of the selenizone are not retained. It is, therefore, not possible to make a precise subgeneric assignment for the species.

The importance of establishing possible exfoliation of part or all of a specimen is exemplified by the case of the holotype of M. (M.) amii, described above. In that specimen, diagnostic spiral cords on the selenizone were lost by exfoliation causing McLearn (1924) to assign the species to M. (Hormotoma) in preference to M. (Murchisonia).

A series of fine crescentic striations on the columellar region of a small internal mould, USNM 188527, text-fig. 12C, represents the attachment scar of a single columellar muscle.

Murchisonia (Hormotoma) sp. A

(Pl. XI, fig. 19)

Figured material. Upper Ross Brook Fm., YPM 28339 from Bambach Colln. A3592(95).

Additional material. Upper Ross Brook Fm., Bambach Colln. A3762(91).

Discussion. The crushed figured specimen shows four whorls. Growth lines preserved on the upper whorl surface of the two largest whorls are steeply inclined prior to passing into the relatively wide slit of unknown depth. The location of the selenizone, low on the whorl, is reminiscent of

M. (Hormotoma) cingulata (Hisinger, 1829) from the Silurian of Gotland but the Arisaig species has fewer whorls with deeper sutural indentation.

Murchisonia (Hormotoma) sp. B

(Pl. XI, fig. 17)

Figured material. Upper McAdam Brook Fm., YPM 28340 from Bambach Colln. A3643(274).

Discussion. A fragment of a single whorl shows growth lines delineating a deep sinus which passes into a slit of unknown depth. On the upper whorl surface growth lines are inclined at about sixty degrees to the selenizone while those on the lower whorl surface have a lower angle of obliquity. The upper edge of the convex selenizone is at midwhorl height. The margins of the selenizone are obscure but seemingly grooved. This species is readily distinguished from other species of Murchisonia (Hormotoma) and M. (Murchisonia) known from Arisaig by its wide, deep sinus.

Subgenus MURCHISONIA (SINUSPIRA) Perner, 1907

Type species. Sinuspira tenera Perner, 1907.

Murchisonia (Sinuspira) cf. M. (S.) tenera (Perner, 1907)

(Pl. XI, fig. 9)

Figured material. Lower McAdam Brook Fm., YPM 28338 from Bambach Colln. A3606(187).

Additional material. Lower McAdam Brook Fm., Bambach  
Collections A3612(201), A3616(197), A3820(196).(4 specimens).

Description. Believed to be the type species of Murchisonia  
(Sinuspira) Perner, 1907 with numerous whorls. Characters  
of early whorls and umbilicus not known. Whorl profile  
gently convex with shallow sutural indentation. Aperture  
poorly known; growth lines indicating a deeply sinuate outer  
lip, the upper margin of which sweeps obliquely back at  
about fifty degrees to the previous suture before passing into  
the deepened culmination of the sinus at just below midheight  
of the exposed whorl face; lower margin similarly oblique.  
Ornamentation of closely spaced, cord-like growth lines.  
Shell structure and thickness unknown.

Discussion. Little difference can be detected between the  
Arisaig specimens and the illustrations of the holotype given  
by Knight (1941, Pl. 45, figs. 7a, b) but, in view of their  
moderate preservation, the assignment to Perner's (1907)  
species is tentative. Murchisonia (Sinuspira), of which  
M. (S.) tenera is the only described species, has previously  
been restricted to the Budnanium of Bubovice, Bohemia.

Undetermined murchisoniid genus and species

(Pl. XI, fig. 20, 21)

Figured material. Moydart Fm., USNM 169470 from Schuchert  
Colln. 52B; YPM 28345 from USNM Colln. 10853(292), Sutherland  
River, Pictou Co.

Additional material. Green Member, Moydart Fm., a number of

fragments in Schuchert Colln. 52B.

Discussion. This high spired species is of uncertain generic affinity. The whorl is divided into upper and lower surfaces by a pronounced peripheral angulation at midwhorl. The profile is concave immediately below the suture with the previous whorl but soon becomes shallowly convex and inclined. At one third of the height of this upper whorl surface the inclination is steepened at a minor angulation. The lower margin of the upper whorl surface is marked by the peripheral selenizone which forms the shallowly convex outer surface of the flange-like angulation. Fine striae along the edges of this upper surface seemingly delimit the margins of the selenizone. Lunulae are shallowly concave and are crossed by two fine spiral grooves at the middle of the selenizone. On the lower whorl surface, a shallowly concave surface separates the lower margin of the selenizone from a spiral cord at about midheight of the base. Below this cord, the lower whorl surface is convex; umbilical characters are unknown. Whorl embracement is at the basal cord, producing sutural indentation which is grossly deep but shallow in detail. Ornamentation on the upper whorl surface is of orthocline growth lines which curve back to form a narrow sinus and in turn pass into the slit of unknown depth; ornamentation below the selenizone is not known. The shell is of moderate thickness, its structure is unknown.

The species resembles certain lophospirinid pleurotomariaceans with regard to the angular periphery and the subperipheral cord. However, the presence of the wide selenizone favours assignment to the Murchisoniidae.

Ectomaria confinus Perner, 1907 from the lower Devonian of Koněprusy is superficially similar but the upper whorl surface

is flat and the peripheral angulation of the Moydart species is replaced by a well developed vertical outer whorl surface.

Family PLETHOSPIRIDAE Wenz, 1938

Subfamily PLETHOSPIRINAE Wenz, 1938

Genus SEELYA Ulrich in Ulrich and Scofield, 1897

Type species. Seelya ventricosa Ulrich in Ulrich and Scofield, 1897.

Discussion. Examination of the holotype, USNM 45996, confirms the presence of a selenizone in this genus. Knight (1941) stated that the feature was not certainly determinable but a small fragment of shell adhering to one of the early whorls clearly shows the selenizone with concave lunulae and bordering lirae.

Seelya moydartensis McLearn, 1924

(Pl. X, figs. 6, 13, 15-17, 19, 22)

Seelya moydartensis McLearn, 1924, p. 145, Pl. XXI,  
figs. 11, 12.

Holotype. Moydart Fm., YPM 464 from Coastal section, Arisaig.

Paratype. YPM 464A, same locality and horizon.

Other figured material. Moydart Fm., YPM 28331, from Twenhofel Colln. 102/3032; GSC 33270 from Univ. of Manchester Colln. Ar Mo 5450; GSC 33274 from Jones Colln. Ar Mo 4900.

Additional material. Moydart Fm., Twenhofel Colln; 102/3032; Bambach Colln. A3849(296); Jones Collections Ar Mo 4820, Ar Mo 4900, Ar Mo 4980, Ar Mo 5450. (About 30 specimens).

Description. Species of Seelya Ulrich in Ulrich and Scofield, 1897 with about four whorls. Nuclear whorls unknown. Whorl profile with peripheral angulation at just below middle of exposed whorl face, at midheight of final whorl. Upper whorl surface shallowly convex, inclined towards periphery; lower whorl surface and base uniformly convex but with minor umbilical shoulder. Whorl embracement slight; sutural indentation moderate overall but deep in detail due to suprasutural spiral cord. Umbilicus seemingly slightly phaneromphalous. Aperture subovoid with height greater than width; outer lip deeply sinuate with growth lines sweeping strongly back from the preceding suture into the deep sinus which culminates in a short slit on the outer edge of the peripheral angulation; growth lines curving strongly forward below selenizone and reaching maximum forward extension just prior to passing over umbilical shoulder into umbilicus. Selenizone raised with upper surface concave between bordering cords. Ornamentation of spiral elements crossed by fine growth lines which become varicose in later growth stages; upper whorl surface with fine spiral striae and as many as three strong spiral cords; lower whorl surface with five or six spiral plications which produce spiral ridges on internal moulds. Shell thick, structure unknown.

Discussion. Seelya moydartensis differs from S. ventricosa Ulrich in Ulrich and Scofield, 1897, the type species from the lower Ordovician of Vermont, in having more convex whorls, greater sutural indentation and a deeper sinus. In

both species the incremental angle is about sixty degrees.

The degree of development of the spiral cords on the upper surface and the elevation of the selenizone vary quite considerably within the available sample. One external mould, GSC 33274, Pl. X, fig. 6, shows the upper whorl surface with only fine spiral striae while in GSC 33270, Pl. X, fig. 22, three spiral cords are present. Similarly, a strong selenizone band occurs in the holotype, Pl. X, fig. 19, but is much less evident in the paratype, Pl. X, figs. 13, 15. Additional variation is seen in the general form of the shell. Most specimens have a similar whorl profile to the paratype but increase in the incremental angle and deepening of the sutures produces a lower spired and more gradate form (YPM 28331, Pl. X, fig. 16).

Order CAENOGASTROPODA Cox, 1959

Superfamily LOXONEMATACEA Koken, 1889

Family LOXONEMATIDAE Koken, 1889

Discussion. Knight et al (1960) considered Morania Horný, 1953 to be a junior subjective synonym of Murchisonia (Sinuspira) Perner, 1907 and not a loxonematacean, as originally suggested by Horný (1953). This opinion is not accepted here and Morania is once more returned to the Loxonematidae. The shape of the emargination in Morania has a loxonematid aspect and is quite unlike the more symmetrical murchisoniid sinus of Sinuspira. Both forms may lie morphologically between the Loxonematacea and Murchisoniaceae but there is little evidence to suggest a phylogenetic relationship between them. The status of Morania relative to Loxonema Phillips, 1841 is, to some extent, uncertain since the shape of the sinus in Loxonema

may show quite considerable ontogenetic and interspecific variation. However, in Loxonema the emargination is normally wide and rounded, and culminates at or near the middle of the exposed whorl surface. In Morania the sinus is narrow with a deepened, angular culmination high on the whorl.

Genus LOXONEMA Phillips, 1841

Type species. Terebra? sinuosa Sowerby in Murchison, 1839.

Loxonema sinuosum (Sowerby in Murchison, 1839)

(Pl. XI, fig. 13)

Terebra? sinuosa Sowerby in Murchison, 1839, p. 619,  
pl. 8, fig. 15.

Loxonema sinuosum; Longstaff, 1909, p. 215, Pl. X,  
figs. 1a, b.

do. ; Knight, 1941, p. 180, Pl. 48,  
figs. 8a, b.

Figured material. Upper Stonehouse Fm., YPM 28337A from  
USNM Colln. 10206(501).

Additional material. Two other specimens in the same  
collection.

Description. Type species of Loxonema Phillips, 1841 with many whorls. Early whorls unknown. Whorl profile of preserved whorls shallowly convex with periphery at just below the middle of the exposed whorl surface. Whorl embracement slight, succeeding whorls embracing earlier ones

at the junction between the outer whorl surface and the flattened base; sutural indentation moderate. Anomphalous. Aperture poorly known, oval with height greater than width; outer lip with sinus occupying the entire outer surface of whorls in the later growth stages. Culmination of sinus at two thirds of height of exposed whorl face with the prosocline upper part of outer lip turning through ninety degrees to form the opisthocline lower part; this opisthocline portion being shallowly convex anteriorly with growth lines at about forty five degrees to the following suture but becoming steeper immediately prior to meeting the suture. Ornamentation of fine growth lines. Shell thick, structure unknown.

Discussion. The only well preserved specimen from Arisaig agrees closely with the illustrations of the holotype given by Knight (1941). Of species described by Donald (1905) and Longstaff (1909) from Britain, Loxonema pseudofasciatum from the Wenlock and lower Ludlow has a less angular sinus and reported spiral striae, L. ledburiense from the Lower Ludlow has a more slender spire while L. planatum and L. perneri from the Wenlock and Ludlow have wider spires and shallower emarginations. Lindström (1884) described five species from the Silurian of Gotland of which L. lindströmii Longstaff, 1909 (L. sinuosum Lindström, 1884 non Sowerby in Murchison, 1839) from the Mulde Beds compares most closely. However, it may be distinguished by its shallow sinus.

Loxonema sp. A

(Pl. XI, fig. 14)

Figured material. McAdam Brook Fm., GSC 33269 from Jones

Description. Species of Loxonema Phillips, 1841 with at least eight whorls. Nuclear whorls unknown. Whorl profile shallowly concave immediately below suture, becoming convex on approaching the whorl periphery which is at just above the middle of the exposed whorl face. Whorl embracement slight, with minor adpression against the previous whorl; sutural indentation relatively deep. Base anomphalous. Aperture poorly known; outer lip with growth lines indicating a deep sinus with an inner notch culminating at the middle of the exposed whorl face. Ornamentation of growth lines. Shell of moderate thickness; structure unknown.

Discussion. This species is characterised by the deepened inner portion of the sinus at midwhorl. Similar emarginations are present in Morania Horný, 1953 and Murchisonia (Sinuspira) Perner, 1907, originally described from the Upper Silurian of Bohemia. However, in the former, the culmination of the sinus is much higher on the exposed whorl face while M. (Sinuspira) has a deeper emargination somewhat lower on the whorl. The form of the spire is typically loxonematid, with the slightly adpressed whorls producing a shallowly concave subsutural area. Loxonema sinuosum (Sowerby in Murchison, 1839) may be distinguished by its uniformly convex whorls and by the absence of a deepened inner portion to the emargination which is located higher on the whorl.

Loxonema sp. B

(Pl. XI, fig. 15)

Figured material. Upper Ross Brook Fm., YPM 28341 from

Bambach Colln. A3760(80).

Additional material. Upper Ross Brook Fm., Bambach Colln. A3592(95), (five specimens).

Discussion. Several crushed specimens from the Upper Ross Brook Fm. have obscure growth lines indicating a wider, shallower emargination than that seen in Loxonema sinuosum or L. sp. A, above. About six whorls are present and the whorl profile is uniformly convex, after the manner of L. sinuosum. L. planatum Longstaff, 1909 from the Wenlockian and Ludlovian of Britain has similar form but differs in its slightly greater degree of adpression of the whorls.

Genus MORANIA Horný, 1953

Type species. Morania v-sinuata Horný, 1953.

Morania(?) boltoni sp. nov.

(Pl. XI, figs. 12, 18)

Holotype. Stonehouse Fm., USNM 192120 from Schuchert Colln. 49D.

Additional material. Stonehouse Fm., Twenhofel Colln. 19j/3032. (1 specimen).

Description. Tentatively a species of Morania Horný, 1953 with at least five whorls. Early whorls unknown. Whorl profile of later whorls convex, with obscure subsutural shoulders. Whorl embracement slight; sutural indentation deep. Shape of aperture poorly known, seemingly ovoid with

height about one and a half times greater than width; growth lines indicating deeply sinuate outer lip. Growth lines prosocline below suture; convex outer edge of subsutural shoulder forming the locus of the deepest part of the sinus; below culmination of sinus, the adaperturally convex growth lines increase in curvature so as to become almost perpendicular to the following suture. Ornamentation of growth lines crossed by obscure spiral striae. Shell thick, structure unknown.

Discussion. Morania (?) boltoni is characterised by the location of the culmination of the sinus on the outer edge of the subsutural shoulder. Morania v-sinuata Horný, 1953 from the Budnanium of Central Bohemia has less shouldered whorls and shallower sutural indentation. In addition, the sinus in Horný's species is narrower and a little deeper with its lower margin less convex. To some extent M. (?) boltoni combines features of the emargination of this latter species with the more arcuate lower portion of the outer lip seen in Loxonema sinuosum (Sowerby in Murchison, 1839). Consequently, the assignment to Horný's genus is tentative. Loxonema costulatum Perner, 1903, from the Budnanium of Bohemia, also has less shouldered whorls and the sinus lower on the whorl, while L. debile Perner, 1903, of similar age, has comparable location of the sinus but lacks the deepened sutures.

Morania(?) sp.

(Pl. XI, fig. 8)

Figured material. Lower McAdam Brook Fm., YPM 28342 from Bambach Colln. A3809(189).

Discussion. This specimen, crushed in mudstone, has five whorls preserved to a total height of 6 mm. The earliest four whorls are poorly preserved but the fifth whorl shows ornamentation of growth lines. These indicate a shallow subsutural sinus similar in configuration to that seen in Morania(?) boltoni, above. However, the latter species is much larger and has a shouldered whorl profile producing deeper sutural indentation. M. v-sinuata Horný, 1953 has a deeper sinus. There is close similarity between the Arisaig specimen and Palaeozygopleura (Palaeozygopleura) devonicans (Perner, 1907) of Horný (1955) in terms of the shape of the outer lip. However, the growth ornamentation in this Devonian species is much more pronounced.

Superfamily SUBULITACEA Lindström, 1884

Family MEEKOSPIRIDAE Knight, 1956

Genus AURIPTYGMA Perner, 1903

Type species. Auriptygma fortior Perner, 1903.

Auriptygma sp.

(Pl. IX, figs. 22, 23)

Figured material. Upper Stonehouse Fm., YPM 28344 from USNM Colln. 10206(501).

Description. Species of Auriptygma Perner, 1903 with about five whorls. Nuclear whorls unknown. Later whorls uniformly convex with whorl embracement at periphery of previous whorl; sutural indentation shallow. Aperture poorly known;

basal lip seemingly with slight siphonal notch; growth lines indicating form of outer lip are shallowly opisthocyrt on the upper whorl surface (the exposed whorl face) but become prosocyrt on outer and lower whorl surfaces. Ornamentation of fine growth lines. Shell thick, structure unknown.

Discussion. Auripitygma fortior Ferner, 1903 from the Budnamium of Bohemia, as illustrated by Knight (1941), has more convex whorls producing deeper sutural indentation. The growth lines are straight and almost orthocline, in contrast to the slightly sinuous form seen in the Arisaig specimen.

#### Undetermined high spired gastropods

Material. Beechhill Cove Fm., USNM Collections 10114(1), 10115, 10116; Jones Colln. Ar Beechhill Cove Loc. 2, Dunn Point. Ross Brook Fm., Bambach Collections A3731(11), A3743(56), A3744(57), A3760(80); Twenhofel Collections 179/3032(62), 179b/3032(61), 180/3032(54). Doctors Brook Fm., USNM Colln. 10165(141). McAdam Brook Fm., USNM Colln. 10809 from McLellan Brook, Pictou Co. Moydart Fm., USNM Collections 10181, 10853(292); Bambach Colln. A3771(293); Twenhofel Colln. 89/3032(305); Schuchert Colln. 52B; Jones Collections Ar Mo 4800, Ar Mo 4820, Ar Mo 5050, Ar Mo 5500. Stonehouse Fm., USNM Collections 10202(498), 10205(500), 10206(501), 10910(496); Bambach Colln. A3685(381); Twenhofel Collections 12-17/3032(482), 15/3032(474), 19a<sup>8</sup>/3032(422), 19a<sup>14</sup>/3032(432), 24i/3032(371), 30-40/3032(355), 67/3032(326); Schuchert Colln. 53; Jones Colln. Ar S 7380. (150 specimens).

Discussion. Poorly preserved, more or less indeterminate

high spired gastropods are found throughout the succession at Arisaig. Most are known only as internal moulds which cannot be referred to the Murchisoniacea or Loxonematacea with any degree of certainty. The presence of an angulation or obscure spiral band on the whorl of such an internal mould may be considered as evidence of murchisoniacean affinity but the absence of such a feature is no basis for placing a specimen into the Loxonematacea.

In the Stonehouse Fm. the majority of the abundant internal moulds no doubt belong to the contemporaneous Murchisonia (Murchisonia) aciculata Hall, 1860, M. (M.) amii (McLearn, 1924), M. (?Hormotoma) arisaigensis (Hall, 1860), Loxonema sinuosum (Sowerby in Murchison, 1839) and Morania(?) boltoni sp. nov. However, with the exception of the distinctively wide M. (?H.) arisaigensis, it is impractical to attempt to refer internal moulds to any particular member of this morphologically similar group of species. As a consequence, stratigraphical records which are based on positive identifications only, are considerably restricted. Several taxa also occur in each of the Moydart and Beechhill Cove Formations. In the former, probable murchisoniaceans are quite common and may attain a height of 35 mm. In contrast, the artificially decalcified coquinas from the Beechhill Cove Fm. collected by Boucot and his coworkers contain smooth internal moulds which have the shallowly convex whorl profile typical of Loxonema. It is unfortunate that this material has not yielded usable external moulds after the acid treatment process.

Undetermined gastropod species

(Pl. VIII, figs. 16, 17)

Figured material. Undetermined gastropod sp. A, YPM 466 from Stonehouse Fm., Arisaig. Undetermined gastropod sp. B, GSC 33278 from topmost Upper Ross Brook Fm. or Doctors Brook Fm., Jones Colln. Ar M 25.

Additional material. Beechhill Cove Fm., USNM Collections 10114(1) and 10115. French River Fm., USNM Colln. 10811(120) from Harri Brook, Pictou Co. Lower McAdam Brook Fm., Bambach Collections A3606(187), A3608(183), A3616(197).

Discussion. Undetermined gastropod sp. A was figured by McLearn (1924, Pl. XXI, fig. 21) as Goniotropha? sp. He commented that it was too poorly preserved for description. The specimen is an internal mould with adherent shell fragments. An obscure band on the whorl may suggest pleurotomariacean affinity.

Undetermined gastropod sp. B is known only from a single internal mould with two and a half whorls. The rounded apical termination of the mould indicates the presence of a septum closing off the nuclear whorls, as is common in many unrelated groups of gastropods. General shape is reminiscent of Siluriphorus Cossman, 1918, species of which may be locally abundant in the Niagaran dolomites of Illinois and Wisconsin, U.S.A. but there is insufficient evidence to warrant further comparison.

Poorly preserved sublenticular gastropods have been observed in the Beechhill Cove Fm. with a more quadrate profile than the contemporaneous Liospira cf. L. affinis

(Foerste, 1885). In terms of profile there is some similarity with Pycnomphalus Lindström, 1884, a species of which is known to exist in the Llandovery of Pembrokeshire and Shropshire but the diagnostic umbilical characters have not been seen. Lenticular specimens from the French River Fm. in Pictou County and the Lower McAdam Brook Fm. at Arisaig are possibly Liospira species.

PLATE I

Figs. 1-3, 6, 7, 11, 12. Phragmosphaera sp., Moydart Fm., x2.

1, 6, 7. USNM 169598, internal mould with transverse dorsal channels produced by thickening of the shell interior. 1, lateral view showing plate-like extension of parietal deposit into aperture; 6, oblique dorsal view; 7, dorsal view.

2, 3. USNM 169599, internal mould with one preserved dorsal channel. 2, oblique dorsal view showing band produced by median selenizone; 3, lateral view.

11. USNM 169597, internal mould with transverse dorsal channels on each side of median dorsal band. Dorsal view.

12. USNM 192113, internal mould with adhering shell patches showing selenizone and obscure growth lines. Dorsal view.

Figs. 4, 5. Undetermined bellerophonacean sp. D, GSC 6216, internal mould, Stonehouse Fm. (?), x1.5. 4, lateral view showing adherent shell closing umbilicus; 5, dorsal view.

Figs. 8, 9. Undetermined bellerophonacean sp. E, GSC 3139a, internal mould, horizon unknown, x2. 8, dorsal view; 9, lateral view.

Figs. 10, 13, 14. Cymbularia sp.

10. YPM 28329, Lower McAdam Brook Fm., dorsal view, x1.3.

13, 14. USNM 169464, internal mould, Doctors Brook Fm., x3. 13, oblique dorsal view showing obscure growth lines meeting undamaged right side of the infilled dorsal slit; 14, dorsal view showing infilled dorsal slit, left side (right side of figure) broken away.

Figs. 15, 20, 23. Bucanopsis sp., Doctors Brook Fm., x2.

15. USNM 169465, internal mould, dorsal view showing median selenizonal band.

PLATE I (cont.)

Bucanopsis sp...

20, 23. USNM 169466, internal mould. 20, lateral view; 23, dorsal view showing obscure growth lines and infilled slit.

Figs. 16-19, 22, 25, 27. Pharetrolites murchisoni (d'Orbigny in Férussac and d'Orbigny, 1840).

16. USNM 169462, internal mould, Moydart Fm., oblique dorsal view with dorsal keel forming locus of rounded culmination of sinus, x3.4.

17. YPM 462, internal mould, Stonehouse Fm., oblique dorsal view, x2.

18, 19, 22, 25. GSC 33268, internal mould, Stonehouse Fm. 18, posterior view, x2; 19, dorsal view, x2; 22, oblique dorsal view showing adhering shell patch with finely crenulate growth lines, x4; 25, lateral view, x2.

27. YPM 28327, internal mould, Stonehouse Fm., dorsal view, x2.

Figs. 21, 24. Pharetrolites bambachi sp. nov., holotype, YPM 28328, Lower McAdam Brook Fm., x4. 21, oblique dorsal view showing crenulate growth lines and deepened inner sinus; 23, lateral view showing minor emargination and spiral fold on umbilical wall.

Fig. 26. Undetermined bellerophonacean sp. C, YPM 28348, French River Fm., dorsal view, x1.5.

PLATE II

Figs. 1, 3, 5. Pharetrolites murchisoni (d'Orbigny in Férussac and d'Orbigny, 1840), USNM 169461, internal mould, Moydart Fm., x3. 1, oblique dorsal view; 3, dorsal view showing traces of growth lines; 5, lateral view.

PLATE I

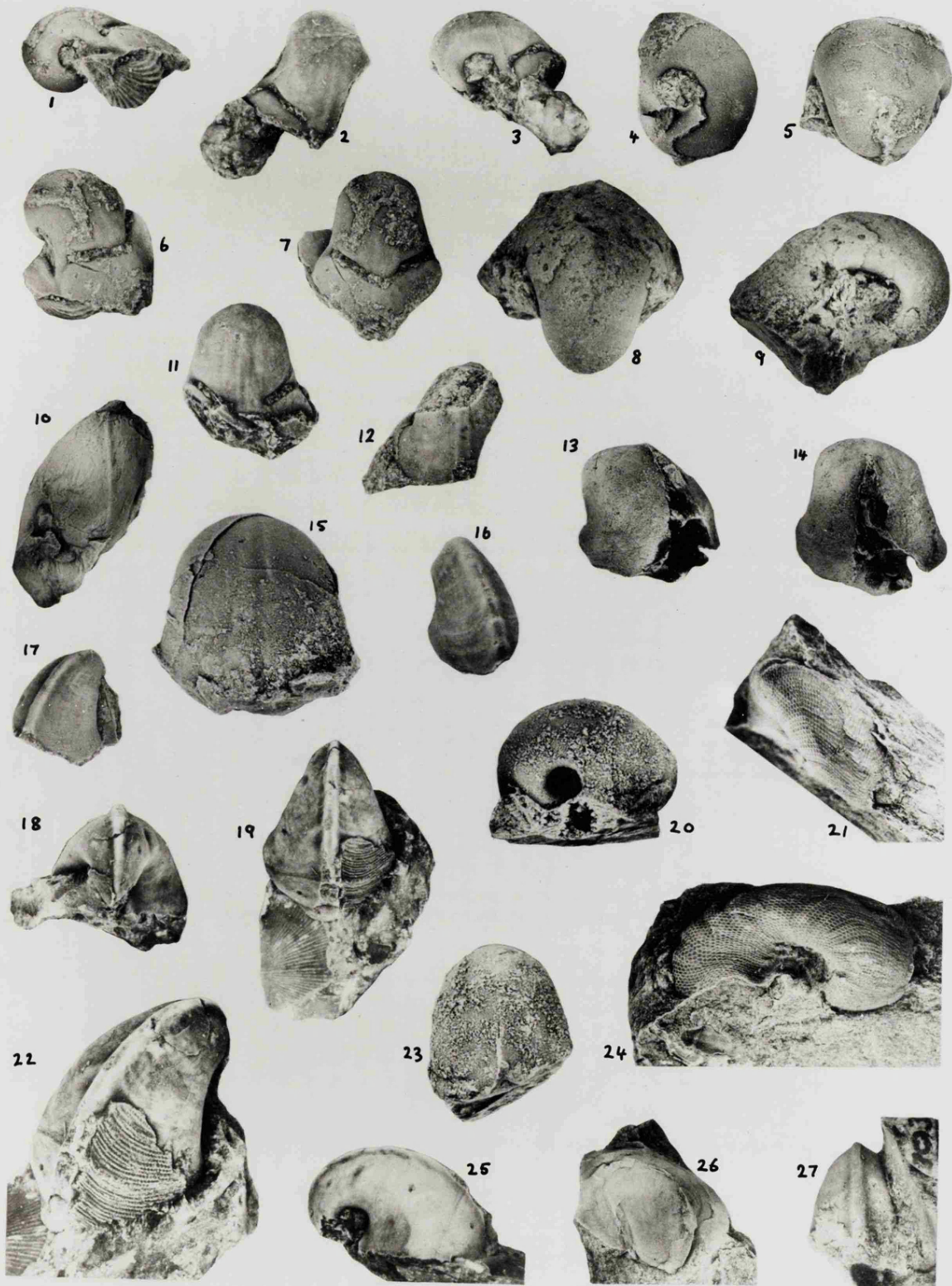


PLATE II (cont.)

Figs. 2, 4, 6-12, 14, 15. Anapetopsis maclearni gen. et sp. nov., Stonehouse Fm., x2.

2, 4. GSC 3140c, paratype, dorsal stereo-pair showing selenizone and ornamentation.

6, 8, 9, 15. GSC 3140a, holotype, internal mould. 6, lateral view showing transverse channel produced by thickening of shell interior; 8, 9, dorsal stereo-pair showing widely expanded aperture with transverse and lateral channels produced by thickening of shell interior; 15, posterior view.

7, 10-12, 14. GSC 3140b, paratype, internal mould. 7, oblique lateral view showing transverse channel; 10, lateral view showing transverse channel; 11, 12, dorsal stereo-pair showing transverse and left lateral channel and median selenizone band; 14, posterior view.

Figs. 13, 16, 17. Anapetopsis lalajae gen. et sp. nov., Stonehouse Fm., x2.

13, 16. GSC 3140, paratype, internal mould. 13, dorsal view showing V-shaped channel produced by thickening of shell interior parallel to growing edge of emargination; 16, lateral view showing V-shaped channel and later transverse channel.

17. USNM 169595, holotype, internal mould, dorsal view showing prominent transverse channel and obscure earlier V-shaped channel.

PLATE III

Figs. 1, 11. Anapetopsis lalajae (?) gen. et sp. nov., Stonehouse Fm.

1. GSC 32781B, apertural view with dorso-lateral margins of aperture broken away, x1.5.

11. USNM 169467, apertural view of specimen crushed in shale showing deep sinus, short slit and small parietal scar, x1.

PLATE II

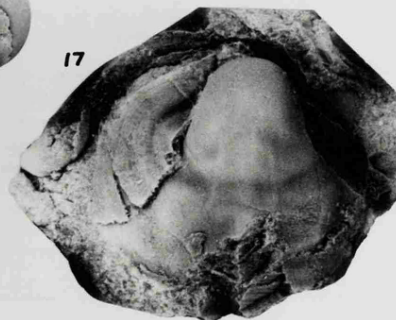
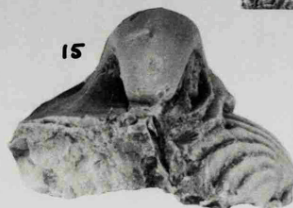
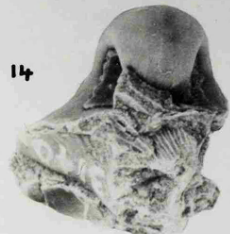
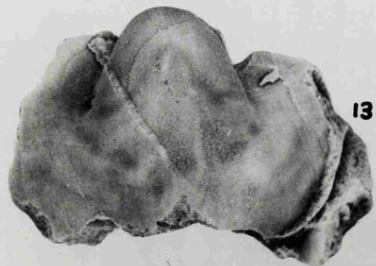
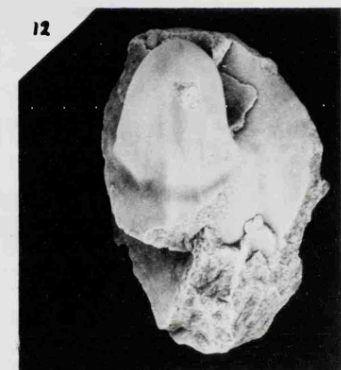
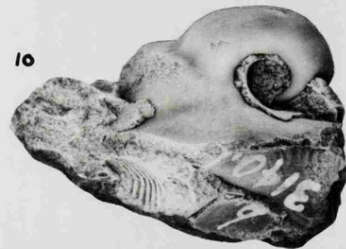
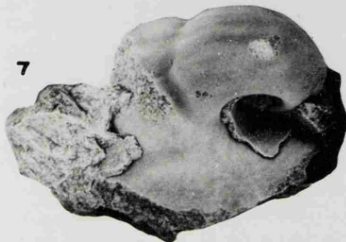
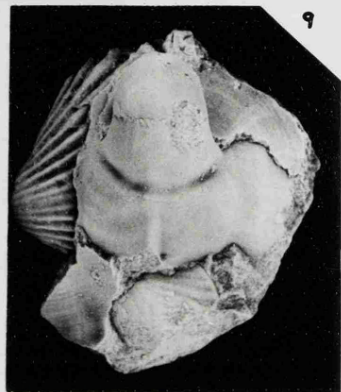
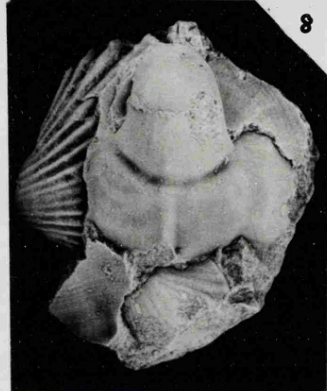
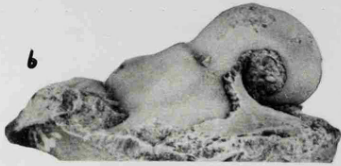
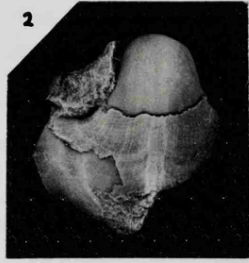


PLATE III (cont.)

Figs. 2, 5. Cymbularia carinata (Sowerby in Murchison, 1839), USNM 169574, internal mould, Moydart Fm., x4. 2, lateral view; 5, dorsal view showing narrow median band.

Fig. 3. Anapetopsis maclearni gen. et sp. nov., GSC 32781A, Stonehouse Fm., apertural view showing apertural boss, x2.

Figs. 4, 7, 10. Anapetopsis lalajae gen. et sp. nov., Stonehouse Fm., x2.

4, 10. USNM 169596, paratype, internal mould showing transverse channel and paired dorsal depressions produced by thickening of the shell interior. 4, oblique dorsal view; 10, dorsal view.

7. USNM 169595, holotype, posterior view.

Figs. 6, 8, 9, 12. Tritonophon sp.

6. YPM 75, Upper Ross Brook Fm., dorsal view showing short slit and selenizone, x3.

8. GSC 33277, Beechhill Cove Fm., oblique dorsal view of internal mould showing lateral margin of slit, x3.

9. YPM 28343, French River Fm., dorsal view of large specimen with obscure selenizone and showing shallow emarginations on lateral lobes, x1.

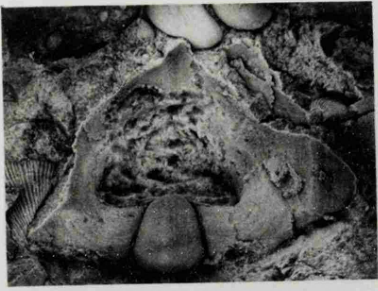
12. YPM 28350, Upper Ross Brook Fm., oblique dorsal view showing selenizone with well developed lumulae, x3.

Figs. 13-21. Tritonophon trilobata (Sowerby in Murchison, 1839).

13. YPM 28347, Moydart Fm., oblique dorsal view of silicon rubber impression showing selenizone and short slit, x4.

14, 16. USNM 169594, Moydart Fm., internal mould, x3. 14, dorsal view; 16, lateral view.

PLATE III



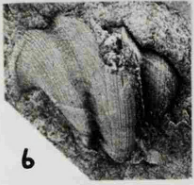
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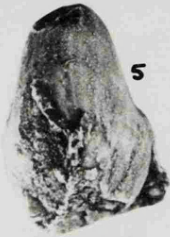
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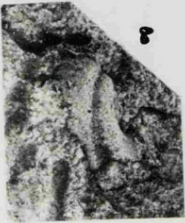
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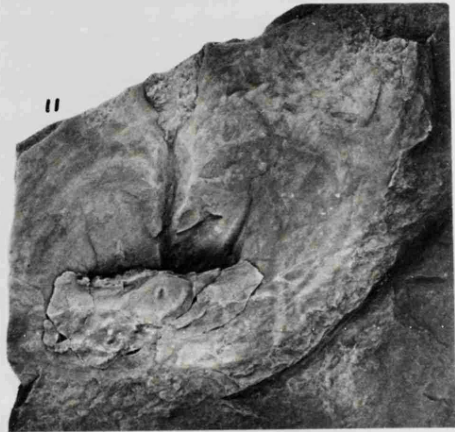
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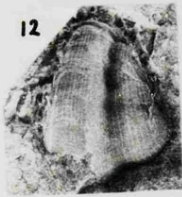
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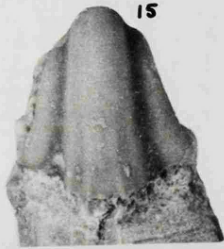
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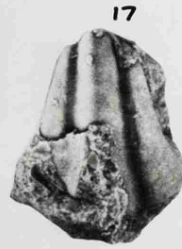
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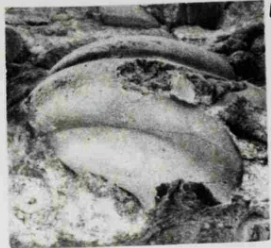
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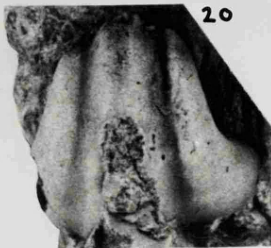
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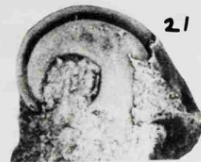
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PLATE III (cont.)

Tritonophon trilobata...

15. USNM 169593, Moydart Fm., dorsal view of internal mould showing median selenizone band, x3.
- 17, 21. GSM 51879, Little Missenden borehole, internal mould, x3.  
17, dorsal view; 21, lateral view.
18. GSC 33276, Moydart Fm., internal mould, x3.
- 19, 20. GSM 51860E, Little Missenden borehole, internal mould showing slit, x2. 19, oblique lateral view; 20, dorsal view.

PLATE IV

Figs. 1-9, 14. Tritonophon trilobata (Sowerby in Murchison, 1839).

- 1, 2. BM PG5002, Felindre, internal mould, x3. 1, lateral view; 2, dorsal view.
- 3, 4. BM PG5004, Felindre, internal mould, x3. 3, dorsal view; 4, lateral view.
5. GSM 51860D, Little Missenden borehole, oblique dorsal view of silicon rubber impression showing selenizone with lunulae, x4.
- 6, 7. GSM Geol. Soc. Coll. 4384, Felindre, internal mould, x3. 6, dorsal view; 7, lateral view showing slight antero-posterior crushing.
- 8, 14. BM PG5003, Felindre, silicon rubber impression showing obscure lunulae, x4. 8, oblique lateral view; 14, dorsal view.
- 9, GSM 51861C, Little Missenden borehole, oblique dorsal view showing selenizone, x4.

Figs. 10-13, 15-22. Tritonophon kivitalonae sp. nov., Stonehouse Fm.

- 10-13. GSC 3138m. 10, 11, apertural and oblique apertural views showing selenizone with lunulae, x5; 12, dorsal view, x3; 13, lateral view, x3.

PLATE IV

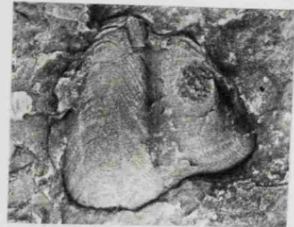
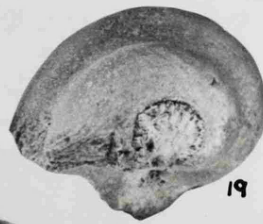
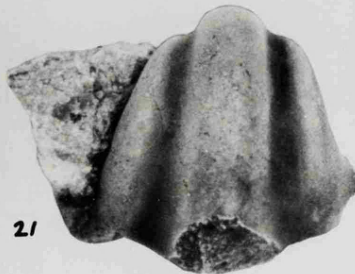
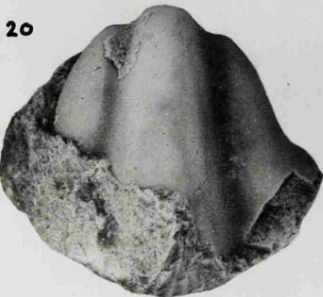
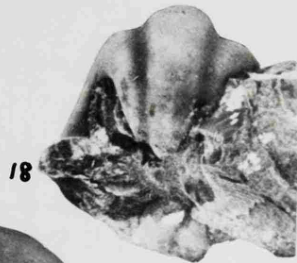
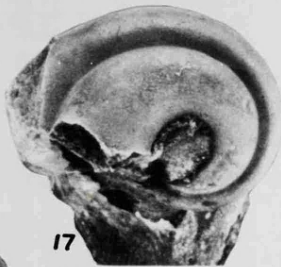
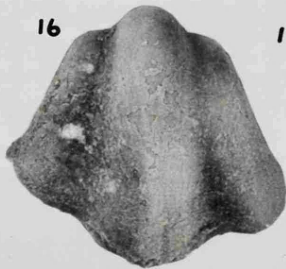
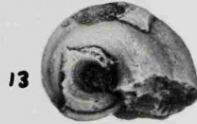
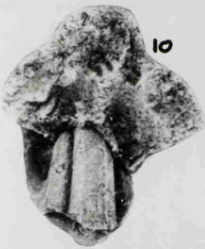
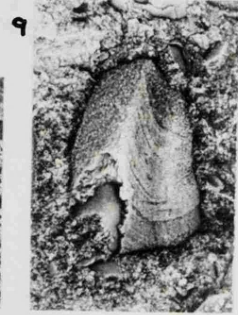
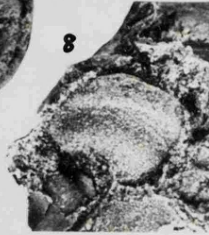
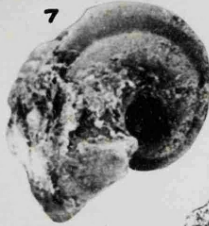
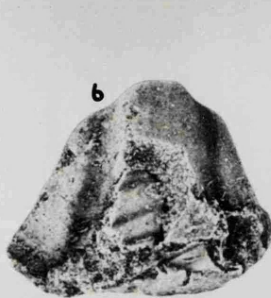
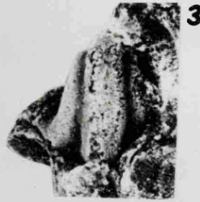
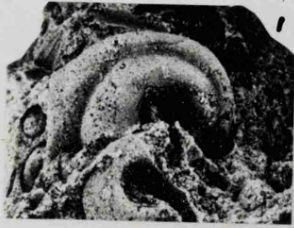


PLATE IV (cont.)

Tritonophon kivitalonae...

- 15, 16, 19. GSC 32782, internal mould, x3. 15, posterior view; 16, dorsal view; 19, lateral view.
- 17, 18, 21. GSC 33275, holotype, internal mould, x3. 17, lateral view; 18, posterior view; 21, dorsal view.
20. GSC 3138a, dorsal view of internal mould showing obscure selenizone band, x2.
22. GSC 5649, dorsal view showing selenizone with lunulae, x2.

PLATE V

Figs. 1-13, 16. Plectonotus chervylae sp. nov., Stonehouse Fm.

- 1, 2. YPM 479, x3. 1, lateral view; 2, oblique dorsal view showing selenizone.
- 3, 4. USNM 169582, holotype, internal mould, x2. 3, lateral view; 4, posterior view showing fragment of selenizone margin.
5. USNM 169578, internal mould, dorsal view, x2.
6. USNM 169580, internal mould, dorsal view, x2.
7. USNM 169468, dorsal view of internal mould of unusually globose specimen, x2.
8. GSC 3138g, internal mould, dorsal view, x2.
9. USNM 169471, juvenile, dorsal view, x5.
- 10-12. USNM 169573, unusually narrow specimen. 10, posterior view of selenizone with lunulae, x4; 11, lateral view, x2; 12, dorsal view, x2.
- 13, 16. USNM 169579, x2. 13, dorsal view; 16, oblique lateral view showing growth lines.

PLATE V

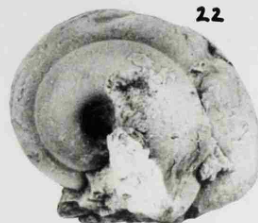
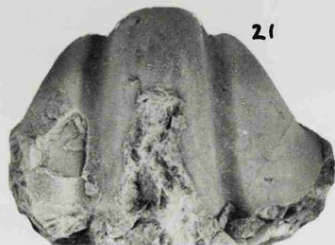
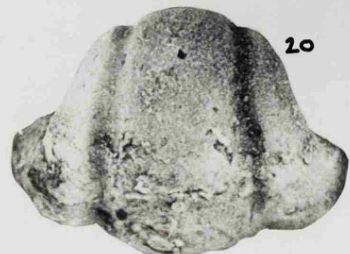
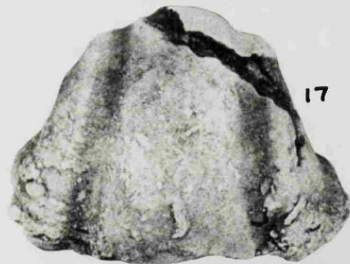
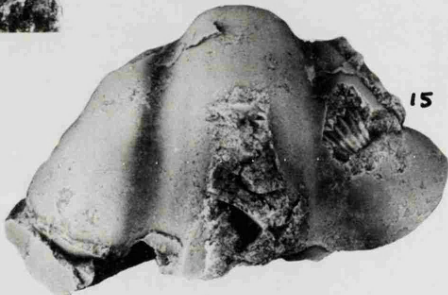
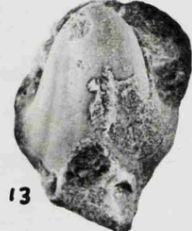
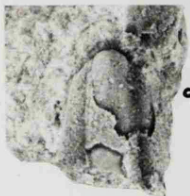
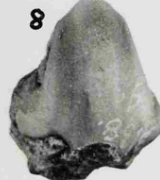
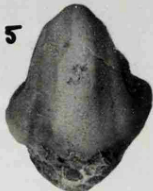
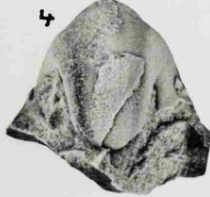
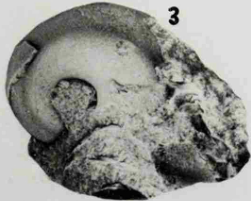
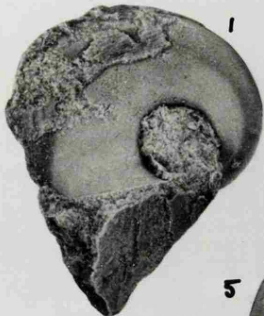


PLATE V (cont.)

Figs. 14, 15, 17-22. Plectonotus boucoti sp. nov.

14. Mo 26567, Gotland, internal mould, oblique dorsal view, x1.  
15. USNM 169589, Doctors Brook Fm., dorsal view of internal mould showing slit, x2.  
17, 18. Mo 26562, Gotland, internal mould, x2. 17, dorsal view; 18, lateral view.  
19, 22. USNM 169590, Doctors Brook Fm., internal mould, x2. 19, dorsal view; 22, lateral view.  
20. Mo 26563, Gotland, internal mould, dorsal view, x2.  
21. GSC 3138, Doctors Brook Fm., dorsal view of internal mould showing slit, x1.5.

PLATE VI

Figs. 1-10, 12, 13, 15, 17, 18. Plectonotus boucoti sp. nov.

- 1-4, 6. USNM 169584, holotype, Doctors Brook Fm. 1, oblique dorsal view showing selenizone, x2; 2, apertural view showing obscure selenizone, x2; 3, lateral view, x2; 4, dorsal view, x2; 6, selenizone area, as in 2, x4.  
5, 10. USNM 169591, Doctors Brook Fm., internal mould, x2. 5, dorsal view; 10, lateral view.  
7. USNM 169583, Doctors Brook Fm., dorsal view showing selenizone and finely pustulose spiral lirae, x5.  
8, 9. USNM 169592, Doctors Brook Fm., internal mould of juvenile, x2. 8, lateral view; 9, dorsal view.  
12. USNM 169588, Doctors Brook Fm., dorsal view showing selenizone and pustulose spiral lirae; the V-shaped trend of the elongate pustules within the selenizone is clearly seen, x6.

PLATE VI (cont.)

Plectonotus boucoti...

13, 15. SM A39165, Tonlegee, Cong, Ireland, internal mould, x2. 13, dorsal view showing part of infilled slit; 15, posterior view.

17, 18. SM A39164, Tonlegee, Cong, Ireland, internal mould, x2.

17, dorsal view showing slit; 18, lateral view.

Figs. 11, 14. Plectonotus derbyi Clarke, 1899b, AMNH 10335/2, lectotype,

Devonian, Rio Maecuru, Para, Brazil, internal mould, x1. 11, dorsal view showing broken anterior margin falsely suggesting shape of the emargination; 14, oblique dorsal view showing median band with obscure lumulae.

Figs. 16, 20. 'Holopea' reversa Hall, 1860, AMNH 1648, holotype, Stonehouse

Fm., internal mould, x4. 16, apical view of basal spire; 20, oblique lateral view showing impression of part of apertural margin.

Figs. 19, 21-23. Mimospira abbae sp. nov.

19. USNM 169571, Moydart Fm., oblique lateral view of internal mould showing basal spire, x4.

21-23. USNM 169489, holotype, McAdam Brook Fm., latex impression.

21. apical view of basal spire showing open coiled protoconch, x6;

22, lateral view, x4; 23, oblique lateral view, x4.

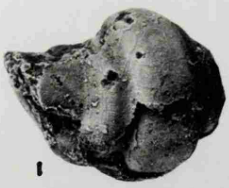
PLATE VII

Figs. 1-4. Liospira marklandensis McLearn, 1924, Stonehouse Fm., x2.

1-3. GSC 5654, holotype. 1, apical view showing forward swing of growth lines; 2, lateral view; 3, oblique lateral view showing obscure peripheral selenizone.

4. USNM 192114, apical view showing ornamentation.

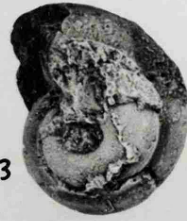
PLATE VI



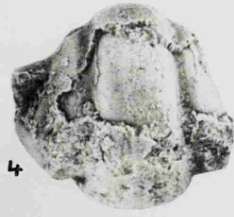
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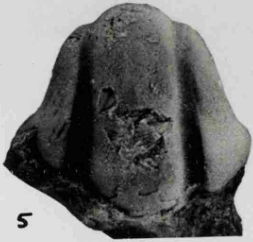
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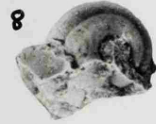
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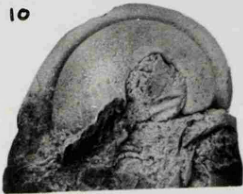
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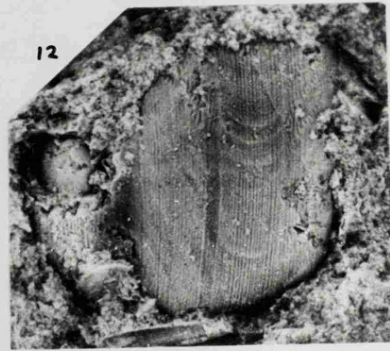
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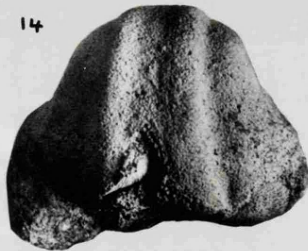
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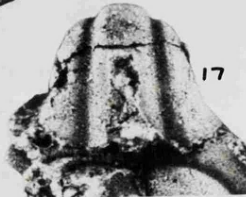
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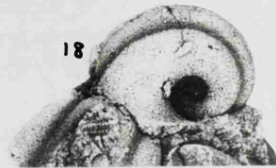
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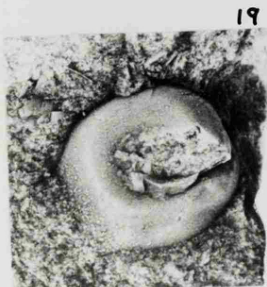
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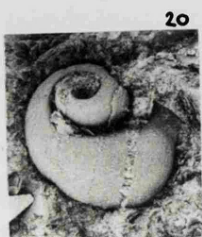
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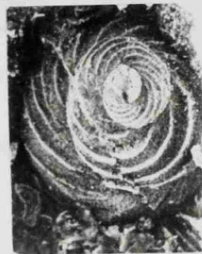
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PLATE VII (cont.)

Figs. 5, 6, 8. Eotomaria sp.

5. YPM 76, Middle Ross Brook Fm., oblique lateral view of crushed specimen,  
x1.

6, 8. USNM 169463, Glencoe Brook Fm., x1.5. 6, apical view; 8, lateral  
view.

Fig. 7. Loxoplocus (Lophospira) sp. B, USNM 169485, Beechhill Cove Fm., lateral  
view of silicon rubber impression, x3.

Figs. 9, 16, 20. Longstaffia centervillensis (Foerste, 1923).

9. YPM 28349, Middle Ross Brook Fm., lateral view of crushed specimen, x2.

16, 20. USNM 188524, Beechhill Cove Fm., x2. 16, lateral view; 20,  
lateral view showing growth lines curving back towards selenizone.

Figs. 10, 11, 14. Liospira cf. L. affinis (Foerste, 1885), Beechhill Cove Fm.,  
x2.

10. YPM 480A, apical view of internal mould.

11, 14. YPM 480B, silicon rubber impression showing peripheral  
selenizone. 11, lateral view; 14, apical view.

Figs. 12, 13. Phanerotrema affin. Ph. jugosum Pitcher, 1939, Beechhill Cove  
Fm., silicon rubber impressions, x1.

12. USNM 169478, oblique lateral view showing selenizone with submedian  
spiral groove.

13. USNM 188520, oblique lateral view.

Fig. 15. Loxoplocus (Lophospira) sp. A, USNM 169482, Beechhill Cove Fm.,  
lateral view of silicon rubber impression, x3.

PLATE VII

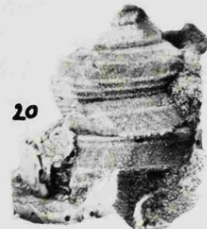
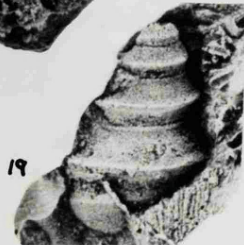
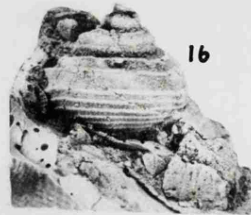
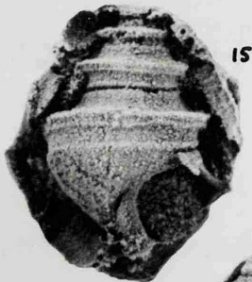
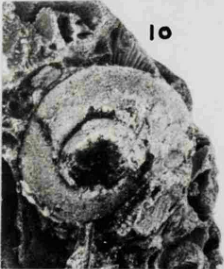
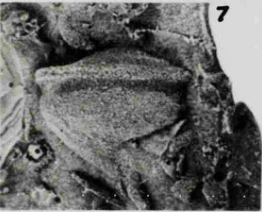
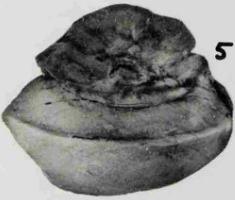
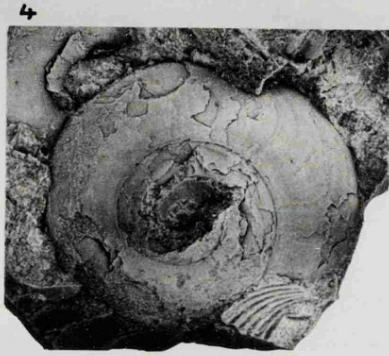
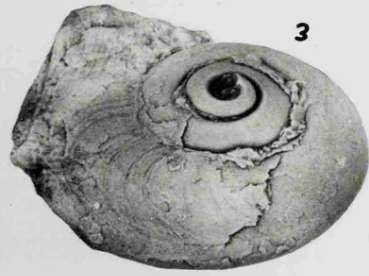
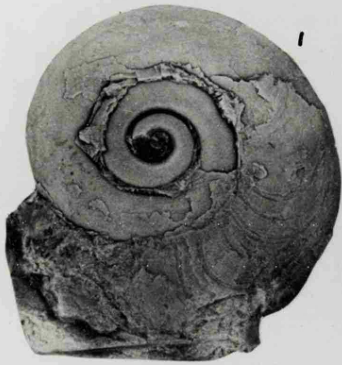


PLATE VII (cont.)

Figs. 17, 18. Longstaffia sp., USNM 169487, Beechhill Cove Fm., silicon rubber impression showing obscure growth lines curving into selenizone, x2. 17, lateral view; 18, oblique lateral view.

Fig. 19. Loxoplocus (Lophospira) sedgwickii (Longstaff, 1906), USNM 169481, Beechhill Cove Fm., lateral view of silicon rubber impression, x4.

PLATE VIII

Figs. 1, 4, 8, 10-12. Ariamannia cancellatula (M'Coy in Sedgwick and M'Coy, 1852).

1. SM A34830, Mulloch Sandstone, Girvan, lateral view, x1.5.

4. SM A34829, holotype, Mulloch Sandstone, Girvan, lateral view, x1.5.

8. USNM 188523, Beechhill Cove Fm., lateral view of silicon rubber impression of juvenile, x2.

10. USNM 169483, Beechhill Cove Fm., oblique lateral view of silicon rubber impression showing reticulation of growth lines and spiral lirae on base, x2.

11. USNM 169484, Beechhill Cove Fm., lateral view of silicon rubber impression showing ornamentation of upper whorl surface and selenizone, x3.

12. USNM 169480, Beechhill Cove Fm., oblique lateral view of silicon rubber impression of large individual, x2.

Figs. 2, 3, 6, 7. Ariamannia inexpectans (Hall and Whitfield, 1875), USNM 85063, Brassfield Limestone, Ohio, x1.5. 2, basal view; 3, 6, lateral views; 7, oblique lateral view.

Fig. 5. Umbospira sp., YPM 28330, Upper Ross Brook Fm., apical view showing sinus in outer lip and spiral crack near periphery, x2.

PLATE VIII (cont.)

Fig. 9. Undetermined trochinid genus and species, USNM 169486, Beechhill Cove Fm., lateral view of silicon rubber impression, x2.

Figs. 13, 14. Ariamannia aulangonensis gen. et sp. nov., USNM 169469, holotype, Doctors Brook Fm., x2. 13, lateral view of silicon rubber impression showing wide selenizone with median groove; 14, lateral view of internal mould with angulation at midwhorl corresponding to position of selenizone.

Fig. 15. Brachytomaria sp., YPM 28326, Stonehouse Fm., lateral view of crushed specimen showing selenizone and growth lines, x4.

Fig. 16. Undetermined gastropod sp. B, GSC 33278, Upper Ross Brook Fm. or Doctors Brook Fm., lateral view of internal mould, x2.

Fig. 17. Undetermined gastropod sp. A, YPM 466, Stonehouse Fm., lateral view of internal mould, x2.

Fig. 18, 19. Ariamannia woodlandi (Longstaff, 1924), USNM 188521, Beechhill Cove Fm., silicon rubber impression, x1.5. 18, apertural view; 19, apical view showing subsutural cord and traces of growth lines.

PLATE IX

Figs. 1-4, 6-8. Naticopsis trevorpatriciorum sp. nov.

1, 2. BM PG5007, Felindre, internal mould, x5. 1, apertural view; 2, oblique lateral view.

3. BM PG5008, Felindre, apertural view of internal mould, x5.

4. BM PG5005, Felindre, silicon rubber impression, lateral view, x4.

PLATE VIII

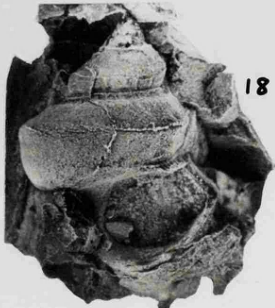
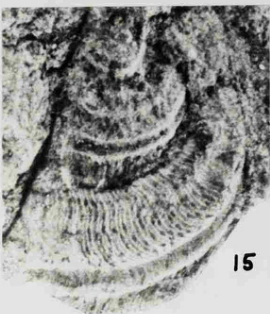
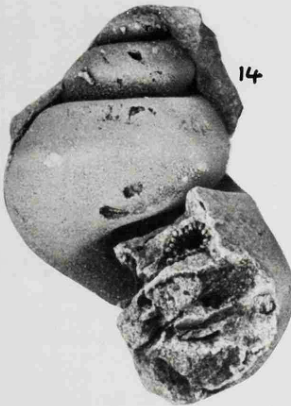
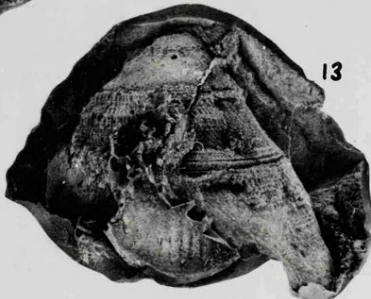
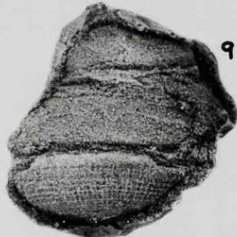
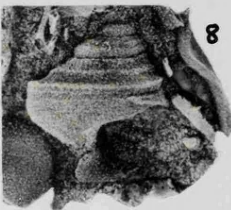
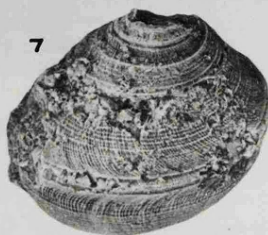
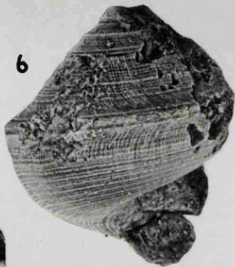


PLATE IX (cont.)

Naticopsis trevorpatriciorum...

- 6, 8. SM A37091, Kirkby Lonsdale, x4. 6, lateral view showing relatively prominent growth lines; 8, basal view showing growth lines deflected backwards into slight anterior notch.
7. BM PG5006, Felindre, apical view of silicon rubber impression showing growth lines on final whorl, x4.

Figs. 5, 9, 11. Cyclonema (Cyclonema) lydiamarianum sp. nov., Felindre, silicon rubber impressions, x5.

5. BM PG5001, oblique lateral view.

9, 11. BM PG5000, holotype. 9, oblique lateral view; 11, lateral view.

Fig. 10. Undetermined gyronematinid genus and species, YPM 28346, Moydart Fm., lateral view of silicon rubber impression showing adpressed whorls and spiral lirae crossed by fine growth lines, x3.

Figs. 12, 13, 16, 17. Naticonema kauffmani sp. nov., Beechhill Cove Fm., silicon rubber impression, x3.

12, 16. USNM 169479, oblique apertural and apertural views showing columella.

13, 17. YPM 462A, holotype, oblique lateral views showing subsutural sinus in obscure growth ornamentation.

Figs. 14, 15. Haplospira sibeliuxeni sp. nov., USNM 192116, holotype, Upper Stonehouse Fm., x4. 14, oblique lateral view; 15, lateral view.

Figs. 18, 21. Holopea sp., Upper Ross Brook Fm.

18. YPM 28334, lateral view, x2.

21. YPM 28333, lateral view, x2.2.

PLATE IX

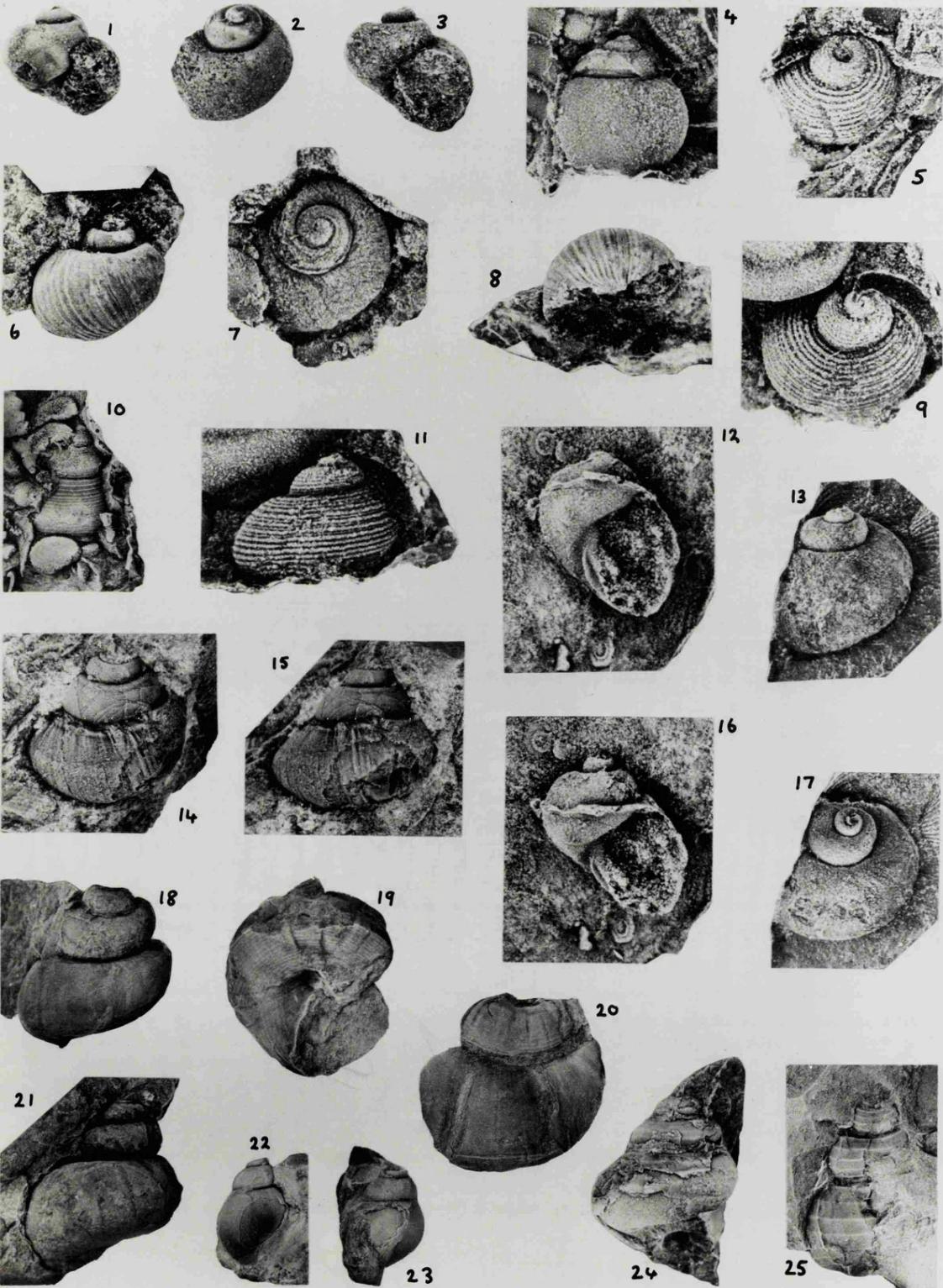


PLATE IX (cont.)

Figs. 19, 20. Undetermined holopeid genus and species, YPM 28336, Middle Ross Brook Fm., x2. 19, basal view showing spiral lirae; 20, lateral view.

Figs. 22, 23. Auripygma sp., YPM 28344, Upper Stonehouse Fm., lateral views, x2.

Fig. 24. Undetermined trochonematid genus and species, USNM 192115, Stonehouse Fm., lateral view, x3.

Fig. 25. Gyronema haliburtoni (McLearn, 1924), YPM 462B, holotype, Ross Brook Fm., lateral view, x3.

PLATE X

Figs. 1-4. Cyclonema (Cyclonema) parvimedius McLearn, 1924, Beechhill Cove Fm., x1.

1, 3. USNM 169475, silicon rubber impression. 1, oblique lateral view; 3, lateral view.

2. USNM 169476 and USNM 169477 (smaller specimen), silicon rubber impression, oblique apertural views showing thickened columella with opercular groove.

4. GSC 5655, holotype, worn specimen with subdued ornamentation.

Figs. 5, 7-12, 14. Platyceras (Platystoma) cornutum (Hisinger, 1837).

5. USNM 192117, Moydart Fm., oblique lateral view of internal mould showing circular muscle attachment scar, x2.

7. USNM 188522, French River Fm., latex impression, apical view, x1.

8, 12. GSC 33272, Moydart Fm., x2. 8, apical view; 12, lateral view.

PLATE X (cont.)

Platyceras (Platvostoma) cornutum...

9. GSC 33273, Moydart Fm., lateral view showing spiral plication, x2.  
10, 11. GSC 5657, holotype of Diaphorostoma cornutum var. arisaigensis McLearn, 1924, Stonehouse Fm., x1.5. 10, oblique apertural view;  
11, apical view.  
14. GSC 5656, holotype of Holopea caecistriata McLearn, 1924, Stonehouse Fm., lateral view showing irregular growth lines and fine spiral ornamentation, x2.

Figs. 6, 13, 15-17, 19, 22. Seelya moydartensis McLearn, 1924, Moydart Fm.

6. GSC 33274, oblique lateral view of silicon rubber impression showing selenizone and finely reticulate ornamentation, x1.5.  
13, 15. YPM 464A, internal mould, x1. 13, lateral view showing growth varices curving to meet selenizonal band; 15, apertural view.  
16. YPM 28331, internal mould, lateral view of small individual with unusually large incremental angle, x1.  
17, 19. YPM 464, holotype, internal mould, x1. 17, basal view; 19, lateral view showing selenizonal band and spiral plications on base.  
22. GSC 33270, internal mould, lateral view showing spiral cords on upper whorl surface, x1.

Fig. 18. Naticopsis trevorpatriciorum sp. nov., YPM 28332, holotype, Moydart Fm., lateral view, x4.

Fig. 20. Cyclonema (Cyclonema) lydiamariarum sp. nov., YPM 28335, Stonehouse Fm., oblique lateral view of crushed specimen, x4.

Fig. 21. Platycomus (?) sp., GSC 32783, Stonehouse Fm., lateral view, x1.

PLATE X

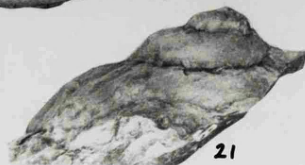
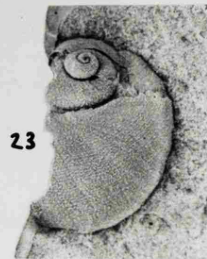
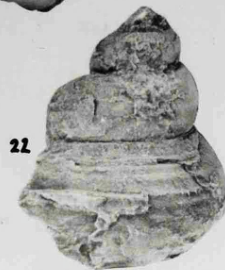
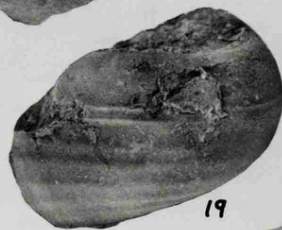
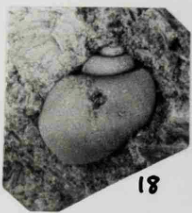
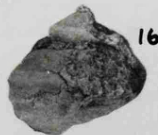
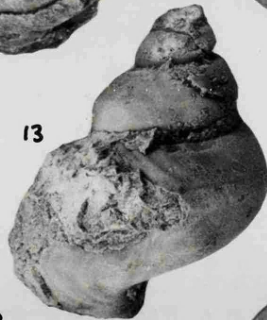
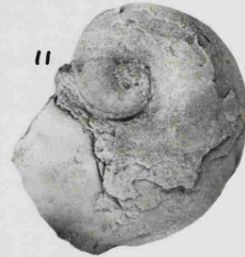
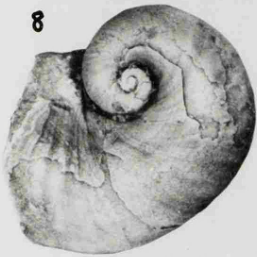
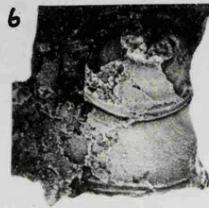
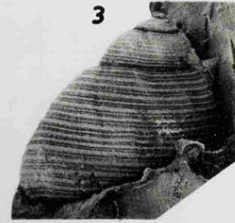
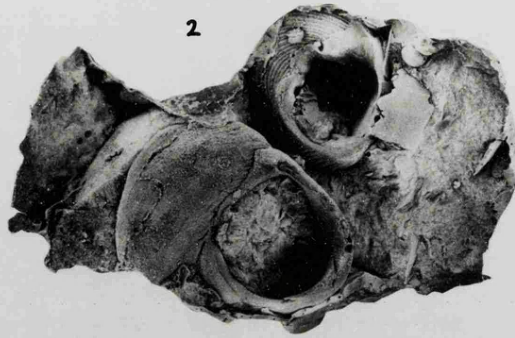


PLATE X (cont.)

- Fig. 23. Platyceras (Platystoma) cf. P. (Pl.) humilis (Billings, 1866),  
USNM 169490, Middle Ross Brook Fm., oblique lateral view of silicon  
rubber impression showing fine spiral striations, x1.5.

PLATE XI

- Figs. 1-3. Murchisonia (Murchisonia) aciculata Hall, 1860, Stonehouse Fm.  
1. GSC 5651, lateral view showing growth lines and selenizone, x4.  
2. GSC 5650, lateral view of internal mould, x2.  
3. AMNH 1649, holotype, lateral view of internal mould, x3.

- Figs. 4, 5, 11. Murchisonia (Murchisonia) amii (McLearn, 1924), Stonehouse Fm.  
4. YPM 28337B, lateral view of silicon rubber impression showing two  
spiral cords lying within the selenizone, x5.  
5. GSC 5652, holotype, lateral view of partly exfoliated specimen lacking  
the spiral cords on the selenizone, x3.  
11. USNM 192121, lateral view showing selenizone below midwhorl, x5.

- Figs. 6, 7, 10, 16. Murchisonia (?Hormotoma) ariscigensis (Hall, 1860),  
Stonehouse Fm.  
6. USNM 192119, lateral view of internal mould, x1.5.  
7. AMNH 1650, lectotype, lateral view of internal mould, x2.1.  
10. AMNH 1650, paralectotype, lateral view of internal mould, x2.1.  
16. USNM 192118, lateral view of juvenile showing obscure band at  
midwhorl, x4.

- Fig. 8. Morania (?) sp., YPM 28342, Lower McAdam Brook Fm., lateral view  
showing obscure growth lines on final whorl, x6.5.

PLATE XI (cont.)

Fig. 9. Murchisonia (Sinuspira) cf. M. (S.) tenera (Permer, 1907), YPM 28338,  
Lower McAdam Brook Fm., lateral view of crushed specimen showing  
sinus, x2.5.

Figs. 12, 18. Morania (?) boltoni sp. nov., USNM 192120, holotype, Stonehouse  
Fm., x2. 12, lateral view; 18, oblique lateral view.

Fig. 13. Loxonema sinuosum (Sowerby in Murchison, 1839), YPM 28337A,  
Stonehouse Fm., lateral view, x3.

Fig. 14. Loxonema sp. A, GSC 33269, McAdam Brook Fm., lateral view, x2.

Fig. 15. Loxonema sp. B, YPM 28341, Upper Ross Brook Fm., lateral view, x1.5.

Fig. 17. Murchisonia (Hormotoma) sp. B, YPM 28340, Upper McAdam Brook Fm.,  
lateral view of a single whorl, x2.

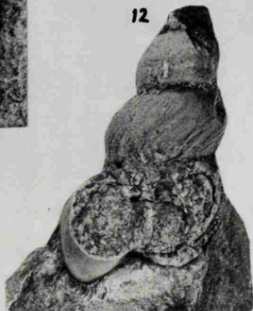
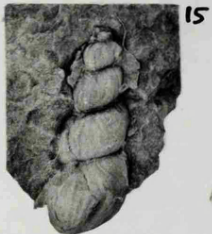
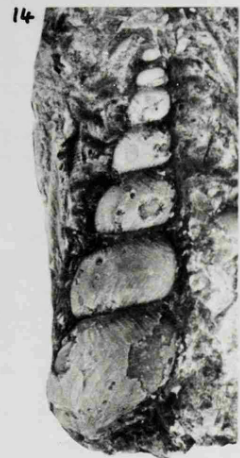
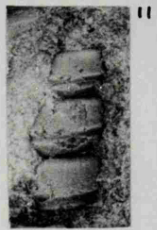
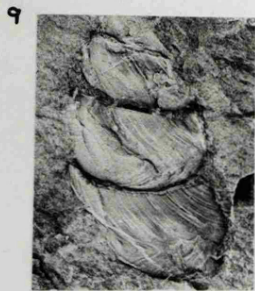
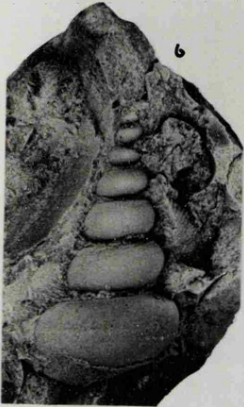
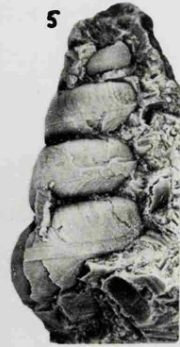
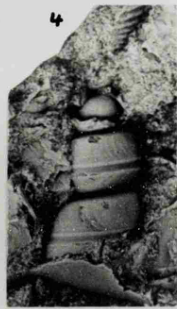
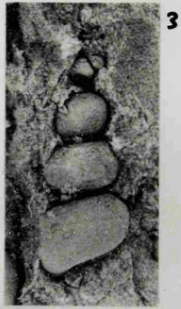
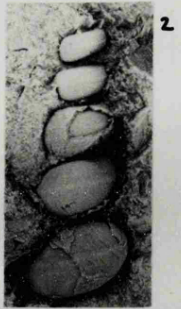
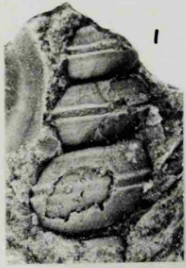
Fig. 19. Murchisonia (Hormotoma) sp. A, YPM 28339, Upper Ross Brook Fm.,  
lateral view of crushed specimen, x5.

Figs. 20, 21. Undetermined murchisoniid genus and species, Moydart Fm.

20. USNM 169470, lateral view showing growth lines above and below the  
raised selenizone, x8.5.

21. YPM 28345, lateral view of silicon rubber impression, x3.5.

PLATE XI



PALAEOECOLOGY

'Indeed it would seem almost difficult to name anything which Arion ater will not eat. A specimen kept two days in captivity was turned out on a newspaper, and commenced at once to devour it. The same specimen ate dead bodies of five other species of slugs, a dead Unio, pupae of Adimonia tanaceti, part of the abdomen of a dragon-fly, and Pear's soap, the latter reluctantly.'

(Cooke, Shipley and Reed, 1895)

## Introduction

Prosobranch gastropods show considerable ecologic diversity in present seas. In a recent review Purchon (1968) noted that archaeogastropods are mainly browsers on algae but some, e.g., Patella Linne, 1758, rasp fine algal growths from the rock surfaces to which they cling. 'Lower' caenogastropods (=Mesogastropoda Thiele, 1925) may also be algal browsers but other members of the group collect plankton, e.g., Crepidula fornicata (Linne, 1758), or are deposit feeders, e.g., Hipponyx DeFrance, 1819; Aporrhais Da Costa, 1778. Some are carnivores and feed on colonial animals, e.g., cowries feeding on ascidians, or actively hunt other molluscs, e.g., naticids. Lanthina Rødding, 1798 and the heteropods are pelagic predacious carnivores while a few members of the group are parasites.

The so-called 'higher' caenogastropods (=Neogastropoda Wenz, 1938) are dominantly scavengers and hunters although some columbellids feed on brown algae. Marine species of the subclass Euthyneura Spengel, 1881 occupy a similar range of habitats to prosobranchs.

In the lower Palaeozoic it is unlikely that gastropod eating habits were so diverse. The great majority of fossil gastropods from rocks of this age (Knight et al., 1960) belong to the prosobranch order Archaeogastropoda Thiele, 1925 and are presumed to be herbivorous, in keeping with most present day members of the order (Keen, 1971; Purchon, 1968). The only common caenogastropods in the lower Palaeozoic are the high spired loxonemataceans and rarer subulitaceans which occur in middle Ordovician and younger strata but it is difficult to suggest that these were predators. Carriker and Yochelson (1968) and Sohl (1969) have reviewed the occurrence of possible

molluscan borings in palaeozoic invertebrates and concluded that there was little evidence to justify referring these to attacks by carnivorous gastropods.

The post Palaeozoic diversification of the Gastropoda and increasing relative abundance of caenogastropods is further emphasised by the changes in the structure of the archaeogastropod fauna itself. Of nearly twenty families of archaeogastropods with representatives in present seas, less than a quarter are known before the Mesozoic while only four families persist at the present of the thirty six recognised in the Palaeozoic (Knight et al, 1960).

The changes which have taken place in the structure and composition of gastropod faunas from the Silurian to the present day clearly cause problems for ecological extrapolation in the reverse direction. There is a need to establish some parallel between present day and fossil morphological adaptations. Ultimately, such comparisons come to be based on similarities in shell morphology, with the necessary assumption that some relationship exists between shell form and mode of life. Unfortunately, functional studies of present day gastropod shells are infrequent although some of the more extreme morphologies do show an obvious correlation to mode of life, for example, the cap-shaped shell of limpets adapted for clinging in high energy environments.

However, a recent study by Vermeij (1971) demonstrates some of the potential of a more precise approach to shell morphology. By utilising the geometrical methods of Raup (1966; 1967; see discussion of Plectonotus boucoti sp. nov. in the systematic section, above), Vermeij was able to demonstrate differences in morphological diversity between the major gastropod taxa.

A notable example, the absence of the high spired form in the Archaeogastropoda, is discussed more fully in a later section. A much more simple demonstration of the usefulness of such an approach for fossil gastropods is given in the final part of this study but increased information about recent gastropods would permit the development of more sophisticated models of analysis.

A brief discussion of palaeogeography is followed in this section by a description of the palaeoecology of the gastropod fauna of the Arisaig Group. The first part is essentially a factual record of the distribution of gastropods and the sedimentary environment prevailing during the accumulation of the particular assemblages. In the second part, an attempt is made to synthesize this information.

The open marine shelf faunas of the Beechhill Cove and Upper Stonehouse Formations are compared and it is concluded that the lophospirid pleurotomariacean fauna of the Beechhill Cove Formation was probably developed on a slightly firmer, more sandy substratum than the high spired loxonematacean and murchisoniacean dominated fauna of the Upper Stonehouse Formation.

Intervening strata may be loosely grouped into two shallowing cycles with passage from deeper water, argillaceous sediments at the base to shallow, barrier and back-barrier deposits at the top. A faunal sequence showing replacement of holopeiform species by bellerophontaceans and, ultimately, by trilobed bellerophontaceans is recognised in each cycle and is apparently related to the shallowing.

Trilobed bellerophontaceans of the subfamily Plectonotinae are characteristic of much of the Arisaig Group

and form an assemblage seemingly indicative of very shallow water conditions. An exploratory study of gastropod faunal composition indicates faunal development during the period of deposition of the Arisaig Group comparable to that recorded by Bambach (1969ms) for the bivalve fauna and suggests that geometric analysis of shell form could prove valuable in the understanding of gastropod palaeoecology.

#### Silurian palaeogeography.

From available palaeomagnetic data (Runcorn, 1962), Bambach (1969ms) estimated that Arisaig lay within the tropics or subtropics during the Silurian and he cited the high taxonomic diversity of the bivalve fauna (text-fig. 17B) as indicative of a warm climate (after Stehli, McAlester and Hellsley, 1967). Well preserved bivalves and nautiloids were submitted to G. Pannella and C. MacClintock at Yale Peabody Museum, New Haven, Conn., who noted only minor seasonal effects in the distribution of growth lines without the extreme crowding produced by slow growth in cold weather.

Irving (1964) drew the Silurian equator along a line from Los Angeles to the Northern tip of the Ungava Peninsula in Quebec which placed Arisaig at about fifteen degrees South on the present configuration of land and sea. In a recent reconstruction by McKerrow and Ziegler (1972) a more tenable arrangement of land and sea has Nova Scotia separated from the rest of North America by a narrow Proto-Atlantic and Arisaig is located more than forty degrees South of the equator (text-fig. 13A). However, it should be noted that the Niagaran reefs around Chicago, which previous restorations (Irving, 1964) have placed near to the equator, are located at more than fifty degrees South by McKerrow and Ziegler (1972)!

TEXT-FIG. 13

A. Silurian continental distributions (after McKerrow and Ziegler, 1972).

Nova Scotia (NS) is near the Southern extremity of a peninsula, incorporating England and Northwest Europe, which is separated from Gaspé and the rest of North America by a narrow Proto-Atlantic (P).

E: Equator; SP: South Pole.

B-D. Typical reef associated gastropods not known from the Arisaig Group.

B. Poleumita Clarke and Ruedemann, 1903, an euomphalacean, x0.7.

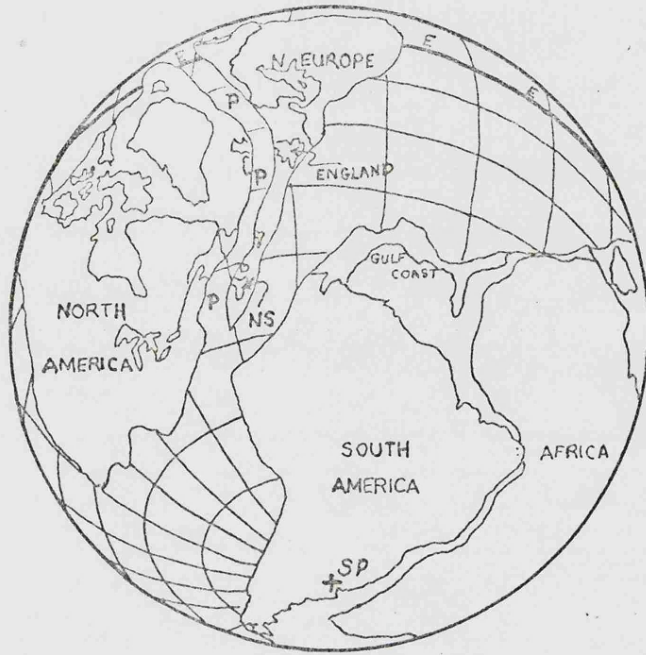
C. Euomphalopterus Roemer, 1876, a pleurotomariacean, x0.7.

D. Tremanotus Hall, 1865, a bellerophonacean, x0.7.

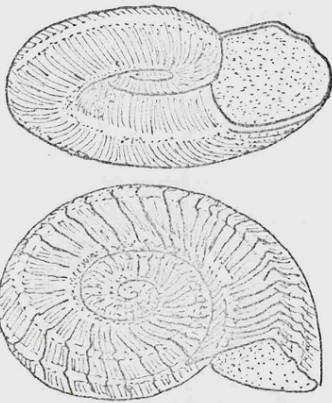
(all drawn after Knight et al, 1960)

Text-fig. 13

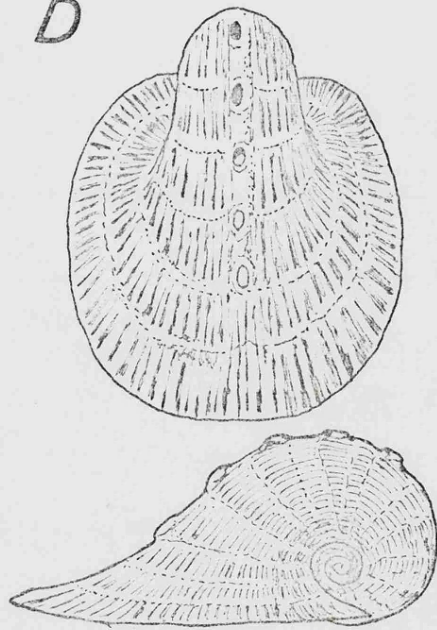
A



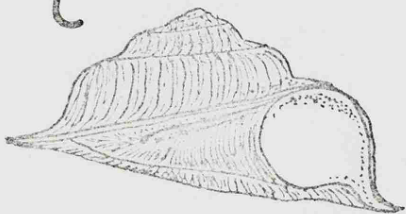
B



D



C



The gastropod fauna of the Arisaig Group is quite unlike the reef associated faunas of Gotland (Lindström, 1884) and the Chicago region where Euomphalopterus Roemer, 1876, Poleumita Clarke and Ruedemann, 1903 and trematoid bellerophontaceans are typical faunal elements (text-fig. 13B-D). None of these genera occur at Arisaig where the fauna is characterised by trilobed bellerophontaceans of the subfamily Plectonotinae (Pls. III-VI). The extent to which these differences can be attributed to latitudinal or other environmental factors is not known. A recent paper by Forney and Boucot (in press) has attempted to elucidate the global distribution of some of the reef associated species noted above but their information, plotted on a present day configuration of land and sea, does not appear to be sufficiently abundant for the task in hand.

#### The Sedimentary Model : Stratigraphic Distribution of Gastropods

As a prelude to his study of bivalve palaeoecology, Bambach (1969ms) attempted to reconstruct the depositional environment at Arisaig throughout the Silurian and lower Devonian. His observations and deductions are combined with those of Boucot et al (in press) to provide a base for all present discussion of gastropod palaeoecology.

Bambach (1969ms) recognised four broad lithological groups within the Arisaig Group. The Beechhill Cove and Ross Brook Formations were interpreted as normal marine rocks with the overlying French River, Doctors Brook and McAdam Brook Formations equated with barrier and lagoonal conditions. The Moydart and Lower Stonehouse Formations accumulated as nearshore and shore line shoal deposits, the intervening red beds of the Upper

Moydart Formation representing a brief nonmarine episode. The Upper Stonehouse Formation marked a return to open marine conditions.

#### Beechhill Cove Formation.

The Beechhill Cove Formation is mainly composed of hard, grey-green quartzose siltstone and thin, micaceous shales, with occasional lenses of fine grained sandstone (Boucot et al, in press). Bambach (1969ms) recorded only lingulid brachiopods and crinoid ossicles in the siltstones and shales laid down as the lower Llandovery sea transgressed across the underlying volcanics but noted that brachiopod rich coquinite commonly formed the basal part of the sandstone lenses.

With eighteen described species, the gastropod fauna of the Beechhill Cove Formation is second only to the Upper Stonehouse Formation in diversity (text-fig. 17G). Common species include Cyclonema (C.) parvimedium, Liospira cf. L. affinis, Phanerotrema affin. Ph. jugosum and lophospirid pleurotomariaceans. Bellerophontaceans and high spired gastropods are less conspicuous (text-figs. 14A).

#### Ross Brook Formation.

In the sedimentary model of Bambach (1969ms) the Lower and lower Middle Members of the Ross Brook Formation represented accumulation under the deepest water conditions experienced at Arisaig during the Silurian. The sediments were fine grained with a high water content and lacked cohesion, producing a soft substratum and turbid water conditions unfavourable to the development of an epifauna. It is unlikely that depth alone was a limiting factor preventing the establishment of an abundant epifauna (Hallam, 1971) and, Boucot et al (in press) and Bambach (1969ms) recorded the presence of the Eocoelia Community. As one of the most shallow

Stratigraphic distribution of gastropods in the Beechhill Cove and Ross Brook Formations.

Stratigraphic thicknesses and numbered strata after Bambach (1969ms).

BC: Beechhill Cove Fm.; LRB, MRB, URB: Lower, Middle, Upper Ross Brook Fm.

A. Beechhill Cove Fm.

Datum: 300ft. for contact of top of Beechhill Cove Fm. with overlying Lower Ross Brook Fm., exposed on West side of Beechhill Cove.

Species recorded from other horizons:

Tritonophon sp.

Longstaffia sp.

Bucanopsis sp.

Arjamannia cancellatula

Undet. bellerophontacean sp. A

Arjamannia woodlandi

Undet. bellerophontacean sp. B

Phanerotrema affin. Ph. jugosum

Liospira cf. L. affinis

Naticonema kauffmani

Eotomaria sp. (Glencoe Brook Fm.)

Cyclonema (C.) parvimedium

Loxoplocus (Lophospira) sedgwickii

Pl. (Platystoma) cornutum

Loxoplocus (Lophospira) sp. A

Undet. trochinid gen. and species

Longstaffia centervillensis

B. Middle and Upper Ross Brook Fm.

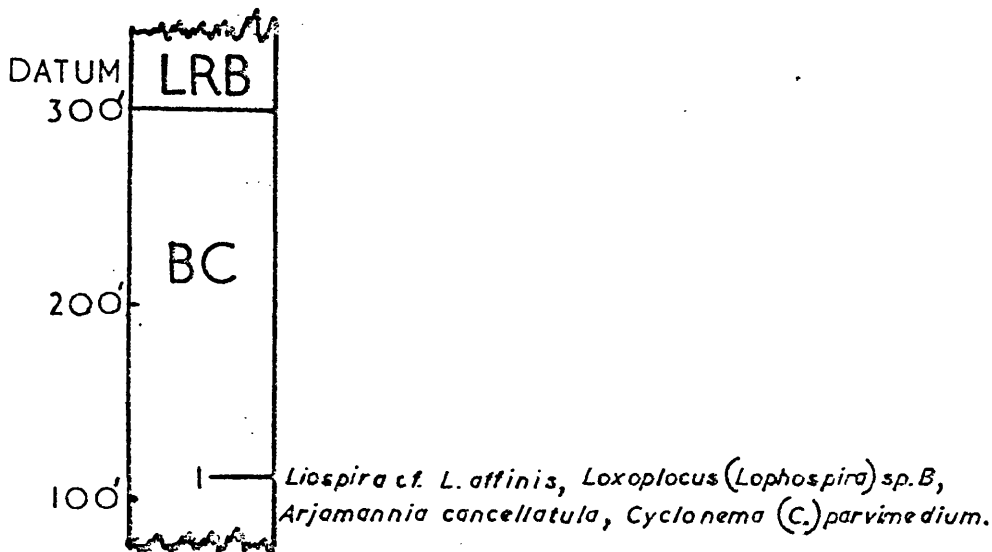
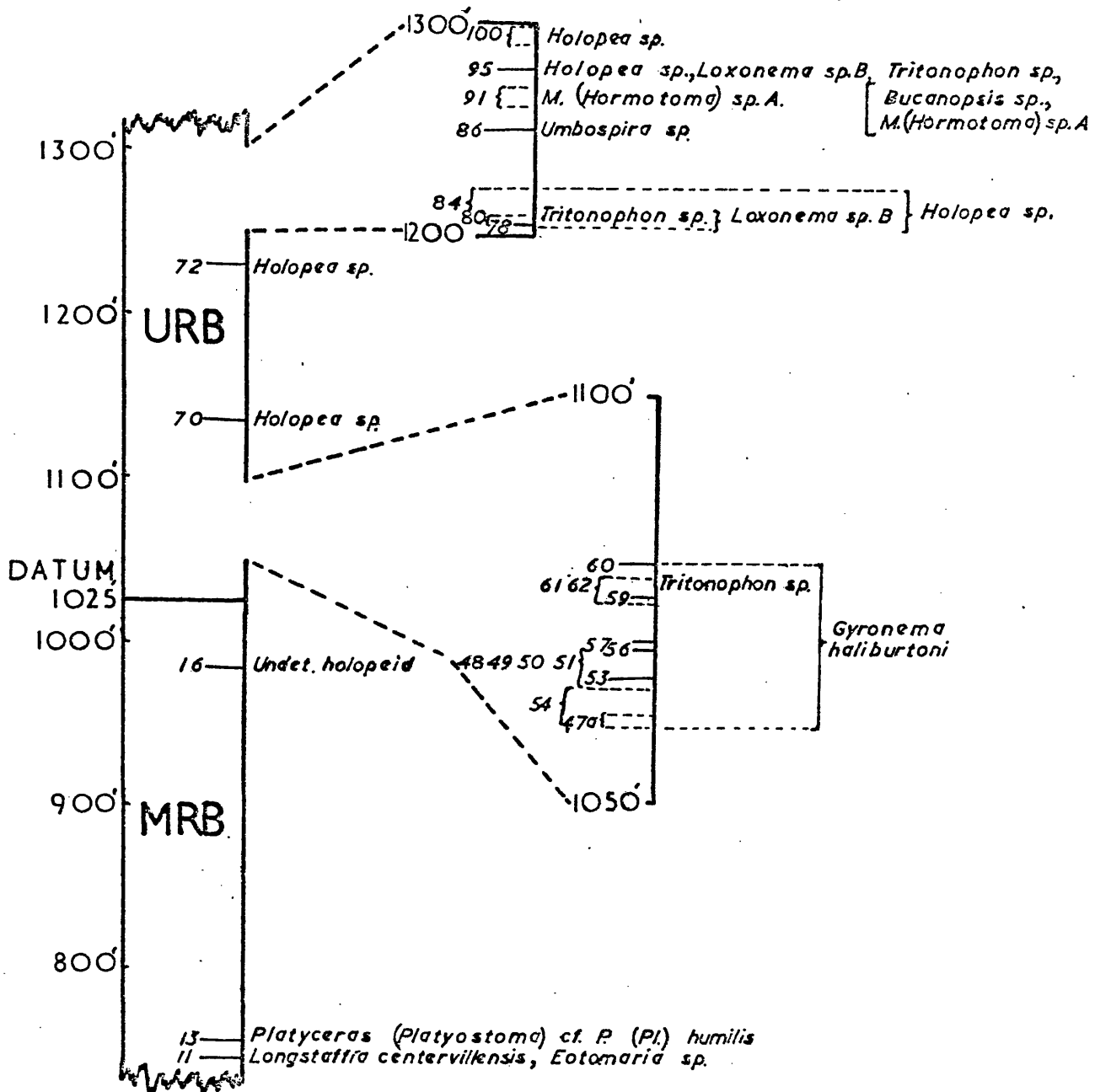
Datum: 1025ft. for contact of top of Middle Ross Brook Fm. with overlying Upper Ross Brook Fm., exposed in first prominent seaward projecting cliff West of Mouth of Arisaig Brook.

Species recorded from other horizons in Upper Member:

Gyronema haliburtoni

(?) Undet. gastropod sp. B

Text-fig. 14



water communities of Ziegler (1965), the Eocoelia Community typically has a diverse gastropod fauna in other areas (Ziegler, Cocksand Bambach, 1968).

During the upper Middle and Upper Members of the Ross Brook Formation thin bedded shoal deposits alternate with more massive silty shales probably laid down in shallow water in the lee of offshore shoals (Bambach, 1969ms). The shoal sediments contain only brachiopod coquinites but a rich epifauna characterises the more massive shale beds.

Gastropods have not previously been recorded from the Lower Ross Brook Formation and no collections were available for study during the present examination. Only four species have been observed in the collections from the Middle Member and two of these are represented by single specimens. Eotomaria sp. and Longstaffia centervillensis also occur in the Beechhill Cove Formation but the undetermined holopeid and Platyceras (Platyostoma) cf. P. (Pl.) humilis are restricted to this member. Gyronema haliburtoni is common in collections from the lower beds of the Upper Member of the Ross Brook Formation and is associated with a possible loxonematacean. In the higher beds, the fauna is dominated by Holopea sp. with Tritonophon sp., Bucanopsis sp., Umbospira sp., Murchisonia (Hermotoma) sp. A and Loxonema sp. B (text-fig. 14B).

#### French River Formation.

Bambach (1969ms) considered that the massively bedded : siltstones of the French River Formation represented a barrier separating the lagoonal sediments of the Doctors Brook and McAdam Brook Formations from the open sea. A thin bed of oolitic ironstone present at Arisaig was probably formed near the shore on the lagoonal side of the barrier as Sheldon (1964; 1970) has suggested for other Silurian ironstones in the Southern Appalachians.

Fossils are scarce in the French River Formation at Arisaig and, with the exception of a single specimen of Platyceras (Platyostoma)

cornutum from Ross Brook, all the gastropods were collected at French River, Pictou County. The fauna is meagre with P. (Pl.) cornutum accompanied by Tritonophon sp., undetermined bellerophontacean species C and undetermined high spired gastropods (text-fig. 15A).

#### Doctors Brook Formation.

The irregular bedding, occasional phosphatic nodules and the presence of oscillation and interference ripples led Bambach (1969ms) to conclude that the Doctors Brook Formation was a back-barrier, lagoonal deposit. Salinity was perhaps slightly reduced but the presence of a diverse fauna indicates that restricted lagoonal conditions were not present.

The gastropod fauna of the Doctors Brook Formation is restricted to only six species (text-fig. 17G). Bellerophontaceans are most conspicuous with Plectonotus boucoti and the micromorphic Tropidodiscus (?) sp. abundant in coquinites. Bucanopsis sp., Cymbularia sp., Arjamannia aulangonensis, Platyceras (Platyostoma) cornutum and rare, undetermined high spired gastropods also occur (text-fig. 15B).

#### McAdam Brook Formation.

The Lower McAdam Brook Formation is composed of dark, sulphide rich shales which represent soft muds accumulating in the centre of a quiet lagoon. The Upper Member is mainly massive siltstone which Bambach (1969ms) interpreted as nearshore deposits in the almost completely infilled lagoon.

Bambach (1969ms) undertook detailed analysis of the bivalve fauna of the McAdam Brook Formation and was able to demonstrate a close relationship between the evolution of the fauna and the infilling of the lagoon. Deposit feeding bivalves dominate the fauna throughout (text-fig. 18B) but closer examination revealed a gradual change from faunas with a preponderance of nonsiphonate deposit feeding bivalves to faunas almost

TEXT-FIG. 15

Stratigraphic distribution of gastropods in the French River, Doctors Brook and McAdam Brook Formations.

Stratigraphic thicknesses and numbered strata after Bambach (1969ms).

FR: French River Fm.

DB: Doctors Brook Fm.

LMB, UMB: Lower, Upper McAdam Brook Fm.

A. French River Fm.

Datum: 1530ft. for Bambach Colln. A3776(115), on East side of French River, Pictou Co.

Species recorded from other horizons:

Tritonophon sp.

Platyceras (Platvostoma) cornutum

B. Doctors Brook Fm.

Datum: 1965ft. for contact of top of Doctors Brook Fm. with overlying Lower McAdam Brook Fm., exposed at East side of mouth of McAdam Brook. (A local datum of 1850ft. was established for the faulted section at the base of the unfaulted section).

Species recorded from other horizons:

Plectonotus boucoti

Cymbularia sp.

Bucanopsis sp.

Arjamannia aulangonensis

C. McAdam Brook Fm.

Datum: 1965ft., as for 15B, above.

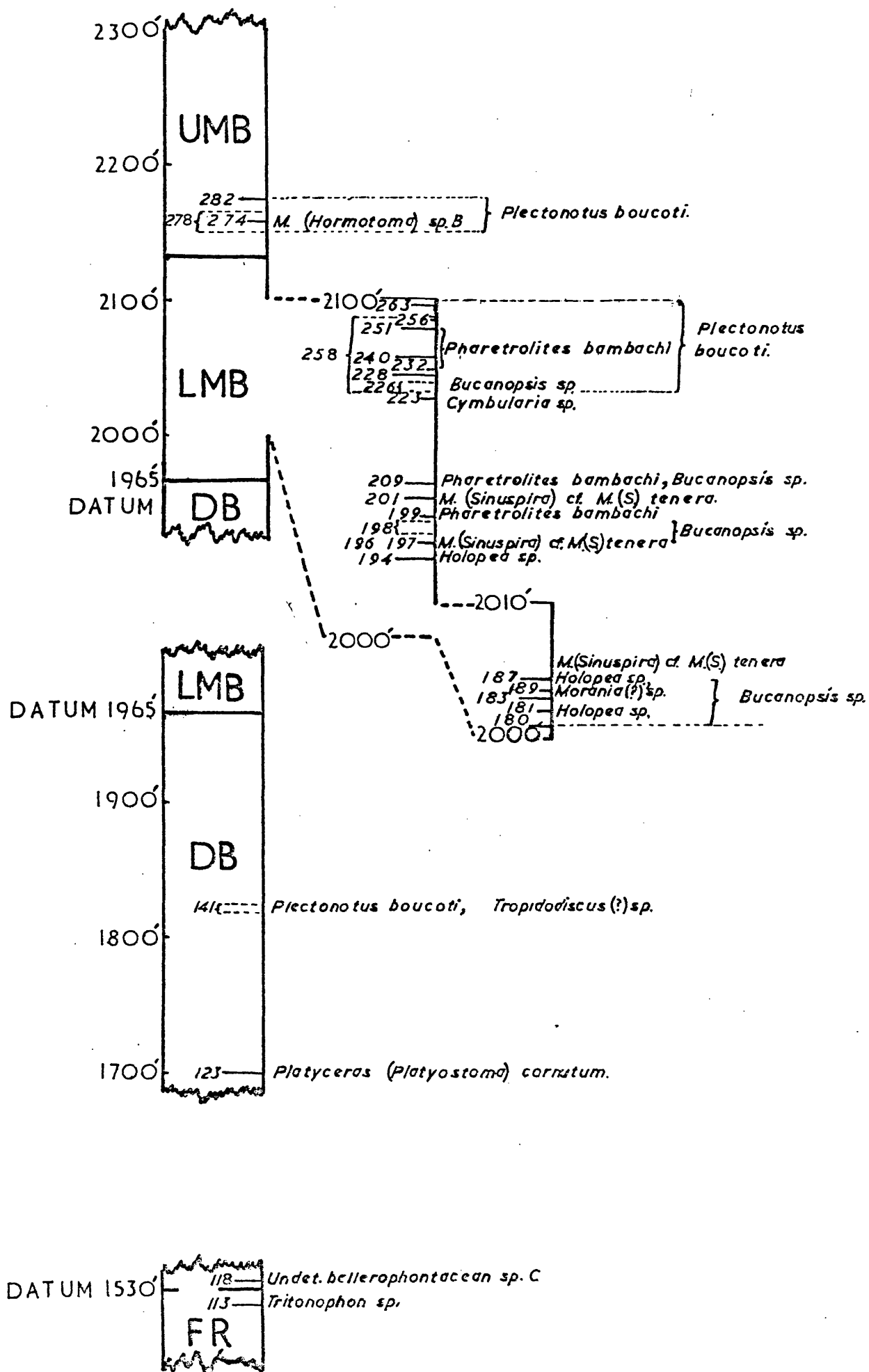
Species recorded from other horizons:

Mimospira abbae

Loxonema sp.

Platyceras (Platvostoma) cornutum

# Text-fig. 15



exclusively composed of siphonate deposit feeders. The proportion of suspension feeders decreased slowly from about thirty percent to ten percent of the total.

The gastropod fauna shows comparable development (text-fig. 15C). The lowest thirty feet of strata have yielded no gastropods but the next twenty feet (Bambach strata 180-194) contain a fauna of Bucanopsis sp. and Holopea sp., with associated Murchisonia (Sinuspira) cf. M. (S.) tenera and a poor lenticular species, probably Liospira or Umbospira. Holopea sp. and the poorly preserved lenticular gastropod are not known above this level but Bucanopsis sp. and M. (S.) cf. M. (S.) tenera continue, with Pharetrolites bambachi coming into the fauna. M. (S.) cf. M. (S.) tenera has not been observed higher than seventy seven feet above the base of the formation (Bambach stratum 201) and some thirty feet higher, in the upper half of the Lower Member, the fauna is dominated by Plectonotus boucoti and Pharetrolites bambachi with occasional Bucanopsis sp. and Cymbularia sp. The sequence is characterised by the gradual replacement of one species by another rather than by the succession of discrete faunas.

#### Moydart Formation.

The Lower (=Green) Member of the Moydart Formation accumulated in the very shallow, almost completely filled lagoon in which the underlying McAdam Brook Formation was deposited. The basal and upper parts of the Green Member represent sedimentation in relatively high energy conditions while the middle part was deposited more slowly in a lower energy environment (Bambach, 1969ms).

The gastropod fauna of the Green Member is distinctive with Seelya moydartensis, Tritonophon trilobata, Cymbularia carinata, Phragmosphaera sp., Naticopsis trevorpatriciorum and undetermined gyronematinid and murchisoniid species associated with numerous undetermined high spired gastropods. Pharetrolites murchisoni continues

into the Upper Stonehouse Formation and the widely distributed Platyceras (Platyostoma) cornutum is frequently present in collections. The presence of rare specimens of the hyperstrophically coiled Mimospira abbae extends the range of the genus from the upper Ordovician to the upper Silurian (text-fig. 16A).

The Upper (=Red) Member of the Moydart Formation is a nonmarine subaerial deposit which Dineley (1963) compared to the lower beds of the Old Red Sandstone of Britain. Boucot et al (in press) recorded nodular limestones similar to the cornstones of the British Dittonian (Devonian).

#### Stonehouse Formation.

The Lower Member of the Stonehouse Formation is essentially similar to the Green Member of the Moydart Formation and represents shoreline deposition following the readvance of the sea into the estuarine and fluviatile regime of the underlying red beds (Bambach, 1969ms). McLearn (1924) recorded rare specimens of Murchisonia (M.) aciculata but no collections were available during the present study.

The diverse and abundant fauna of the shales and siltstones of the Upper Stonehouse Formation announces a return to open marine conditions. The waters were still shallow, however, with more massive siltstone beds indicating periodic high energy conditions (Bambach, 1969ms).

The gastropod fauna of the Upper Stonehouse Formation is the most varied in the Arisaig Group with twenty described species (text-figs. 16B, 17G). High spired forms are typical with abundant Murchisonia (M.) aciculata, M. (M.) amii, M. (?Hormotoma) arisaigensis and less frequent loxonemataceans. Unlike the Beechhill Cove Formation, pleurotomariaceans are rare, with the exception of the ubiquitous Liospira marklandensis. Six species of bellerophonaceans are present with the trilobed Plectonotus cherylae widely distributed. Only Pharetrolites murchisoni and Platyceras(Platyostoma) cornutum occur in other formations.

Stratigraphic distribution of gastropods in the Moydart and Stonehouse Formations.

Stratigraphic thicknesses and numbered strata after Bambach (1969ms).

GMO: Green Member, Moydart Fm.; US: Upper Stonehouse Fm.

A. Moydart Fm.

Datum: 2615ft. for contact of top of Green Member, Moydart Fm. with the overlying Red Member, exposed on West side of McDonald Cove.

Species recorded from other horizons:

Pharetrolites murchisoni

Platyceras (Platvostoma) cornutum

Tritonophon trilobata

Naticopsis trevorpatriciorum

Phragmosphaera sp.

Undet. murchisoniid gen. and species

Cymbularia carinata

Seelya moydartensis

B. Upper Stonehouse Fm.

Datum: 3623ft. for bed at mouth of McEachern Brook (contact between zones 39 and 40 of Twenhofel(1909)).

Species recorded from other horizons:

Pharetrolites murchisoni

Undet. trochonematid gen. and species

Plectonotus chervylae

Platyceras (Platvostoma) cornutum

Tritonophon kivitalonae

Murchisonia (M.) aciculata

Anapetopsis maclearni

Murchisonia (M.) amii

Anapetopsis lalajae

M. (?Hormotoma) arisaigensis

Undet. bellerophontacean sp. D

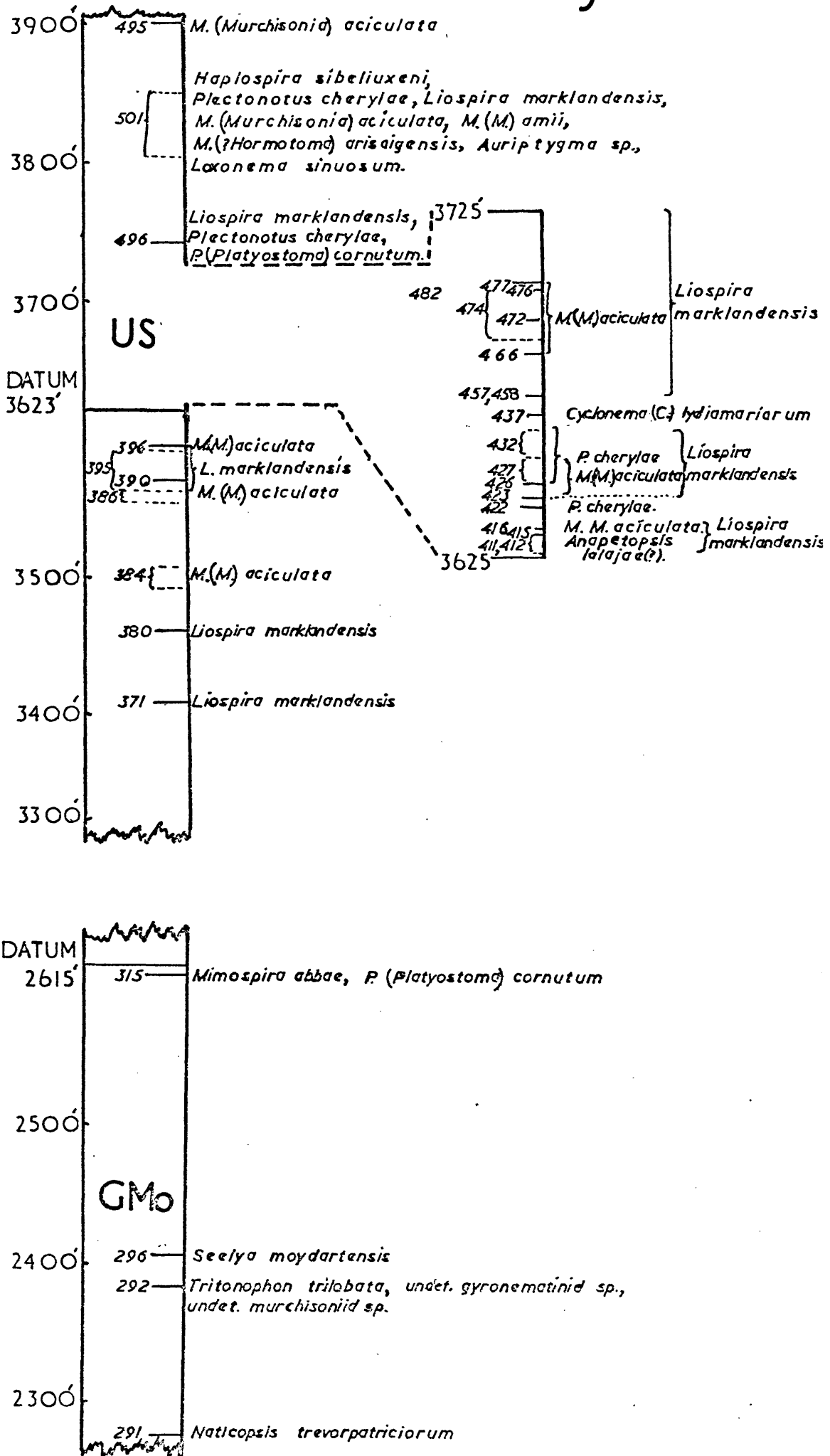
Morania (?) boltoni

Liospira marklandensis

Undet. gastropod sp. A

Brachytomaria sp.

Text-fig. 16



## Synthesis

### Faunas of the Beechhill Cove and Upper Stonehouse Formations.

The gastropod fauna of the Arisaig Group is most diverse, in terms of number of species, in the Beechhill Cove Formation (eighteen species) and the Upper Stonehouse Formation (twenty species). In the intervening strata fewer than half this number of species are present in any one member (text-fig. 17G).

Examination of the faunal lists of McLearn (1924) shows similar high diversity in the Upper Stonehouse Formation for brachiopods, bivalves, trilobites and cephalopods (text-fig. 17A-F). The abundance of species is no doubt equated with the return to full marine conditions after the more restricted environments of earlier deposits.

The high number of gastropod species present in the Beechhill Cove Formation is not echoed by any of the major fossil groups listed by McLearn (1924) where even gastropods are limited to three species against the eighteen noted here. To some extent, the paucity of previous records can be equated with the difficulty of collecting from the hard coquinites. This is partly demonstrated by the greatly increased numbers of brachiopods and gastropods in collections made by Boucot and co-workers which were decalcified by acid treatment prior to detailed examination in the laboratory. The number of brachiopod species recorded by Boucot et al (in press) is twice that documented by McLearn (1924) while gastropods show a sixfold increase.

The gastropod faunas of the Beechhill Cove and Upper Stonehouse Formations are quite distinct even though both formations were deposited under shallow water, open marine conditions. In the former, pleurotomariaceans account for more than a half of the recorded species (text-fig. 14A) with lophospirids particularly well represented (seven species). In the Upper Stonehouse Formation lophospirids are completely absent and three of the four described pleurotomariaceans are rare

TEXT-FIG. 17

Distribution of species in the Arisaig Group.

A-F. After McLearn (1924).

A. Total fauna.

B. Bivalves.

C. Brachiopods.

D. Trilobites.

E. Cephalopods.

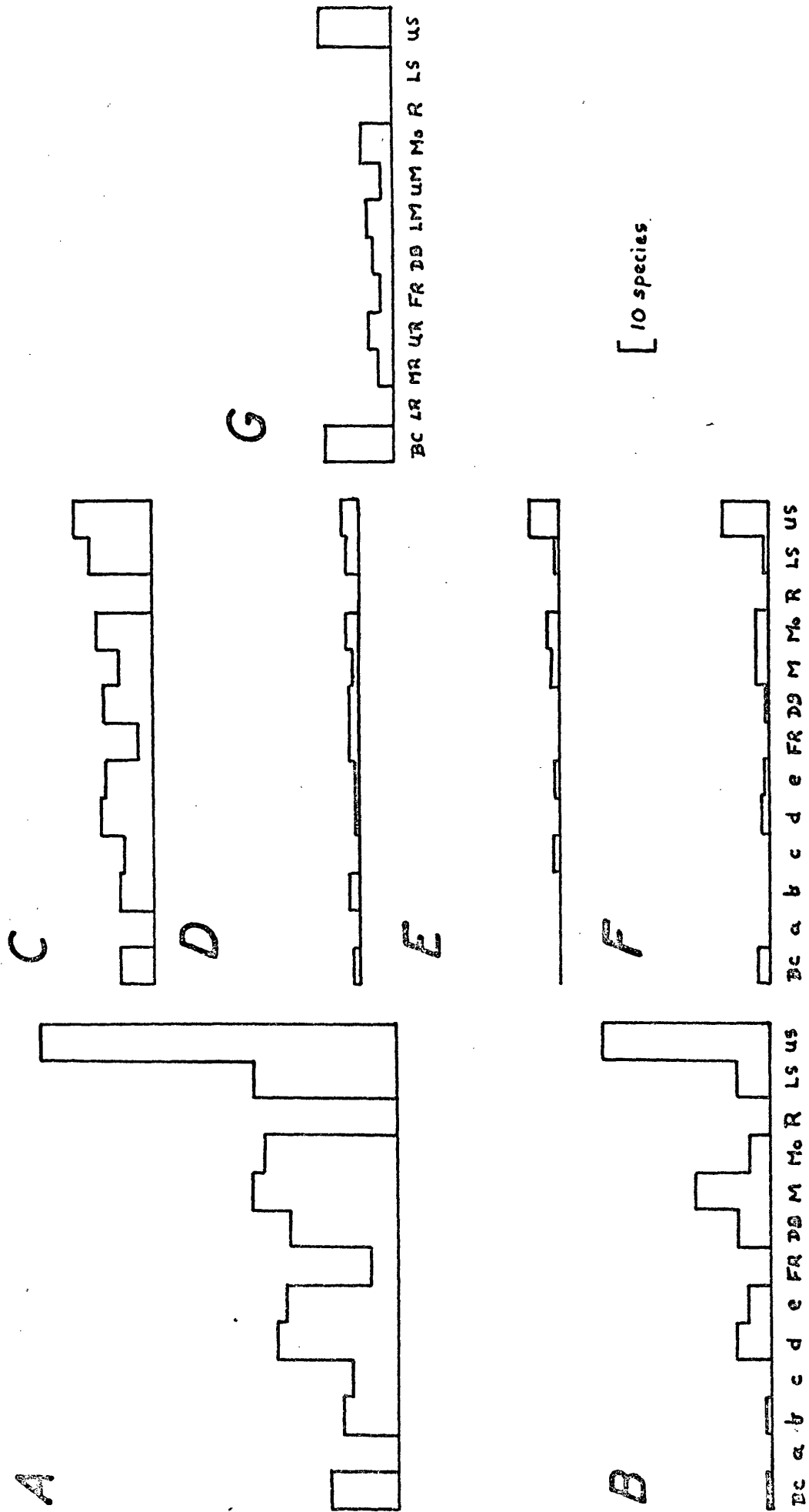
F. Gastropods.

BC: Beechhill Cove Fm.; a-e: McLearn's (1924) zones of the Ross Brook Fm., see text-fig. 2; FR: French River Fm.; DB: Doctors Brook Fm.; M: McAdam Brook Fm.; Mo: Green Member, Moydart Fm.; R: Red Member, Moydart Fm.; LS, US: Lower, Upper Stonehouse Fm.

G. Distribution of gastropods, present study.

BC: Beechhill Cove Fm.; LR, MR, UR: Lower, Middle, Upper Ross Brook Fm.; FR: French River Fm.; DB: Doctors Brook Fm.; LM, UM: Lower, Upper McAdam Brook Fm.; Mo: Green Member, Moydart Fm.; R: Red Member, Moydart Fm.; LS, US: Lower, Upper Stonehouse Fm.

Text-fig. 17



(text-fig. 16B). The exception is Liospira marklandensis which is widely distributed in the Upper Stonehouse Formation and forms a possible equivalent to L. cf. L. affinis of the Beechhill Cove Formation.

The Upper Stonehouse Formation is characterised by murchisoniaceans and loxonemataceans. At least two species of probable loxonemataceans are known amongst the undetermined high spired gastropods of the Beechhill Cove Formation but high spired gastropods are never as conspicuous as in the Upper Stonehouse Formation (text-fig. 20A).

Trochinids are equally developed, with a species of Cyclonema (Cyclonema) accompanying Platyceras (Platyostoma) cornutum in each fauna. Naticonema kauffmani and the undetermined trochinid genus and species are restricted to the lower formation, however, and Haplospira sibelixeni to the upper. Bucanopsis sp. is the only common bellerophontacean in the Beechhill Cove Formation while the trilobed Plectonotus cherylae and Tritonophon kivitalonae, with associated Anapetopsis and Pharetrolites murchisoni, are typical of the Upper Stonehouse Formation.

The dominance of lohospirid pleurotomariaceans in the Beechhill Cove Formation, and of murchisoniaceans and loxonemataceans in the Upper Stonehouse Formation, appears to be the principal difference between the two faunas. The distribution of trilobed bellerophontaceans is discussed later.

Lophospirids are not known in rocks younger than the Triassic and have no close relatives amongst the depleted pleurotomariacean faunas of the present day. There is some similarity in form between Arjamannia and Longstaffia and recent pleurotomariids but the fourteen living species of Entemnotrochus Fischer, 1885, Peretrochus Fischer, 1885 and Mikadotrochus Lindholm, 1927 described by Bayer (1966; 1967) are generally restricted to depths greater than fifty fathoms (Batten, 1958) in conditions quite unlike those envisaged for the fauna of the Beechhill

Cove Formation. As with other archaeogastropods, the lophospirids are thought to have possessed aspidobranch ctenidia. The tendency for these relatively complex bipectinate ctenidia to become fouled (Yonge, 1947) effectively restricts the group to a firm substratum in clear water.

Members of the extinct superfamily Loxonematacea probably had a single monopectinate ctenidium as is the case with other caenogastropods. The greater efficiency of the mantle cavity associated with the pectibranch condition, together with the modified foot and the development of an anterior siphon, enables caenogastropods to move freely over a soft substratum in turbid water (Yonge, 1947). The mode of life of loxonemataceans is not known. At the present day, high spired gastropods follow a number of different habits. Terebrids are active carnivores living infaunally in sand (Wilson and Gillet, 1971), many cerithiids are grazers on algal mats (Taylor, 1971) while turritellids are infaunal detrital feeders (Graham, 1938; Yonge, 1946). Carriker and Yochelson (1968) and Sohl (1969) have discussed the presence of carnivorous gastropods in the lower Palaeozoic on the basis of bored shells of other invertebrates but there is insufficient evidence to demonstrate that gastropods were responsible for the attacks. It is possibly best to presume that loxonemataceans were herbivorous, in keeping with the great majority of coexistent species.

Regardless of feeding habits, there does seem to be some correlation between the high spired form and low energy environments, in a wide sense to also include infaunal occurrences. Vermeij (1971) commented that the absence of the high spired shell form in the order Archaeogastropoda is probably due to the group being restricted by the structure of the ctenidia to hard substrata in relatively high energy environments where a stable shell form is a prerequisite. Only in low energy environments, or infaunally, can a high spired shell develop. The common equivalence of low energy environments with a soft substratum could reasonably limit the high spired form to the pectinibranch

caenogastropods as aspidobranth ctenidia of the type found in modern archaeogastropods would not be able to cope with the turbid conditions.

Murchisoniaceans present ecologic and phylogenetic problems. Knight et al (1960) tentatively placed the suborder Murchisoniina within the Archaeogastropoda while recognising that the high spired form and incipient anterior siphonal notch suggested affinity with the Caenogastropoda. A well developed slit and selenizone probably indicate a pair of ctenidia by analogy with the Pleurotomariina and Bellerophonina but the structure of the ctenidia of this extinct group is not known. The stability arguments put forward by Vermeij (1971) promote the hypothesis that the murchisoniaceans lived in low energy environments, or infaunally, and had pectinibranch or possibly modified aspidobranth ctenidia. This interpretation was also propounded by Bretsky (1970).

It might be argued that aspidobranth ctenidia could function if the gastropod lived amongst the foliage of marine phanerogams above the possibly turbid sediment-water interface. Stratification of faunas into foliage and sediment-water interface associations is well known at the present day (Warmke and Almodovar, 1963; Starmühlner, 1968; 1969; Duffus, 1969; Taylor, 1971) with several high spired cerithiid species living high above the substratum. In a study of the relationship between molluscs and algae in Puerto Rico, Warmke and Almodovar (1963) noted that gastropods accounted for ninety nine percent of the molluscs in their samples and that the great majority of these were under two millimetres in length - very small when compared to the average size of known fossil murchisoniaceans. Consequently, a more likely mode of life would be as a grazer on algal mats in a low energy environment as Taylor (1971) described for several cerithiids from the Indian Ocean.

Whether pectinibranch or modified aspidobranth, the efficiency of the respiratory system of the Murchisoniina is attested to by their abundance from the lower Ordovician to the upper Triassic. In many cases, specimens are prolific in sediments indicative of a soft substratum (Foerste, 1923; Bretsky, 1970).

The development of the lophospirid fauna in the Beechhill Cove Formation and the murchisoniacean and loxonematacean fauna in the Upper Stonehouse Formation cannot readily be explained in terms of variation in water depth. Bambach (1969ms) and Boucot et al (in press) were emphatic about the extreme shallowness during the period of accumulation of both. The gross lithology of the formations is also comparable, with siltstones forming more than half of both the sedimentary sequences. There is, however, a difference in the nature of the main fossil bearing beds. In the Beechhill Cove Formation fossils are mainly restricted to the lower part of sandstone lenses which fill scour depressions in the upper surface of siltstone beds. Bambach (1969ms) recorded only linguloid brachiopods and crinoid ossicles from the siltstones and shales while disarticulated brachiopods characterised the transported sandstone lenses. All available collections are from the coquinite basal beds of the lenticular sandstones.

In the Upper Stonehouse Formation Boucot et al (in press) noted that fossils were concentrated in thin siltstones and thicker limestone lenses. The thin siltstones contained abundant brachiopods, bivalves, gastropods, crinoids and bryozoans with many of the bivalves articulated. Boucot et al (in press) concluded that the siltstones were formed by the gentle winnowing out of the finer clay elements from the sediment with minimal reworking and transportation of the shells. The limestones occur in scours and are composed of coquinite grading up into fine sand and silt. Brachiopods comprise ninety percent of the fauna and are usually more fragmented than in the siltstones, with their convex sides oriented uppermost (Boucot et al, in press). M. J. Copeland (Geological Survey of Canada, oral communication, 1970) found little difference between the faunas of the siltstones and the limestone lenses in the Upper Stonehouse Formation and concluded that the degree of transportation of the latter was slight.

It is clear that the fauna of the Upper Stonehouse Formation

is more or less in situ but the lack of fossils in the siltstones and shales argues against such an interpretation for the fauna of the sandstone lenses of the Beechhill Cove Formation. In view of the predominance of lophospirid pleurotomariaceans, it is concluded that the fauna of the latter formation was probably derived from an area with a firm, sandy substratum and low turbidity. It is unlikely, from the nature of the enclosing sediment, that the assemblages were transported far but the nature of the fauna does not require this. It is of interest that Bambach (1969ms) noted that the few bivalves seen by him from the Beechhill Cove Formation were quite unlike those from other formations of the Arisaig Group.

Bretsky (1970) recognised a similar separation of lophospirids and murchisoniids in the upper Ordovician of the Central Appalachians. Lophospirids occurred in a Sowerbyella-Onniella Community developed on outer sublittoral sands and silts while murchisoniids were the characteristic gastropod element in an inner to outer sublittoral Zygospira-Hebertella Community developed on calcareous muds. Bretsky (1970) considered that the occurrence of murchisoniids in an argillaceous environment demonstrated the affinity of the group with the Caenogastropoda.

#### Faunas of the shallowing cycles.

The strata occurring between the open marine Beechhill Cove and Upper Stonehouse Formations can be regarded as forming two shallowing cycles with passage from deeper water fine muds at the base of each cycle to silty shoal and barrier deposits at the top.

The first cycle commenced in the Lower Member of the Ross Brook Formation where fissile shales probably represent the deepest water conditions experienced during the deposition of the Arisaig Group. Gradual passage to shoal deposition during the upper Middle and Upper

Members was followed by the accumulation of the barrier deposits of the French River Formation, with the Doctors Brook Formation representing a shoal sequence in the lee of the barrier.

The second cycle occurs in the McAdam Brook Formation with the transition from fissile shales in the lower beds of the Lower Member to a series of shoal deposits in the Upper McAdam Brook Formation marking the readvance of barrier conditions into the general Arisaig area. Shallowing continued during the deposition of the Lower Member of the Moydart Formation with eventual emergence for the accumulation of the red beds of the Upper Member.

Bambach (1969ms) considered the Ross Brook Formation to have been laid down in normal marine conditions due to the high species diversity and similarity of the bivalve fauna to that of the Upper Stonehouse Formation. The McAdam Brook Formation has a less diverse fauna (text-fig.17) and was thought to have accumulated in open lagoonal conditions behind the barrier represented by the deposits of the French River Formation. The gastropod faunas of the two cycles are remarkably similar and add some supporting evidence to the ecologic distinction made by Bambach (1969ms) whose remarks appear quite justified when the fauna as a whole is considered.

The generalised faunal sequence present in each cycle shows a gradual replacement of holopeiform species by bellerophontaceans and, ultimately, trilobed bellerophontaceans of the subfamily Plectonotinae. However, it should be noted that successive faunal elements replace each other gradually so that occasional specimens of trilobed bellerophontaceans may occur in sediments characterised by holopeiform species. Holopea sp., Bucanopsis sp. and Plectonotus boucoti are common to both cycles and are associated in each case with equivalent, but different, species of Loxonematacea, Murchisoniacea and a lenticular gastropod.

The sequence from the Ross Brook Formation to the French River and Doctors Brook Formations provides the fullest record (text-figs. 14B, 15A, 15B). A fauna composed entirely of Gyronema haliburtoni in the lowest part of the Upper Member of the Ross Brook Formation is succeeded in the upper part of the member by Holopea sp., in equal abundance, associated with Bucanopsis sp., Umbospira sp., Loxonema sp. B., Murchisonia (Homotoma) sp. A and sporadic Tritonophon sp. In the overlying French River and Doctors Brook Formations bellerophontaceans dominate with the trilobed Tritonophon and Plectonotus boucoti most in evidence.

The early Gyronema phase is not present in the McAdam Brook Formation cycle (text-fig. 15C). Holopea sp. and Bucanopsis sp., with Murchisonia (Sinuspira) cf. M. (S.) tenera and Morania (?) sp., are succeeded by Pharetrolites bambachi and Bucanopsis sp. and, finally, by Plectonotus boucoti in the lower part of the Upper Member. A rather different fauna characterises the Green Moydart Formation but Tritonophon trilobata is a prominent species (see discussion in later section).

The absence of Gyronema haliburtoni in the McAdam Brook Formation cycle possibly supports Bambach's (1969ms) interpretation of a reduced connection with the open sea in the second cycle, when compared to the initial open sea conditions of the earlier cycle of the Ross Brook, French River and Doctors Brook Formations. An alternative explanation could invoke differences in depth and depth related environmental parameters. This is supported by the association of Bucanopsis sp. with Holopea sp. in even the lowest (and presumably deepest) collections from the McAdam Brook Formation whereas Holopea sp. occurs without the bellerophontacean on its first appearance in the Upper Ross Brook Formation. The suggestion would be that the cycle of the McAdam Brook Formation commenced at a shallower water depth than that of the cycle of the Ross Brook, French River and Doctors Brook Formations, to the exclusion of the Gyronema haliburtoni phase and the

Holopea sp. (without Bucanopsis sp.) phase of the earlier cycle.

The similarity in faunal development between the two shallowing cycles suggested by the gastropods is also supported by the sequence of bivalve associations (text-fig. 18).

Trophic analysis of the bivalve associations by Bamback (1969ms) showed that epifaunal suspension feeding bivalves are dominant in the Middle and Upper Ross Brook Formation although a fauna from near the base of the Middle member is composed almost entirely of deposit feeders. In the overlying French River and Doctors Brook Formations deposit feeders predominate. The general developmental trend for this lower cycle, therefore, is towards increased abundance of deposit feeding bivalves (text-fig. 18A).

Deposit feeders are the most common bivalve trophic element throughout the McAdam Brook Formation (text-fig. 18B). However, an increase in abundance from sixty percent of the total bivalve fauna at the base to ninety percent at the top of the formation parallels the trend seen in the previous cycle.

Functional morphology and palaeoecology of the Plectonotinae,  
(Bellerophontacea).

Trilobed bellerophontaceans of the subfamily Plectonotinae are perhaps the most characteristic group in the gastropod fauna of the Arisaig Group. Two species of Plectonotus and three of Tritonophon are distributed through the sequence and trilobed specimens are present in all formations. Greatest abundance is seen in the Upper Stonehouse Formation where Plectonotus cherylae and Tritonophon kivitalonae are widely distributed and common. Tritonophon trilobata is common in the Green Member of the Moydart Formation while Plectonotus boucoti is the representative species in the Doctors Brook and McAdam Brook Formations. Specimens of plectonotinids are less frequently present in collections from the lower beds of the Arisaig Group but Tritonophon

TEXT-FIG. 18

Bivalve trophic associations of the shallowing cycles.

(after Bambach, 1969ms).

A. Trophic association of the shallowing cycle of the Ross Brook, French River and Doctors Brook Formations. With the exception of association 1, the trend is towards an increase in the proportion of deposit feeding bivalves.

1. lower Middle Member, Ross Brook Fm.

2, 3, 4. Upper Member, Ross Brook Fm.

5. French River Fm.

6, 7, 8, 9. Doctors Brook Fm.

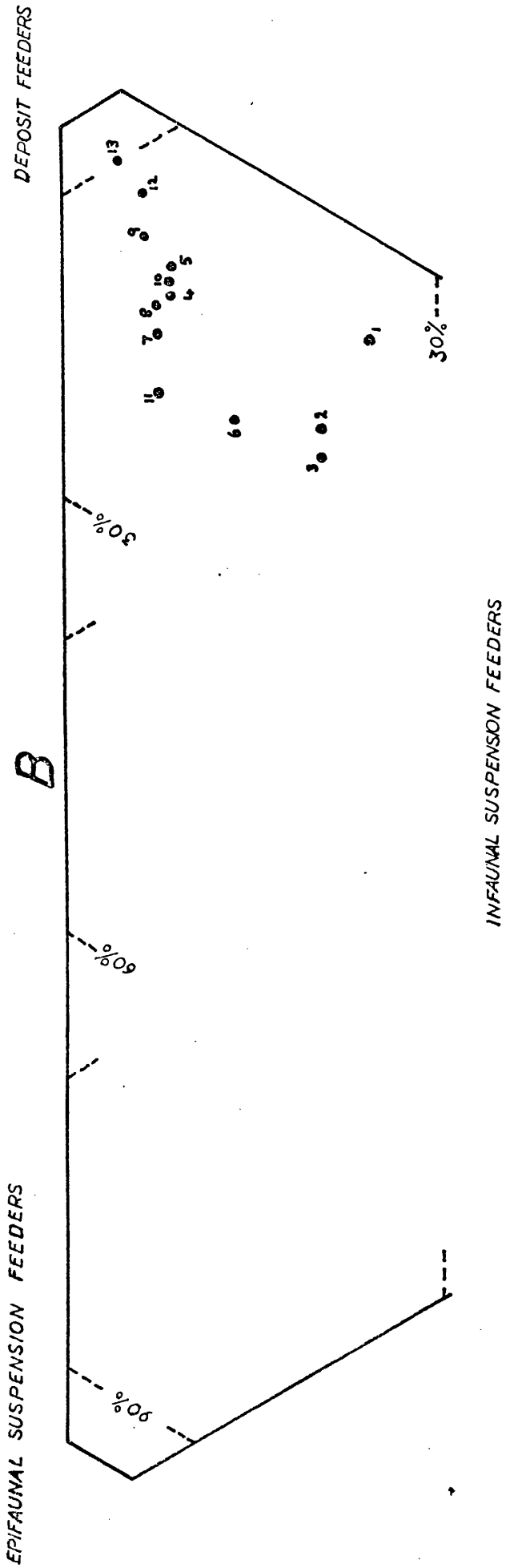
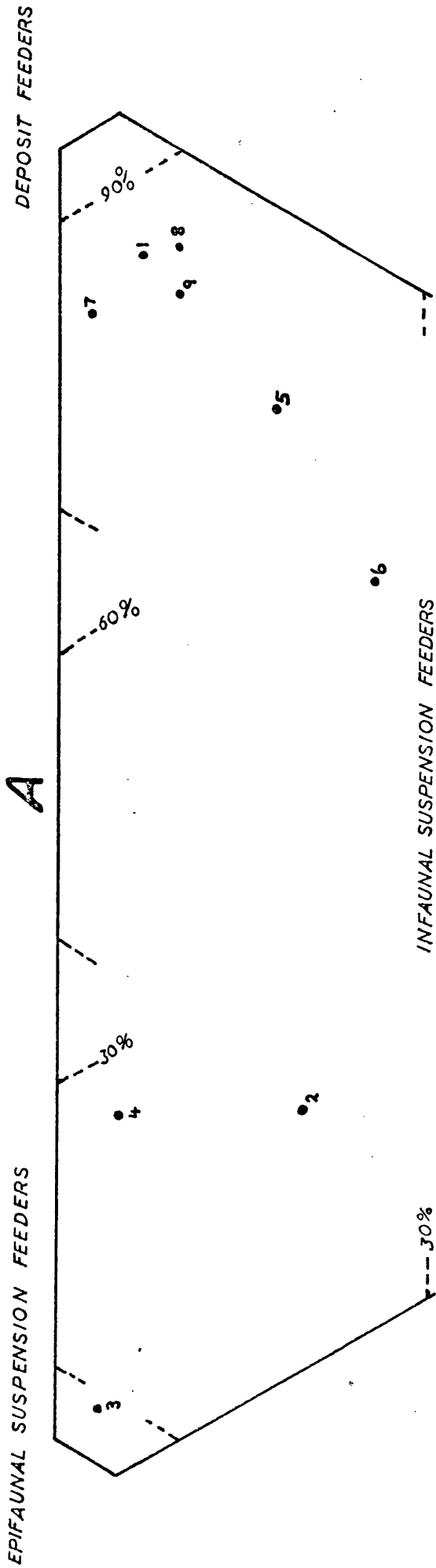
B. Trophic associations of the shallowing cycle of the McAdam Brook Fm.

Deposit feeding bivalves dominate throughout but increase in abundance from 60% of the bivalve fauna at the base to 90% at the top.

1-13. McAdam Brook Fm., numerical sequence from stratigraphically lowest to stratigraphically highest collection.

Percentages are based upon specimen counts

Text-fig. 18



sp. has been recorded from the Beachhill Cove, Upper Ross Brook and French River Formations. No specimens are known from the Middle Ross Brook Formation and collections were not available from the Lower Ross Brook and Lower Stonehouse Formations.

Functional morphology: Following the classic studies of J. B. Knight (1947; 1952) it is commonly supposed that bellerophontaceans are archaeogastropods showing the same general anatomical organisation as recent pleurotomariaceans although some authors still propose a lack of torsion in the group (Termier and Termier in Grassé, 1968). Knight (1947) inferred the presence of a pair of pedal retractor muscles in the Bellerophontacea on the basis of supposed muscle scars on finely preserved internal moulds. Similar scars have been described by Peel (1972; copy appended at rear) in other bellerophontacean species and are much more common on fossil specimens than the rather sparse literature would suggest. However, the description of the coiled sinus-bearing monoplacophoran Sinuitopsis acutilira (Hall, 1861) by Rollins and Batten (1968) serves to emphasise some of the problems accompanying systematic determination of the many remaining taxa of bellerophontiform molluscs.

The nature of the musculature in Plectonotus and Tritonophon has not been conclusively demonstrated but obscure circumbilical spiral traces have been observed on several specimens. Thin, possible myostracal deposits occur on the umbilical walls of transverse thin sections of Plectonotus boucoti but it has not proved possible to equate these deposits with structures on the surface of the internal moulds.

Of more immediate interest, in terms of life habit, is the structure of the mantle cavity. Knight (1952) discussed the periodic paired extensions of the dorsal lip in Knightites (K.) multicornutus Moore, 1941 and concluded that the 'horns' were canals indicating

the position of inhalant currents. By analogy with recent pleurotomariaceans, Knight (1952) suggested that the mantle cavity housed a pair of aspidobranch ctenidia symmetrically disposed about the median anus (text-figs. 19A, 19B). Water circulation patterns within the mantle cavity were considered comparable to those described by Crofts (1937) and Yonge (1947) in the living Haliotis Linné, 1758.

The paired inhalant canals of Knightsites (Knightsites) are unique amongst the Bellerophontacea where evidence of the position of the presumed inhalant currents is usually wanting. However, Opik (1953) described without comment a pair of lateral emarginations in Kokenospira trisinuata Opik, 1953 from the lower Silurian of Victoria, Australia (text-fig. 19C). Horný (1963) noted similar, but better developed, emarginations on the lateral lobes of the strongly trilobed Tritonophon (?) bohémica (Perner, 1903) from the upper Ordovician of Bohemia (text-figs. 19D, 19E). Horný (1963) commented on the importance of the lateral emarginations but offered no explanation as to their function. Occasional specimens of Tritonophon (Pl. III, fig. 9) and Plectonotus from the Arisaig Group show lateral emarginations of the type illustrated by Horný (1963) but the feature is variable in degree of development and occurrence.

It is suggested that the lateral emarginations indicate the position of the inhalant currents in the same way as the paired extensions of the dorsal lip in Knightsites (Knightsites) and that the ctenidia are located under the lateral lobes (text-figs. 19F-H). Trilobation would then be a modification of the shape of the mantle cavity designed to increase efficiency. The deepening of the grooves between the median and lateral lobes would tend to produce partial barriers separating the clean water of the inhalant streams from the fouled and deoxygenated exhalant current (text-fig. 19F).

TEXT-FIG. 19

The Mantle Cavity in the Bellerophontacea.

A, B. Knightites (Knightites) multicornutus Moore, 1941, x3.

Restoration of the mantle cavity after Knight (1952).

C. Kokenospira trisimata Opik, 1953, x10.

View of left side after Opik (1953) showing the lateral, inhalant emargination.

D, E. Tritonophon (?) bohémica (Perner, 1903), x6.

Dorsal and oblique dorsal views after Horný (1963) showing well developed lateral, inhalant emargination on right lateral lobe. The sides of the median, exhalant emargination are not quite parallel so that a true slit is not present in this specimen.

F, G, H. Suggested reconstruction of the mantle cavity in Plectonotus and Tritonophon. F, cross-section of whorl showing location of the ctenidia under the lateral lobes. G, dorsal view. H, lateral view with the form of the coiled shell taken from a longitudinal section along the plane of symmetry rather than from the umbilical view as in 19B.

A: Anus

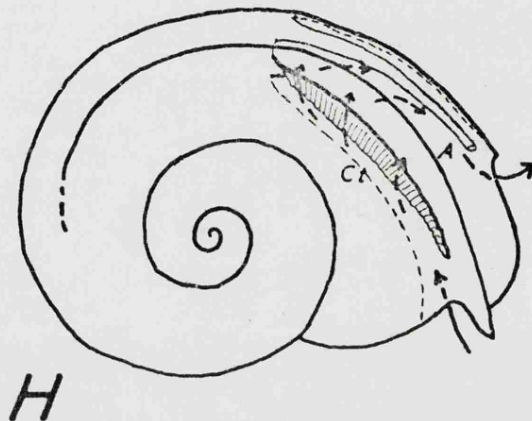
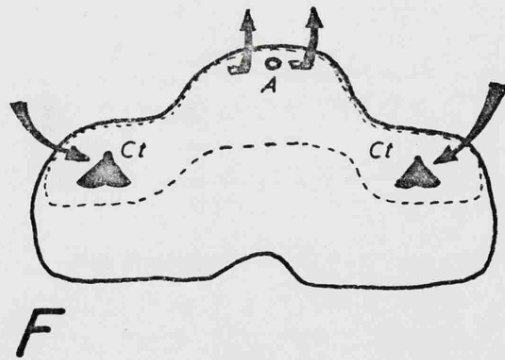
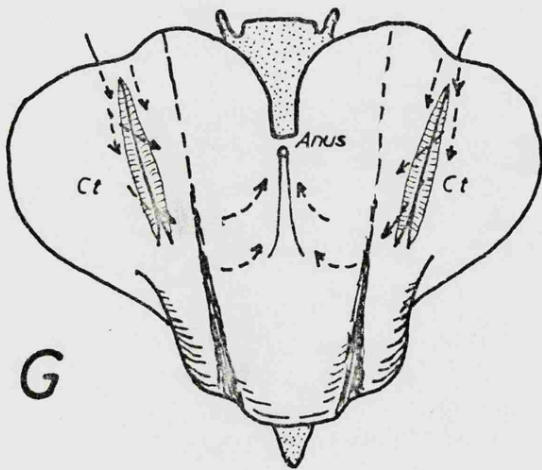
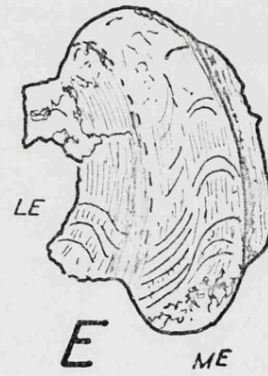
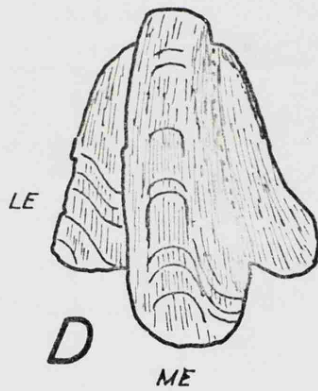
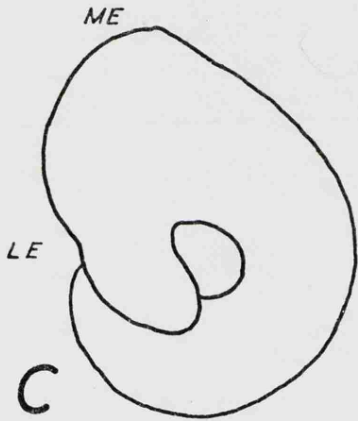
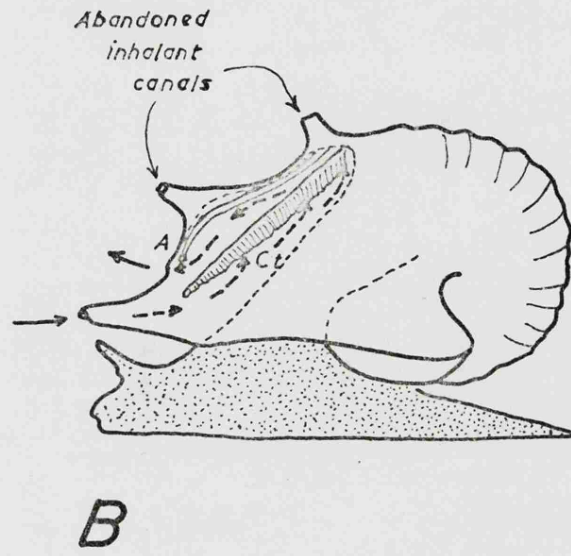
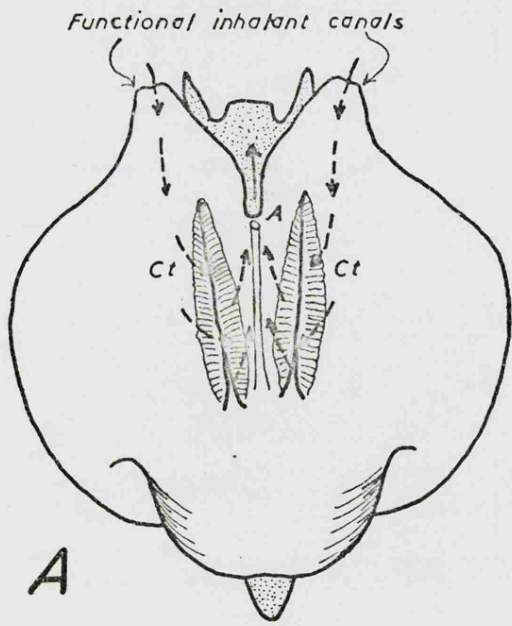
LE: Lateral, inhalant emargination

Ct: Ctenidium

ME: Median, exhalant emargination

Inferred water currents are shown by heavy dashed lines within the mantle cavity (finely broken line).

# Text-fig. 19



Mode of life: If the presence of aspidobranch ctenidia is accepted, plectonotinids would be expected to favour a firm substratum in clear water in the same manner as most other archaeogastropods. Alternatively, they might have lived amongst the foliage of marine phanerogams and high above the possibly turbid sediment-water interface. Stratification of marine faunas in algal grass beds is well known at the present day (Taylor, 1971) with distinctive faunas developed amongst the foliage, at the sediment-water interface and infaunally.

A browsing existence of this type was suggested by Bretsky (1970) for Plectonotus (?) sp. in the upper Ordovician of the Central Appalachians. Bretsky noted that specimens were commonly found grouped together in patches of sediment which were locally richer than usual in organic debris. He argued that these assemblages represented algal fronds and their associated fauna.

The shallow water conditions operative during the accumulation of the Arisaig Group would have been conducive to the development of extensive algal meadows in all of the postulated marine environments. An abundance of fucoids was observed by Bambach (1969ms) in the Upper Stonehouse Formation and he concluded that these probable algal remains would have provided suitable attachment sites for the pterioid element of the bivalve fauna. The local abundance of Plectonotus cherylae and Tritonophon kivitalonae can perhaps be attributed to the presence of such a well developed algal meadow.

The plectonotinid association: Plectonotinid bellerophontaceans are present in rocks of upper Ordovician to Devonian age throughout the world and several authors have commented upon the common association of the group with shallow water sediments.

The elucidation of the concept of animal communities in the upper Llandovery by Ziegler (1965) prompted Boucot, Johnson and Talent (1969) to describe a homolanotid-Plectonotus Community from the Silurian

and Devonian. No detailed description of faunal composition was given but the community was considered to occur to the landward of the Eocoelia Community of Ziegler (1965), in the Silurian. Cited examples included the Arisaig Group. Boucot, Johnson and Talent (1969) gave no indication of the relationship of the homolanotid-Plectonotus Community to the Lingula Community of Ziegler (1965) which the latter author described to the immediate landward of the Eocoelia Community.

Ziegler, Cocks and Bambach (1968), in a discussion of the structure of the upper Llandovery Eocoelia Community, noted the occurrence of Tritonophon ("Plectonotus trilobatus") in their type sample from the Damery Beds of the Tortworth Inlier, Gloucs. The same species is also present in a collection from the upper Llandovery of Anvil Bay, Pembrokeshire which Ziegler et al (1969) referred to a diverse Lingula, bordering upon Eocoelia Community.

A detailed discussion of the occurrence of plectonotinids was given by Bretsky (1970) in his study of the ecology of the upper Ordovician of the Central Appalachians. Bretsky described an Orthorhynacula-Ambonychia Community developed under inner sublittoral and intertidal conditions. The substratum varied from muddy silt to coarse, well sorted sand deposited in variable conditions of salinity. The most inshore fauna, the <sup>n</sup>liguloid population, was characterised by large numbers of Lingula (?) sp., Plectonotus (?) sp., Bucania sp. and one species each of nuculoid and modiomorphid bivalves. Bretsky considered Plectonotus (?) sp. to have browsed on algal fronds which grew on the organically rich, silty muds of extremely nearshore lagoons. All preserved specimens were recorded on the seaward side of the barriers behind which the lagoons formed but Bretsky argued that the conditions in the lagoons were unsuited to the preservation of calcareous shells. Bretsky appears to have considered that algal fronds were mainly developed in the lagoonal areas. The restriction is not easy to justify since present day algal meadows 'occur on all but the most exposed shores'

(Taylor, 1971) of reef platforms in the Indian Ocean and are similarly well developed around rocky shores (Lewis, 1964).

The concept of a shallow water plectonotid association is supported by the distribution of Plectonotus and Tritonophon in the Arisaig Group. Bambach (1969ms) and Boucot et al (in press) noted the overall shallow water conditions with the period of deepest water in the Lower Ross Brook Formation still falling within the Eocoelia Community (Ziegler and Boucot, 1970), the second most inshore community of Ziegler (1965). The absence of plectonotids in the deeper parts of the two shallowing cycles (see earlier section) and their dominance in the shallower parts adds further confirmation.

In the Lower (=Green) Member of the Moydart Formation Tritonophon trilobata is associated with Cymbularia carinata, Pharetrolites murchisoni, Naticopsis trevorpatriciorum, an undetermined murchisoniid genus and species and large specimens of Platyceras (Platyostoma) cornutum, Phragmosphaera sp., Seelya moydartensis and possible loxonemataceans. The small bellerophontaceans, Naticopsis trevorpatriciorum and the undetermined murchisoniid were probably algal browsers, with most of the larger species living at the sediment-water interface. The larger bellerophontacean, Phragmosphaera sp., has a widely expanded aperture at maturity which possibly relates to an unusually large foot. The increased size of the foot could be an adaptation enabling the bellerophontacean to move over a softer substratum than is normal for aspidobranch gastropods. The relationship between crinoids and coprophagous platyceratid gastropods which live on the echinoderm calyx is well known (Bowsher, 1955). The abundance of P. (Pl.) cornutum can be equated with the increased abundance of crinoids in the Lower Moydart Formation where the only well articulated specimens of echinoderms from the Arisaig Group have been recorded (Bambach, 1969ms).

Comparable plectonotid associations with Tritonophon trilobata occur in the <sup>"</sup>Oved-Ramsåsa Series of Scania, Sweden (Moberg

and Grönwall, 1909), in the borehole into Downtonian strata at Little Missenden, Bucks., (Straw, 1933) and in the uppermost Ludlow of Felindre, Radnorshire (Sowerby in Murchison, 1839). The close stratigraphic relationship to fish beds at Little Missenden and red beds at Felindre indicates the proximity of the shore in the latter two examples.

Shaw (1971) described a similar association in the Kirkby Moor Flags (Ludlow-Pridoli) of the English Lake District. He also claimed that "Bellerophon trilobatus" (= Tritonophon) exhibited an antipathetic relationship with "Gyronema cf. octavia". A similar situation is present in the Arisaig Group where Tritonophon sp. succeeds Gyronema haliburtoni in the shallowing cycle of the Ross Brook Formation. However, Shaw maintained that "G. cf. octavia" dominated the more stable areas of slow sedimentation with "B. trilobatus" more typical of the possibly deeper water, more rapidly sedimented areas to the South. If a difference in depth occurs in the manner suggested by Shaw (1971) the evidence from the Kirkby Moor Flags would appear to contradict the currently held view of Tritonophon being characteristic of shallow water associations, with Gyronema occurring in deeper waters. The occurrence of "G. cf. octavia" in the relatively slowly sedimented 'stable' conditions and the restriction of "B. trilobatus" to the rapidly sedimented 'unstable' areas offers some accord with the situation in the Arisaig Group where Gyronema haliburtoni is typical of the quiet water conditions of the lower part of the Upper Ross Brook Formation. The plectonotids of the French River, Doctors Brook and Upper McAdam Brook Formations occur in the higher energy shoal environments associated with the advance of barrier conditions into the Arisaig area, in conditions which are perhaps not unlike those proposed by Shaw (1971).

Shaw (1971) gave few details of individual assemblages or the palaeogeographic setting and the faunal aspects of the study remain

unclear. However, the similarity of the fauna of the Kirkby Moor Flags to that of the Lower Moydart Formation and the proximity of the two areas in reconstructions of Silurian continental distributions (text-fig. 13A) makes the reinvestigation of the fauna of the English strata an attractive project.

The characteristic murchisoniacean and loxonematacean element of the fauna of the Upper Stonehouse Formation, discussed above, occurs in association with abundant plectonotinids and the lenticular pleurotomariacean Liospira marklandensis. The presence of the last named species is a point of contrast with the fauna of the Lower (=Green) Moydart Formation where lenticular species are unknown. Morphologically similar species are recorded from the Beechhill Cove Formation (Liospira cf. L. affinis), Upper Ross Brook Formation (Umbospira sp.) and the Lower McAdam Brook Formation (poor Liospira (?) sp.). The almost planispiral form of the shell of lenticular species produces a form of similar proportions to a laterally compressed bellerophontacean. The low stability (Vermeij, 1971) suggests a browsing life amongst algal foliage in a similar manner to plectonotinids. However, the absence of lenticular species in the higher energy environments of the French River, Doctors Brook and, possibly, Lower Moydart Formation might indicate a preference for quieter water conditions.

The association of abundant Turbocheilus helicites (Sowerby in Murchison, 1839) with the transition from marine Ludlow to nonmarine Downtonian in the Silurian of the Welsh Borderlands also suggests a shallow water habitat for at least some lenticular species. The Platyschisma helicites Beds of Radnorshire (Earp, 1938; 1940) follow strata with Tritonophon trilobata and a fauna of Lower Moydart Formation type which probably accumulated in conditions of reduced salinity (Allen and Tarlo, 1963).

Bivalve and gastropod faunal development ; a comparison.

The apparently congruent development of the bivalve and gastropod faunas of the shallowing cycles, discussed above, naturally promotes enquiry into the relative development of the two molluscan classes throughout the Arisaig Group.

In an exploratory investigation into faunal composition, the gastropod fauna of each formation of the Arisaig Group was resolved into three components on a numerical basis. The components were chosen so as to encompass the greatest possible variation in shell form with the planispiral coiling of the Bellerophontacea and the high spired shells of the Murchisoniacea and Loxonematacea being the two main determinative groups. The third group included all other gastropods and consisted mainly of turbiniform species.

The resolution is clearly crude but the data, consisting simply of specimen counts on the four major collections, are insufficient to merit a more sophisticated approach.

The results are illustrated in text-fig. 20A and show a sequence from faunas dominated by 'other gastropods' in the Beechhill Cove Formation (1) and Middle and Upper Ross Brook Formation (2,3) to bellerophontacean domination in the Doctors Brook (5) and McAdam Brook (6) Formations and, finally, equal representation of the three groups in the ~~Green~~ Member of the Moydart Formation (7) and the Upper Stonehouse Formation (8).

The major feature is an increase and subsequent decrease in the proportion of bellerophontaceans in the fauna. A peak is reached in the Doctors Brook and McAdam Brook Formations (5,6) where some seventy percent of observed specimens are bellerophontaceans. Associated with this trend is a general reduction in the proportion of 'other gastropods' from seventy five percent in the lower formations to near twenty five percent in the upper strata. The proportion of high spired gastropods is generally low until the Moydart (7) and Upper Stonehouse (8)

Comparison of gastropod and bivalve associations in the Arisaig Group.

A. Morphological analysis of the gastropod fauna.

The faunas of the respective formations are resolved into three components of contrasting morphology: planispiral bellerophontacean; high spired murchisoniacean and loxonematacean; 'other gastropods', a group including all other species and consisting mainly of turbiniform elements (data from Bambach, Twenhofel, Schuchert and U.S. National Museum Collections).

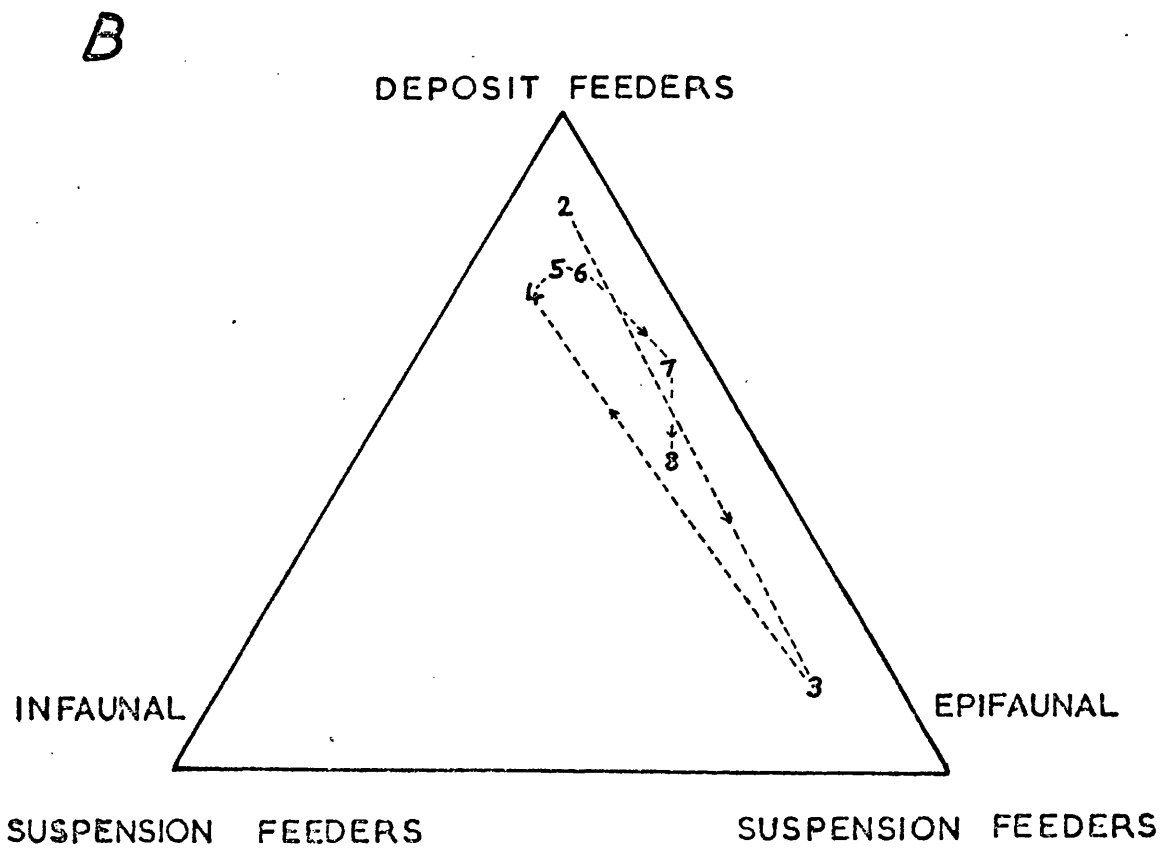
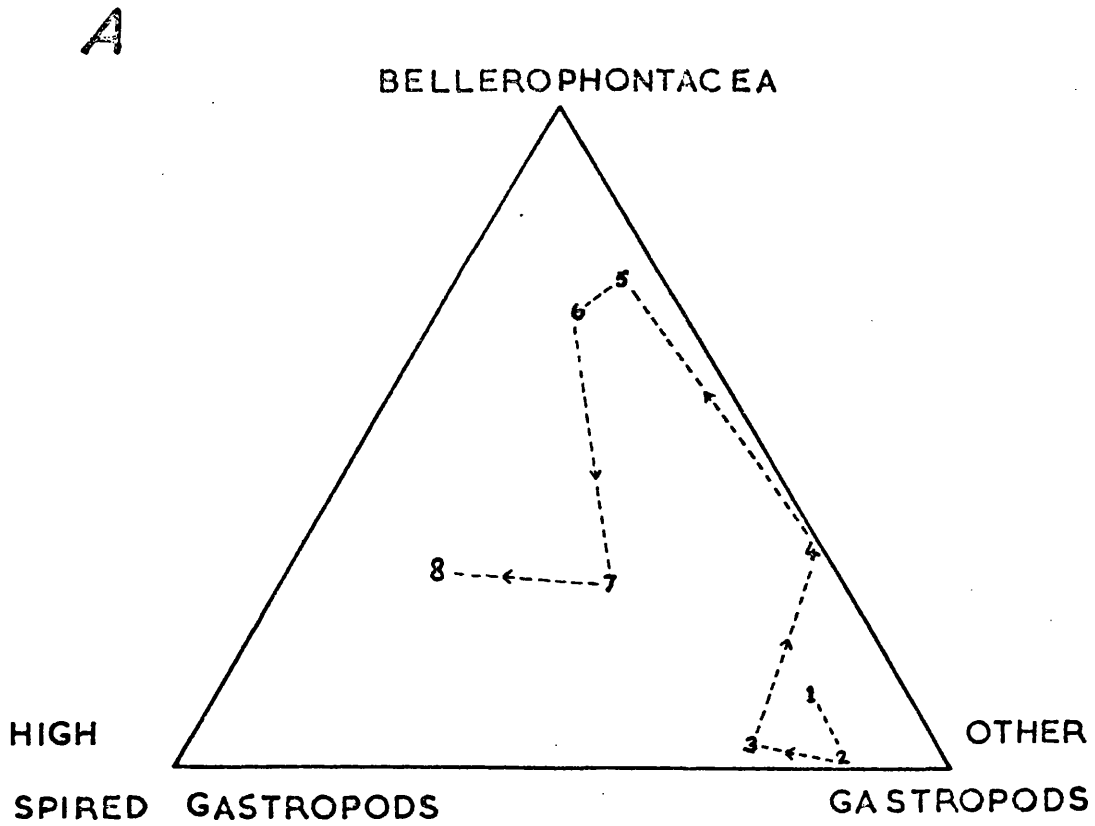
B. Summation of bivalve trophic associations.

(data from Bambach, 1969ms).

1. Beechhill Cove Fm.
2. Middle Member, Ross Brook Fm.
3. Upper Member, Ross Brook Fm.
4. French River Fm.
5. Doctors Brook Fm.
6. McAdam Brook Fm.
7. Green Member, Moydart Fm.
8. Upper Member, Stonehouse Fm.

Percentages are based upon specimen counts

Text-fig. 20



Formations, where about half the observed specimens belong to this category.

The critical question relates to the amount of meaning that can be read into this essentially morphological analysis. The three component groups have distinctive shell form and it is to be presumed, with support from the recent study of Vermeij (1971), that these differences in coiling have some palaeoecological significance.

As previously observed in the discussion of the gastropod faunas of the Beechhill Cove and Upper Stonehouse Formations, above, most archaeogastropods are restricted to a firm substratum in clear water (Yonge, 1947; Purchon, 1968). While high spired murchisoniaceans and loxonemataceans are frequently present in these conditions, they are more typical of a softer substratum and more turbid water unsuited to the aspidobranch ctenidia of archaeogastropods (Yonge, 1947; Bretsky, 1970). Two components of the analysis are thus concerned to some extent with the nature of the substratum since the group of 'other gastropods' is entirely composed of aspidobranch archaeogastropods. Domination by high spired gastropods is indicative of a soft substratum while a preponderance of 'other gastropods' suggests a firm substratum with clear water.

The association of plectonotid bellerophontaceans with extreme shallow water has been described by Boucot, Johnson and Talent (1969) and Bretsky (1970) and is discussed in the previous section. The high proportion of members of this subfamily in the bellerophontacean dominated associations of the Doctors Brook (5) and McAdam Brook (6) Formations correlates with proximity to land and the somewhat reduced marine conditions of the barrier complex, unsuited to the establishment of a diverse fauna. Plectonotids are also common in the Lower (=Green) Member of the Moydart Formation (7) and the Upper Stonehouse Formation (8) but the prevailing open marine conditions allow the development of a more diverse benthonic fauna in these cases. The

bellerophonacean component is, therefore, apparently an indicator of proximity to shore which, when dominant over other components, may also suggest some departure from full marine conditions.

Summation of all the bivalve trophic associations given by Bambach (1969ms) produces a comparable figure to that seen for the gastropods (text-fig. 20B). The faunas of the French River (4), Doctors Brook (5) and McAdam Brook (6) Formations are dominated by deposit feeders and quite unlike the trophic associations of the Upper Ross Brook Formation (3) in which epifaunal suspension feeders are more abundant. Faunas from the Green Member of the Moydart Formation (7) and the Upper Stonehouse Formation (8) show admixing of the two extremes although Bambach (1969ms) considered the latter, in particular, to be similar to the Upper Ross Brook Formation (3).

The single bivalve trophic association from the lower part of the Middle Member of the Ross Brook Formation (2) represents an apparent anomaly in having the highest proportion of deposit feeding bivalves of any formation. However, Bambach (1969ms) noted that this association of infaunal siphonate deposit feeders had the lowest species diversity of any of his described trophic associations and was developed in offshore soft muds accumulating under the deepest water conditions experienced during the deposition of the Arisaig Group.

In each molluscan class the culmination of the respective trend coincides with the advance into the Arisaig area of the barrier complex of the French River (4), Doctors Brook (5) and McAdam Brook (6) Formations (text-fig. 20). Subsequent reversal of the trends accompanies the re-establishment of open marine conditions.

The component units employed in the analysis of the gastropod fauna (text-fig. 20A) are not trophic (i.e., feeding pattern) groups, as is the case for the bivalves (text-fig. 20B). It has been noted, above, that most lower Palaeozoic gastropods were probably

herbivores but there is little currently available information which permits recognition of more precise feeding patterns. The present inability to recognise morphological adaptations to different modes of life comparable to those well known in the bivalves (Stanley, 1970; Rhoads, Speden and Waage, 1972) necessitates the adoption of a morphological (as distinct from trophic) analysis of the gastropod fauna. However, it is possible to give the component shell forms some degree of meaning in an ecologic sense, as shown here.

The inelegance of the present model is apparent but the measure of agreement between bivalve and gastropod trends in text-fig. 20 suggests that the representation of the structure of gastropod faunas in this manner does have some validity. A more elaborate survey of the distribution of gastropod shell forms could well prove profitable for the increased understanding of the palaeoecology of fossil gastropod associations.

## APPENDIX

### Collection Notes.

#### Bambach Collection, Yale Peabody Museum.

Form of citation: "Bambach Colln. A3606(187)" A3606 being the Yale Peabody Museum Collection Number and 187 the stratum number of Bambach (1969ms).

During 1964-65 Dr. R. K. Bambach made detailed collections from measured sections mainly along Arisaig shore. Each assemblage was given a different Yale Peabody Collection Number and these numbers are on file in the Division of Invertebrate Paleontology, Yale Peabody Museum, New Haven, Conn., with descriptions of field localities. Stratigraphic charts and maps indicating the position of all collection localities are given by Bambach (1969ms, Pl. 1-5).

Bambach assigned his individual collections to a series of numbered strata in a sequence 1-509 from bottom to top of the Arisaig section. The stratigraphic position of each stratum was referred to a datum point for the major stratigraphic unit in which it was located, enabling a collection to be precisely located relative to any other collection within the same unit. In addition, Bambach incorporated into his scheme of numbered strata most of the accurately documented collections made by Twenhofel some sixty years previously, together with more recently made collections of Boucot and collaborators, and thereby partly integrated the three major collections from Arisaig.

The relative stratigraphic position of all the cited numbered strata of Bambach (1969ms) is shown in text-figs. 14-16. Precise geographic co-ordinates are not given since this information is available at Yale Peabody Museum, in Bambach (1969ms) and on the large scale maps of Boucot et al (in press). Unless otherwise stated all Bambach Collections are from the coastal section, Arisaig shore.

Collections bearing U. S. National Museum Collection Numbers.

Form of citation: "USNM Colln. 10114(1)"; where 10114 is the U. S. National Museum Collection Number and 1 the stratum number of Bambach (1969ms) where applicable.

The greater part of the material amassed since 1953 by Dr. A. J. Boucot, his collaborators and students is located in the U. S. National Museum, Washington, D.C., although some material with USNM Collection Numbers was donated to Yale Peabody Museum for study by Bambach (1969ms). Full details of field localities are filed in the Dept. of Paleobiology, U. S. National Museum but as most of the cited localities are inland and do not have Bambach stratum numbers, brief details are given below.

Beechhill Cove Fm.

- 10114(1) Shore 2050ft. NE of McGillivray Brook in upper half of formation, Boucot et al (in press) Pl. 3.
- 10115 McGillivray Brook 50ft. upstream of contact with underlying volcanics, Boucot et al (in press) Pl. 3.
- 10116 Shore 2175ft. NE of McGillivray Brook, Boucot et al (in press) Pl. 3.
- 10819 Wallace Brook, Pictou Co., Maehl (1960ms) map fig. 6.

Glencoe Brook Fm.

- 11262 Brook 2 miles E of Sunnybrae, Pictou Co., Maehl (1960ms) map fig. 14.
- 11267 Road NE of Kerrowgare, Pictou Co., Maehl (1960ms) map fig. 14.

Ross Brook Fm. (Middle Member)

- 11224 French River, Pictou Co., Maehl (1960ms) map fig. 14.
- 11291 Pictou Co., Maehl (1960ms) map fig. 4.

Ross Brook Fm. (Upper Member)

- 10129(100) Shore 10ft. SW of French Brook, Boucot et al (in press) Pl. 5.

French River Fm.

- 10153 Ross Brook, South Branch, Boucot et al (in press) Pl. 6.  
10158 Iron ore mine NE of Arisaig Brook, Boucot et al (in press)  
Pl. 7.  
11247 Pictou Co., Maehl (1960ms) map fig. 6.

Doctors Brook Fm.

- 10164(123) Shore 440ft. SW of French Brook, Boucot et al (in press)  
Pl. 4.  
10165(141) Shore 1450ft. NE of McAdam Brook, Boucot et al (in press)  
Pl. 4.  
10919 Doctors Brook, Boucot et al (in press) Pl. 5.

McAdam Brook Fm.

- 11183 'Molson's Brook', Lochaber.  
11217 Harri Brook, Pictou Co., Maehl (1960ms) map fig. 8.

Moydart Fm. (Green Member)

- 10174 Smith Brook 280ft. NNW of Route 45 bridge, Boucot et al  
(in press) Pl. 4.  
10175 Smith Brook 190ft. N of Route 45 bridge, Boucot et al (in  
press) Pl. 4.  
10181 Shore 1380ft. SW of McAdam Brook, Boucot et al (in press)  
Pl. 4.  
10183(315) Shore 270ft. W of McDonald Brook, Boucot et al (in press)  
Pl. 4.  
10853(292) Sutherland River, Pictou Co., Maehl (1960ms).

Stonehouse Fm. (undifferentiated)

- 10843(505) Cape George, collected by Griffin, 1959.  
11214 do.

Stonehouse Fm. (Upper Member)

- 10202(498) McAdam Brook, Boucot et al (in press) Pl. 8.  
10205(500) do.  
10206(501) do.

10211 Arisaig Brook, Boucot et al (in press) Pl. 7.

10910(496) Arisaig shore, collected by Boucot, 1953.

Geological Survey of Canada Collections.

Form of citation: "GSC loc. 1302".

Precise locality details for the old collections of Honeyman, Ami, Fletcher, Williams (1914) and McLearn (1924) are not known. Most specimens are referred to "Arisaig" or "Arisaig shore" without accompanying stratigraphic information. Some specimens collected by T. C. Weston in the middle of the last century have paper labels stating that they were collected from E2, 3 and 6, presumably of Fletcher (1887). These three units embrace the entire Arisaig Group with the exception of the Beechhill Cove Fm. It is clear that the labels were added some considerable time after collection. Collections made recently by M. J. Copeland are accurately localised.

GSC loc. 1302 Arisaig, Nova Scotia. T. C. Weston, 1867.

GSC loc. 39089 Blocks from ditch 400ft. NE of North Branch of McAdam Brook, 10ft. SW of Highway 245. M. J. Copeland, 1959.

Jones Collection, Manchester University.

Form of citation: "Jones Colln. Ar S 7820" where S indicates Stonehouse Fm. and 7820 is the paced distance in feet along the shore from the origin.

O. T. Jones made a largely uncurated collection which is now preserved in the Dept. of Geology, Manchester University. Individual collection numbers refer to a sketch section of the coast based on a paced traverse along the shore. There were possibly two such sections but only one concerning Western outcrops is preserved. Explanatory notes have not been found.

The stated origin is 300ft. Southwest of the present (1925) mouth of Arisaig Brook and the distance along the shore to the end of the Stonehouse Fm. outcrop is given as a little more than 8,000ft., compared to some 11,000ft. noted by Bambach (1969ms). Jones indicated the base of the Moydart and

Stonehouse Formations on the sketch and also named the Stonehouse Brook (=MacEachern Brook of current usage, see text-fig. 3). These points are accurately located relative to the Southwest extremity of the section (as distinct from the stated origin) and it would appear that Jones mistakenly identified Smith Brook as Arisaig Brook. A copy of the section is lodged with the Geological Survey of Canada, Ottawa, to accompany figured specimens from the Jones Collection which have been kindly donated to the Canadian Survey by Manchester University.

Localities cited in text but not located on sketch section:

Ar B. Cove Loc. 2, Dunn Point. Beechhill Cove Fm., Dunn Point, precise locality unknown.

Ar B. Cove Loc. 4. Beechhill Cove Fm., locality unknown.

Ar 1900 Upper Ross Brook Fm. (from presence of Gyronema haliburtoni), precise locality unknown.

Localities cited in text and located on sketch section:

0 Origin redefined as about 300ft. SW of Smith Brook, Arisaig shore, mistakenly identified as Arisaig Brook by Jones.

Ar M 25 Probably top of Upper Ross Brook Fm., but possibly Doctors Brook Fm.

2800 Base of McAdam Brook Fm.

Ar M 3480 McAdam Brook Fm., about 400ft. SW of McAdam Brook.

4550 Base of Moydart Fm.

Ar Mo 4700, Ar Mo 4800, Ar Mo 4820, Ar Mo 4900, Ar Mo 4980, Ar Mo 5050, Ar Mo 5300, Ar Mo 5420, Ar Mo 5450, Ar Mo 5500...all Moydart Fm., Green Member.

5620 Mouth of McDonald Brook.

5940 Base of Stonehouse Fm.

Ar S 7380 Stonehouse Fm., Upper Member.

7800 Mouth of MacEachern Brook.

Ar S 7815 Stonehouse Fm., Upper Member.

Ar S 7820 do.

Schuchert Collection, U. S. National Museum.

Form of citation: "Schuchert Colln. 53!"

Charles Schuchert visited Arisaig in 1900 and his collections contain a large number of well preserved specimens not seen by McLearn (1924) or Bambach (1969ms). Unfortunately, locality information is imprecise although it is usually possible to determine the formation from which the specimens were collected. Details of localities are recorded at the U. S. National Museum, Dept. of Paleobiology, and the following are relevant abstracts:

Schuchert Colln. 49. Arisaig zone D of Honeyman = Ludlow. Arisaig shore and near Stonehouse Brook, Nova Scotia.

49A. In beds 30ft. from the top of the series.

49D. In beds 70ft. from the top of the series.

Comment: The 'Stonehouse Brook' is that currently referred to as the MacEachern Brook (see text-fig. 3) and the collections are from the Upper Stonehouse Fm.

Schuchert Colln. 52. Arisaig zone C of Honeyman. Arisaig shore in region of McAdam Brook, N. S.

52B. Bed 7 (upper half) of Fletcher (1837), NE of McPherson's Brook.

Comment: The pale grey-green limestone of this collection is clearly from the Green Member of the Moydart Fm. The brook referred to is apparently the McAras Brook of present usage.

52D. Loose limestone pebbles along the shore but apparently from zone C of Honeyman.

Comment: The presence of Plectonotus boucoti and the lithology of this coquinite suggest Doctors Brook Fm.

Schuchert Colln. 53. Arisaig zone B' of Honeyman. Arisaig shore N of Arisaig Brook, N. S.

Comment: Notes accompanying Schuchert's collection state that the base of B'

occurs at the mouth of Arisaig Brook. B' would consequently outcrop along the shore to the Southwest of the brook with zone B of Honeyman outcropping to the Northeast. This contradicts the stated locality information although it should be noted that the mouth of the Arisaig Brook is now located some 300ft. to the Southwest of the pre-1897 course. It is not known to which position of the mouth of the brook Schuchert referred his comments.

Honeyman's zones B and B' are approximately equivalent to the Ross Brook Fm. However, the lithology and fauna of Schuchert Colln. 53 suggests derivation from the Stonehouse Fm. Dr. Jean Berdan (oral communication, 1969) considered the ostracodes to be of Stonehouse Fm. type while Dr. R. K. Bambach (oral communication, 1970) noted the presence of Nuculites concentricus (Hall, 1860), Pteronitella venusta Billings, 1874 and other bivalves indicating the same source. The gastropod fauna contains only Stonehouse Fm. species and is quite unlike the fauna of the Ross Brook Fm.

It is presumed that the collection has been incorrectly labelled and, in view of the palaeontological evidence, it is considered quite justifiable to regard the Stonehouse Fm. as the stratum of origin.

Twenhofel Collection, Yale Peabody Museum.

Form of citation: "Twenhofel Colln. 24a/3032(380)" being the assemblage from W. H. Twenhofel locality 24a, Yale Peabody Museum Accession No. 3032. The stratum number of Bambach (380) is given where applicable.

Twenhofel (1909) amassed a large and accurately documented collection from the Arisaig coastal section. Locality details are filed in the Division of Invertebrate Paleontology, Yale Peabody Museum and are not given here. The majority of Twenhofel's individual assemblages have been given stratum numbers by Bambach (1969ms) and their stratigraphic positions are illustrated in text-figs. 14-16. Some localities are shown on the large scale maps of Boucot et al (in press).

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Observations on some Lower Palaeozoic  
trematiform Bellerophonacea  
(Gastropoda) from North America

BY

JOHN S. PEEL

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# 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 *Bellerophon*idae. 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 *Bellerophon*idae 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 Hupisch first noted their existence in 1781. By reference to *Tremanotus chicagoensis* (McChesney 1859), Meek reiterated de Koninck's (1842-1844) interpretation of the *Bellerophon*aceans as proso-branchiate 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 *Bellerophon*iform molluscs. A notable contribution was the demonstration by Wenz (1940) of the tryblidiid affinity of the coiled *Cyrtionella mitella* (Hall 1862) which, of necessity, cast doubt upon the status of the remaining members of the group. Wenz (1940) presumed that all *Bellerophon*aceans 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 *Bellerophon*acea of then current usage could itself no longer be maintained as a single entity.

The distinction between the coiled *Cyclomya* (*Monoplacophora*) and the *Bellerophon*acea (*Gastropoda*) is now well recognized, principally through the works of Horný (1962, 1963a, 1963b, 1965a, 1965b, 1966). Recent summaries are given by Yochelson (1967), Rollins (1969), and Starobogatov (1970). Muscle scars are known in an increasing number of *Bellerophon*iform molluscs, though the description by Rollins and Batten (1968) of the sinus-bearing *Monoplacophora* *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-

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 retractor 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.

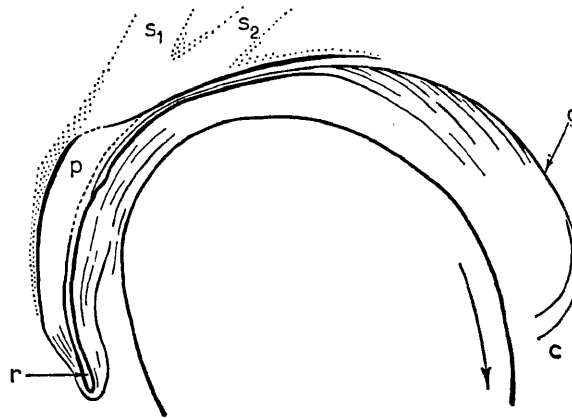
Two internal moulds assigned to *Bellerophon* show well-preserved muscle scars. The larger specimen (USNM 169475), apparently from the Pennsylvanian of the U.S.A. and hereafter referred to as *Bellerophon* specimen *A*, lacks the apertural margin, though the last preserved growth stage is almost certainly 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 ( $\times 6$ ).

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*<sub>1</sub>; *s*<sub>2</sub>) 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 trans-dorsal 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)

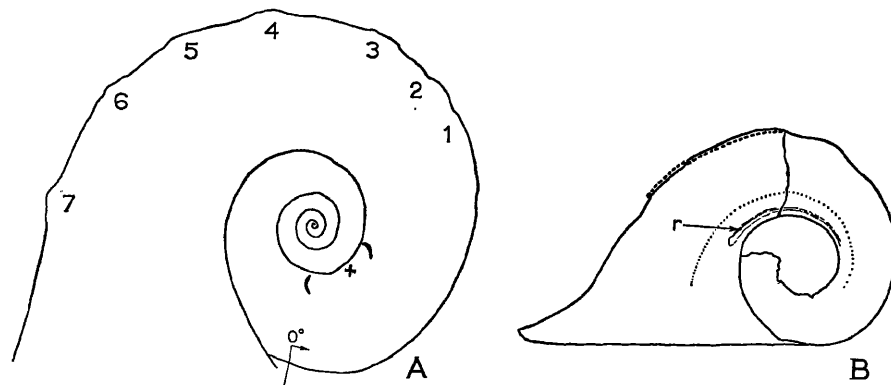
A full description of this species is given by Ulrich and Scofield (1897, pp. 900-901). The two specimens discussed here are internal moulds from the Middle Ordovician (Black River) Plattville Fm. at Beloit, Wisconsin. The more complete (USNM 15641) shows the bell-shaped final growth stage and explanate 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 ( $\times 1$ ) of *Tremannotus 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 tremata noted in text-fig. 3 is omitted. The origin of the radial scale employed in text-fig. 3 is shown.

B, lateral view ( $\times 1$ ) 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

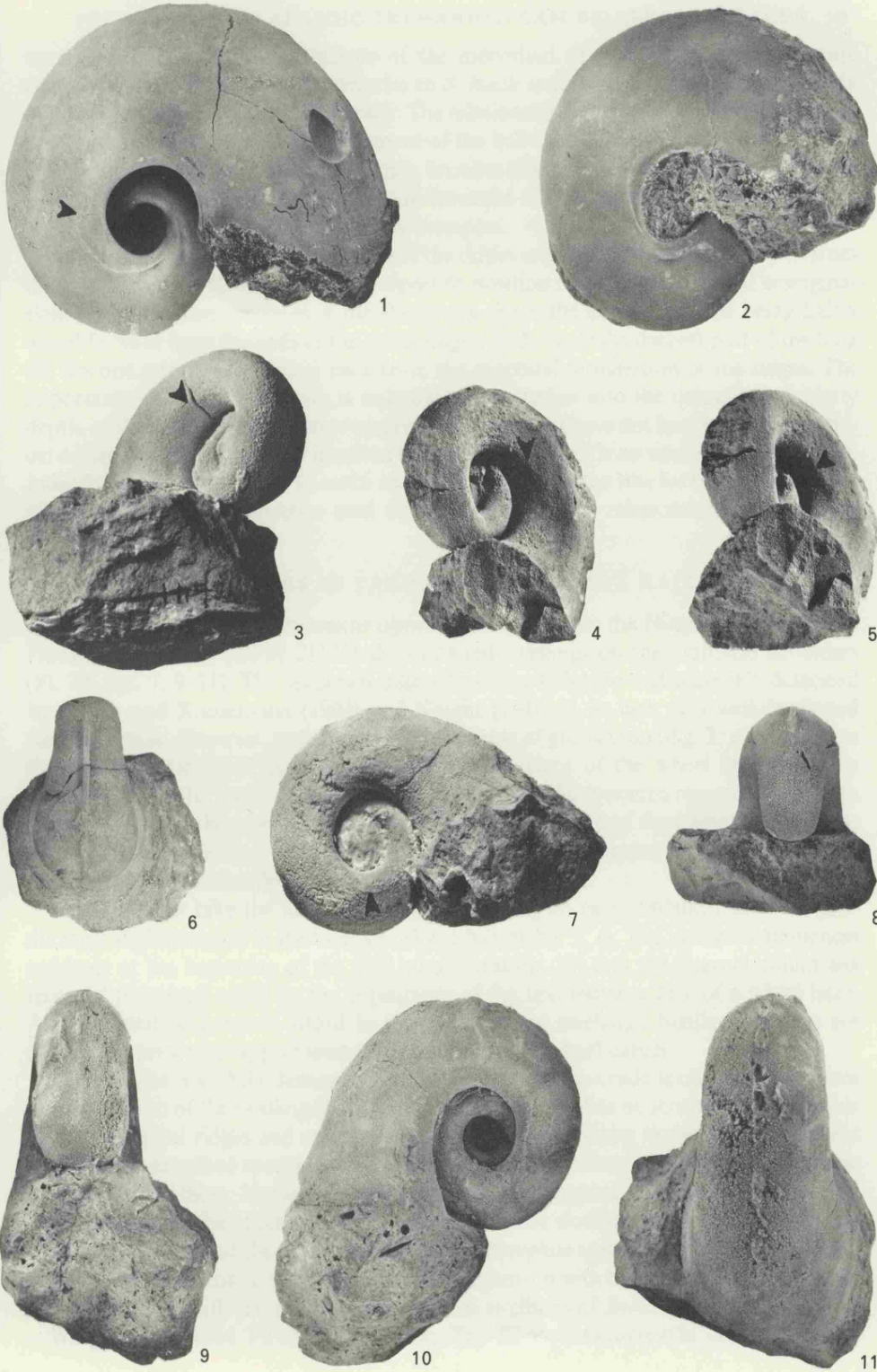
#### EXPLANATION OF PLATE 79

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,  $\times 1$ .

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

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,  $\times 1$ ; 6, dorsal view,  $\times 0.75$ ; 8, posterior view,  $\times 0.75$ ; 4, 5 (USNM 169472); oblique views illustrating the circumbilical spiral ridge,  $\times 1$ .

Figs. 7, 9-11. *Tremannotus alpheus* Hall 1865 (GPM 21123), Hawthorne, Illinois, U.S.A. 7, oblique lateral view showing ridge on ad-dorsal margin of swelling,  $\times 0.75$ ; 9, posterior view showing swellings,  $\times 0.75$ ; 10, lateral view,  $\times 0.75$ ; 11, dorsal view illustrating the dorsal tremata,  $\times 0.75$ .



PEEL, Lower Palaeozoic Bellerophontacea

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 apertural 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

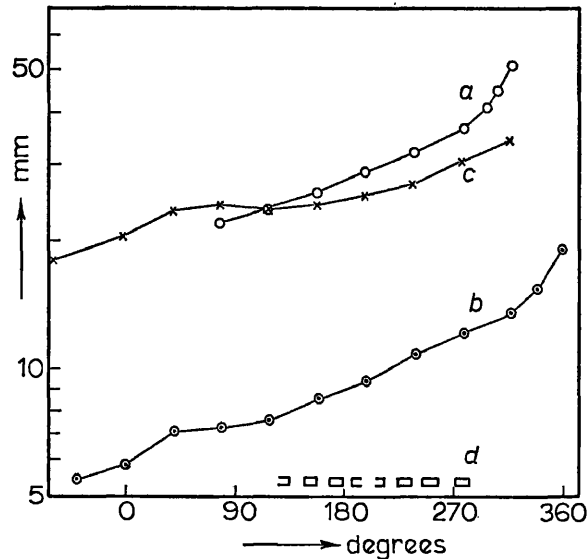
An internal mould of *Tremanotus alpheus* Hall 1865 from the Niagaran dolomites at Hawthorne, Illinois (GPM 21123) shows paired swellings on the umbilical shoulders (Pl. 79, figs. 7, 9-11). The specimen differs from the holotype and materials described by Clarke and Ruedemann (1903) and Knight (1941) 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 opisthoclinal, 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 Bellerophonitidae.

In discussing *Tremanotus* Horný (1963a, 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 tremanotid 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. dilatatus* (Sowerby 1839) of  
Northrop 1939

*S. inornatum* 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 referral to *Salpingostoma* would seem justified, on the basis of Twenhofel's (1928) description and illustrations.

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Abstract

A fauna of more than sixty species of Silurian Gastropoda is described from the Arisaig Group of Nova Scotia. Two new genera, Anapetopsis and Arjamannia, are proposed and thirteen new species: Pharetrolites bambachi, Plectonotus boucoti, Plectonotus cherylae, Tritonophon kivitalonae, Anapetopsis maclearni, Anapetopsis lalajae, Mimospira abbae, Arjamannia aulangonensis, Haplospira sibliuxeni, Naticonema kauffmani, Cyclonema (C.) lydiamariarum, Naticopsis trevorpatriciorum and Morania (?) boltoni.

Particular emphasis is given to the systematics, ontogeny, functional morphology and palaeoecology of members of the subfamily Plectonotinae (Bellerophontacea) which characterise much of the Arisaig Group.

The palaeoecology of other gastropod associations from the Arisaig Group is discussed and the sequence of faunas is related to the advance of barrier conditions into the shallow marine environment prevailing at Arisaig during the Silurian.