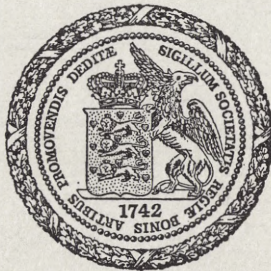


JOHN S. PEEL

SYSTEMATICS AND PALAEOECOLOGY  
OF THE SILURIAN GASTROPODS OF THE  
ARISAIG GROUP, NOVA SCOTIA

Det Kongelige Danske Videnskabernes Selskab  
Biologiske Skrifter 21, 2



Kommissionær: Munksgaard  
København 1977

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## Synopsis

A fauna of more than 60 species of Silurian (Llandovery – Pridoli) gastropods is described from the Arisaig Group of Nova Scotia, Canada, and compared to similar faunas from Britain. The following new species are described: *Tropidodiscus* (?) *arisaigensis*, *Umbospira yochelsoni*, *Holopea rossbrookiensis*, and *Murchisonia* (*s. l.*) *antigonishensis*.

The mode of life of Lower Palaeozoic gastropods in general is discussed prior to examination of the palaeoecology of gastropods from the nearshore, level-bottom sequence of communities at Arisaig.

Three basic gastropod faunas are recognised. A trochiform pleurotomariacean dominated shallow marine platform fauna in the Beechhill Cove Formation is related to a hard substratum. Most later formations have assemblages adapted to softer substrata which can be referred either to an open lagoon fauna or to a soft substratum shallow marine platform fauna. Morphologically similar representatives of these faunas characterise successive regressive phases of sedimentation.

The abundance of trilobed plectonotid bellerophonaceans throughout the sequence is equated with the nearshore environment of deposition.

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## INTRODUCTION

The small village of Arisaig, Nova Scotia (Fig. 1) has given its name to one of the best exposed and most complete Silurian sections in the Appalachian mountain system. The 1300 metres thick siltstone dominated sequence includes deposits ranging in age from the lower Llandovery, through Wenlock, Ludlow, Pridoli and into the lower Gedinne (Devonian). BOUCOT *et al.* (1974) commented that the Arisaig Group is unique in providing an almost continuous faunal record of shallow marine conditions throughout the Silurian, although subsequent analysis of brachiopod communities has demonstrated some variation in depth with the recognition of Benthic Assemblage 2 (nearshore) and Benthic Assemblage 4 (offshore) faunas by WATKINS and BOUCOT (1975). Nevertheless, the detailed collecting of W. H. TWENHOFEL, R. K. BAMBACH, A. J. BOUCOT and other workers does allow the fauna of the essentially clastic, shelf sequence to form a standard for comparison with sections elsewhere which are less complete, or of another lithofacies.

HALL (1860) first described gastropods from Arisaig, his paper including two of the common murchisoniids of the upper Stonehouse Formation (*Murchisonia* (*M.*) *aciculata*; *M.*(*M.*) *arisaigensis*) and the still unique specimen of *Onychochilus* (?) *reversa*. DAWSON in HONEYMAN (1860) supplied notes on several species some of which, although not illustrated, are also readily identifiable as from the Stonehouse Formation. The general faunal monograph of McLEARN (1924) included six new species and one new variety in a total of eighteen gastropod species, less than one third of the presently recognised total.

The present paper is the fifth in a current series concerned with the systematics and palaeoecology of the gastropods of the Arisaig Group. PEEL (1974) discussed the functional morphology, and described the systematics, of the trilobed bellerophonaceans *Plectonotus* and *Tritonophon*—the catch-all *Bellerophon trilobatus* SOWERBY in MURCHISON, 1839 of many previous authors. Five species assigned to these genera are distributed through the Arisaig Group, some being of wide occurrence also outside of the Arisaig area. SOWERBY's true *B. trilobatus*, a species of *Tritonophon*, is known in upper Ludlow and Pridoli strata from Gotland and Scania in Sweden, the Little Missenden borehole in Buckinghamshire, England, the Welsh Borderlands and Arisaig.

A new genus, *Anapetopsis*, was proposed by PEEL (1975a) for two rare bellerophonacean species from the Pridoli strata of the upper Stonehouse Formation. In a

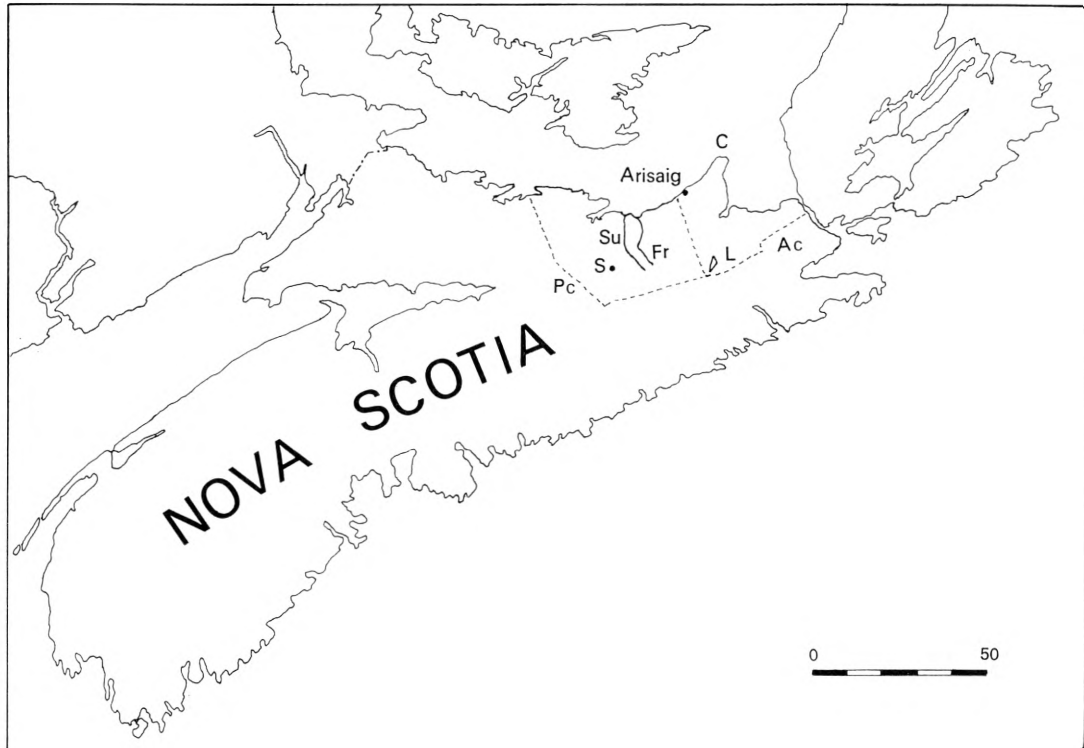


Fig. 1. Silurian localities of the Arisaig region, Nova Scotia. Ac, Antigonish County. Pc, Pictou County. C, Cape George. Fr, French River. L, Lochaber. S, Springville. Su, Sutherland River. Scale in miles.

third paper the occurrence of a new pleurotomariacean genus, *Arjamannia*, in the upper Ordovician and Silurian of North America and Britain was discussed (PEEL, 1975b). Three species of this genus, one new, were recorded from Llandovery and Wenlock strata at Arisaig. Finally, PEEL (1975c) described eight species of gastropods, seven new, from the Silurian of Arisaig, with supplementary material from the upper Silurian of Britain.

Insofar as the present paper is the cumulative work in the series, the gastropods described in the previous papers are nominally included, and some are illustrated. However, discussion of these species is generally restricted to notes on stratigraphic distribution and references to the earlier descriptions.



## FAUNAL RELATIONSHIPS

Over 1000 gastropods, distributed amongst more than 60 species have been examined from the Arisaig Group (Fig. 2), forming the largest gastropod fauna described from a single Silurian sequence in more than half a century. No specimens have been seen from the highest beds of the Stonehouse Formation, exposed inland from the coastal section at Arisaig, which HARPER (1973) and BOUCOT *et al.* (1974) referred to the lower Gedinne (Devonian). The described fauna is consequently entirely of Silurian (Llandovery-Pridoli) age.

The gastropod fauna of the Arisaig Group developed under shallow marine shelf conditions without influence from reefs or reef associated facies. In consequence, many of the gastropods most familiar to workers in the Silurian of Britain, Gotland and North America are completely absent. No specimens of the spirally ornamented euomphalid *Poleumita*, the flange-bearing pleurotomariacean *Euomphalopterus* or the large bellerophontaceans *Tremanotus* and *Boiotremus* have been recorded. Instead, the Arisaig fauna is characterised by small bellerophontaceans, especially the trilobed *Plectonotus* and *Tritonophon*, lophospirid and liospirinid pleurotomariaceans, and frequently abundant high spired gastropods.

In consequence, few comparisons can be drawn between the Arisaig fauna and the much larger (180 species) reef associated fauna of Gotland excellently described by LINDSTRÖM (1884). However, the trilobed bellerophontaceans *Plectonotus boucoti* and *Tritonophon trilobata*, while common at Arisaig, also occur rarely in Gotland. Similarly, the gastropod faunas from North American carbonate sequences (HALL, 1852; WHITEAVES, 1895; NORTHROP, 1939; POULSEN, 1974) are also generally dissimilar.

As might be expected, a much closer resemblance is observed with British and North American faunas from comparable shelf environments. Many Llandovery species from Arisaig or their near relatives are also known from Britain (PITCHER, 1939; LONGSTAFF, 1924). The upper Ludlow fauna of the Moydart Formation at Arisaig (Fig. 2) is remarkable in its similarity to faunas of the same age in the Welsh Borderlands (SOWERBY *in* MURCHISON, 1839), but also shares species with younger, Pridoli, faunas from Scania and Little Missenden, Buckinghamshire (MOBERG and GRÖNWALL, 1909; STRAW, 1933).

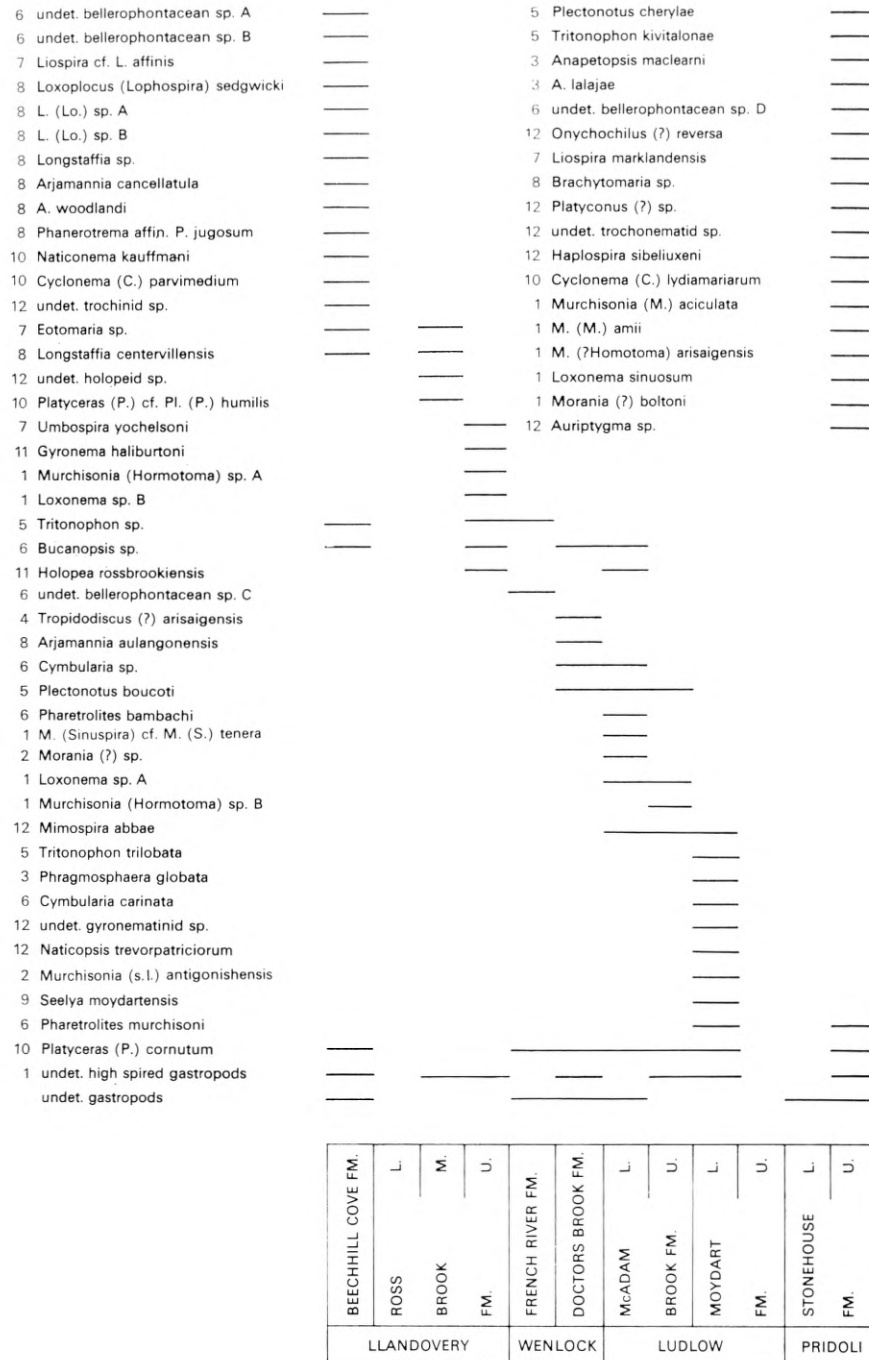


Fig. 2. Stratigraphic distribution of Arisaig Group gastropods. 1, high spired. 2, micromorphic high spired. 3, explanate bellerophontacean. 4, micromorphic bellerophontacean. 5, trilobed bellerophontacean. 6, other bellerophontaceans. 7, lenticular pleurotomariacean. 8, trochiform pleurotomariacean. 9, trochiform murchisoniacean. 10, trochiform platyceratid. 11, trochiform holopeid. 12, other gastropods.

### Beechhill Cove Formation

The gastropod fauna of the Beechhill Cove Formation, with eighteen described species against three noted by McLEARN (1924), is closely comparable to Llandovery faunas from Britain described by PITCHER (1939) and LONGSTAFF (1924). *Loxoplocus* (*Lophospira*) *sedgwicki*, *Arjamannia woodlandi* and *A. cancellatula* were originally described from the Girvan area in southern Scotland. The latter, in particular, is common in the Beechhill Cove Formation but has been recorded from the Gasworks Mudstone of Pembrokeshire, Wales, in strata of equivalent age (PEEL, 1975b). *Cyclonema* (*C.*) *parvimedium*, another characteristic Beechhill Cove Formation species, has also been identified from the Gasworks Mudstone. Species of *Phanerotrema* and *Bucanopsis* closely resembling the Arisaig specimens occur at Girvan and in Shropshire.

There is a similar but less precise resemblance to faunas from the late Llandovery Brassfield Formation of Ohio, U.S.A. (FOERSTE, 1923). *Liospira affinis* is originally a Brassfield species but poorly known liospirinid pleurotomariaceans are of generally wide occurrence in the Llandovery. *Arjamannia* is represented in both faunas by closely related, although distinct, species (PEEL, 1975b). *Longstaffia centervilleensis* occurs in lower Llandovery shales below the Brassfield Formation at Centerville, Ohio, but the fauna differs from that of the Beechhill Cove Formation in being dominated by Murchisoniids.

### Ross Brook Formation

No gastropods have been seen from the lower member of the Ross Brook Formation. The sparse fauna of the middle member includes *Longstaffia centervilleensis*, known from the Beechhill Cove Formation and lower Llandovery strata in Ohio (FOERSTE, 1923).

The gastropod fauna of the upper member of the Ross Brook Formation is larger but only three of the species are assigned names at the specific level (Fig. 2). *Gyronema haliburtoni* and *Holopea rossbrookiensis*, the most common species, were originally described from Arisaig but the former is present in collections from the Silurian of Maryland, U.S.A., preserved in Yale Peabody Museum. PITCHER (1939) described a similar late Llandovery specimen from Shropshire as *Gyronema octavia* var. *multicarinata*, a name employed by LINDSTRÖM (1884) for an upper Wenlock form from Gotland.

Trilobed bellerophonaceans assigned to *Tritonophon* sp. occur occasionally in the upper member of the Ross Brook Formation and a single specimen is known from the underlying Beechhill Cove Formation. The same species is probably present in the equivalent Rose Hill Formation of Maryland (SWARTZ and PROUTY, 1923) and the Brassfield Formation of Ohio (FOERSTE, 1923) but poor preservation prevents precise determination. PITCHER (1939) described possibly similar specimens from the upper Llandovery of Shropshire as *Bucaniella trilobata* CONRAD non SOWERBY in MURCHISON (see discussion in PEEL, 1974, p. 257).

### French River Formation

The four species recorded from the French River Formation are too imperfectly known to permit comparison with other faunas.

### Doctors Brook Formation

*Plectonotus boucoti*, the characteristic bellerophontacean of the Doctors Brook Formation, occurs infrequently in the upper Wenlock and early Ludlow strata of Gotland, but is apparently more common in upper Llandovery rottenstones from Tonlegee, Cong, Galway, Ireland (PEEL, 1974). The species is probably also present in the Wenlock and Ludlow of Britain (REED, 1920–21) but this occurrence requires confirmation. The *Bucanella trilobata* CONRAD var. *viramundo* of CLARKE (1899) from the Silurian of Brazil appears to be a *Plectonotus* closely related to *P. boucoti* (PEEL, 1974).

*Tropidodiscus* (?) *arisaigensis* sp. nov., described below, also occurs in the basal Wenlock of the Tortworth Inlier, Gloucestershire, England. *Arjamannia aulangonensis*, described by PEEL (1975b) as the youngest presently known representative of the genus, is currently recorded only from the Arisaig Group.

### McAdam Brook Formation

Many of the species present in the McAdam Brook Formation are not determined at the specific level and cannot be readily compared with faunas from elsewhere (Fig. 2). *Plectonotus boucoti*, *Bucanopsis* sp. and *Pharetrolites bambachi* are characteristic bellerophontaceans. The distribution of the former is discussed in the preceding section. The latter is not yet known outside of its type area (PEEL, 1975c).

*Murchisonia* (*Sinuspira*) cf. *M.(S.) tenera*, from the lower member of the McAdam Brook Formation, represents the first record of the genus outside of the upper Silurian of Bohemia. The rare *Mimospira abbae* extends the range of this characteristic Ordovician genus from Scandinavia into the Silurian (PEEL, 1975c).

### Moydart Formation

Most of the gastropods reported from the lower member of the Moydart Formation were originally described by SOWERBY in MURCHISON (1839) from the upper Ludlow of the Welsh Borderlands. *Tritonophon trilobata* is present in upper Ludlow strata at Felindre, Radnorshire, Wales, and in southern Gotland (PEEL, 1974). It is present in Pridoli strata in the Little Missenden borehole (STRAW, 1933; PEEL, 1974) and in Scania (MOBERG and GRÖNWALL, 1909). The somewhat uncertainly known *Phragmosphaera globata*, the recently redefined *Naticopsis trevorpatriciorum* (PEEL, 1975c) and *Pharetrolites murchisoni* are also characteristic Felindre species. In addition to its occurrence in the upper Ludlow of Britain and the Moydart Formation of Arisaig,

*Cymbularia carinata* is represented in the Pridoli Öved-Ramsåsa Series of Scania by small specimens named *Bellerophon lenticularis* by MÖBERG and GRÖNWALL (1909).

The upper member of the Moydart Formation is a non-marine deposit containing nodular limestones similar to the cornstones of the British Dittonian (BOUCOT *et al.*, 1974).

### Stonehouse Formation

The only gastropods seen from the lower member of the Stonehouse Formation are rare indeterminate high spired and holopeiform species. McLEARN (1924) recorded rare *Murchisonia* (*M.*) *aciculata*, but this occurrence has not been verified.

The fauna of the upper member is the most abundant and diverse, in terms of number of species, encountered from the Arisaig Group (Fig. 2). With the exception of the ubiquitous *Platyceras* (*Platyostoma*) *cornutum*, only *Pharetrolites murchisoni*, known also from the upper Ludlow of Britain, is present in earlier formations. High spired murchisoniaceans and loxonemataceans are most commonly represented in collections but only two of the species are currently known outside of Arisaig. *Murchisonia* (*M.*) *amii* was recorded from Pridoli strata in the Little Missenden borehole by STRAW (1933) under the name *Hormotoma* cf. *articulata*. *Loxonema sinuosum* was originally described from the lower Ludlow of Britain but its range is otherwise not well known.

The trilobed bellerophontacean *Tritonophon kivialonae* is reported from the Pridoli Jones Creek Formation of New Brunswick (PEEL, 1974), but the related *Plectonotus cherylae* is confined to Arisaig at the present time. *Cyclonema* (*C.*) *lydiamarium*, described from the upper Ludlow of Felindre, Radnorshire, by PEEL (1975c), is also documented from the upper member of the Stonehouse Formation.

*Brachytomaria* sp. and *Haplospira sibelixeni* provide the first Silurian records of otherwise Ordovician genera (PEEL, 1975c). However, these, and the remaining specifically determined species in Fig. 2 were originally described from the Arisaig Group.

No gastropods have been seen from the inland exposures of the highest beds of the Stonehouse Formation which BOUCOT *et al.* (1974) considered to be of lower Devonian age.

## SYSTEMATIC PALAEOONTOLOGY

An abbreviated classification of the gastropod fauna of the Arisaig Group is given in table 1. Formalised systematics have then been omitted from the text in the interests of brevity. Classification mainly follows KNIGHT *et al.* (1960).

The following abbreviations are employed in the systematic text: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM); Geological Survey of Canada, Ottawa (GSC); Institute of Geological Sciences, London (GSM and GSM Geol. Soc. Coll.); Sedgwick Museum, Cambridge (SM); U.S. National Museum, Washington D.C. (USNM); Yale Peabody Museum, New Haven (YPM).

### **Pharetrolites bambachi** PEEL, 1975c

Plate 2, fig. 9

1975c. *Pharetrolites bambachi* Peel, p. 1526–8, Pl. 1, figs. 16, 18.

*Figured material* – Lower McAdam Brook Fm., YPM 28328, holotype, from YPM Colln. A3822.

*Additional material* – Lower McAdam Brook Fm., YPM Collections A3620, A3637, A3822, A3836, A3844.

### **Pharetrolites murchisoni** (D'ORBIGNY in FÉRUSSAC and D'ORBIGNY, 1840)

Plate 1, figs. 21–24, 26–29

1839. *Bellerophon striatus* SOWERBY in MURCHISON, p. 604, Pl. 3, fig. 12e, *non* BRONN, 1835.  
1840. *Bellerophon murchisoni* D'ORBIGNY in FÉRUSSAC and D'ORBIGNY, p. 210, Pl. VII, figs. 1–3.  
1921. *Temnodiscus murchisoni*; REED, p. 49–51, Pl. IX, figs. 8, 9.  
1924. *Bellerophon* sp.; McLEARN, p. 141, Pl. XX, figs. 28, 29.  
*non* 1842. *Bellerophon murchisoni*; D'ARCHIAC and DE VERNEUIL, p. 353, Pl. XXVIII, figs. 7, 8.

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

TABLE 1. Classification of Arisaig gastropods.

ORDER ARCHAEOGASTROPODA	Family Phanerotrematidae
Suborder Bellerophonina	<i>Phanerotrema</i> affin. <i>P. jugosum</i>
Superfamily Bellerophonata	<i>Brachytomaria</i> sp.
Family Sinuitidae	Family uncertain
Subfamily Temnodiscinae	<i>Platyconus</i> (?) sp.
<i>Pharetrolites bambachi</i>	Superfamily Trochonematacea
<i>Pharetrolites murchisoni</i>	Family Trochonematidae
Family Bellerophonitidae	Undetermined trochonematid species
Subfamily Plectonotinae	
<i>Plectonotus boucoti</i>	Suborder Trochina
<i>Plectonotus cherylae</i>	Superfamily Platyceratacea
<i>Tritonophon trilobata</i>	Family Holopeidae
<i>Tritonophon kivitalonae</i>	Subfamily Holopeinae
<i>Tritonophon</i> sp.	<i>Holopea rossbrookiensis</i>
Subfamily Bucaniinae	Undetermined holopeid species
<i>Anapetopsis maclearni</i>	<i>Haplospira sibieliuxeni</i>
<i>Anapetopsis lalajae</i>	Subfamily Gyronematinae
Subfamily Carinaropsinae	<i>Gyronema haliburtoni</i>
<i>Bucanopsis</i> sp.	Undetermined gyronematid species
<i>Phragmosphaera globata</i>	Family Platyceratidae
Subfamily Cymbulariinae	<i>Naticonema kauffmani</i>
<i>Cymbularia carinata</i>	<i>Cyclonema</i> (C.) <i>parvimedium</i>
<i>Cymbularia</i> sp.	<i>Cyclonema</i> (C.) <i>lydiamarium</i>
Subfamily Tropicodiscinae	<i>Platyceras</i> ( <i>Platygostoma</i> ) cf. <i>P. (Pl.) humilis</i>
<i>Tropicodiscus</i> (?) <i>arisaigensis</i>	<i>Platyceras</i> ( <i>Platygostoma</i> ) <i>cornutum</i>
Suborder Macluritina	Suborder Neritopsina
Superfamily Macluritacea	Superfamily Neritacea
Family Onychochilidae	Family Neritopsidae
<i>Onychochilus</i> (?) <i>reversa</i>	Subfamily Naticopsinae
Superfamily Clisospiracea	<i>Naticopsis trevorpatriciorum</i>
Family Clisospiridae	
Subfamily Clisospirinae	Suborder Murchisoniina
<i>Mimospira abbae</i>	Superfamily Murchisoniacea
	Family Murchisoniidae
Suborder Pleurotomariina	<i>Murchisonia</i> (M.) <i>aciculata</i>
Superfamily Pleurotomariacea	<i>Murchisonia</i> (M.) <i>amii</i>
Family Sinuopeidae	<i>Murchisonia</i> (? <i>Hormotoma</i> ) <i>arisaigensis</i>
Subfamily Platyschismatinae	<i>Murchisonia</i> ( <i>Hormotoma</i> ) sp. A
<i>Umbospira yochelsoni</i>	<i>Murchisonia</i> ( <i>Hormotoma</i> ) sp. B
Family Raphistomatidae	<i>Murchisonia</i> ( <i>Sinuspira</i> ) cf. <i>M. (S.) tenera</i>
Subfamily Raphistomatinae	<i>Murchisonia</i> (s. l.) <i>antigonishensis</i>
<i>Liospira marklandensis</i>	Family Plethospiridae
<i>Liospira</i> cf. <i>L. affinis</i>	Subfamily Plethospirinae
Family Eotomariidae	<i>Seelya moydartensis</i>
Subfamily Eotomariinae	
<i>Eotomaria</i> sp.	ORDER CAENOGASTROPODA
Family Lophospiridae	Superfamily Loxonematacea
Subfamily Lophospirinae	Family Loxonematidae
<i>Loxoplocus</i> ( <i>Lophospira</i> ) <i>sedgwicki</i>	<i>Loxonema sinuosum</i>
<i>Loxoplocus</i> ( <i>Lophospira</i> ) sp. A	<i>Loxonema</i> sp. A
<i>Loxoplocus</i> ( <i>Lophospira</i> ) sp. B	<i>Loxonema</i> sp. B
Subfamily Ruedemanniinae	<i>Morania</i> (?) <i>boltoni</i>
<i>Longstaffia centervillensis</i>	<i>Morania</i> (?) sp.
<i>Longstaffia</i> sp.	Superfamily Subulitacea
<i>Arjamannia cancellatula</i>	Family Meekospiridae
<i>Arjamannia woodlandi</i>	<i>Auriptygma</i> sp.
<i>Arjamannia aulangonensis</i>	

*Additional material* – Moydart Fm., infrequent in Schuchert Colln. 52B. Upper Stonehouse Fm., 3 specimens from Jones Colln. Ar S 7820.

*Discussion* – *Pharetrolites evolvens* (PERNER, 1903) from the Ashgill of Bohemia is similar in profile and ornamentation to individuals of *P. murchisoni* of comparable size but differs in having a deeper sinus. Plaster casts in the U.S. National Museum of *P. cristatus* (PERNER, 1903) from the Silurian of Bohemia indicate more widely spaced growth ornamentation and a wider, deeper sinus.

SOWERBY, (*in* MURCHISON, 1839) stated that *Bellerophon murchisoni* occurs at Felindre, Radnorshire. REED (1920–1921) 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.

The greater tumidity of specimens from the Upper Stonehouse Formation reflects their increased size (Pl. 1, figs. 21, 24, 26).

### **Plectonotus boucoti** PEEL, 1974

Plate 1, fig. 12

1884. *Bellerophon trilobatus*; LINDSTRÖM, p. 80–81, Pl. IV, figs. 13–15.

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

1974. *Plectonotus boucoti* PEEL, p. 252–254, Pl. I, figs. 14, 15, 17–22; Pl. II, figs. 1–9, 11–13, 16, 17.

*non* 1839. *Bellerophon trilobatus* SOWERBY *in* MURCHISON, p. 604, Pl. 3, fig. 16.

*Figured material* – Doctors Brook Fm., USNM 169590 from Schuchert Colln. 52D.

*Additional material* – Doctors Brook Fm., USNM 169583, USNM 169584, the holotype, USNM 169585, USNM 169587, USNM 169588, USNM 169591, USNM 169592, USNM 188526, USNM 192123 and more than 100 other specimens from USNM Colln. 10165; GSC 3138 from Arisaig; USNM 169589, USNM 169590 from Schuchert Colln. 52D. Lower McAdam Brook Fm., YPM Collections A3633, A3635, A3640, A3844, 117/3032. Upper McAdam Brook Fm., YPM Collections A3645–6.

*Discussion* – PEEL (1974) described this species from Arisaig, noting its occurrence in the Silurian of Britain, Ireland and Gotland.

### **Plectonotus cherylae** PEEL, 1974

Plate 1, fig. 10

1924. *Plectonotus trilobatus*; McLEARN, (pars), p. 140–141, Pl. XX, figs. 30, 31, *non* figs. 18, 32.

1974. *Plectonotus cherylae* PEEL, p. 254–255, Pl. 1, figs. 1–13, 16.

*non* 1839. *Bellerophon trilobatus* SOWERBY *in* MURCHISON, p. 604, Pl. 3, fig. 16.



*Figured material* – Upper Stonehouse Fm., USNM 169582, holotype, from Schuchert Colln. 53.

*Additional material* – Upper Stonehouse Fm., USNM 169573 from USNM 10206; USNM 169468, USNM 169471, USNM 169576–81, USNM 188527 from Schuchert Colln. 53; GSC 3138g from Arisaig; YPM 479 from Springville, Nova Scotia; and more than 50 other specimens from the same formation.

*Discussion* – *Plectonotus cherylae* is distinguished from *P. boucoti* by its less severe trilobation and greater lateral compression (PEEL, 1974). The species is currently restricted to the upper Stonehouse Formation of the Arisaig area.

### **Tritonophon trilobata** (SOWERBY *in* MURCHISON, 1839)

Plate 1, fig. 4

1839. *Bellerophon trilobatus* SOWERBY *in* MURCHISON, p. 604, Pl. 3, fig. 16.  
 1909. *Bellerophon trilobatus*; MOBERG and GRÖNWALL, p. 43–44, Pl. III, figs. 13, 14.  
 1933. *Plectonotus trilobatus*; STRAW, p. 125, Pl. IX, figs. 26, 27.  
 1974. *Tritonophon trilobata*; PEEL, p. 256–258, Pl. II, figs. 15, 18–22, 24, 25; Pl. III, figs. 1–9, 14.  
 non 1924. *Plectonotus trilobatus*; McLEARN, p. 140–141, Pl. XX, figs. 18, 30–32.

*Figured material* – Moydart Fm., USNM 169594 from Schuchert Colln. 52B.

*Additional material* – Moydart Fm., USNM 169593 and a number of un-numbered specimens from Schuchert Colln. 52B; YPM 28347 from USNM Colln. 10853 from Sutherland River, Pictou County; GSC 33276 from Jones Colln. Ar Mo 4800.

*Discussion* – The systematics of this poorly known, but widely quoted species have recently been revised (PEEL, 1974). The species occurs in strata of Upper Ludlow and Pridoli age in Scania, Gotland, Felindre in Radnorshire (the type locality), and the borehole at Little Missenden, Bucks. The high degree of lateral compression and the strongly vaulted median lobe serve to distinguish *Tritonophon trilobata* from other trilobed bellerophonaceans at Arisaig.

### **Tritonophon kivialonae** PEEL, 1974

Plate 1, fig. 15

1924. *Plectonotus trilobatus*; McLEARN, p. 140–141, Pl. XX, fig. 32, *non* figs. 18, 30, 31.  
 1974. *Tritonophon kivialonae* PEEL, p. 258–260, Pl. III, figs. 10–13, 15–22.  
 non 1839. *Bellerophon trilobatus* SOWERBY *in* MURCHISON, p. 604, Pl. 3, fig. 16.

*Figured material* – Upper Stonehouse Fm., GSC 32782 from GSC loc. 1302.

*Additional material* – Upper Stonehouse Fm., GSC 33275, holotype, GSC 33279 from Jones Colln. Ar S 7820; GSC 3138a, GSC 3138m, GSC 5649 from Arisaig. A number

of poor specimens from the Stonehouse Fm. may belong here or in *Plectonotus cherylae*, above.

*Discussion* – *Tritonophon kivialonae* is distinguished from *T. trilobata* by its greater rate of whorl expansion, and from *Plectonotus boucoti* by its narrower median lobe with the selenizone occupying the full width of the upper surface. In the latter species the selenizone covers only about half of the upper surface of the median lobe.

*T. kivialonae* was originally described from the higher beds of the upper Stonehouse Formation exposed along the coast at Arisaig but the species is also present in the Jones Creek Formation of New Brunswick, of equivalent Pridoli age.

### **Tritonophon** sp.

1974. *Tritonophon* sp.; PEEL, p. 260–261, Pl. II, figs. 23, 26–28.

*Material* – Beechhill Cove Fm., GSC 33277 from Jones Colln. Ar B Cove loc. 4. Upper Ross Brook Fm., YPM 75 from YPM Colln. A3592; YPM 28350 from YPM Colln. A3760 and one specimen from YPM 179b/3032. French River Fm., YPM 28343 and one specimen from YPM Colln. A3775 French River, Pictou County; one specimen from USNM 11247. Pictou County.

*Discussion* – Poorly preserved *Tritonophon* sp. from the lower part of the Arisaig Group may be comparable to species in the Llandovery of Britain (PITCHER, 1939) and Maryland (SWARTZ and PROUTY, 1923). Unfortunately, the relationship of these specimens to *Planorbis trilobatus* CONRAD, 1839 or *Tritonophon trilobata* SOWERBY in MURCHISON, 1839 is not known (PEEL, 1974).

### **Anapetopsis maclearni** PEEL, 1975a

Plate 2, fig. 15

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

1975a. *Anapetopsis maclearni* PEEL, p. 510–512, pl. 1, figs. 1–8, 10.

*Figured material* – Upper Stonehouse Fm., GSC 3140a, holotype, from Arisaig.

*Additional material* – Upper Stonehouse Fm., GSC 3140b, GSC 3140c from Arisaig; GSC 32781A from GSC loc. 1302.

### **Anapetopsis lalajae** PEEL, 1975a

1924. *Bucanopsis?* sp.; McLEARN, p. 141, Pl. XX, fig. 20.

1975a. *Anapetopsis lalajae* PEEL, p. 512–513, Pl. 1, figs. 9, 11–16.

*Material* – Upper Stonehouse Fm., USNM 169595, holotype, USNM 169596 from Schuchert Colln. 53; GSC 3140 from Arisaig shore; USNM 169467 from Schuchert Colln. 49A; GSC 32781B from GSC loc. 1302.

*Discussion* – *Anapetopsis lalajae* differs from *A. maclearni* in having a wider whorl profile and deeper sinus. Both species were originally described from the upper Stonehouse Formation at Arisaig (PEEL, 1975a).

**Bucanopsis** sp.

Plate 1, figs. 9, 16, 17

*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 County. Upper Ross Brook Fm., YPM Colln. A3592, Doctors Brook Fm., USNM Colln. 10919. Lower McAdam Brook Fm., YPM Collections A3604, A3606, A3607, A3608, A3616, A3620, A3811/A3815, A3820, A3826.

*Discussion* – Several poor internal moulds from the Beechhill Cove and Doctors Brook Formations possess the carina on the floor of the whorl allegedly characteristic of this genus. Similarly, many crushed specimens occur in shales from the upper Ross Brook and lower McAdam Brook Formations, showing a well developed selenizone and prominent reticulate ornamentation. However, as HORNÝ (1963) has observed, *Bucanopsis* is a poorly known genus although the name has been widely employed for many unrelated bellerophonacean gastropods from throughout the Palaeozoic. Many Devonian-Permian species are now referred to *Retispira* KNIGHT, 1945 which lacks the keel on the floor of the whorl. The type species, *B. carinifera* ULRICH and SCOFIELD, 1897, is from the middle Ordovician of Kentucky but the status of many Ordovician and Silurian species commonly placed here is in great need of reinvestigation.

**Phragmosphaera globata** (SOWERBY *in* MURCHISON, 1839)

Plate 1, figs. 1–3, 6, 7. Fig. 3

1839. *Bellerophon globatus* SOWERBY *in* MURCHISON, p. 604, Pl. 3, fig. 15; Pl. 4, fig. 50.

*Figured material* – Moydart Fm., USNM 169597–600, USNM 192113 from Schuchert Colln. 52B.

*Additional material* – Moydart Fm., 15 specimens in Schuchert Colln. 52B and Jones Colln. Ar Mo 4820.

*Discussion* – The internal mould described by SOWERBY (*in* MURCHISON, 1839) from the Ludlow of the Welsh Borderlands has similar proportions to the Arisaig specimens and exhibits comparable transverse channels on the dorsum. M'COY (*in* SEDGWICK and M'COY, 1855) thought that there could be 'not the slightest doubt of the propriety

of uniting' *Bellerophon globatus* with *B. expansus* SOWERBY *in* MURCHISON, 1839, the former being a juvenile of the latter. However, REED (1920–21) commented that the type of *B. globatus* could not be located and the relationship to *B. expansus* therefore could not be established. Until such time as SOWERBY'S two species are reinvestigated the Arisaig specimens are referred to *Phragmosphaera globata* and the issue is left in abeyance.

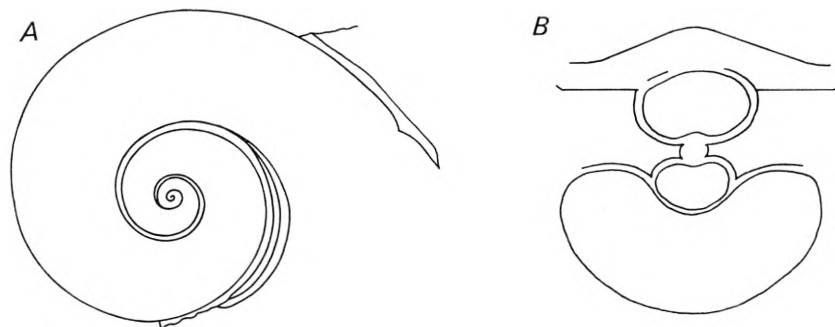


Fig. 3. *Phragmosphaera globata*. Lower Moydart Formation, x 5. A, USNM 169600, median section showing parietal deposit within aperture. B, USNM 169597, reconstructed transverse section.

*Phragmosphaera lyra* (HALL, 1861) of ROLLINS (*in* ROLLINS, ELDREDGE and SPILLER, 1971) from the Devonian of New York State has more prominent spiral ornamentation and a shallower dorsal sinus than the Arisaig specimens.

### ***Cymbularia carinata* (SOWERBY *in* MURCHINSON, 1839)**

Plate 1, figs. 13, 18

1839. *Bellerophon carinatus* SOWERBY *in* MURCHISON, p. 604, pl. 3, figs. 4, 1d.

1921. *Cymbularia carinata*; REED, p. 64–66, Pl. X, fig. 12.

1897. *Bellerophon lenticularis* GRÖNWALL, p. 237 (*nom. nud.*).

1909. *Bellerophon lenticularis* MOBERG & GRÖNWALL, p. 43, Pl. III, figs. 12a, b.

*Figured material* – Moydart Fm., USNM 169574, USNM 169575 from Schuchert Colln. 52B.

*Additional material* – Moydart Fm., 4 specimens from Schuchert Colln. 52B and Jones Colln. Ar Mo 4820.

*Discussion* – The type specimen of *Cymbularia carinata* from the Ludlow of Britain is an internal mould (GSM Geol. Soc. Coll.) providing little information concerning the shell exterior. In contrast, *Bellerophon lenticularis* was described by MOBERG and GRÖNWALL (1909) on the basis of finely preserved material from Scania. The Arisaig material, although poorly preserved, provides a link between the two since it would appear that *B. lenticularis* is merely the juvenile form of *C. carinata*. Increase in

ontogeny produces a relative increase in whorl width which obscures the lenticular form of the earlier growth stages (Fig. 4). The Scanian specimens are certainly referable to *Cymbularia* and following REED (1920–21) it should be noted that, if the separate identity of *B. lenticularis* is recognised, the name *Cymbularia lenticularis* is preoccupied by a species of KOKEN (1897).

*C. carinata* is similar to *Joleaudella mansuyi* PATTE, 1929 from the Silurian or Devonian of Tonkin. KNIGHT *et al.* (1960) considered this genus to be a junior sub-

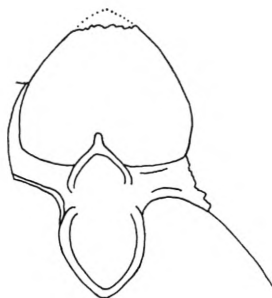


Fig. 4. *Cymbularia carinata*. Lower Moydart Formation, USNM 169575. Transverse section showing median dorsal keel on inner whorl and closed umbilici, x 6.25.

jective synonym of *Tropidodiscus* MEEK and WORTHEN, 1866 but PATTE's genus is readily distinguished from *Tropidodiscus* by its narrow umbilici and cymbularioid emargination. *C. carinata* has closed umbilici, is less laterally compressed and lacks the crenulate ornamentation of the oriental species.

### ***Cymbularia* sp.**

Plate 1, figs. 11, 19

*Figured material* – Doctors Brook Fm., USNM 169464 from USNM Colln. 10919. Lower McAdam Brook Fm., YPM 28329 from YPM Colln. A3623.

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

*Discussion* – The poor fragments placed here exhibit the gross form and configuration of emargination typical of *Cymbularia*, namely a wide dorsal sinus with a deepened inner portion.

### ***Tropidodiscus* (?) *arisaigensis* n. sp.**

Fig. 5

*Holotype* – Doctors Brook Fm., USNM 169586 a transverse thin section associated with *Plectonotus boucoti* from USNM Colln. 10165, Arisaig shore, Nova Scotia.

*Additional material* – Doctors Brook Fm., a further specimen in the same thin section as the holotype and three specimens on a transverse polished section associated with *P. boucolti*, USNM 188526 from USNM Colln. 10165. BM PG5009, a small internal mould from a limestone band in the basal Wenlock of Brinkmarsh Quarry, Tortworth Inlier, Gloucestershire, England.

*Description* – A minute species with at least four whorls, tentatively assigned to *Tropidodiscus* MEEK and WORTHEN, 1886. Earliest two and a half whorls transversely elliptical



Fig. 5. *Tropidodiscus* (?) *arisaigensis* n. sp. Doctors Brook Formation, USNM 169586, holotype. Transverse thin section showing ontogenetic variation in whorl profile suggestive of a micromorphic adult, x 25.

with whorl width greater than whorl height. Third and fourth whorls with pronounced dorsal expansion producing a highly vaulted profile, whorl height exceeding whorl width. At this late stage, the umbilical walls becoming 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. Umbilici phaneromphalous, about one sixth of the total length at maturity. Ornamentation and shell structure unknown.

*Discussion* – The small size of *Tropidodiscus* (?) *arisaigensis* (length less than 2 mm) might be considered to support an interpretation as the nuclear whorls of some macrogastropod. However, the well marked ontogenetic change between the third and fourth whorls of the holotype (Fig. 5) suggests that the specimens are mature individuals of a 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 (PEEL, 1974).

The genus *Microceras* HALL, 1845 was proposed for a group of morphologically similar species which may be locally abundant in strata 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 bellerophontaceans but KNIGHT (1941) expressed conviction that all HALL's specimens of the type species from Cincinnati were nuclei. 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 . . . '.

It is clearly undesirable to refer the described specimens to *Microceras*. The widely phaneromphalous umbilici and discoid form suggest the macromorphic *Tropidodoscus* MEEK and WORTHEN, 1886, to which tentative assignment is made while recognising the discrepancy in size. *T. (?) arisaigensis* differs from most species of the genus in its extreme diminutive size, greater rate of whorl expansion, fewer number of whorls and probably greater width of the selenizone, as exemplified in the greater width of the flat dorsal band.

The species is also present in the basal Wenlock of Brinkmarsh Quarry, near Tortworth, Gloucestershire, where phosphatised internal moulds occur in residues left after acid digestion.

### Undetermined bellerophontacean genera and species

Plate 1, figs. 5, 8, 14, 20, 30

*Material* – Beechhill Cove Fm., species A, USNM 188525 from USNM Colln. 10115; species B, USNM 169488 from USNM Colln. 10115. French River Fm., species C, YPM 28348 from YPM Colln. A3777, Pictou County. Upper Stonehouse Fm., species D, GSC 6216 from Arisaig. Species E, GSC 3139a, Cape George (?), locality and stratum unknown.

*Discussion* – Several specimens discussed here are too imperfectly known to merit formal description. Species A, not figured, is a poor internal mould associated with figured specimens of *Arjamannia cancellatula* and *Longstaffia centervillensis*. The rate of whorl expansion is great and the umbilici narrow, while a deep groove on the axial surface presumably corresponds to a carina on the previous whorl.

Species B, not figured, is a large laterally compressed internal mould with a rounded dorsum occurring on a small slab with a figured specimen of *Longstaffia* sp. The umbilici are narrow but a grooved axial surface of the type characteristic of the previous species is not present.

Species C, Plate 1, fig. 30, has a rapidly expanding shell with many fine spiral lirae. The crushed specimen shows a shallow median sinus and selenizone. Species D, Plate 1, figs. 5, 8, was referred by McLEARN (1924, p. 141, Pl. XX, figs. 13, 14) to *Bucania* HALL, 1847. The degree of whorl impression is high and the umbilici are closed, precluding retention in the widely phaneromphalous *Bucania*.

Species E, Plate 1, figs. 14, 20, is a poor internal mould labelled *Bucania profunda* which was supposedly collected at Arisaig. However, its preservation in a buff, coarsely crystalline limestone is quite unlike any other examined Arisaig specimen. AMI (1895) applied the same name to a specimen from the Stonehouse Formation of Cape George, Antigonish County and it seems likely that this is the specimen in question.

**Onychochilus (?) reversa** (HALL, 1860)

Plate 2, fig. 3

1860. *Holopea reversa* HALL, p. 154, fig. 14.1868. *Holopea reversa*; DAWSON, p. 605, fig. 211.1924. *Holopea reversa*; MCLERN, p. 148.

*Figured material* – Upper Stonehouse Fm., AMNH 1648, the holotype, 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. However, without evidence of the nature of the ornamentation precise placement is not possible. *Mimospira abbae* is higher spired with more whorls. There is some similarity in gross form with *Versispira contraria* PERNER, 1903 from the Bohemian Ordovician, and the middle Devonian *Hyperstrophomena devonicans* HORNÝ, 1964. AMI (1895) recorded the occurrence of HALL’s species in strata of equivalent age at Cape George, Antigonish County but the specimen in question has not been located.

**Mimospira abbae** PEEL, 1975c

Plate 2, fig. 8

1975c. *Mimospira abbae* PEEL, p. 1528–9, pl. 1, figs. 10, 11, 14.

*Figured material* – McAdam Brook Fm., USNM 169489, holotype, from USNM Colln. 11183 at Lochaber, Antigonish County.

*Additional material* – Moydart Fm., USNM 169571 from USNM Colln. 10183.

*Discussion* – This rare hyperstrophic species is the first Silurian record of the genus (PEEL, 1975c).

**Umbospira yochelsoni** n. sp.

Plate 2, fig. 6

*Holotype* – Upper Ross Brook Fm., YPM 28330 from YPM Colln. A3582.

*Additional material* – Five specimens in the same collection.

*Description* – Species of *Umbospira* PERNER, 1903 with about three whorls. Profile poorly known but seemingly rotelliform with shallowly convex upper whorl surfaces. Nature of umbilicus and basal surface unknown. Whorl embracement at just above periphery of previous whorl, producing shallow sutural indentation. Growth lines slightly prosocyrct on upper whorl surface, increasing in convexity with passage into



the deep, U shaped sinus which is located at just above the whorl periphery. Ornamentation of fine growth lines. Shell seemingly thin, structure unknown.

*Discussion* – McLEARN (1924, p. 144) seems to have included similar specimens in *Liospira* ULRICH and SCOFIELD, 1897 but the Ross Brook Formation specimen lacks a true slit and selenizone. Several examples do 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*. However, in the holotype (Plate 2, fig. 6) the form of the U shaped sinus with subparallel sides is clearly visible. The crack approximately corresponds to the upper edge of the sinus which is presumably a line of weakness because of the very closely spaced, almost parallel growth lines.

*U. nigricans* PERNER, 1903, the type species from the upper Silurian of Czechoslovakia, has a more open sinus than the Arisaig species in which the emargination is U shaped with subparallel sides. A minute species from the Silurian of Scania was referred to *Umbospira* sp. by HEDE (1915) but the material is too poorly known to compare with the Arisaig specimens.

### ***Liospira marklandensis* McLEARN, 1924**

Plate 2, figs. 11–14

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

*Figured material* – Upper Stonehouse Fm., GSC 5654, holotype, Arisaig; USNM 169572 from USNM Colln. 10206; USNM 192114 from Schuchert Colln. 53.

*Additional material* – Common in the Upper Stonehouse Fm.

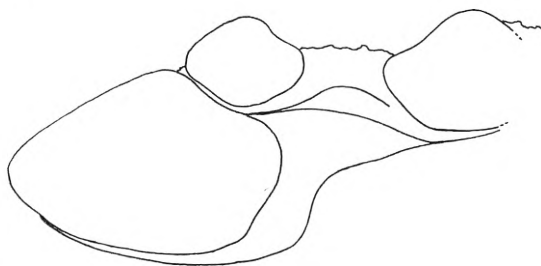


Fig. 6. *Liospira marklandensis*. Upper Stonehouse Formation, USNM 169572. Transverse section showing closed umbilicus, x 6.

*Discussion* – The prosocyrte growth lines on the upper whorl surface distinguish *Liospira marklandensis* from other species of the genus, in which the growth lines are prosocline. The degree of closure of the umbilicus is apparently variable, ranging from completely closed by a callus deposit and thickened columellar lip (Fig. 6) to widely phaneromphalous with just minor development of a funicle on the umbilical shoulder.

**Liospira cf. L. affinis** (FOERSTE, 1885)

Plate 2, figs. 4, 7, 10

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

*Figured material* – Beechhill Cove Fm., YPM 480, YPM 83 from McGillivray Brook (*sensu* BOUCOT *et al.*, 1974).

*Additional material* – Beechhill Cove Fm., about 15 specimens from USNM Collections 10114 and 10115.

*Discussion* – This species differs from the former in having a more perfectly formed conical spire which is relatively more elevated. In *Liospira marklandensis* the incremental angle approaches  $150^\circ$  whereas in *L. cf. L. affinis* it is some  $30^\circ$  less. The shape of the apertural lip above the selenizone is not known in the Arisaig specimens but type materials of *L. affinis* from Ohio show a prosocline lip as distinct to the prosoclyrt lip in *L. marklandensis*.

**Eotomaria** sp.

Plate 3, figs. 8, 13

*Figured material* – Glencoe Brook Fm., (Beechhill Cove Fm. equivalent), USNM 169463 from USNM Colln. 11267, Pictou County. Middle Ross Brook Fm., YPM 76 from YPM Colln. A3731.

*Discussion.* – The two poorly preserved specimens placed here lack the apical and apertural portions. There is some similarity with *Lophospira ehlersi* FOERSTE, 1923 from lower Llandovery shales below the Brassfield Limestone of Ohio but the latter is higher spired and possesses an obscure basal angulation.

**Loxoplocus (Lophospira) sedgwicki** (DONALD, 1906)

Plate 2, fig. 23

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

*Figured material* – Beechhill Cove Fm., USNM 169481 from USNM Colln. 10819, Pictou County.

*Additional material* – A further specimen from the same collection.

*Discussion* – The Arisaig specimens agree closely with the original description by DONALD (1906) of this species in equivalent strata of lower Llandovery age from Mulloch Hill, Ayrshire, Scotland.

**Loxoplocus (Lophospira) sp. A**

Plate 2, fig. 18

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

*Discussion* – The single specimen differs from the former species in being lower spired and having the more strongly defined peripheral flange located lower on the whorl face.

**Loxoplocus (Lophospira) sp. B**

Plate 3, fig. 1

*Figured material* – Beechhill Cove Fm., USNM 169485 from USNM Colln. 10114.

*Discussion* – This species, known only from a fragmentary external mould, shows a much lower inclination of the upper whorl surface than *L. (Lo.) sedgwicki*. Immediately below the peripheral flange, the whorl surface is excavated into a narrow channel. In *L. (Lo.) sedgwicki* and *L. (Lo.)* sp. A this subperipheral excavated band is better differentiated, forming a well marked outer whorl surface with a prominent angular junction with the base.

**Longstaffia centervillensis** (FOERSTE, 1923)

Plate 2, figs. 17, 19; Plate 3, fig. 4

1923. *Lophospira (Ruedemannia?) centervillensis* FOERSTE, 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 YPM Colln. A3731.

*Additional material* – Beechhill Cove Fm., an additional specimen associated with the figured example.

*Discussion* – KNIGHT *et al.* (1960) referred *Longstaffia* to the subfamily Lophospirinae Wenz, 1938. However, the relatively well developed selenizone and prominent spiral ornamentation on the base seem more characteristic of the Ruedemanniinae Knight, 1956. The genus is accordingly transferred to this subfamily of the Lophospiridae Wenz, 1938 to lie alongside *Ruedemannia* FOERSTE, 1914, *Worthenia* DE KONINCK, 1883 and *Arjamannia* PEEL, 1975b.

FOERSTE (1923) described *Longstaffia centervillensis* from shales below the Brassfield Limestone at Centerville, Ohio, which appear to be equivalent to the Belfast Member (lower Llandovery) and, hence, of comparable age to the Beechhill Cove Formation. *Longstaffia tubulosa*, 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*.

**Longstaffia** sp.

Plate 2, figs. 21, 22

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

*Additional material* – Beechhill Cove Fm., fragment associated with *Arjamannia cancellatula*, USNM 188523 from USNM Colln. 10115.

*Discussion* – *Longstaffia* sp. is distinguished from the contemporaneous *L. centervillensis*, above, by its narrower incremental angle of 70°. In the latter species, which also has a more gradate profile, the angle approaches 90°.

PITCHER (1939) referred specimens from the upper Llandovery of Shropshire to *Gyronema octavia* (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 of the type present in *L. centervillensis* and *Longstaffia* sp. 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.

**Arjamannia cancellatula** (M'COY in SEDGWICK and M'COY, 1852)

Plate 2, fig. 5

1852. *Murchisonia cancellatula* M'COY in SEDGWICK and M'COY, p. 292–293, Pl. 1L, figs. 20, 20a.

1924. *Lophospira cancellatula*; LONGSTAFF, p. 419–420. Pl. XXXIII, figs. 1, 2.

1975b. *Arjamannia cancellatula*; PEEL, p. 386–8, Pl. 53, figs. 1–5, 7.

*Figured material* – Beechhill Cove Fm., USNM 169484 from USNM Colln. 10114.

*Additional material* – About 13 specimens from the Beechhill Cove Fm.

*Discussion* – This species occurs in approximately equivalent deposits in Scotland, Pembrokeshire and Arisaig (PEEL, 1975b).

**Arjamannia woodlandi** (LONGSTAFF, 1924)

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

1939. *Lophospira woodlandi*; PITCHER, p. 88–89, Pl. II, figs. 1–4.

1975b. *Arjamannia woodlandi*; PEEL, p. 390, Pl. 53, figs. 14, 15.

*Material* – Beechhill Cove Fm., USNM 188521 from USNM Colln. 10819, Pictou County.

*Discussion* – This species is known from Llandovery deposits in southern Scotland, Shropshire and at Arisaig (PEEL, 1975b).

**Arjamannia aulangonensis** PEEL, 1975b

Plate 2, fig. 16

1975b. *Arjamannia aulangonensis* PEEL, p. 389–90, Pl. 53, figs. 12, 13.

*Figured material* – Doctors Brook Fm., USNM 169469, holotype, from USNM Colln. 10919.

*Additional material* – A few poor fragments associated with the holotype.

*Discussion* – *Arjamannia aulangonensis*, the youngest species of the genus, is only known from Arisaig.

**Phanerotrema** affin. **P. jugosum** PITCHER, 1939

Plate 2, figs. 1, 2

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

*Additional material* – About 30 specimens from the same collection.

*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 upper whorl surface. *P. jugosum* has two or three strong spiral cords, *P. occidens* (HALL, 1867) about nine, and *P. lindstroemi* (BOUCOT and JOHNSON in BOUCOT *et al.*, 1966; the type species of *Pseudoscalites* BOUCOT and JOHNSON in BOUCOT *et al.*, 1966 which is apparently a junior synonym of *Phanerotrema* FISCHER, 1885) 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.

**Brachytomaria** sp.1975c. *Brachytomaria* sp.; PEEL, p. 1529, Pl. 1, fig. 17.

*Material* – Upper Stonehouse Fm., YPM 28326, from YPM Colln. 19e/3032.

*Discussion* – This specimen represents the first Silurian record of the genus (PEEL, 1975c).

**Platyconus** (?) sp.

Plate 4, fig. 19

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

*Discussion* – A large, poorly preserved specimen resembles *Platyconus carinatus* (SOWERBY *in* MURCHISON, 1839) from the Ludlow of the Welsh Borderlands. Ornamentation is not preserved but a ramp on the lower part of the final whorl suggests the raised selenizone found in SOWERBY'S species. *Prosolarium scalatum* NORTHROP, 1939 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* PERNER, 1903.

### Undetermined trochonematid genus and species

Plate 3, fig. 20

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

*Additional material* – A further specimen in the same collection.

*Discussion* – The illustrated specimen is an internal mould with adhering shell fragments. The convex final whorl has a peripheral flat band suggestive of a selenizone or pseudoselenizone. A subsutural cord is present and it appears that ornamentation consists of spiral lirae and intervening concave areas. There is some similarity to *Proturritella gracilis* KOKEN, 1889 from the Baltic Ordovician in whorl profile and ornamentation but imperfect preservation hinders further comparison.

### *Holopea rossbrookiensis* n. sp.

Plate 3, figs. 6, 11

*Holotype* – Upper Ross Brook Fm., YPM 28333 from YPM Colln. A3592.

*Paratype* – Upper Ross Brook Fm., YPM 28334 from YPM Colln. A3759.

*Additional material* – Upper Ross Brook Fm., abundant in YPM Colln. A3592, but also in YPM Collections A3583, A3586, A3759, A3760, 175/3032 and USNM Colln. 10129. Lower McAdam Brook Fm., YPM Collections A3604, A3606, A3611.

*Description* – Species of *Holopea* HALL, 1847 with at least four whorls. Nuclear whorls unknown. Later whorls inflated 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 orthocone outer lip. Ornamentation of growth lines only. Shell seemingly thin, structure unknown.

*Discussion* – *Holopea rossbrookiensis* n. sp. has a slightly greater rate of whorl expansion and relatively larger final whorl than *H. symmetrica* HALL, 1847, the type species from the Ordovician of New York State (KNIGHT, 1941). *H. striatella* (SOWERBY *in* MURCHISON, 1839) from the Ordovician of Shropshire has similar proportions to the Arisaig

species, but the growth lines appear to have a slightly different angle and the sutures are less indented. *Haplospira sibliuxeni* PEEL, 1975c, from the upper Stonehouse Formation of Arisaig, is readily distinguished by a strong subsutural cord and its shallower sutural indentation.

### Undetermined holopeid genus and species

Plate 3, fig. 10

*Figured material* – Middle Ross Brook Fm., YPM 28336 from YPM Colln. A3556.

*Additional material* – One specimen in the same collection.

*Discussion* – This minutely phaneromphalous species is characterised by strong spiral lirae located mainly below the periphery of the rather globose whorls. In the figured specimen the final whorl has about fifteen lirae on the base of the final whorl crossed by nearly orthocline growth lines. *Threavia gulosa* LAMONT, 1946 from the upper Ordovician of the Girvan area is distinguished by only having a single spiral lira on the lower part of the whorl. In *Gyronema* fewer, relatively more coarse lirae are distributed over all the whorl surface.

### *Haplospira sibliuxeni* PEEL, 1975c

Plate 3, fig. 24

1975c. *Haplospira sibliuxeni* PEEL, p. 1529–30, Pl. 1, fig. 19.

*Figured material* – Upper Stonehouse Fm., USNM 192116, holotype, from USNM Colln. 10206.

*Additional material* – Upper Stonehouse Fm., associated with the holotype of *Onychochilus (?) reversa* (HALL, 1860), AMNH 1648.

*Discussion* – This species is currently restricted to the Arisaig Group of Nova Scotia.

### *Gyronema haliburtoni* (McLEARN, 1924)

Plate 3, fig. 7

1924. *Cyclonema haliburtoni* McLEARN, p. 147, Pl. XXI, fig. 3.

*Figured material* – Ross Brook Fm., YPM 462B, holotype, from the coastal section, Arisaig.

*Additional material* – Common in the lower part of the upper Ross Brook Fm.

*Discussion* – *Gyronema haliburtoni* differs from most of the varieties of *G. 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 variety *multicarinata* from the Mulde Beds of Gotland in terms of profile, but this form is said to have more abundant spiral ornamentation. One of the specimens illustrated by PITCHER (1939) as *G. octavia* var. *multicarinata* from the upper Llandovery of Shropshire 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., above. Specimens identical with McLEARN's species occur in Yale Peabody Museum from the Silurian around Cumberland, Maryland.

### Undetermined gyronematinid genus and species

Plate 3, fig. 19

*Figured material* – Moydart Fm., YPM 28346 from USNM Colln. 10853, Sutherland River, Pictou County.

*Discussion* – The whorl profile of the single fragment described here is concave below the suture but soon becomes convex prior to passing onto the convex base. Sutural indentation is slight. Ornamentation is of spiral lirae and intervening concave bands crossed by prosocline growth lines, the spiral lirae becoming finer away from the preceding suture. Although assigned to the subfamily Gyronematinae the generic position of this species is uncertain. The nature of the adpressed subsutural area and the spiral ornamentation find no close equivalent in other members of the group but the material is insufficient to delimit a new taxon.

### *Naticonema kauffmani* PEEL, 1975c

Plate 4, fig. 27

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

1975c. *Naticonema kauffmani* PEEL, p. 1530, Pl. 1, figs. 12, 15.

*Figured material* – Beechhill Cove Fm., YPM 462A, the holotype, from West Point, Beechhill Cove, Arisaig.

*Additional material* – Beechhill Cove Fm., USNM 169479 from USNM Colln. 10116.

### *Cyclonema (Cyclonema) parvimedium* McLEARN, 1924

Plate 3, figs. 22, 23, 25, 26

1924. *Cyclonema parvimedium* McLEARN, p. 146, Pl. XXI, figs. 13, 14.

*Figured material* – Beechhill Cove Fm., GSC 5655, holotype, from Arisaig; USNM 169473, 169476, 169477 from USNM Colln. 10114.



*Additional material* – About twenty five specimens from the Beechhill Cove Fm., USNM Collections 10114, 10115.

*Discussion* – This species is characterised by the subtrochoidal form which is manifested in the narrowly shouldered whorls and slightly convex, inclined outer whorl faces. *Cyclonema (C.) daytonense* FOERSTE, 1899 from the Brassfield Formation of Ohio, Illinois and Missouri may have similar ornamentation but is distinguished by its lower rate of whorl expansion. This produces a relatively smaller final whorl, with relatively greater width, than in *C. (C.) parvimum*. *C. (C.) crebistria* (M'COY) var. *rugatum* PITCHER, 1939 from the upper Llandovery of Shropshire is a lower, more vertically compressed form while *C. (C.) bellulum* BILLINGS, 1866, as figured by TWENHOFEL (1928) and BOLTON (1972) from the lower Silurian of Anticosti Island, has more convex whorls. *C. (C.) varians* BILLINGS, 1859, another Anticosti species, is delimited by its turbinate form.

A single specimen (SM A32391) has been observed from the Gasworks Mudstone, Pembrokeshire, of similar age to the Arisaig occurrence.

#### ***Cyclonema (Cyclonema) lydiamariarum* PEEL, 1975c**

1975c. *Cyclonema (Cyclonema) lydiamariarum* PEEL, p. 1530–1, Pl. 1, figs. 9, 13, 21.

*Material* – Upper Stonehouse Fm., YPM 28335 from YPM Colln. A3717.

*Discussion* – This species was described on the basis of well preserved specimens from the upper Ludlow of Felindre, Radnorshire, and the single poor specimen from Arisaig (PEEL, 1975c).

#### ***Platyceras (Platyostoma) cf. P. (Pl.) humilis* (BILLINGS, 1866)**

Plate 3, fig. 5

*Figured material* – Middle Ross Brook Fm., USNM 169490 from USNM Colln. 11291, Pictou County.

*Additional material* – Middle Ross Brook Fm., USNM Colln. 11224, Pictou County; YPM Colln. A3732.

*Discussion* – Poor specimens from the middle Ross Brook Fm. show the rapidly expanding turbinate form characteristic of this species from Anticosti Island. Ornamentation consists of somewhat irregularly spaced and slightly rippled spiral striae, with flat intervening areas, crossed by prosocline growth lines.

**Platyceras (Platyostoma) cornutum** (HISINGER, 1837)

Plate 3, figs. 9, 15, 21; Plate 4, figs. 18, 21, 22, 25

1837. *Pileopsis cornuta* HISINGER, Pl. 12, fig. 11.1884. *Platyceras cornutum*; LINDSTRÖM, p. 63, Pl. 2, figs. 29–51; Pl. 3, figs. 6–9, 19–26.1924. *Diaphorostoma cornutum* var. *arisaigensis* MCLEARN, p. 148, Pl. XXI, figs. 8–10.1924. *Holopea caecistriata* MCLEARN, 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. Upper Stonehouse Fm., GSC 5656, GSC 5657 from Arisaig shore.

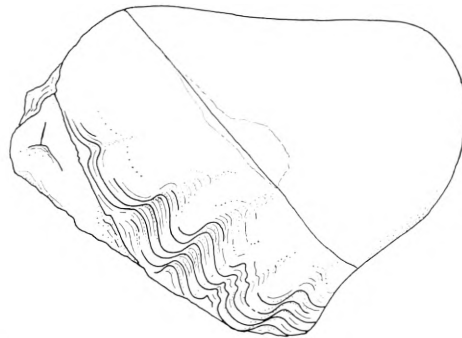


Fig. 7. *Platyceras (Platyostoma) cornutum*. Upper Stonehouse Formation, GSC 33271. Lateral view showing irregular growth lines. The minor emarginations probably correspond to the shape of the echinoderm calyx with which the coprophagous gastropod was associated, x 2.

*Additional material* – Present in all formations but particularly common in the Moydart and upper Stonehouse Formations.

*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 rapidly expanding, naticiform, commonly with a sunken spire. The whorl profile is strongly convex; ornamentation consists of irregular growth lines (Fig. 7) with spiral striae on earlier whorls. *Holopea caecistriata* MCLEARN, 1924 is merely a juvenile example with well developed spiral ornamentation.

### Undetermined trochinid genus and species

Plate 2, fig. 20

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

*Discussion* – The single fragment preserves parts of two whorls. The subtrochoidal shell has a convex base and moderately elevated spire. The junction between the base and the upper whorl surface is marked by a strong peripheral carina, above which lies a deep spiral channel. A fine reticulate ornament is present on the base. The species is superficially similar to some Mesozoic Proconulinae but has orthocone growth lines on the base as distinct to the strongly prosocline condition characteristic of many trochids.

### *Naticopsis trevorpatriciorum* PEEL, 1975c

Plate 3, fig. 2

1975c. *Naticopsis trevorpatriciorum* PEEL, p. 1531–2, Pl. 1, figs. 1–8.

*Figured material* – Moydart Fm., YPM 28332 from YPM Colln. 103a/3032.

*Additional material* – Four specimens from the same formation.

*Discussion* – A full discussion and synonymy of this species, *Natica glaucinoides* J. DE C. SOWERBY in MURCHISON, 1839 *non* J. SOWERBY, 1812, is given by PEEL (1975c).

### *Murchisonia (Murchisonia) aciculata* HALL, 1860

Plate 4, figs. 1–3

1860. *Murchisonia aciculata* HALL, p. 154.

1868. *Murchisonia aciculata*; DAWSON, p. 605.

1924. *Goniotropha aciculata*; McLEARN, p. 142, Pl. XXI, figs. 21, 25.

*Figured material* – Upper Stonehouse Fm., AMNH 1649, the holotype; GSC 5650, GSC 5651, the figured specimens of McLEARN (1924), Arisaig.

*Additional material* – Common in the upper Stonehouse Fm.

*Discussion* – 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 given by HALL (1860) which cannot be satisfactorily applied to other contemporaneous species. *Murchisonia (M.) cambria* (DONALD, 1905) from the Ludlow of Wales has the selenizone a little lower on the whorl face while in *M. (M.) elegans* SOLLAS, 1879, a Wenlock species, the upper whorl surface is concave and lacks the subsutural shoulder. Ornamentation is unfortunately unknown in both these species.

McLEARN (1924) recorded this species from the Moydart Formation and the lower member of the Stonehouse Formation at Arisaig but these records have not been confirmed during the present study.

**Murchisonia (Murchisonia) amii** (McLEARN, 1924)

Plate 4, figs. 4, 12, 13

1924. *Hormotoma amii* McLEARN, p. 143, Pl. XX, fig. 22.1933. *Hormotoma* cf. *articulata*; STRAW, p. 124, Pl. IX, figs. 23, 24.non 1839. *Pleurotoma articulatum* SOWERBY in MURCHISON, p. 612, Pl. 5, fig. 25.

*Figured material* – Upper Stonehouse Fm., GSC 5652, the holotype; YPM 28337B from USNM Colln. 10206; USNM 192121 from Schuchert Colln. 53.

*Additional material* – Uncommon in the upper Stonehouse Fm.

*Discussion* – *Murchisonia (M.) amii* differs from *M. (M.) dudleyensis* DONALD, 1902 and *M. (M.) cambria* (DONALD, 1905) from the Wenlock and Ludlow of Britain, respectively, in having a less angular whorl profiles with shouldered whorls. *M. (M.) cava* LINDSTRÖM, 1884 from the Slite Beds of Gotland has a similar profile but lacks the deeper 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 within 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 marine Downtonian (= Pridoli) strata of the Little Missenden Borehole, Buckinghamshire as *Hormotoma* cf. *articulata* (SOWERBY in MURCHISON, 1839) are placed here. In GSM 51876, the original of STRAW (1933, Pl. IX, fig. 23), the shouldered whorls, near orthocline growth lines above the selenizone and the characteristic two spiral cords entirely within the selenizone margins are well displayed. The holotype of SOWERBY'S species (DONALD, 1899, Pl. XXII, fig. 7) has more open sutures and greater inclination of the growth lines above the selenizone.

In the holotype of *M. (M.) amii* a thin outer shell layer bearing the selenizone cords has been exfoliated in all but the earliest of the five whorls. Presumably it was the absence of these spiral elements which caused McLEARN (1924) to refer the then only known specimen to *Hormotoma* SALTER, 1859.

**Murchisonia (?Hormotoma) arisaigensis** (HALL, 1860)

Plate 4, figs. 7–9, 26

1860. *Murchisonia arisaigensis* HALL, p. 154.1868. *Murchisonia arisaigensis*; DAWSON, p. 604.1924. *Goniotropha?* *arisaigensis*; McLEARN, p. 143.

*Lectotype* – Here designated as the larger of two specimens bearing the number AMNH 1650 from the upper Stonehouse Fm., Arisaig. The smaller specimen in the same collection is designated paralectotype.

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

*Additional material* – Upper Stonehouse Fm., seventeen specimens from USNM Collections 10205, 10206 and Schuchert Colln. 53.

*Discussion* – *Murchisonia* (?*Hormotoma*) *arisaigensis* has a greater incremental angle ( $25^\circ$ ) than the contemporaneous *M. (M.) aciculata* and *M. (M.) amii* (both  $15^\circ$ ). HALL's syntypes, not figured by McLEARN (1924), are internal moulds showing no indication



Fig. 8. *Murchisonia* (?*Hormotoma*) *arisaigensis*. Upper Stonehouse Formation, USNM 192122. Internal mould showing a single columellar muscle scar, x 6.25.

of external characters other than a possible selenizone band at the periphery. Preserved shell is only known in USNM 192118, a partially exfoliated juvenile, but even here the upper surface of the selenizone is not preserved, making precise subgeneric assignment impossible. A series of fine crescentic striae on the columellar region of a small internal mould (Fig. 8) represents the attachment scar of a single columellar muscle.

### ***Murchisonia* (*Hormotoma*) sp. A**

Plate 4, fig. 23

*Figured material* – Upper Ross Brook Fm., YPM 28339 from YPM Colln. A3592.

*Discussion* – The location of the selenizone, low on the whorl, in this specimen is reminiscent of *Murchisonia* (*Hormotoma*) *cingulata* (HISINGER, 1829) from the Silurian of Gotland but the Arisaig species has fewer whorls with deeper sutural indentation.

### ***Murchisonia* (*Hormotoma*) sp. B**

Plate 3, fig. 3

*Figured material* – Upper McAdam Brook Fm., YPM 28340 from YPM Colln. A3643.

*Discussion* – A fragment of a single whorl is readily distinguished from other species of *Murchisonia* (*Hormotoma*) and *M. (Murchisonia)* known from Arisaig by its wide, deep sinus passing into a slit of unknown depth at midwhorl.

**Murchisonia (Sinuspira) cf. M. (S.) tenera** (PERNER, 1907)

Plate 4, fig. 6

*Figured material* – Lower McAdam Brook Fm., YPM 28338 from YPM Colln. A3606.

*Additional material* – Lower McAdam Brook Fm., four specimens from YPM Collections A3612, A3616, A3820.

*Discussion* – The Arisaig specimens scarcely differ from the illustrations of the holotype given by KNIGHT (1941) but, in view of the moderate preservation, assignment to PERNER'S (1907) species is tentative. *Murchisonia (Sinuspira)* has apparently not previously been described outside of Bohemia.

**Murchisonia (s. l.) antigonishensis** n. sp.

Plate 4, figs. 20, 24

*Holotype* – Moydart Fm., USNM 169470 from Schuchert Coll. 52B, a fragment showing ornamentation.

*Figured material* – Moydart Fm., YPM 28345 from USNM Colln. 10853, Sutherland River, Pictou County.

*Additional material* – Moydart Fm., a number of fragments and internal moulds in Schuchert Colln. 52B.

*Description* – A small high spired murchisoniacean of uncertain generic position, with many whorls. Nucleus and early whorls unknown. Later whorls with angular whorl profile and anomphalous base. Sutural indentation deep, accentuated in detail by a subsutural cord. Upper whorl surface shallowly convex between the subdued subsutural cord and a prominent peripheral angulation located with its upper edge at midwhorl height. Outer surface of angulation flattened, the locus of a wide selenizone. Lower whorl surface shallowly concave between lower edge of the peripheral angular band and a prominent cord which marks the transition to the shallowly convex base. Aperture poorly known; growth lines indicate a shallow sinus passing into a wide slit of unknown, but probably shallow, depth. Ornamentation of fine growth lines with spiral striae at the upper and lower edges of the selenizone and at just below its midheight. Shell seemingly thick; its structure unknown.

*Discussion* – The generic position of this high spired species is uncertain. The angular whorl periphery and subperipheral cord suggest relationship to certain lophospirinitid pleurotomariaceans (Plate 2, figs. 18, 23) but the high spire and wide selenizone favour assignment to the Murchisoniidae. The Arisaig species most closely resembles *Ectomaria* KOKEN, 1896 but this characteristic Ordovician genus lacks a true slit.

'*Ectomaria*' *confinis* PERNER, 1907 from the lower Devonian of Koněprusy is superficially similar but the upper whorl surface is flat, with the peripheral angulation of the Arisaig specimens replaced by a well developed outer whorl.

***Seelya moydartensis* McLEARN, 1924**

Plate 3, figs. 12, 14, 16–18

1924. *Seelya moydartensis* McLEARN, p. 145, pl. XX, figs. 11, 12.

*Figured material* – Moydart Fm., YPM 464, holotype, YPM 464A, paratype, Arisaig; YPM 28331 from YPM Colln. 102/3032; GSC 33270 from Jones Colln. Ar Mo 5450; GSC 33274 from Jones Colln. 4900.

*Additional material* – Moydart Fm., about 30 specimens from YPM Collections 102/3032, A3849 and Jones Collections Ar Mo 4820, 4900, 4980, 5450.

*Discussion* – *Seelya ventricosa* ULRICH in ULRICH and SCOFIELD, 1897, the type species from the lower Ordovician of Vermont, differs in having less convex whorls, shallower sutural indentation and a shallower sinus. The available sample shows quite considerable variation in the degree of development of spiral cords on the upper whorl surface and the elevation of the selenizone. The number of spiral cords varies from zero (Plate 3, fig. 16) to as many as three (Plate 3, fig. 14) while the strong selenizone band seen in the holotype is much less evident in the paratype. A few specimens show increase in the incremental angle and consequent deepening of the sutures (Plate 3, fig. 18).

***Loxonema sinuosum* (SOWERBY in MURCHISON, 1839)**

Plate 4, fig. 10

1839. *Terebra?* *sinuosa* SOWERBY in MURCHISON, p. 619, pl. 8, fig. 15.

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

1941. *Loxonema sinuosum*; KNIGHT, p. 180, Pl. 48, figs. 8a, b.

*Figured material* – Upper Stonehouse Fm., YPM 28337A from USNM Colln. 10206.

*Additional material* – Two specimens in the same collection.

*Discussion* – Of species described by DONALD (1905) and LONGSTAFF (1909) from Britain, *Loxonema pseudofasciatum* has a less angular sinus and reported spiral striae, *L. ledburiense* has a more slender spire, while *L. planatum* and *L. perneri* have wider spires and shallower emarginations. *L. lindstroemii* LONGSTAFF, 1909 (= *L. sinuosum* LINDSTRÖM, 1884 non SOWERBY in MURCHISON, 1839) is the closest Gotland species but may be distinguished by its shallower sinus.

**Loxonema sp. A**

Plate 4, fig. 11

*Figured material* – McAdam Brook Fm., GSC 33269 from Jones Colln. Ar M 3480.

*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 from the upper Silurian of Bohemia. However, in the former, the culmination of the sinus is higher on the whorl while the latter has a deeper emargination somewhat lower on the whorl. The shape of the spire in the Arisaig species is typically loxonematiform with the slightly adpressed whorls producing a shallowly concave subsutural area. *Loxonema sinuosum* has more uniformly convex whorls while the culmination of the more open sinus is located higher on the whorl.

**Loxonema sp. B**

Plate 4, fig. 14

*Figured material* – Upper Ross Brook Fm., YPM 28341 from YPM Colln. A3760.

*Additional material* – Upper Ross Brook Fm., 5 specimens in YPM Colln. A3592.

*Discussion* – Several crushed specimens placed here have obscure growth lines indicating a wider, more shallow emargination than is seen in other species of *Loxonema* from Arisaig. *L. planatum* LONGSTAFF, 1909 from the Wenlock and Ludlow of Britain differs in having a slightly greater degree of adpression of the whorls.

***Morania* (?) *boltoni* PEEL, 1975c**

Plate 4, fig. 15

1975c. *Morania* (?) *boltoni* PEEL, p. 1532, Pl. 1, fig. 20.

*Figured material* – Upper Stonehouse Fm., USNM 192120, the holotype, from Schuchert Colln. 49D.

*Additional material* – Upper Stonehouse Fm., 1 specimen in YPM Colln. 19j/3032.

*Discussion* – PEEL (1975c) reinstated *Morania* as a genus within the family Loxonemataidae (*contra* KNIGHT *et al.*, 1960) and described *M. (?) boltoni* from Arisaig.

***Morania* (?) sp.**

Plate 4, fig. 5

*Figured material* – Lower McAdam Brook Fm., YPM 28342 from YPM Colln. A3809.



*Discussion* – This tiny, crushed specimen has poorly preserved growth ornamentation on the final whorl indicating a subsutural sinus similar to *Morania* (?) *boltoni* above. However, the latter species is much larger and has a shouldered whorl profile with deeper sutures, while the type species, *M. v-sinuata* HORNÝ, 1953, has a deeper sinus. There is close similarity with *Palaeozygopleura* (*P.*) *devonicans* (PERNER, 1907) of HORNÝ (1955) in terms of the shape of the outer lip but the growth ornamentation in this Devonian species is much more pronounced.

### **Auriptygma** sp.

Plate 4, fig. 16

*Figured material* – Upper Stonehouse Fm., YPM 28344 from USNM Colln. 10206.

*Discussion* – *Auriptygma fortior* PERNER, 1903, 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 shallowly opisthocyrt form characteristic of the subsutural area in the Arisaig specimen.

### **Undetermined high spired gastropods**

*Material* – About 150 specimens from all formations at Arisaig except the French River Fm.

*Discussion* – Poorly preserved high spired gastropods, mainly internal moulds, occur throughout the Arisaig Group. The presence of an obscure spiral band on many of the specimens may suggest a selenizone indicative of the Murchisoniacea but there can be little justification in referring those specimens without such a band solely to the Loxonematacea. The internal moulds are most common in the upper Stonehouse Fm. and the majority are no doubt referable to the several high spired species known from this formation. However, with the exception of the distinctively wide *Murchisonia* (?*Hormotoma*) *arisaigensis*, it is impractical to attempt to distinguish between any other members of the morphologically uniform group. As a consequence, stratigraphical records of these species, which are based only on positive identifications, may be considerably restricted. Several taxa also occur in each of the Moydart and Beechhill Cove Formations.

### **Undetermined gastropod species**

Plate 1, fig. 25; Plate 4, fig. 17

*Figured material* – Species A, YPM 466 from the upper Stonehouse Fm., Arisaig. Species B, GSC 33278 seemingly from the basal Doctors Brook Formation, Jones Colln. Ar M 25.

*Additional material* – Beechhill Cove Fm., USNM Collections 10114, 10115. A few poor fragments of a lenticular gastropod, probably *Liospira*, from the French River and lower McAdam Brook Formations.

*Discussion* – Species A was figured by McLEARN (1924, Pl. XXI, fig. 21) as *Goniotropha?* sp. An obscure band on the whorl may suggest pleurotomariacean affinity (Plate 1, fig. 25). Species B is reminiscent, in terms of gross form, of *Siluriphorus* COSSMAN, 1918, species of which may be locally abundant in the Niagaran dolomites of the Chicago area, Illinois, but there is insufficient evidence to warrant further comparison (Plate 4, fig. 17). Poorly preserved sublenticular gastropods in the Beechhill Cove Formation have a more quadrate profile than the contemporaneous *Liospira* cf. *L. affinis*. There is some similarity with *Pycnomphalus* LINDSTRÖM, 1884, a species of which does exist in the Llandovery of Pembrokeshire and Shropshire, but the diagnostic umbilical characters have not been seen.

## PALAEOECOLOGY

### Introduction

There can be little doubt that the classic study by YONGE (1947) of the evolution of the pallial organs within the Gastropoda and other Mollusca is fundamental to any discussion of the palaeoecology of Lower Palaeozoic gastropods. Unfortunately, too stringent adherence to YONGE'S excellent thesis, or the palaeontological version by KNIGHT (1952), can stifle appreciation of the adaptive significance of the great range of shell morphologies employed by Lower Palaeozoic gastropods, when combined with the conservative classification widely used at the present (KNIGHT *et al.*, 1960). Consequently, a brief discussion of the mode of life of Lower Palaeozoic gastropods in general is given below, as a prelude to the subsequent account of the palaeoecology of gastropods within the Arisaig Group.

Morphological evidence is presented to suggest that Lower Palaeozoic gastropods followed a relatively wide range of adaptive strategies. With this principle in mind, the life habits of a number of morphological groups forming components of each of the various gastropod faunas of the Arisaig Group are discussed. The inferences concerning mode of life derived from discussion of each morphological component are later assembled to provide a picture of the palaeoecological setting of the gastropod fauna of each of the formations of the Arisaig Group. A final section summarises the ecological history of gastropods throughout the Silurian at Arisaig.

### Mode of Life of Lower Palaeozoic Gastropods

The great majority of Lower Palaeozoic gastropods are referred to the Order Archaeogastropoda with caenogastropods (= Mesogastropoda + Neogastropoda) much less conspicuous (KNIGHT *et al.*, 1960). Thus, the Silurian gastropod fauna of the Arisaig Group of Nova Scotia, the basis of the present discussion, contains only six caenogastropod species in a total of more than sixty described species (table 1). Since the Lower Palaeozoic, gastropods have diversified considerably and caenogastropods have passed from a state of relative obscurity to comprise two thirds of the prosobranch fauna of present day seas. Their success relative to archaeogastropods is to a large extent attributable to the acquisition of a monopectinate ctenidium. The development of this superior ctenidium, together with a modified foot and an anterior siphon, has enabled caenogastropods to move freely into environments characterised by soft sediments. The inability of archaeogastropod bipectinate ctenidia to cope with fine suspended sediment generally serves to limit the group to clear water over hard substrata (YONGE, 1947).

Unfortunately, the rise to dominance of the caenogastropods since the Lower Palaeozoic provides some difficulty for ecological extrapolation in the reverse direction. It is quite possible that there has been a diminution of the habitat range of archaeogastropods through geological time as a result of direct competition with caenogastropods in habitats near the tolerance limits imposed on archaeogastropods by their bipectinate ctenidia. In consequence, the widely held belief that Lower Palaeozoic 'archaeogastropods' were necessarily herbivores limited to hard substrata in similar fashion to most extant archaeogastropods probably should not be accepted without qualification. Indeed, the not infrequent occurrence of Palaeozoic 'archaeogastropods' in fine sediments seemingly indicative of a soft substratum (e.g. FOERSTE, 1923; BRETSKY, 1970a; GROMCZAKIEWICZ-LOMNICKA, 1972) provides an immediate apparent contradiction.

The ecological and dietary constraints of recent archaeogastropods are widely known, although there are some significant exceptions. MORTON (1967) noted that present day archaeogastropods are microphagous deposit feeders, algal rasps and browsers but further commented that only minor changes were needed to convert from the ancestral microphagous habit to a macroherbivore, ciliary feeder or carnivore. Some fissurellids no longer feed on algae but graze on sponges (MORTON, 1967) while the recent *Mikadotrochus* includes the latter organism in its microphagous scavenging habit (FRETTER, 1964). This assumption of carnivorism by some of the most primitive of extant archaeogastropods, relics of the pleurotomarians which flourished during the Palaeozoic, would seem to demonstrate the possible existence of similar sluggish carnivores and scavengers in the archaeogastropod faunas of the past.

Similarly, the development of ciliary feeding has generally been considered to be restricted to caenogastropods. However, FRETTER (1975) has recently observed this

feeding pattern in the trochid *Umbonium vestiarium*, one of the tropical archaeogastropods most familiar to European conchologists.

That there are some exceptions to the belief that all archaeogastropods were herbivores has also been established in the Palaeozoic. The coprophagous habit of many platyceratids on echinoderms is widely known (BOWSHER, 1955) and comparable to the settling of *Hipponyx* on *Turbo* at the present day. Other platyceratids, for example, *Cyclonema (C.) parvimedium* from the Beechhill Cove Formation at Arisaig, lack the irregular shells typical of the more or less sedentary coprophagous forms and were probably sluggish carnivores or scavengers.

Direct evidence of predation by gastropods in the Lower Palaeozoic is lacking. CARRIKER and YOCHELSON (1968) and SOHL (1969) reviewed the occurrence of borings in Palaeozoic invertebrates and concluded that there was little evidence to justify referring the attacks under discussion to carnivorous gastropods. However, the absence of this single specialised form of predation does not preclude the existence of other carnivorous feeding patterns, in particular, browsing on stationary prey such as sponges or coelenterates.

There is a need to establish some parallel between present day and fossil morphological adaptations, with the necessary but logical assumption that some relationship exists between shell form and mode of life. The process is not easy for the average trochiform gastropod since shells of this type can be found in most environments at the present. Similarly, different ranges of shell morphologies are present in Palaeozoic and recent gastropod faunas. VERMEIJ (1975) illustrated this problem in noting that present day marine planispiral shells are always small, generally less than 10 mm in diameter, whereas a variety of Palaeozoic planispiral gastropods may be a factor of ten larger. Since most Palaeozoic gastropods are interpreted as archaeogastropods (KNIGHT *et al.*, 1960) and lack the inhalant siphonal channel characteristic of caenogastropods, a wide range of shell forms resulting from modification of the whorl profile associated with the siphon is not available. Thus, there are no Palaeozoic morphological analogues of the familiar cone or cowrie shells. It may be argued that the latter bears some resemblance to a planispiral bellerophontacean shell but the analogy is clearly deficient when the orientation of the shell during life is considered. In cowries and many caenogastropods the axis of coiling parallels the direction of movement while in bellerophontaceans and other archaeogastropods the shell is coiled about an axis perpendicular to this direction, or nearly so.

There are naturally dangers associated with the uncritical comparison of similar shell morphologies, as may be seen from comparing present day pleurotomariids such as *Perotrochus* or *Mikadotrochus* with their very close morphological analogues from the Palaeozoic. The former are restricted to deeper water while the many Palaeozoic species are demonstrably shallow water dwellers. However, some progress can be made with more unusual morphologies. Thus, the suggestion by PEEL (1975a) that the repeated development of an explanate aperture within the Bellerophontacea reflects adaptation to life on a soft substratum gains support from reference to the present

day pelican's foot shells *Aporrhais pespelicani* and *A. serresiana*. The latter species lives in soft sediment and has a larger expanded stage than the former, which burrows into firmer muddy gravels (YONGE, 1937). Hyperstrophic open coiling in the soft bottom dwelling *Nevadaspira* from the Devonian of the U.S.A. led YOCHELSEN (1971) to suggest a sedentary ciliary feeding existence and a similar mode of life has been inferred for other Palaeozoic gastropods, including forms resembling *Vermicularia* (PEEL, 1975d). A less spectacular but considerably more important example of morphological analysis, the notable discussion by VERMEIJ (1971) concerning the high spired shell form amongst present day gastropods, is more closely examined below.

### Foliage supported Faunas

At the present day a great abundance of gastropods lives amongst the foliage of marine algae and sea-grasses. The vegetation provides a dense protective habitat, above a possibly turbid sea floor, and food is often abundant either in the form of the host plants or as numerous small epiphytes. The faunas of algae and sea-grasses are often well stratified with distinctive suites of species living at the sediment surface, amongst holdfasts or roots, and at various levels within the foliage (DUFFUS, 1969; MORTON and MILLER, 1973; STARMÜHLNER, 1969; TAYLOR, 1971; TAYLOR and LEWIS, 1970). Ecologically mixed assemblages result upon the death of individuals within stratified faunas, since undisturbed shell accumulations may include species from any stratum within the foliage, from the sediment surface or from the infauna. Pelagic species may also be present.

Stratification provides a possible explanation for the occurrence of archaeogastropods with ctenidia unsuited to turbid water in soft sediments. Species living amongst the foliage may be effectively raised above fine suspended, gill clogging, particles near the sediment-water interface. However, a general theory of foliage support for Palaeozoic archaeogastropod faunas in fine grained sediments cannot satisfactorily be invoked without consideration of several problems.

At the present day the dominant vegetation of soft sediment in shallow water is provided not by algae but by sea-grasses (MORTON and MILLER, 1973). Algal stands are more characteristic of rocky shores. However, some algae do occur associated with sea-grasses (e.g. BATHURST, 1975, p. 137, fig. 153) in otherwise soft sediments, although sometimes attached to hard substrates such as dead shells. Meadows of *Zostera*, *Thalassia* and other marine angiosperms probably developed during the Tertiary (BRAZIER, 1975) but were certainly not present during the Lower Palaeozoic. Thus, it is necessary to suggest that any widespread marine vegetation in areas of soft sediment during the Lower Palaeozoic was provided by a group of plants no longer a dominant component of that habitat. The supposition might require a diminution in the habitat range of algae since the Lower Palaeozoic, and assumes that Lower Palaeozoic algae were capable of developing stands comparable to those around present rocky shores (LEWIS, 1964).

The molluscs living on sea weed are generally small, although the relationship is clearly complex involving consideration of the size and supporting ability of the plant, and individual and population size of the molluscs. 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 vast majority of these were less than 2 mm in length. BRAZIER (1975) commented that an abundance of small gastropods may be one criterion for the recognition of former grass beds. MORTON and MILLER (1973) have made similar qualitative remarks about the small size of gastropods, mainly rissoids, dwelling upon algae and sea-grasses around the New Zealand coast. These authors also described larger gastropods (e.g. *Trochus viridis*, height 18 mm) living on kelp in high energy, rocky shore environments, although large algae of this type are not present on present day soft shores. MORTON and MILLER (1973) did find some large trochids associated with *Zostera* on muddy sand flats but the characteristic trochid, *Micrelenchus huttoni*, reaches a maximum size of about 9 mm.

Few currently described Palaeozoic gastropods are of a comparable size to most present day foliage dwellers, although this is not to say that small species did not occur. Indeed, a number of gastropod faunas characterised by diminutive size are referred to in the literature (e.g., HARRISON and HARRISON, 1975; GROMCZAKIEWICZ-LOMNICKA, 1972), although the commonly poor preservation of gastropods of this size means that the systematics of micromorphic species has been neglected. Rather, the implication with regard to size is that Palaeozoic gastropods as generally present in collections and discussed in the literature tend to be significantly larger than most recent foliage supported species at the present day. A general statement that many of these 'average' Palaeozoic gastropods could be foliage dwellers is consequently difficult to accept. Of more than sixty species of gastropods known from the Arisaig Group only *Tropidodiscus* (?) *arisaigensis* is characterised by diminutive size. Other micromorphic species, perhaps foliage dwellers, were probably present and the fact that none are represented in collections could be due to collecting and preservational bias. Many smaller Arisaig gastropods (size about 5 mm) may also have been foliage dwellers, as may some gastropods reaching two or even three times this size. However, it is not tenable to presume that a high proportion of Arisaig gastropods of this larger size of 15–20 mm or more lived in the same way.

Drifting masses of algae comparable to the present day widely distributed *Sargassum* may have provided an additional form of foliage support above soft substrata in the Lower Palaeozoic. RUEDEMANN (1934) strongly propounded this view as an explanation for the occurrence of benthic faunas in his classic discussion of black graptolitic shale faunas. Similar size parameters in terms of gastropods inhabiting floating algal masses to those in other foliage faunas might be expected, although EKMAN (1953) noted a tendency for the invertebrates in *Sargassum* to be smaller. RUEDEMANN's material unfortunately included just a single gastropod, but this was a slender, high spired shell only 9 mm high.

The presence of similar drifting algal masses was recently invoked by DUFF (1975) to provide suitable attachment sites for abundant pendent bivalves above the soft substratum of the lower Oxford Clay (Jurassic) of central England. The most abundant gastropods are the high spired *Procerithium* (20 mm) and pelican's foot shells of the genus *Dicroloma*. Both were probably deposit feeding caenogastropods although the former may equally well have been a foliage browser in similar fashion to *Bittium* at the present day (PARKER, 1975; DUFFUS and JOHNSTON, 1969).

SURLYK (1972) considered a similar floating seaweed hypothesis in the context of the brachiopod faunas of the soft bottom environment of the Danish Chalk. He concluded that the mechanism did not provide a suitable explanation for the occurrence of brachiopods in this environment and recognised a series of adaptations to life on the soft substratum.

The present day Venus' necklace, *Hormosira banksii*, occurs in an unattached form lying on the soft mud surface in front of mangrove swamps in New Zealand (MORTON and MILLER, 1973). Movement is often confined to rise and fall with the tides, unlike the widely drifting *Sargassum*, but a comparable mechanism exists for supporting gastropods above the inhospitable mud. Characteristic gastropods in this particular environment include opisthobranchs, the high spired *Zeacumantus*, the carnivorous caenogastropod *Cominella* and the mud flat trochid *Zediloma subrostrata*, the latter grazing on the algal film covering the muds or clustering around local harder substrates.

Algae may be present in areas of accumulation of soft sediment as films on the sediment surface. TAYLOR (1971) described sheltered sites in front of mangrove fringes in the Indian Ocean in which abundant caenogastropods occur on green algal coatings to dark, fetid muds. Water conditions in this Indian Ocean environment are frequently turbid and presumably unsuited to archaeogastropods. BATHURST (1975) described a subtidal algal mat developed on soft muds on the Great Bahama Bank. In this case, however, broad fluctuations in salinity produced a high stress environment and the only recorded gastropod was the high spired caenogastropod *Cerithidea costata*.

Algal mats are capable of binding the upper surface of sands and muds to the extent that currents of several times greater strength than those required to move the unprotected sediment are withstood (BATHURST, 1975). The mat may provide a firm substratum and an abundant source of food but it is uncertain if the binding effect is sufficiently strong to prevent the resuspension of fine, gill clogging sediment.

It must be concluded that none of the discussed examples of snail—seaweed—algal associations provides an overall adequate explanation for the occurrence of Lower Palaeozoic gastropods in sediments indicative of a soft substratum. It is probable that examples comparable to each can be found, although the cumulative effect is still somewhat unsatisfactory. However, additional explanations can be supplied by the gastropods themselves. Obviously, the opinion expressed by KNIGHT *et al.* (1960) in the *Treatise on Invertebrate Paleontology* that most gastropods were archaeogastropods could be questioned. It may be that a number of caenogastropods have been

mistakenly assigned to the wrong order. Distinction between the two orders can only be based on features of shell morphology, namely the presence or absence of an anterior siphonal canal, and some degree of overlap is present. Equally, some Palaeozoic gastropods may lie outside our current concept of ordinal classification of proso-branch gastropods. Thus, we may be seeing the gastropods preserved in their actual benthic habitats because of the presence of monopectinate or functionally equivalent gills.

Alternatively, some Lower Palaeozoic archaeogastropods may have become adapted to life on a soft substratum. As stated above, a general absence of soft-bottom adapted archaeogastropods at the present day may be partly a reflection of decreased ecological diversity resulting from competition with the more advanced caenogastropods. Many of the distinctive lineages of Lower Palaeozoic archaeogastropods may have played adaptive roles that have been denied to their descendents.

### **Autecology of Arisaig Gastropods**

In this section the mode of life of characteristic elements of the Arisaig gastropod fauna is elucidated from the standpoint of shell morphology. Morphologically similar species, often but not necessarily systematically close to each other, are grouped together to effect a classification of gastropod adaptive strategies capable of application elsewhere in the Lower Palaeozoic (table 2).

In general, several of these morphological groups are present in varying proportions within the individual gastropod assemblages, the extent to which particular groups are represented providing a strong clue to the nature of the environment. The mutual relationship of the component morphological groups within the gastropod fauna of each of the Arisaig formation is discussed in a later section as a base for the description of the environmental and ecological history of the Arisaig Group.

### **Morphological analysis**

Most gastropod shells can be referred to one of three major morphological groups—high spired, planispiral or trochiform. Quantitative resolution of a gastropod assemblage into these components can provide a crude ecological measure, although in the present context of the Arisaig Group such a model is too simple. Thus, in fig. 9A the dominance of high spired gastropods in the lower Moydart (M) and upper Stonehouse Formations (US) provides a pointer towards the interpreted soft substratum. Unfortunately, the trochiform dominated faunas of the Beechhill Cove Formation (BC) and upper Ross Brook Formation (URB) lie in close morphological juxtaposition whereas the discussion below suggests that these were preserved in rather different environments, the former on a relatively firm substratum and the latter on a soft substratum.



TABLE 2. Life habits of Arisaig gastropods.

High spired gastropods	
a. macromorphic	epifaunal deposit feeders in low energy environments infaunal deposit feeders ciliary feeders(?)
b. micromorphic	grazers amongst algal foliage
Explanate bellerophontaceans	epifaunal deposit feeders on soft substratum
Micromorphic bellerophontacean	grazer amongst algal foliage
Trilobed bellerophontaceans	epifaunal deposit feeders grazers amongst algal foliage
Other bellerophontaceans	epifaunal deposit feeders grazers amongst algal foliage
Lenticular pleurotomariaceans	epifaunal deposit feeders grazers amongst algal foliage
Trochiform pleurotomariaceans	epifaunal deposit feeders on firm substratum in clear water
Trochiform murchisoniacean	epifaunal deposit feeder on soft substratum
Trochiform platyceratids	coprohagous feeders on echinoderms scavengers or browsing carnivores
Trochiform holopeids	epifaunal deposit feeders on soft substratum

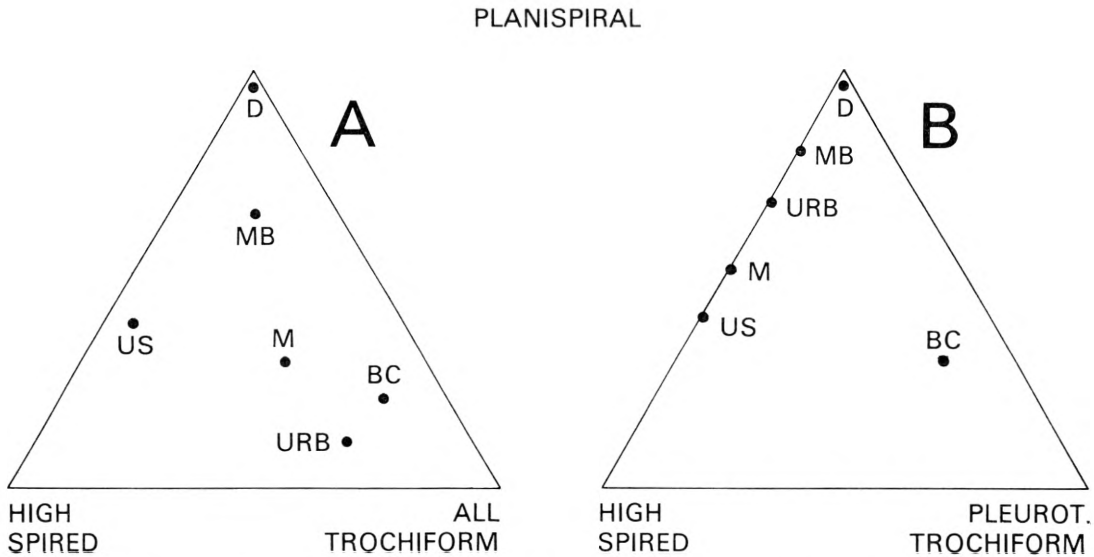


Fig. 9. Morphological composition of Arisaig gastropod faunas. The fauna of each formation is resolved numerically into planispiral (bellerophontacean + lenticular pleurotomariacean), high spired and trochiform components (A), and planispiral, high spired and trochiform pleurotomariacean components (B). BC, Beechhill Cove Formation, 146 specimens. URB, upper Ross Brook Formation, 67 specimens. D, Doctors Brook Formation, 139 specimens. MB, McAdam Brook Formation, 54 specimens. M, lower Moydart Formation, 159 specimens. US, upper Stonehouse Formation, 353 specimens.

If the three morphological groups are subdivided on the basis of other systematic characters a more meaningful resolution is possible. In this context the trochiform group, for example, is subdivided into pleurotomariacean, holopeid, platyceratid and murchisoniacean components, to each of which is attributed a different ecological setting. The demonstrated importance of the trochiform pleurotomariacean component in indicating the fundamental difference between the harder substratum gastropod fauna of the Beechhill Cove Formation and the softer substratum faunas of most of the remaining formations of the Arisaig Group is clearly apparent (fig. 9B).

Assignment of individual morphological units to trophic groups is to some extent unsatisfactory since several of the units contain gastropods that probably employed different modes of feeding, the precise delimitation of which may not be possible. Thus, at the present day, the high spired group incorporates a diversity of gastropod life habits. Turritellids are infaunal ciliary feeders, cerithiids are grazing herbivores while terebrids are active infaunal predators. However, all are united by similar morphological and physical shell stability parameters which can be readily applied to comparable Palaeozoic high spired lineages. Inferences regarding the possible feeding patterns of the extinct Palaeozoic analogues must then depend on information other than simple shell shape.

### High spired gastropods

High spired gastropods are common, both in numbers and taxa, throughout much of the Arisaig Group (fig. 2; table 1; plates 3 and 4). Two species of *Murchisonia* (*M.*), three of *M. (Hormotoma)*, one of *M. (Sinuspira)* and one of *Murchisonia s. l.* are associated with three species of *Loxonema* and two of the related *Morania* (?). A number of indeterminate species are also represented. Two species, *Morania* (?) sp., and *Murchisonia s. l. antigonishensis*, are small (c. 6 mm) but most of the others vary from 25 to 40 mm height.

The tendency for the bipectinate ctenidia of recent archaeogastropods to become fouled by fine suspended sediment generally restricts members of the order to life on a firm substratum in clear water (YONGE, 1947). VERMEIJ (1971) argued that the absence of the high spired shell form amongst recent archaeogastropods is probably a consequence of this limitation since a more stable shell form is a prerequisite of the relatively high energy conditions commonly associated with hard substrata. Only in low energy environments, or infaunally, is a high spired shell advantageous. The general equivalence of low energy environments with soft substrata could reasonably limit the high spired form to the monopectinate Caenogastropoda since bipectinate ctenidia of the type found in extant archaeogastropods would not be able to cope with the turbid conditions in such an environment.

Members of the extinct superfamily Loxonematacea (plate 4, figs. 10, 11, 15) are the only common caenogastropods in the Lower Palaeozoic and, after the murchisoniids, the second most important group of Palaeozoic high spired gastropods.

Loxonemataceans probably had a single monopectinate ctenidium, as is the case with other members of the order, and were able to move freely over soft substrata in turbid water (YONGE, 1947).

Murchisoniids, the most common Lower Palaeozoic high spired gastropods, present phylogentic and ecological problems. KNIGHT *et al.* (1960) tentatively placed the group within the Archaeogastropoda while recognising that the high spired form and supposed incipient anterior siphonal notch suggested affinity with the Caenogastropoda. The well developed slit and selenizone (plate 4, figs. 3, 12, 23) were considered to indicate a pair of ctenidia by analogy with the Pleurotomariina and Bellerophonina. However, the nature of the ctenidia in the Murchisoniina is unknown.

The stability arguments advanced by VERMEIJ (1971) promote the hypothesis that murchisoniids were monopectinate caenogastropods which lived in low energy environments or infaunally. Unfortunately, there is a strong risk of circular argument inherent in this line of thought since murchisoniids are now extinct. Their extinction, together with that of many other important Palaeozoic groups in the great change in gastropod faunal composition that has taken place from the Lower Palaeozoic to the present, may have resulted in a partial diminution of the ecological diversity of the Archaeogastropoda through geological time. The fact that the high spired realm is now occupied exclusively by caenogastropods might merely reflect this diminution. Indeed, the greater adaptive potential of the caenogastropod mantle cavity was probably responsible for it. It is therefore necessary to at least entertain the possibility that murchisoniids were bipectinate archaeogastropods, although some degree of ctenidial modification may have taken place. Whatever the structure of the mantle cavity, the efficiency of the murchisoniid respiratory system is attested to by the abundance of the group throughout much of the Palaeozoic. In many cases murchisoniids are prolific in sediments indicative of a soft substratum (FOERSTE, 1923; BRETSKY, 1970a) and this association itself prompted BRETSKY (1970a) to suggest affinity to the Caenogastropoda.

The arguments advanced by VERMEIJ (1971) enumerate the restrictions in terms of stability governing acquisition of the high spired shell but offer no direct explanation of the functional advantage of a shell form of this type to the individual gastropod. Such a functional analysis was presented by ANDREWS (1974) for a Paleocene *Turritella* from Virginia. By analogy to living forms (GRAHAM, 1938; YONGE, 1946), ANDREWS concluded that the multiwhorled shell with a small aperture developed in association with the elongation of the gill in response to the ciliary food gathering mechanism. In addition, he proposed that the large surface area of the high spired shell may provide better anchorage in possibly moving sediment and prove to be more easily buried by the burrowing animal than would be the case with a globose shell.

However, high spired gastropods follow several other habits at the present day in addition to the ciliary feeding employed by *Turritella*, although some of the functional parameters may be similar. Terebrids and some mitrids are active carnivores and scavengers living infaunally in sand (WILSON and GILLETT, 1971) and the shape

of the anterior-posteriorly oriented shell may reduce resistance to movement through the sediment. Many cerithiids and potamidids are grazers on algal mats (TAYLOR, 1971) while some small species browse amongst algal or sea-grass foliage (DUFFUS, 1969; PARKER, 1975).

The mode of life of loxonemataceans and murchisoniids is not known although the groups display sufficient morphological variation to suggest that considerable variation in mode of life may also have occurred. CARRIKER and YOCHELSON (1968) and SOHL (1969) have discounted a gastropod origin for various Palaeozoic borings. It is equally unlikely that the active hunting methods employed by terebrids were used since such techniques are confined to the most advanced caenogastropods at the present day. However, predation on sedentary animals is plausible. In this context it should be noted that present day, high spired epitoniids feed on coelenterates although the shell aperture is simple, a feature commonly indicative of a herbivorous manner (KEEN, 1971).

PEEL (1975d) discussed the existence of ciliary feeding patterns in Palaeozoic gastropods in relation to uncoiled or open coiled shells. *Loxoplocus* (*Loxoplocus*), a pleurotomariacean with probable bipectinate ctenidia, was considered to be a possible ciliary feeder on the basis of its morphological similarity to the present day *Vermicularia*. *Loxoplocus* (*L.*) and related pleurotomariaceans are often morphologically similar to murchisoniids. When considered in conjunction with the clear morphological similarity to the present day ciliary feeding *Turritella*, it is not difficult to suggest that some Palaeozoic murchisoniids may have been ciliary feeders.

It may be argued that the bipectinate ctenidia of murchisoniids (if present) would be unsuited to the development of ciliary feeding mechanisms since ctenidia of this type cannot cope with fine suspended sediment—hence the restriction of most archaeogastropods to hard substrata. The common occurrence of murchisoniids in soft sediments would seem to negate this argument but it is perhaps more likely that the latter occurrence is evidence in favour of the presence of a monopectinate ctenidium or its functional equivalent. Murchisoniids would then be caenogastropods, together with loxonemataceans, with ctenidia suited to the development of ciliary feeding. The issue is not necessarily clear cut since, among the archaeogastropods, the trochid *Umboium* has developed a monopectinate ctenidium and is a periodic ciliary feeder (FRETTER, 1975).

The not infrequent occurrence of murchisoniids and loxonemataceans in higher energy deposits may indicate that some species were infaunal, for example, some of the undetermined high spired gastropods in the Beechhill Cove Formation.

Considered in conjunction with the common association with soft substrata it is perhaps most satisfactory to presume that these Palaeozoic high spired gastropods displayed a comparable ecological range to modern, herbivorous, cerithiids. Some live on the algal coated surface of lagoonal muds and sheltered carbonate banks (TAYLOR, 1971; BATHURST, 1975) while others are microherbivores living in sand or under stones (KEEN, 1971; MORTON and MILLER, 1973). Some tiny species, for example

*Bittium*, live amongst algal or sea-grass foliage (DUFFUS, 1969; PARKER, 1975) and this habit may be inferred for the two smallest high spired gastropods from Arisaig, *Morania* (?) sp. (plate 4, fig. 5) and *Murchisonia s. l. antigonishensis* (plate 4, figs. 20, 24). Ciliary feeding or carnivorous habits may have been occasionally developed but there seems little chance of estimating the proportion of high spired gastropods in the Palaeozoic which may have employed these methods.

High spired gastropods are known from nearly all formations at Arisaig (fig. 2). Their dominance over other groups in the Moydart and upper Stonehouse Formations reflects the interpreted soft substratum in shallow water conditions.

### Explanate bellerophontaceans

A number of bellerophontaceans markedly increase the rate of whorl expansion in the latest growth stages such that the apertural margins become explanate, *i. e.*, tangential to the plane of the substratum when the gastropod is placed in presumed life position with the aperture opening downwards. The condition is well illustrated among Arisaig species by *Anapetopsis* PEEL 1975a from the Stonehouse Formation (plate 2, fig. 15). It has previously been suggested that this morphology may reflect adaptation to life on a soft substratum. The expansion of the aperture is probably associated with enlargement of the gastropod foot which could result in a lowering of the quantity of fine sediment raised into suspension and, by virtue of its increased surface area, tend to prevent submergence in a soft substratum.

Reference to the arguments of YONGE (1947), discussed above, once more serves to stress the importance of the development of mechanisms of this kind to prevent clogging of the presumed bipectinate ctenidia by suspended sediment, if bipectinate gastropods are to leave the cleaner waters over hard substrata.

In addition to *Anapetopsis*, represented by two uncommon species in the Stonehouse Formation, this morphological component is exemplified by *Phragmosphaera globata*, a common species in the lower member of the Moydart Formation (plate 1, figs. 1–3, 6, 7). *P. globata* differs from *Anapetopsis* by expanding more obliquely forward to produce a lower shell than the somewhat bell shaped *Anapetopsis*. In addition, the coiled early whorls of *P. globata* may protrude outside the plane of the aperture, indicating that the apertural margin was probably more highly raised above the substratum during life than in the more perfectly explanate *Anapetopsis*.

The higher degree of whorl expansion, the bell shaped final growth stage and the finely tapering apertural margins may suggest that *Anapetopsis* was adapted to more quiet, softer conditions, than *P. globata*. An analogous situation occurs amongst present day pelican's foot shells where the outer margin of the aperture is drawn out into a series of finger-like digitations. The deeper water, soft bottom dwelling *Aporrhais serresiana* has a proportionally larger expanded late growth stage with longer, more slender digitations than does its shallower water, thick shelled, muddy sand dwelling counterpart *A. pospelicani*. YONGE (1937) concluded that one of the

functions of the expanded final stage in *A. serresiana*, and the related spider shell *Lambis*, was to prevent the animal sinking into the bottom sediment.

A comparable explanate bellerophontacean association was described by GROMCZAKIEWICZ-LOMNICKA (1972) from the Carboniferous of Poland. *Patellilabia aplanata*, a homeomorph of *Anapetopsis*, is the only large gastropod in a fauna of otherwise diminutive gastropod species occurring in a black shale. GROMCZAKIEWICZ-LOMNICKA considered the smaller gastropods to be inhabitants of algal foliage, above the soft substratum. The much larger, thin shelled *P. aplanata* probably lived on the soft bottom in comparable manner to *Anapetopsis* in the Stonehouse Formation at Arisaig.

Bellerophontaceans became extinct just after the close of the Palaeozoic and explanate bellerophontaceans are therefore absent from Mesozoic and Cenozoic strata. However, the development of an expanded aperture in association with a soft substratum appears to be repeated in these younger strata by the pelican's foot shells. An essentially high spired shell replaces the planispirally coiled bellerophontacean shell but this is of little consequence in the low energy environment—the high spired shell form is itself often equated with these conditions, as discussed above. In discussing the palaeoecology of the Jurassic lower Oxford Clay of central England, DUFF (1975) noted that the benthic fauna of the dominant deposit-feeder bituminous shale biofacies was characterised by the high spired gastropod *Procerithium damonis* (27%), the bivalve *Mesosaccella morrisoni* (19%) and the expanded, finely digitate pelican's foot shell *Dicroloma trifida* (14%). Both gastropod shell forms are in accord with the soft, muddy substratum.

### Micromorphic bellerophontacean

The minute *Tropidodiscus* (?) *arisaigensis* (fig. 5), in which the maximum observed length of the laterally compressed shell does not exceed 2 mm, has only been identified in thin sections from the Doctors Brook Formation, at Arisaig, but could have a much greater stratigraphic range. The pronounced ontogenetic changes in whorl profile seem to indicate that *T. (?) arisaigensis* is a mature, micromorphic gastropod rather than the juvenile of some larger, otherwise unrecognised, species. At the present day, most of the gastropods dwelling amongst algal foliage are of similar size to *T. (?) arisaigensis* and the latter is one of the very few Arisaig species that can be considered as a possible foliage dweller with any degree of confidence.

Similar micromorphic gastropods may be occasionally common in the Palaeozoic but their frequent poor preservation has resulted in a general neglect of micromorphic systematics. *Microceras* HALL, 1845 was proposed for a morphologically similar species from the upper Ordovician of Cincinnati. ULRICH and SCOFIELD (1897) considered many of the specimens examined by themselves to be adults of small gastropods but KNIGHT (1941) expressed conviction that HALL's types were embryos.

HARRISON and HARRISON (1975) recently described a fauna with small gastropods (1–5 mm) from the lower Silurian Brassfield Formation of Ohio which they compared to a similar fauna from the upper Ordovician Maquoketa Formation. Physical, chemical and genetic size control mechanisms in a high-stress environment were cited as possible explanations for the diminutive size of the gastropods. However, following the discussion of foliage faunas above, the general size range seems in accordance with the authors' suggestion of life amongst the foliage of algal stands.

GROMCZAKIEWICZ-LOMNICKA (1972) discussed the ecology of minute gastropods in describing a lower Carboniferous fauna from Poland occurring in black, pyritous shales. She considered the supporting ability of algal foliage as the possible factor limiting the size of the gastropods which could only exist amongst the algae developed above an inhospitable, soft substratum. The presence of the large explanate bellerophontacean *Patellilabia aplanata* in the fauna of otherwise diminutive forms adds confirmatory evidence as to the soft nature of the substratum.

### Trilobed bellerophontaceans

Trilobed bellerophontaceans of the subfamily Plectonotinae are one of the most characteristic groups in the gastropod fauna of the Arisaig Group, with two species of *Plectonotus* and three of *Tritonophon* distributed through the sequence. Greatest abundance is seen in the upper Stonehouse Formation (*Plectonotus cherylae* and *Tritonophon kivialonae*, plate 1, figs. 10, 15), the lower member of the Moydart Formation (*T. trilobata*, plate 1, fig. 4) and the Doctors Brook and McAdam Brook Formations (*P. boucoti*, plate 1, fig. 12). Plectonotinids are less frequent in the lower beds of the Arisaig Group but *Tritonophon* sp. has been recorded from the Beechhill Cove, upper Ross Brook and French River Formations (fig. 2).

PEEL (1974) recently discussed the functional morphology and systematics of trilobed bellerophontaceans from Arisaig and concluded that spiral trilobation of the dorsum effected a spatial separation of inhalant and exhalant currents, with a consequent increase in the efficiency of the mantle cavity. As a result of the generally accepted presence of bipectinate ctenidia, plectonotinids would be expected to favour a firm substratum in clear water in the same manner as most other archaeogastropods (YONGE, 1947). Alternatively, life amongst algal foliage, high above the possibly turbid sediment-water interface, may be postulated (BRETSKY, 1970a). However, specimens may reach more than 10 mm in length which is large, although not prohibitively so, when comparison is made with most modern foliage dwellers.

Several authors have commented upon the common association of plectonotid bellerophontaceans with shallow water sediments. The elucidation of the concept of animal communities in the Llandoverby 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 ZIEGLER's *Eocoelia* brachio-

pod community in the Silurian. Cited examples included the Arisaig Group. The authors 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. Trilobed forms are 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 plectonotids was given by BRETSKY (1970a) in his study of the ecology of the upper Ordovician of the Central Appalachians. He described an *Orthorhynacula-Ambonychia* Community developed under inner sublittoral and intertidal conditions in which the substratum varied from muddy silt to coarse, well sorted sand deposited in variable conditions of salinity. The most inshore fauna, the linguloid population, was characterised by large numbers of *Lingula* (?) sp., *Plectonotus* (?) sp., *Bucania* sp. and one species each of nuculoid and modiomorphid bivalves. BRETSKY considered the trilobed *Plectonotus* (?) sp. to have browsed on algal fronds which grew on the organically rich, silty muds of extremely nearshore lagoons.

The concept of a shallow water plectonotid association is supported by the distribution of *Plectonotus* and *Tritonophon* in the Arisaig Group. In both the Ross Brook and McAdam Brook Formations plectonotids occur in the higher, more silty beds which BAMBACH (1969ms) and LEVINTON and BAMBACH (1975) considered to be shallow water shoal deposits. In the Doctors Brook Formation *Plectonotus boucoti* is abundant in coquinites in occasionally phosphatic siltstones which BAMBACH (1969ms) concluded to have been shallow water, back barrier deposits. Shallow, open marine shelf conditions are reflected in the abundance of *Tritonophon trilobata* in the lower Moydart Formation and *T. kivialonae* and *P. cherylae* in the upper Stonehouse Formation. WATKINS and BOUCOT (1975) have recorded brachiopods of Benthic Assemblage 2 (nearshore) from all these formations.

Comparable plectonotid associations with *Tritonophon trilobata* occur in the Öved-Ramsåsa Series of Scania (MOBERG and GRÖNWALL, 1909), in the borehole into Pridoli strata at Little Missenden, Buckinghamshire (STRAW, 1933), in the uppermost Ludlow at Felindre, Radnorshire (SOWERBY *in* MURCHISON, 1839) and possibly in the Kirkby Moor Flags (Ludlow-Pridoli) of the Lake District (SHAW, 1971). The close stratigraphic relationship to fish beds at Little Missenden and red beds at Felindre indicates the proximity to shore in the latter two examples. Unidentified plectonotids, probably *Tritonophon*, are also common in nearshore upper Llandovery deposits in Shropshire (PITCHER, 1939) in the Brassfield Limestone of Ohio (FOERSTE, 1923) and in the Rose Hill and Rochester Formations of Maryland (SWARTZ and PROUTY, 1923).

WALKER (1972) attempted to trace comparable *Lingula* communities through the Palaeozoic, principally by synthesising the data presented by earlier authors. He drew



parallels between the upper Ordovician linguloid population of BRETSKY (1970a), discussed above, in which plectonotids are conspicuous, and the *Lingula* community of ZIEGLER, COCKS and BAMBACH (1968) in which plectonotids may also be common, although not recorded in this specific instance by either party. The community was also recognised in the Carboniferous Top Hosie Shale of Scotland, where *Bucanopsis striatus* (a species of *Retispira*) was considered to take the place of the then extinct plectonotids.

### Other bellerophontaceans

A number of small bellerophontaceans are present in the Arisaig Group, although generally less abundant than the trilobed plectonotids (fig. 2; table 1; *Pharetrolites*, *Cymbularia* and *Bucanopsis*). A generally similar, shallow water deposit feeding or browsing existence to that proposed for plectonotids can be suggested, although some possibly significant differences are evident.

*Bucanopsis* sp. (plate 1, figs. 9, 16, 17) appears to be associated with members of the trochiform holopeid component in the upper McAdam Brook Formation prior to the incoming of plectonotids (fig. 12). The partial separation of the bellerophontaceans may reflect a preference by *Bucanopsis* sp. for either the less cohesive sediment or slightly deeper water of the lower beds of the unit. The former alternative is less attractive since *Bucanopsis* p. is well represented in the firm substratum fauna of the Beechhill Cove Formation, in association with members of the trochiform pleurotomariacean component. The latter alternative, a preference for deeper water, would suggest that the Beechhill Cove Formation with *Bucanopsis* and very rare plectonotids (only a single observed specimen) developed in slightly deeper water than the fauna of the upper Stonehouse Formation, in which plectonotids are common but *Bucanopsis* sp. or close morphological analogues virtually absent.

The depth difference is supported by BRETSKY'S (1970a) study of communities in the Upper Ordovician of the Appalachians. Here, the plectonotid rich association developed under inner sublittoral and intertidal conditions while the trochiform pleurotomariacean component, characteristic of the Beechhill Cove Formation at Arisaig, see below, was developed on outer sublittoral sands.

BOWEN, RHOADS and McALESTER (1974) have described a *Bellerophon* community from the Upper Devonian of New York dominated by bivalves and a bellerophontacean seemingly of similar shell morphology to the *Bucanopsis* sp. from Arisaig. The community, in which *Bellerophon* was considered to be a browser on relatively large benthic algae, developed on the nearshore area of the delta platform and adjacent channels during periods of moderate delta progradation favourable to the development of algal meadows.

*Pharetrolites murchisoni* (plate 1, figs. 21–24, 26–29) and *Cymbularia carinata* (plate 1, figs. 13, 18) from the lower Moydart Formation, are associated with several

other small gastropods (*Murchisonia s. l. antigonishensis*, *Naticopsis trevorpatriciorum*) probably comprising a foliage supported assemblage.

### Lenticular pleuromariaceans

The lenticular pleuromariacean *Liospira marklandensis* (plate 2, figs. 11–14) is common and widely distributed in the upper Stonehouse Formation. *L. cf. L. affinis* (plate 2, figs. 4, 7, 10) is less common, but still conspicuous, in the Beechhill Cove Formation while morphologically similar species occur occasionally in the upper Ross Brook Formation (*Umbospira yochelsoni*, plate 2, fig. 6) and the lower McAdam Brook Formation (indeterminate, possibly *Liospira* sp.). The almost planispiral shell of lenticular species produces a morphology of similar proportions to a laterally compressed bellerophonacean. The low physical stability of such a shell suggests a preference for quiet water conditions and a deposit feeding, or possible foliage browsing mode of life in similar fashion to small bellerophonaceans. However, the not infrequent occurrence of specimens upto 20 mm in diameter may cause difficulties with interpretation as a foliage dweller.

It is possible that abundance of lenticular pleuromariaceans may also be correlated with shallow water. The association of abundant *Turbocheilus* (= "*Platyschisma*") *helicitis* (SOWERBY in MURCHISON, 1839) with the transition from marine Ludlow to non-marine Downtonian in the Silurian of the Welsh Borderlands (the *Platyschisma* community of BOUCOT, 1975) may be cited as support for this hypothesis. The *Platyschisma* Beds of Radnorshire (EARP, 1938; 1940) follow marine strata with a fauna of lower Moydart Formation type, and probably accumulated in shallow water conditions with reduced salinity (ALLEN and TARLO, 1963).

WATKINS (1975) recognised a *Trepsospira* association in the Carboniferous of California characterised by a low density of the lenticular pleuromariacean *Trepsospira* ULRICH and SCOFIELD, 1897 and an aviculopectinid bivalve. He concluded that the association probably indicated a very restrictive environment but was unable to suggest whether salinity, oxygen content or bottom composition was the limiting factor.

The distribution of lenticular pleuromariaceans at Arisaig is not clearly in accord with palaeoecological distinctions made on the basis of other groups. Lenticular species are well represented in the Beechhill Cove and upper Stonehouse Formations which, as discussed below, are considered to represent relatively hard and soft substrata respectively. This independence of bottom type could support interpretation as a foliage dweller, which would satisfy the need for the bipectinate ctenidia of the pleuromariacean to avoid turbid conditions near the sediment surface although, as stated above, many of the specimens appear somewhat large to be easily fitted into this life pattern. However, the size difference involved is not an insurmountable obstacle since, although the greatest dimension of the lenticular shell may be as much as 20 mm, the volume relative to a trochiform gastropod of this height is much less.

The lower Member of the Moydart Formation has several small bellerophonaceans and other gastropods which could possibly be interpreted as foliage dwellers in a fauna which is reminiscent of that of the upper Stonehouse Formation. Unfortunately, lenticular pleurotomariaceans have not been recorded from the Moydart Formation, although they occur frequently in the upper Stonehouse Formation.

### **Trochiform pleurotomariaceans**

Trochiform pleurotomariaceans form a characteristic element in the gastropod fauna of the Beechhill Cove Formation with 7 species of the lophospirids *Arjamannia*, *Longstaffia* and *Loxoplocus* (*Lophospira*) (fig. 2; table 1; plate 2, figs. 5, 16–19, 21–23; plate 3, figs. 1, 4) and 1 species of *Phanerotrema* (plate 2, figs. 1, 2). Lophospirids occur throughout the Palaeozoic but phanerotrematids do not persist beyond the Devonian (KNIGHT *et al.*, 1960). Close relatives amongst the depleted pleurotomariacean faunas of the present day are lacking, although there is some degree of morphological similarity with *Entemnotrochus* FISCHER, 1885, *Perotrochus* FISCHER, 1885 and *Mikadotrochus* LINDHOLM, 1927. However, the fourteen extant species of these rare and poorly known genera are restricted to deep waters in conditions quite unlike those envisaged for their Palaeozoic ancestors (BATTEN, 1958; BAYER, 1966; 1967).

Following YONGE (1947), the bipectinate ctenidia would be expected to limit trochiform pleurotomariaceans to relatively firm substrata in conditions of clear water and this pattern is reflected in their distribution at Arisaig. Many of the Arisaig examples are more than 25 mm in height and, when allowance is made for the relatively great volume associated with the trochiform shape, life amongst algal foliage is scarcely tenable. A deposit feeding, benthic existence is presumed.

A comparable association of lophospirid, trochiform, pleurotomariacean gastropods was described by BRETSKY (1970a) in a *Sowerbyella-Onniella* Community developed on outer sublittoral sands in the Upper Ordovician of the central Appalachians. The association also occurred in an equivalent *Dalmanella-Sowerbyella* Community of the same age in New York State (BRETSKY, 1970b).

### **Trochiform murchisoniacean**

*Seelya moydartensis* (plate 3, figs. 12, 14, 16–18), a characteristic species in the Moydart Formation, closely resembles members of the trochiform pleurotomariacean group in possessing a trochiform shell and a well developed slit and selenizone. The presence of an incipient anterior siphonal notch led KNIGHT *et al.* (1960) to place *Seelya* within the Murchisoniina, in proximity to the high spired murchisoniids. This placement implies a similar ability to live on soft substrata to that shown by murchisoniids, which appears to be substantiated by the Arisaig occurrence. A greater degree

of ecological freedom therefore exists than that shown by trochiform pleurotomariaceans which are restricted to harder substrata by their ctenidial structure.

*Seelya moydartensis* is the next largest Arisaig gastropod, attaining a maximum observed height of 45 mm. Life as an epifaunal deposit feeder is most likely.

### Trochiform platyceratids

The coprophagous relationship between some platyceratids and echinoderms is well known, with the gastropod being closely associated with the anal area of the echinoderm and ingesting expelled faeces (BOWSER, 1955). The shape of the platyceratid aperture commonly reflects in some detail irregularities in the shape of the upper surface of the calyx (fig. 7; plate 4, fig. 25). However, other platyceratids, e.g. *Cyclonema (C.) parvimedium* from the Beechhill Cove Formation (plate 3, figs. 22, 23, 25, 26), show little irregularity in their growth lines and some appear to have been members of the mobile benthos. In this latter situation, a general scavenging mode of life is more applicable.

Trochiform platyceratids occur throughout the Arisaig Group (fig. 2) but are most conspicuous in the Beechhill Cove Formation (the scavenger *C. (C.) parvimedium* with rarer, corprophagous *Naticonema kauffmani*, plate 4, fig. 27) and the lower member of the Moydart Formation (coprophagous *Platyceras (Platyostoma) cornutum*, plate 3, figs. 9, 15, 21; plate 4, figs. 18, 21, 22, 25). The latter formation contains the only well preserved crinoid remains known from Arisaig (BAMBACH, 1969ms).

### Trochiform holopeids

Fissile, graptolitic shales in the lower part of the upper member of the Ross Brook Formation contain the trochiform holopeid *Gyronema haliburtoni* in abundance (plate 3, fig. 7). BAMBACH (1969ms) concluded that the shales represent muds with a high original water content, lacking in cohesion. On ascending the sequence the silt contents of the muds increases and *G. haliburtoni* is succeeded by the morphologically similar holopeid *Holopea rossbrookiensis* (plate 3, figs. 6, 11).

As with trochiform pleurotomariaceans, above, and other archaeogastropods, the structure of the ctenidia would be expected to limit holopeids to firm substrata in clear water, by comparison with living members of the order. However, the abundance of *G. haliburtoni* and *H. rossbrookiensis* in this argillaceous environment clearly argues against such an all embracing restriction. It is therefore desirable to recognise a separate trochiform holopeid group, apparently developed on a relatively soft substratum, as distinct from a trochiform pleurotomariacean association developed on harder substrata.

It should not automatically be assumed, however, that members of the holopeid group lived in direct contact with the sea floor. A foliage supported existence is possible although the relatively large size and volume of both species (height upto 30 mm)

argues against such an interpretation. A possible recent analogue to a foliage supported mode of life has been described by MORTON and MILLER (1973) from *Zostera* flats in New Zealand. Although developed on rather soft, muddy sands, a rich prosobranch fauna living on and around the *Zostera* includes the small trochid archaeogastropods *Micrelenchus huttoni* (9 mm) and *Zediloma subrostrata* (c. 10 mm) and occasional much larger *Lunella smaragda* (50 mm).

An additional possibility is that the gastropods in question may not be archaeogastropods in our usual understanding of the term. Both species have 'average' shapes which can be closely compared to present day gastropods in other orders. If monopectinate ctenidia were present, life on a soft substratum, as appears to be the case at Arisaig, would not be prevented by the inability of the ctenidia to cope with the turbid sediment.

In view of the simplicity of shape of the trochiform holopeids from Arisaig, no attempt is made to recognise this group in other Palaeozoic environments, although its presence is suspected. However, several other holopeiform species which are rare at Arisaig may possibly be placed here—an undetermined holopeid from the middle member of the Ross Brook Formation (plate 3, fig. 10), *Haplospira sibeluixeni* from the upper Stonehouse Formation (plate 3, fig. 24) and an undetermined gyronematid from the lower member of the Moydart Formation (plate 3, fig. 19).

### Other gastropods

Several species are not readily integrated into the above scheme on account of their rarity at Arisaig. This rarity itself may suggest that some of the species were scavengers or carnivores (BOUCOT, 1975), although there is little other evidence to support or deny the supposition.

Three species, *Haplospira sibeluixeni*, an undetermined holopeid and an undetermined gyronematid, may possibly be members of the trochiform holopeid group, discussed above (plate 3, figs. 10, 19, 24). The first named is a small species from the upper Stonehouse Formation which may have been a foliage dweller. Foliage supported modes of life may also be invoked for two small hyperstrophic species. *Onychochilus (?) reversa* (plate 2, fig. 3) and *Mimospira abbae* (plate 2, fig. 8), represented by a total of three specimens, and the globose *Naticopsis trevorpatriciorum* (plate 3, fig. 2). All are between 5 and 10 mm in height.

A single large specimen from the upper Stonehouse Formation referred to *Platyconus (?)* was probably a deposit feeder (plate 4, fig. 19) as were the contemporaneous undetermined trochonematid (plate 3, fig. 20) and an undetermined trochinid (plate 2, fig. 20) from the Beechhill Cove Formation. The single subtrochiform specimen from the upper Stonehouse Formation assigned to the caenogastropod genus *Auriptygma* may have been a sluggish carnivore or scavenger (plate 4, fig. 16).

### Gastropod Palaeoecology of the Arisaig Group

Combination of the autecological information derived from the discussion of gastropod morphological groups in the previous section with a sedimentary facies model proposed by BAMBACH (1969ms), indicates a positive correlation between gastropod faunal composition, expressed in terms of shell morphology, and the physical environment during the deposition of the Arisaig Group. A series of distinctive gastropod faunas characterises successive formations (fig. 2), with variation in faunal composition relating to differences in the nature of the substratum and water depth. Periodicity in the depositional environment, in the form of three regressive phases, is reflected in the partial repetition of morphologically similar gastropod faunas in successive phases.

TABLE 3. Gastropod faunas of the Arisaig Group.

Formation	Fauna	Comment
Upper Stonehouse	B	plectonotinids abundant
Lower Stonehouse	–	gastropods rare, non-diagnostic
Upper Moydart	–	non-marine red beds
Lower Moydart	B	plectonotinids abundant
McAdam Brook	C	succeeded by shallow water equivalent
Doctors Brook	?A	abundant plectonotinids
French River	–	gastropods rare, non-diagnostic
Ross Brook	C	succeeded by shallow water equivalent
Beechhill Cove	A	plectonotinids very rare

### Environmental setting

Contrasting palaeoecological studies of the invertebrates of the Arisaig Group have been presented by BAMBACH (1969ms) and WATKINS and BOUCOT (1975). The latter paper discussed brachiopod communities in a regional sense, drawing on the earlier systematic and stratigraphic work of HARPER (1973) and BOUCOT *et al.* (1974). The unpublished thesis of BAMBACH examined the ecological development of bivalves through the Arisaig Group, a selected study of the bivalves of the McAdam Brook Formation being published by LEVINTON and BAMBACH (1975). The difference in approach between the two studies inevitably leads to some differences in interpretation. Most of the brachiopods were collected from coquinites probably representing storm layers which, in the Beechhill Cove Formation in particular, appear to have been transported into their depositional environment from elsewhere. In contrast, BAMBACH (1969ms) principally collected bivalves from more or less *in situ* assemblages in the intervening shales and mudstones.

BOUCOT *et al.* (1974) commented that the Arisaig Group is unique in providing an almost continuous faunal record of shallow marine conditions throughout the Silurian. Subsequent analysis of brachiopod assemblages by WATKINS and BOUCOT (1975) suggested a range from Benthic Assemblages 3 or 4 (offshore) in the French River Formation to Benthic Assemblage 2 (nearshore) in the remaining formations.

BAMBACH (1969ms) recognised four major events in the sedimentological history of the nearshore Arisaig Group sequence (fig. 2). A transgression across underlying non-marine volcanics is represented by the Beechhill Cove Formation. The Ross Brook and French River Formations represents a regressive phase, with passage from the deepest water sediments known from the Arisaig Group (in the lower member of the Ross Brook Formation) to barrier deposits in the French River Formation. The Doctors Brook Formation contains shallow water siltstones laid down in the lee of this barrier. A second regression is recorded by the McAdam Brook and Moydart Formations, with passage from lagoonal muds into massive shore-line siltstones and, ultimately, sub-aerial red beds. Shore-line deposited massive siltstones in the lower Stonehouse Formation were succeeded by open marine shelf conditions in the upper Stonehouse Formation. A final regressive phase culminated in the fish-bearing Devonian red beds of the Knoydart Formation.

The principal difference of interpretation between the environmental models proposed by WATKINS and BOUCOT (1975) and BAMBACH (1969ms) concerns the depositional environment of the French River Formation. The former authors suggested an offshore, Benthic Assemblage 3 or 4, origin. BAMBACH preferred to interpret the formation as a shallow water barrier behind which the coastal, open lagoonal deposits of the Doctors Brook and McAdam Brook Formations were laid down.

Unfortunately, the gastropod fauna of the French River Formation (fig. 2) is too meagre to contribute meaningfully to the discussion of origin. However, BAMBACH's sedimentary facies model is otherwise employed and appears to be supported by the distribution and composition of gastropod assemblages within the Arisaig Group.

### **Beechhill Cove Formation**

The Beechhill Cove Formation is mainly composed of hard, grey-green quartzose siltstones and micaceous shales, with occasional lenses of fine grained sandstone (BOUCOT *et al.*, 1974). 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 coquinities commonly formed the basal layer of the sandstone lenses. Since all available gastropods originate from the coquinities it is clear that the following comments may relate to the fauna of a transported assemblage.

The gastropod fauna of the Beechhill Cove Formation is the second most diverse in terms of number of species in the Arisaig Group, with eighteen recorded species (fig. 2). The fauna is dominated by trochiform gastropods (figs. 9–11) with trochiform

pleurotomariaceans (*Arjamannia*, *Loxoplocus* (*Lophospira*), *Longstaffia* and *Phanerotrema*) and the scavenging trochiform platyceratid *Cyclonema* (*C.*) *parvimedium* forming the principal elements. Trochiform holopeids and trochiform murchisoniaceans are absent. Planispiral forms (lenticular pleurotomariaceans; the bellerophontacean *Bucanopsis* sp.) and high spired gastropods (mainly indeterminate) are equally represented.

The dominance of trochiform pleurotomariaceans, absence of trochiform holopeids, and the low representation of high spired gastropods (in comparison to the Moydart and Stonehouse Formations) is interpreted as indicating an environment with a firm substratum in clear water.

WATKINS and BOUCOT (1975) recognised three brachiopod communities of Benthic Assenblage 2 (nearshore) in the Beechhill Cove Formation at Arisaig. Only single collections with gastropods are available from each of these communities so that details of variation in faunal composition are not known. Gastropods in USNM Collections 10114 (*Mendacella* community) and 10115 (*Cryptothyrella* community) are similar, although the latter is dominated by *Cyclonema* (*C.*) *parvimedium* and lacks bellerophontaceans (fig. 10). WATKINS and BOUCOT (1975) commented that in other regions both these brachiopods commonly occur together, which would appear to be in agreement with the rather limited evidence supplied by the gastropods. USNM Collection 10116 (*Dalmanella* community) is markedly different, containing all the twenty nine recorded Arisaig specimens of the trochiform pleurotomariacean *Phanerotrema* and a single *Naticonema kauffmani*, a coprophagous platyceratid. An additional collection, USNM 10819 from Wallace Brook in Pictou Country, contains the brachiopods *Leptostrophia beechhillensis* and *Leptaena* cf. *martinensis* (HARPER, 1973) associated with a small gastropod fauna comparable to USNM 10114 and 10115, although *Cyclonema* is absent.

### Ross Brook Formation

No gastropods were available from the lower member of the Ross Brook Formation. Four species are known from the middle member with the pleurotomariaceans *Eotomaria* and *Longstaffia centervillensis* represented by single specimens. There are two specimens of an undetermined holopeid and a few more of *Platyceras* (*Platystoma*) cf. *P. (Pl.) humilis*, although the fauna is too scant for meaningful evaluation (fig. 2). BAMBACH (1969ms) concluded that the fissile graptolitic shales represented fine muds with a high original water content unsuited to the establishment of an epifauna.

In the upper part of the formation siltstones gradually become more common and brachiopod coquinas and rich epifaunas are present. In the upper member the trochiform holopeids *Gyronema haliburtoni* and *Holopea rossbrookiensis*, with occasional high spired species (indeterminate, possible loxonemataceans) are succeeded by bellerophontaceans (*Bucanopsis* sp. and *Tritonophon* sp.), the lenticular pleurotomariacean *Umbospira yochelsoni* and infrequent high spired gastropods. The incoming



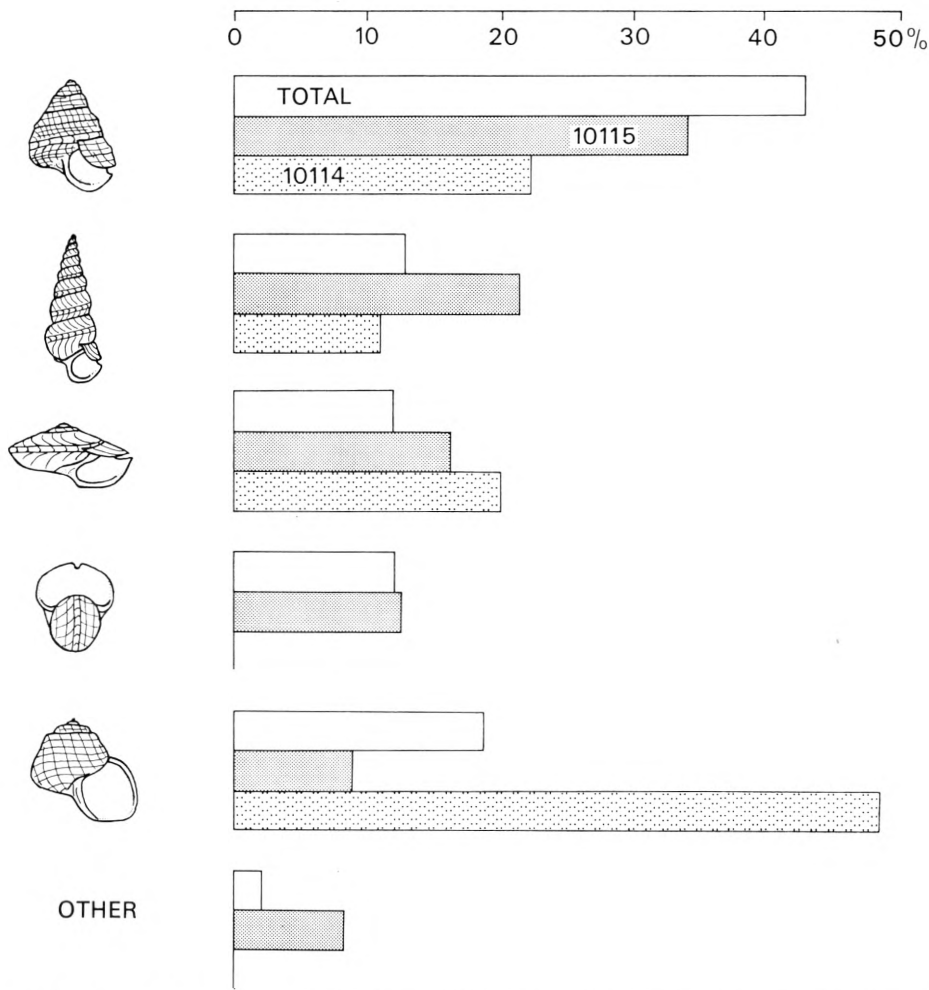


Fig. 10. Composition of the Beechhill Cove Formation gastropod fauna. The faunas of the formation as a whole (TOTAL; based on 146 specimens) and collections from the *Mendacella* community (10114; 45 specimens) and the *Cryptothyrella* community (10115; 56 specimens) of WATKINS and BOUCOT (1975) are expressed in terms of trochiform pleurotomariaceans, high spired gastropods, lenticular pleurotomariaceans, the bellerophonacean *Bucanopsis* sp., and trochiform platyceratids (almost exclusively *Cyclonema* (*C.*) *parvimedium*), in descending order.

planispiral bellerophonaceans and the lenticular pleurotomariacean probably reflect some degree of shallowing or stabilising of the substratum associated with the increasing silt content.

The difference in faunal composition between the gastropod faunas of the Beechhill Cove Formation and the upper member of the Ross Brook Formation is demonstrated in fig. 11. In fig. 11A the two faunas are resolved into the three basic morphological groups: high spired; planispiral (= bellerophonaceans + lenticular

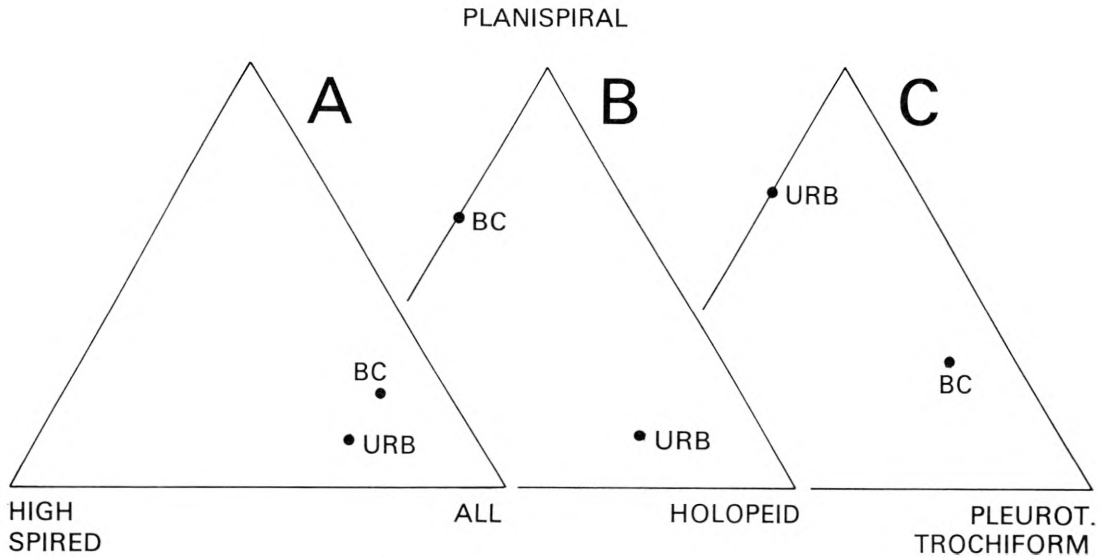


Fig. 11. Morphological comparison of the gastropod faunas of the Beechhill Cove Formation (BC) and upper Ross Brook Formation (URB). For explanation see text. Lower right component consists of all trochiform specimens (A), trochiform holopeids (B), and trochiform pleurotomariaceans (C). 146 specimens from BC, 67 from URB. One horizon in the upper Ross Brook Formation, yielding many hundreds of uncounted trochiform holopeids, is not included; its inclusion would accentuate the separation seen in figure B.

pleurotomariaceans); and trochiform. The similarity between the two faunal plots is evident. In fig. 11 B the same high spired and planispiral elements are plotted against trochiform holopeids of any type, *i.e.*, the two definitive species of the trochiform holopeid group and a few other rare holopeids (see table 1). Holopeids are absent from the Beechhill Cove Formation where the trochiform component of the fauna is entirely hard substratum associated trochiform pleurotomariaceans, or scavenging and coprophagous platyceratids (*Cyclonema*, *Naticonema*). In fig. 11 C the trochiform component is restricted to hard substratum associated pleurotomariaceans and the relationship expressed in fig. 11 B is reversed.

SHAW (1971) claimed that '*Bellerophon trilobatus*' (= *Tritonophon*) exhibited an antipathetic relationship with '*Gyronema cf. octavia*' in the Ludlow-Pridoli Kirkby Moor Flags of the Lake District. He maintained that the latter dominated the more stable areas of slow sedimentation while '*B. trilobatus*' was typical of more rapidly sedimented, perhaps deeper water areas. The conclusion reached by SHAW with regard to difference in depth seems to be possibly in contradiction to the evidence from Arisaig where it is tentatively concluded that *Tritonophon* had a more shallow water mode of life than *Gyronema haliburtoni*. However, the presence of *G. haliburtoni* in the lower, finer grained beds of the Ross Brook Formation may be in accordance with the observation by SHAW concerning slow sedimentation. Similarly, *Tritonophon* is present

in higher beds of the formation, interbedded with siltstones which BAMBACH (1969ms) referred to as shoal deposits, in conditions perhaps not unlike those envisaged by SHAW (1971).

BAMBACH (1969ms) considered the lower member and early middle member of the Ross Brook Formation to represent the deepest water conditions experienced during the deposition of the Arisaig Group. WATKINS and BOUCOT (1975) record the *Eocoelia* brachiopod community, Benthic Assemblage 2, from the middle and upper members and consider the formation to be of nearshore origin. However, the only brachiopods from the lower member identified by HARPER (1973) are rare specimens of *Pentlandina*.

### French River Formation

With the exception of a single *Platyceras (Platyostoma) cornutum*, the meagre gastropod fauna of this formation was collected at French River, Pictou County (fig. 1). WATKINS and BOUCOT (1975) recorded the offshore *Plagiorhynchia* cf. *plastica* Community, although BOUCOT *et al.* (1974) concluded that a shallow water oolitic ironstone represented no radical change from the environment operative during deposition of the rest of the dominantly siltstone formation. BAMBACH (1969ms) suggested that the French River Formation represented a barrier behind which the Doctors Brook and McAdam Brook Formations accumulated.

### Doctors Brook Formation

BAMBACH (1969ms) concluded that the shallow water siltstones of the Doctors Brook Formation were laid down in the lee of an offshore barrier represented by the French River Formation. WATKINS and BOUCOT (1975) recorded the nearshore *Salopina submedia* – *Camarotoechia* aff. *planorugosa* brachiopod community. The gastropod fauna has few species (fig. 2) but the great abundance of *Plectonotus boucoti* in coquinites confirms the suggestion of shallow water. The occasional presence of *Arjamannia aulangonensis* may indicate a firm stratum comparable to that developed in the Beechhill Cove Formation, where *Arjamannia* and other trochiform pleurotomariaceans are conspicuous, but specimens are too few to be significant.

### McAdam Brook Formation

The McAdam Brook Formation displays a change in sediment composition comparable to that seen in the Ross Brook Formation. Dark, sulphide rich shales at the base of the lower member gradually give way to massive siltstone, shoal deposits in the upper member. LEVINTON and BAMBACH (1975) undertook a detailed analysis of the bivalve fauna and were able to demonstrate a close relationship between the

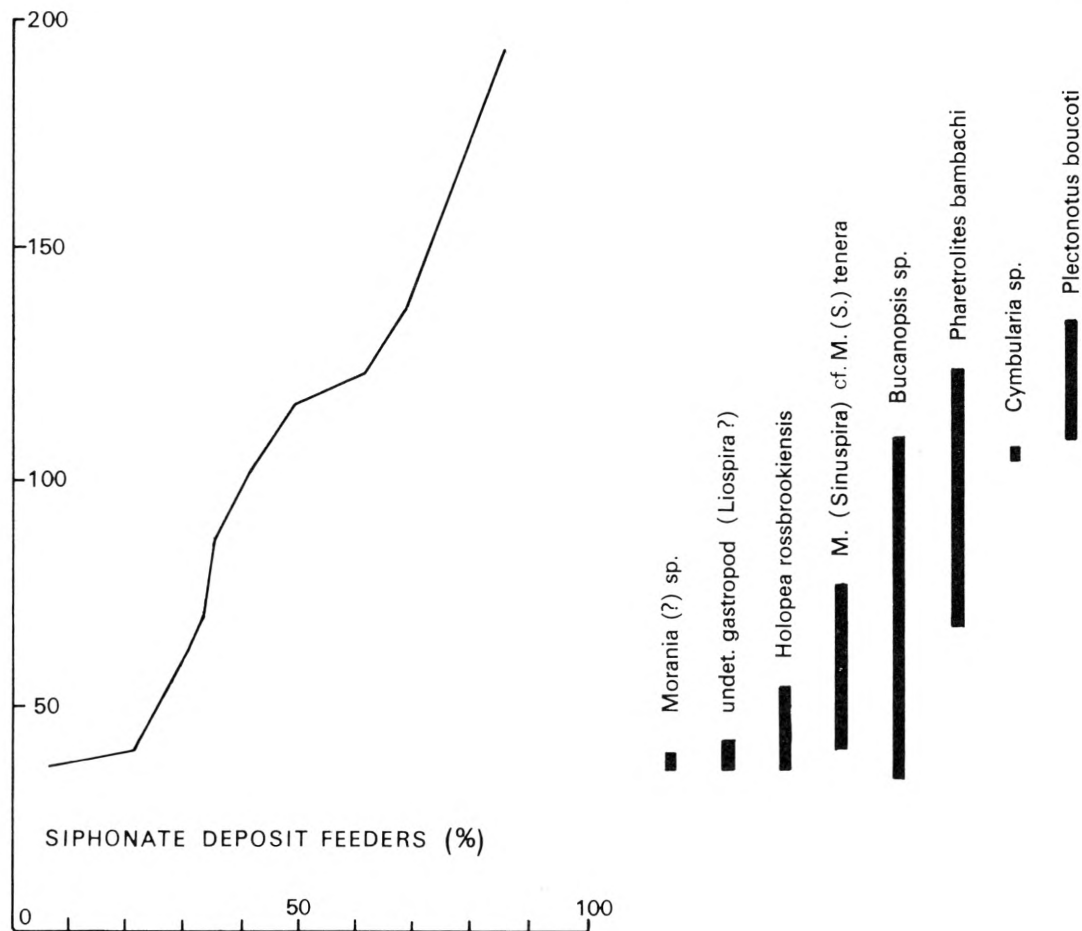


Fig. 12. Bivalve and gastropod faunal changes in the lower member, and basal upper member, of the McAdam Brook Formation. Increasing cohesiveness of the sediment is reflected in an increase in the proportion of siphonate deposit feeding bivalves (left; redrawn after BAMBACH, 1969ms and LEVINTON and BAMBACH, 1975) and a gradual change in the composition of the gastropod fauna. Stratigraphic thickness (extreme left; in feet) after BAMBACH (1969ms).

evolution of faunal composition in the lower member and the lower part of the upper member and the changing sedimentological environment. Deposit feeding bivalves dominate the fauna throughout but siphonate forms gradually replace non-siphonate deposit feeders as the sequence is ascended (fig. 12). LEVINTON and BAMBACH (1975) concluded that the change was related to the increasing cohesiveness of the substratum with non-siphonate forms dominating in the earlier uncompacted, watery sediments and siphonate deposit feeders preferring the firmer substratum associated with the increased silt content of the later, shallower water deposits.

The gastropod fauna shows similar development (fig. 12). Faunas with the trochiform holopeid *Holopea rossbrookiensis*, the high spired *Murchisonia* (*Sinuspira*) cf. *M. (S.) tenera* (plate 4, fig. 15) and an indeterminate lenticular species in the earlier, softer sediments give way to an association of the bellerophontaceans *Pharetrolites bambachi* and *Plectonotus boucoti* developed on the later, more cohesive muds. The latter species is first known in the siltstones of the underlying Doctors Brook Formation and reappears in the more silty upper part of the lower member of the McAdam Brook Formation after having been absent from the intervening soft muds.

Similarity between the lower member of the McAdam Brook Formation and the older Ross Brook Formation is reflected in the reappearance of *Holopea rossbrookiensis* and *Bucanopsis* sp., together with morphological equivalents of the respective high spired, lenticular pleurotomariacean and trilobed bellerophontacean species. Both faunas are characterised by the gradual incoming of 'planispiral' elements (bellerophontacean + lenticular pleurotomariacean) in association with increase in silt content and possible shallowing. The absence of a *Gyronema haliburtoni* analogue and the marked less abundance of the other trochiform holopeid, *Holopea rossbrookiensis*, in the McAdam Brook Formation may reflect slight differences in water depth, nature of substratum or salinity. BAMBACH (1969ms) concluded that the McAdam Brook Formation may have been deposited under open lagoonal conditions behind the offshore bar represented by the French River Formation.

### Moydart Formation

The lower and upper parts of the lower member of the Moydart Formation consist of mainly massive siltstones deposited in shallow, relatively high energy shoaling conditions. Intervening strata were deposited in a lower energy environment (BAMBACH, 1969ms). The upper member is a non-marine subaerial deposit, lacking invertebrates, which DINELEY (1963) compared to the lower beds of the Old Red Sandstone in Britain.

The gastropod fauna of the lower member of the Moydart Formation is distinctive with *Seelya moydartensis*, *Tritonophon trilobata*, *Platyceras* (*Platystoma*) *cornutum* and *Phragmosphaera globata* associated with abundant, but generally indeterminate, high spired gastropods (figs. 2, 13). There is some similarity in terms of gross morphological composition with the Beechhill Cove Formation (fig. 14A, B). However, the trochiform platyceratid element in the latter is mainly *Cyclonema* (*C.*) *parvimum*, a probable benthic scavenger, while the more inflated, probably sedentary, coprophagous *P. (Pl.) cornutum* is the representative platyceratid in the Moydart Formation. True trochiform pleurotomariaceans are absent from the Moydart Formation, although characteristic of the Beechhill Cove Formation (fig. 14C).

The trochiform murchisoniacean *Seelya moydartensis*, although morphologically reminiscent of hard bottom dwelling trochiform pleurotomariaceans, was probably a caenogastropod and therefore capable of inhabiting soft muds. Its presence, together with the absence of pleurotomariaceans, suggests that the substratum during deposition

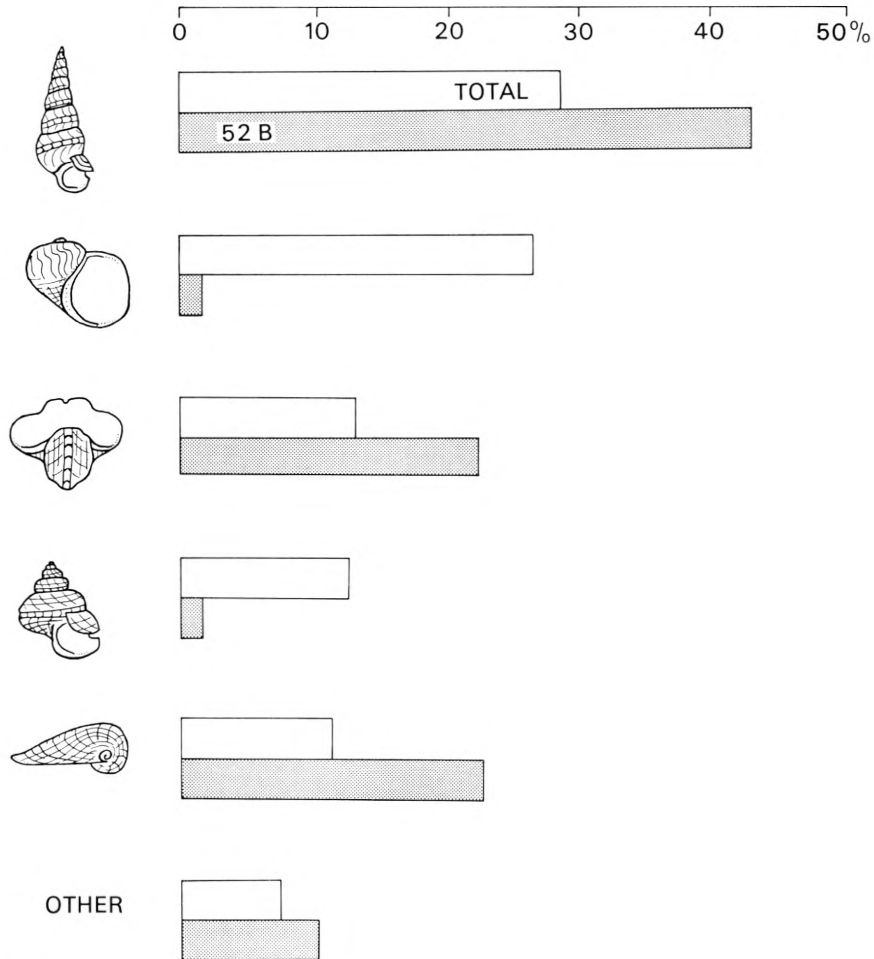


Fig. 13. Composition of the gastropod fauna of the lower member of the Moydart Formation. The faunas of the formation as a whole (TOTAL; based on 159 specimens) and a single, large coquinite collection made by CHARLES SCHUCHERT (52B; 85 specimens) are expressed in terms of high spired gastropods, the trochiform platyceratid *Platyceras* (*Platystoma*) *cornutum*, the trilobed bellerophontacean *Tritonophon* *trilobata*, the trochiform murchisoniacean *Seelya* *moydartensis*, and the explanate bellerophontacean *Phragmosphaera* *globata*, in descending order.

of the lower Moydart Formation was somewhat softer than that of the Beechhill Cove Formation. This conclusion is supported by the frequent presence in the lower Moydart Formation of the explanate bellerophontacean *Phragmosphaera globata* and more abundant high spired gastropods.

### Stonehouse Formation

Only a very few indeterminate high spired and holopeiform gastropods have been observed from the shoal deposited siltstones of the lower member of the Stone-

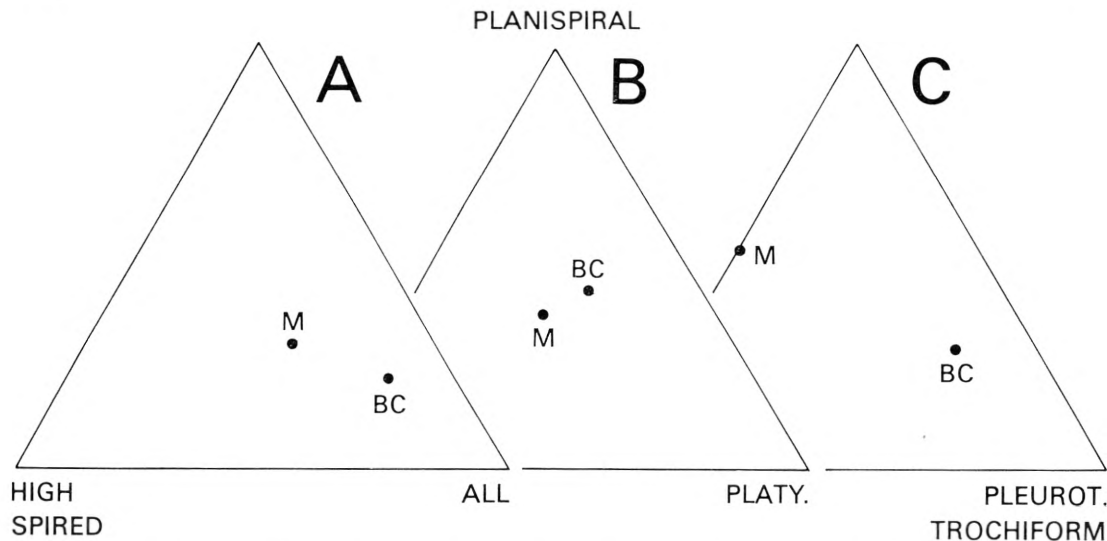


Fig. 14. Morphological comparison of Beechhill Cove Formation (BC) and lower Moydart Formation (M) gastropod faunas. For explanation see text. Lower right component consists of all trochiform specimens (A), trochiform platyceratids (B), and trochiform pleurotomariaceans (C), 146 specimens from BC, 159 from M.

house Formation. In contrast, the siltstones, shales and thin lenticular limestones of the upper member have yielded the largest gastropod fauna from the Arisaig Group, with twenty recorded species (fig. 2).

The dominance by high spired gastropods (figs. 9, 15) and an almost total lack of trochiform pleurotomariaceans (only a single specimen of *Brachytomaria* sp.) indicates that a softer substratum was present during the deposition of the upper Stonehouse Formation than in the Beechhill Cove Formation, where trochiform pleurotomariaceans are characteristic (fig. 9B). A similar separation of high spired gastropods (murchisoniids) and trochiform pleurotomariaceans (lophospirids) was described from the Upper Ordovician of the central Appalachians by BRETSKY (1970a). The major delimiting factor was considered to be the nature of the substratum, as is also the case in the Arisaig Group. 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.

The presence of a softer substratum in the upper Stonehouse Formation is also inferred from the presence of the explanate bellerophontaceans *Anapetopsis maclearni* and *A. lalajae*. Comparable morphotypes are absent from the Beechhill Cove Formation.

The abundance of trilobed bellerophontaceans in the upper Stonehouse Formation (fig. 15) may suggest slightly shallower water than during the Beechhill Cove Formation, where only a single *Tritonophon* sp. has been recorded. This is again supported by BRETSKY's (1970a) work on the Upper Ordovician of the Appalachians.

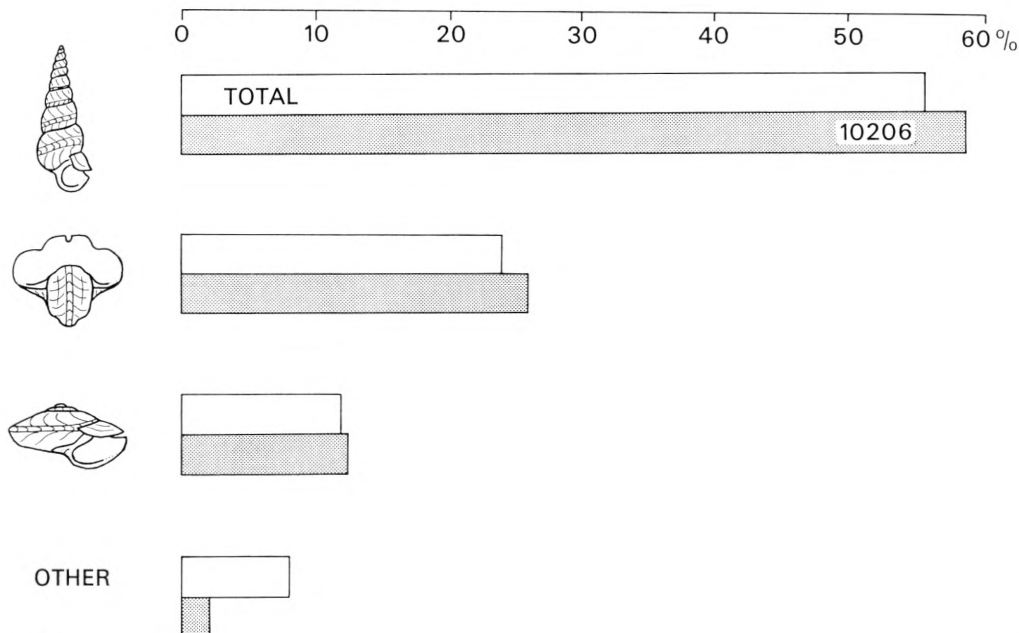


Fig. 15. Composition of the gastropod fauna of the upper Stonehouse Formation. The faunas of the formation as a whole (TOTAL; based on 353 specimens) and a coquinite collection (USNM 10206; 95 specimens) are expressed in terms of high spired gastropods, the trilobed bellerophontaceans *Plectonotus cherylae* and *Tritonophon kivitalonae*, and the lenticular pleurotomariacean *Liospira marklandensis*, in descending order.

Trilobed bellerophontaceans occurred in the most inshore faunule of the *Orthorhynchula-Ambonychia* community developed under intertidal and inner sublittoral conditions. As noted above, trochiform pleurotomariaceans of the type characteristic of the Beechhill Cove Formation were present in outer sublittoral sands and silts. Any difference in depth between the Beechhill Cove and upper Stonehouse formations appears to lie completely within the ecological range of planispiral pleurotomariaceans which are common in both formations and, as suggested above, may favour shallow water.

BAMBACH (1969ms) considered the diverse bivalve fauna of the upper Stonehouse Formation to be reminiscent of that of the older upper Ross Brook Formation, although the greater variety of detrital feeders may indicate an upper Stonehouse association adapted for higher energy, shallower nearshore environments. There is no such similarity in faunal composition between the gastropod faunas of the two formations even though both have been interpreted as developed on relatively soft substrata. The fauna of the upper Ross Formation is dominated by trochiform holopeids with minor representation of high spired gastropods and bellerophontaceans. The upper Stonehouse fauna has abundant high spired gastropods, trilobed bellerophontaceans and lenticular pleurotomariaceans. BAMBACH'S inference with regard to difference in water depth is supported by the greater abundance of trilobed bellerophontaceans.



phontaceans indicative of shallower water in the upper Stonehouse Formation, when compared to the upper Ross Brook Formation. However, coquinites in both units yield brachiopods of Benthic Assemblage 2.

The gastropod fauna of the upper Stonehouse Formation shows greatest similarity to that of the underlying Moydart Formation, although there are only two determined species in common (fig. 2). Both faunas are dominated by high spired gastropods (mainly indeterminate in the Moydart Formation), with trilobed bellerophontaceans, trochiform platyceratids and explanate bellerophontaceans also present. The principal difference lies in the unexplained absence of lenticular pleurotomariaceans in the Moydart Formation. Both contain elements indicative of soft substrata (high spired gastropods and explanate bellerophontaceans) and shallow water (trilobed bellerophontaceans, high spired gastropods). Any suggestion of slightly higher energy conditions in the Moydart Formation exceeding the stability limits of the lenticular shell seems to be inadequate since members of the group are conspicuous in the higher energy fauna of the Beechhill Cove Formation.

## Synthesis

The pronounced difference between the relatively hard substratum associated gastropod fauna of the Beechhill Cove Formation and the soft substratum faunas from elsewhere in the Arisaig Group has already been briefly noted (fig. 9B). There would appear to be a tendency towards the development of a similar hard substratum fauna in the Doctors Brook Formation but the evidence is inconclusive. BAMBACH (1969ms) did not specifically investigate the bivalve fauna of the Beechhill Cove Formation but commented that the few specimens available were quite unlike those of later formations, supporting the present distinction.

A partial repetition of morphologically similar gastropod faunas characterises the three regressive cycles represented by the deposits of the Ross Brook, French River, Doctors Brook, McAdam Brook, Moydart and Stonehouse Formations in BAMBACH's facies model. In the first regressive cycle (Ross Brook Formation) trochiform holopeids are succeeded by trilobed and other small bellerophontaceans, and lenticular pleurotomariaceans. The abundance of trilobed bellerophontaceans continues into the Doctors Brook Formation where rare trochiform pleurotomariaceans may suggest conditions approaching those seen in the Beechhill Cove Formation.

In the second cycle (McAdam Brook Formation) trochiform holopeids are less well represented but are again succeeded by small bellerophontaceans. Subsequently, a diverse shallow marine platform fauna with abundant high spired gastropods was established in the lower Moydart Formation to be followed by non-marine red beds in the upper Moydart Formation.

The third regressive cycle (upper Stonehouse Formation) yields only a shallow marine platform fauna, comparable to that seen in the lower Moydart Formation, prior to passage into the red beds of the Knoydart Formation (Devonian).

The sequence of gastropod faunas within the regressive cycles suggests a general shallowing tendency during the deposition of the Arisaig Group, confirmed by reference to BAMBACH's facies model. Deepest water conditions occur in the first cycle with fine, dark muds of the open lagoonal phase well represented. The lagoonal phase is less well developed in the second regressive cycle and completely absent from the third cycle, where only a sheltered shallow marine platform fauna is preserved.

### Conclusions

The palaeoecological history of gastropods within the Arisaig Group can be viewed in terms of three generalised gastropod faunas (table 3).

*Fauna A: hard substratum, shallow marine platform.*

This fauna is characterised by an abundance of trochiform pleurotomariaceans. The fauna is virtually restricted to the Beechhill Cove Formation but may be represented in the Doctors Brook Formation.

*Fauna B: soft substratum, shallow marine platform.*

The gastropod fauna is diverse but dominated by high spired gastropods. The fauna is typically developed in the upper Stonehouse Formation but also occurs during a lull in the deposition of massive strand-line siltstones in the lower Moydart Formation.

*Fauna C: soft substratum, open lagoon.*

Trochiform holopeids are characteristic of this fauna which is most clearly developed in the lower beds of the upper member of the Ross Brook Formation. A similar fauna occurs in the lower McAdam Brook Formation. With decrease in water depth and hardening of the substratum the trochiform holopeids give way to faunas dominated by small bellerophontaceans, with occasional lenticular pleurotomariaceans and high spired gastropods. These shallow water representatives of the fauna may be transitional to faunas A and B, above, although the characteristic elements of those faunas are absent or rare.

Trilobed plectonotid bellerophontaceans, known from all formations of the Arisaig Group, and other small bellerophontaceans are seemingly associated with shallow water and a variable substratum. As such, the bellerophontaceans may be expected to occur in any of the three faunas A, B, and C. The presence of small bellerophontaceans in the shallower water equivalent of fauna C is noted above, and well documented in the upper Ross Brook and lower McAdam Brook Formations (fig. 12). Small bellerophontaceans, notably plectonotids, are also abundant in fauna B in both the lower Moydart and upper Stonehouse Formations. However, plectonotids are very rare in fauna A of the Beechhill Cove Formation, although the small bellerophontacean *Bucanopsis* sp. is common. Their absence is interpreted as being a result

of slightly too great water depth. The fauna of the Doctors Brook Formation, with abundant *Plectonotus boucolti* and rare trochiform pleurotomariaceans, could be a shallower water equivalent, although possibly transitional to fauna C.

### Summary

A series of papers (PEEL, 1974; 1975a,b,c) concerning the systematics and palaeoecology of Silurian (Llandovery – Pridoli) gastropods from the Arisaig Group of Nova Scotia is concluded with the present cumulative paper. Four additional new species are described from a fauna of more than sixty species of gastropods (fig. 2; table 1) which shows particular affinity to contemporaneous faunas from Britain.

Characteristic faunal elements include trilobed plectonotid bellerophontaceans of the genera *Plectonotus* and *Tritonophon*; trochiform pleurotomariaceans (*Loxoplocus* (*Lophospira*), *Arjamannia*, *Longstaffia*, *Phanerotrema*); lenticular pleurotomariaceans (*Liospira*, *Umbospira*); trochiform holopeids (*Holopea*, *Gyronema*) and frequently abundant high spired murchisoniaceans and loxonemataceans.

It is proposed that Lower Palaeozoic so-called archaeogastropods followed a greater range of adaptive strategies than indicated by direct comparison with recent archaeogastropods. In particular, there is evidence to suggest that many may have lived in environments with a soft substratum, although the bipectinate ctenidia of archaeogastropods are generally considered to be unsuited to life under such conditions. It is also possible that our current concept of the systematics of Lower Palaeozoic gastropods is too rigid, notably at the level of Order, and that reappraisal of the the relationships between many of the major groups of Palaeozoic gastropods may be desirable.

A number of morphological groups of gastropods are recognised in the Arisaig fauna, with differing modes of life (table 2). High spired gastropods are compared to present day deposit feeding and herbivorous cerithiids. Some Palaeozoic high spired gastropods may have been ciliary feeders of sluggish infaunal carnivores but such modes of life are difficult to demonstrate.

Explanate bellerophontaceans, trochiform murchisoniaceans and trochiform holopeids probably lived on soft substrata. Abundance of trochiform pleurotomariaceans is correlated with a hard substratum. Small bellerophontaceans, including the widely distributed trilobed plectonotids, and the bellerophontacean-like lenticular pleurotomariaceans were possibly grazers amongst algal foliage or epifaunal deposit feeders. Trochiform platyceratids with irregular growth followed a coprophagus habit on echinoderms, while the more regularly coiled forms were possibly benthic scavengers or sluggish carnivores.

The environment of deposition of each of the formations of the Arisaig Group can be deduced by examining each gastropod assemblage in terms of the previously established morphological groups, and by reference to a sedimentary facies model proposed by BAMBACH (1969ms). All the gastropod assemblages discussed are derived

from faunas referred to the nearshore Benthic Assemblage 2 of BOUCOT (1975) by WATKINS and BOUCOT (1975). However, variation in the composition of the gastropod fauna from formation to formation is recognised and attributed to differences in substratum and water depth (table 3). Distinctive faunas are partially repeated as a result of repetition of environments in three regressive phases.

A hard substratum shallow marine platform fauna, characterised by dominant trochiform pleurotomariaceans, is preserved in the Beechhill Cove Formation. The Ross Brook Formation yields a soft substratum open lagoonal fauna with trochiform holopeids, which gives way to a small bellerophontacean dominated fauna in the shallowing waters of the first regressive phase. The French River Formation, considered to have an offshore origin by WATKINS and BOUCOT (1975) but to represent a shallow water shoaling barrier deposit by BAMBACH (1969ms), yields only rare non-diagnostic gastropods. The fauna of the Doctors Brook Formation is dominated by shallow water trilobed plectonotid bellerophontaceans but may represent a reoccurrence of the hard substratum shallow marine platform fauna. The soft substratum open lagoonal fauna is again present in the early part of the second regressive phase (McAdam Brook Formation). It is succeeded by its shallow water equivalent and, ultimately, by a soft substratum shallow marine platform fauna in the lower Moydart Formation. Non-marine red beds of the upper Moydart Formation lack gastropods. Only a few non-diagnostic specimens are known from the lower Stonehouse Formation but during this third regressive phase a diverse soft substratum shallow marine platform fauna was present in the upper Stonehouse Formation environment.

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## Collections and Localities

### Yale Peabody Museum, Bambach and Twenhofel Collections

W. H. TWENHOFEL amassed a large and accurately documented series of collections from Arisaig (*e.g.* YPM 24a/3032) during the early part of the century. R. K. BAMBACH made detailed collections from measured sections principally located along Arisaig shore. BAMBACH (1969ms) assigned individual collections (*e.g.*, YPM Colln. A3582) so a series of numbered strata throughout the Arisaig Group. Each collection is precisely located relative to others in the same major stratigraphic unit. In addition, BAMBACH incorporated into his scheme most of the earlier collections of TWENHOFEL, together with recent collections made by BOUCOT *et al.* (1974), and thereby partially integrated the three major groups of Arisaig collections. Full locality details are on file at Yale.

### Material with USNM Collection Numbers

Most of the material obtained since 1953 by BOUCOT *et al.* (1974) is lodged in the U.S. National Museum, although some is present in Yale Peabody Museum. Details of localities are given by HARPER (1973) and BOUCOT *et al.* (1974). Unlike other collectors, BOUCOT and coworkers collected extensively from inland exposures of the Arisaig Group.

### Geological Survey of Canada Collections

Precise locality details for the old collections of HONEYMAN, AMI, MCLEARN (1924) and other workers are not known. Most specimens are simply referred to 'Arisaig'. It is clear that some specimen labels were added a considerable time after the original collection date. Recent collections from the Stonehouse Formation made by M. J. COPELAND are accurately localised.

### Jones Collection, Manchester University, England

A largely uncurated collection made by O. T. JONES during the twenties is preserved in the Department of Geology, Manchester University. Individual collection numbers refer to a sketch section based on a paced traverse along the shore. The stated origin is 300 ft. southwest of the present (1925) mouth of the Arisaig Brook. However, comparison with maps in BOUCOT *et al.* (1974) suggests that JONES mistakenly identified Smith Brook as Arisaig Brook. Correction of this error gives the otherwise considerably forshortened section a remarkable accuracy. A copy of the section accompanies figured specimens from the Jones Collection, donated to the Geological Survey of Canada.

### Schuchert Collection, U.S. National Museum

CHARLES SCHUCHERT visited Arisaig in 1900 and his collections contain a large number of well preserved specimens not seen by McLEARN (1924). Locality information is sometimes imprecise but the formation of origin can usually be determined.

*Schuchert Colln.* 49 – “Arisaig zone D of HONEYMAN . . . Arisaig shore and near Stonehouse Brook, Nova Scotia. 49A, in beds 30 ft. from the top of the series; 49D, in beds 70 ft. from the top of the series.” *Comment:* The “Stonehouse Brook” is that now referred to as MacEachern Brook; the collections are from the upper Stonehouse Formation.

*Schuchert Colln.* 52 – “Arisaig zone C of HONEYMAN. Arisaig shore in region of McAdam Brook, N.S. 52B, Bed 7 (upper half), NE of McPherson’s Brook.” *Comment:* Clearly from the green member of the Moydart Formation near the McAras Brook of current usage. “52D, loose pebbles along the shore . . .” *Comment:* The presence of *Plectonotus boucoti* and the lithology indicates Doctors Brook Formation.

*Schuchert Colln.* 53 – “Arisaig zone B’ of HONEYMAN. Arisaig shore N of Arisaig Brook, N.S.” *Comment:* Schuchert’s notes state that the base of B’ occurs at the mouth of Arisaig Brook. B’ would consequently outcrop to the southwest along the shore and zone B of HONEYMAN (see McLEARN, 1924) to the northeast, which contradicts the stated locality information. The zones B and B’ are approximately equivalent to the Ross Brook Formation of present usage. However, the ostracodes (Dr. JEAN BERDAN, oral communication, 1969), the bivalves (Dr. R. K. BAMBACH, oral communication, 1970) and the gastropods clearly indicate derivation of collection 53 from the Stonehouse Formation. It is presumed that the collection has been incorrectly labelled.

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PLATES

## PLATE 1

Figs. 1-3, 6, 7. *Phragmosphaera globata* (SOWERBY in MURCHISON, 1839). Moydart Fm.,  $\times 2$ . 1, 7, USNM 169598, internal mould with transverse dorsal channels. 2, USNM 192113, dorsal view showing raised selenizone. 3, USNM 169599, internal mould. 6, USNM 169597, internal mould with transverse dorsal channels located laterally of selenizone band.

Fig. 4. *Tritonophon trilobata* (SOWERBY in MURCHISON, 1839). USNM 169594, Moydart Fm., internal mould,  $\times 3$ .

Figs. 5, 8. Undetermined bellerophonacean sp. D, GSC 6216, upper Stonehouse Fm., partially exfoliated internal mould,  $\times 1.5$ .

Figs. 9, 16, 17. *Bucanopsis* sp. Internal moulds, Doctors Brook Fm.,  $\times 2$ . 9, 16, USNM 169466, showing infilled slit and growth ornamentation. 17, USNM 169465.

Fig. 10. *Plectonotus cherylae* PEEL, 1974. USNM 169582, holotype, upper Stonehouse Fm., internal mould,  $\times 2$ .

Figs. 11, 19. *Cymbularia* sp. 11, USNM 169464, Doctors Brook Fm., internal mould with obscure growth lines meeting undamaged right side of infilled slit,  $\times 3$ . 19, YPM 28329, Lower McAdam Brook Fm.,  $\times 1.3$ .

Fig. 12. *Plectonotus boucoti* PEEL, 1974. USNM 169590, Doctors Brook Fm., internal mould,  $\times 2$ .

Figs. 13, 18. *Cymbularia carinata* (SOWERBY in MURCHISON, 1839). USNM 169574, Moydart Fm., internal mould,  $\times 4$ .

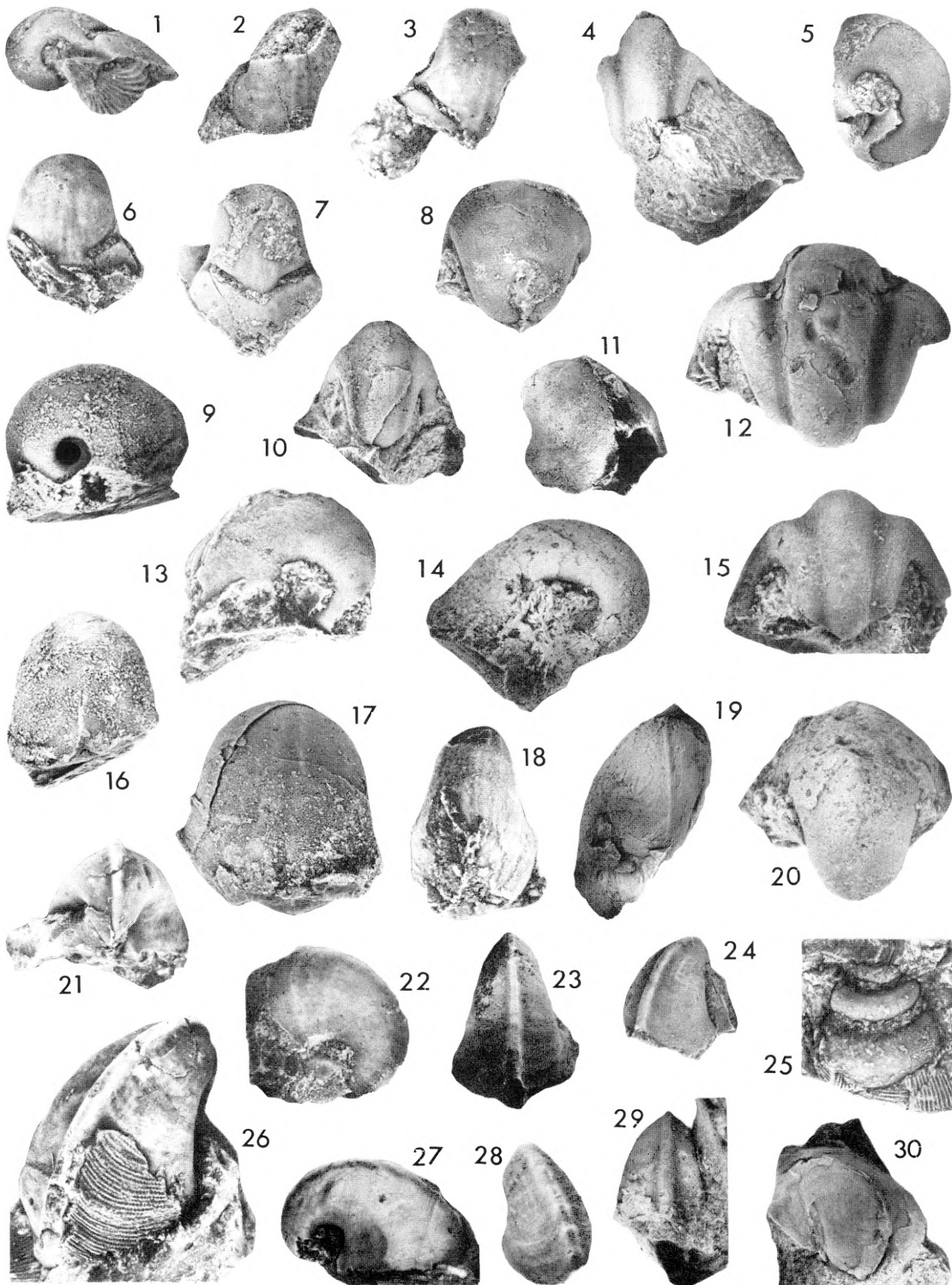
Figs. 14, 20. Undetermined bellerophonacean sp. E, GSC 3139a, internal mould,  $\times 2$ .

Fig. 15. *Tritonophon kivalonae* PEEL, 1974. GSC 32782, upper Stonehouse Fm., internal mould,  $\times 3$ .

Figs. 21-24, 26-29. *Pharetrolites purchisoni* (D'ORBIGNY in FÉRUSAC and D'ORBIGNY, 1840). 21, 26, 27, GSC 33268, upper Stonehouse Fm. 21, posterior view,  $\times 2$ . 26, oblique dorsal view showing ornamentation,  $\times 4$ . 27, lateral view,  $\times 2$ . 22, 23, USNM 169461, Moydart Fm., internal mould,  $\times 2$ . 24, YPM 462, upper Stonehouse Fm., internal mould,  $\times 2$ . 28, USNM 169462, Moydart Fm., internal mould showing sinus,  $\times 3.4$ . 29, YPM 28327, upper Stonehouse Fm., internal mould,  $\times 2$ .

Fig. 25. Undetermined gastropod sp. A, YPM 466, upper Stonehouse Fm., internal mould,  $\times 2$ .

Fig. 30. Undetermined bellerophonacean sp. C, YPM 28348, French River Fm.,  $\times 1.5$ .



## PLATE 2

Figs. 1, 2. *Phanerotrema* affin. *P. jugosum* PITCHER, 1939. Beechhill Cove Fm., silicon rubber impressions,  $\times 1$ . 1, USNM 169478, selenizone with submedium groove. 2, USNM 188520.

Fig. 3. *Onychochilus* (?) *reversa* (HALL, 1860). AMNH 1648, holotype, upper Stonehouse Fm., oblique view of basal spire of internal mould,  $\times 4$ .

Figs. 4, 7, 10. *Liospira* cf. *L. affinis* (FOERSTE, 1885). Beechhill Cove Fm.,  $\times 2$ . 4, YPM 480, apical view of internal mould. 7, 10, YPM 83, silicon rubber impression showing selenizone.

Fig. 5. *Arjamannia cancellatula* (M'COY in SEDGWICK and M'COY, 1852). USNM 169484, Beechhill Cove Fm., silicon rubber impression,  $\times 3$ .

Fig. 6. *Umbospira yochelsoni* n. sp. YPM 28330, holotype, Upper Ross Brook Fm., apical view showing sinus,  $\times 2$ .

Fig. 8. *Mimospira abbae* PEEL, 1975c. USNM 169489, holotype, McAdam Brook Fm., latex impression,  $\times 4$ .

Fig. 9. *Pharetrolites bambachi* PEEL, 1975c. YPM 28328, holotype, Lower McAdam Brook Fm.,  $\times 4$ .

Figs. 11–14. *Liospira marklandensis* McLEARN, 1924. Upper Stonehouse Fm,  $\times 2$ . 11–13, GSC 5654, holotype, with characteristic prosocyrt growth lines. 14, USNM 192114.

Fig. 15. *Anapetopsis maclearni* PEEL, 1975a. GSC 3140a, holotype, upper Stonehouse Fm., dorsal view,  $\times 2$ .

Fig. 16. *Arjamannia aulangonensis* PEEL, 1975b. USNM 169469, holotype, Doctors Brook Fm., latex impression,  $\times 2$ .

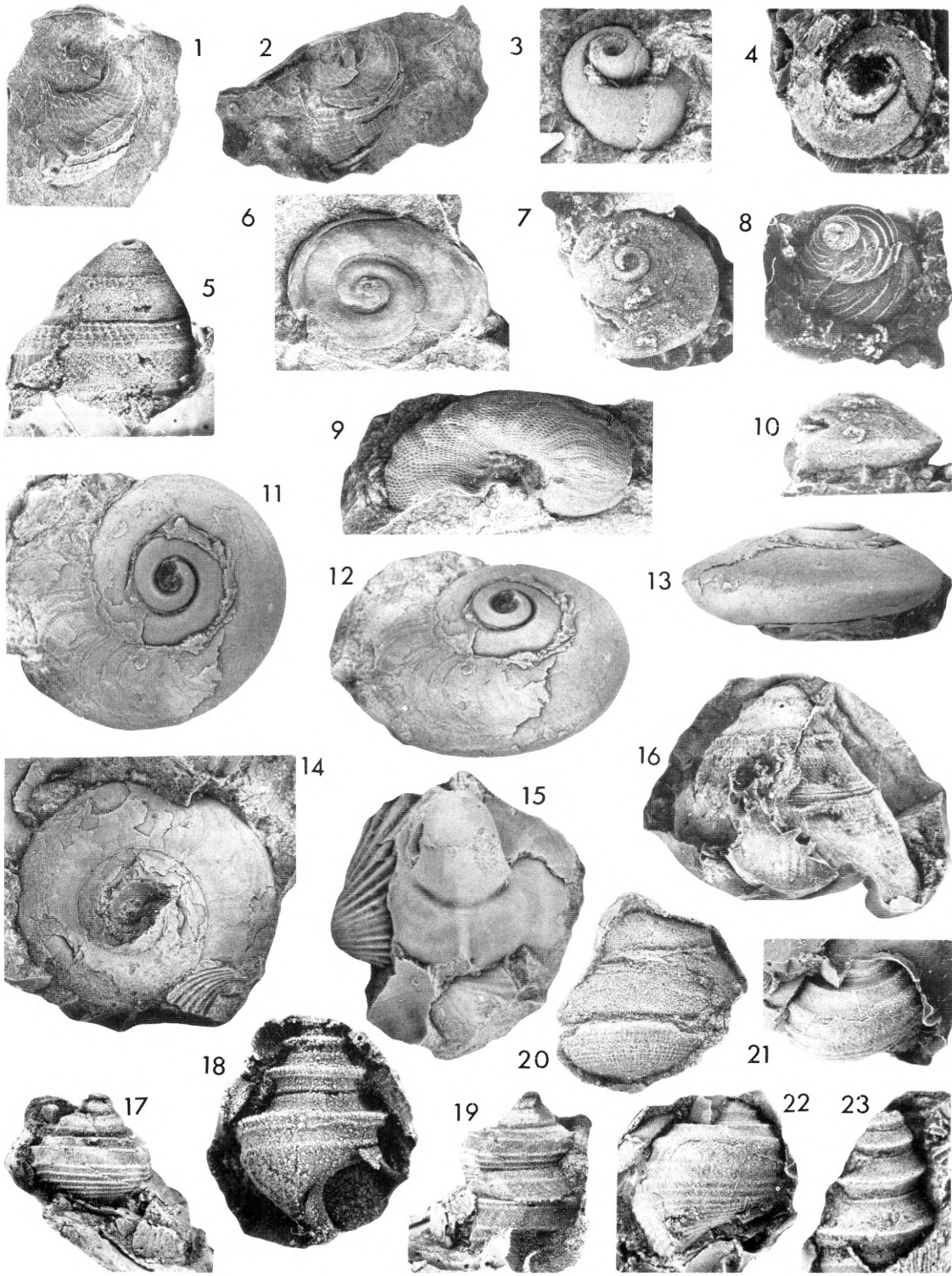
Figs. 17, 19. *Longstaffia centervillensis* (FOERSTE, 1923). USNM 188524, Beechhill Cove Fm., silicon rubber impression showing selenizone,  $\times 2$ .

Fig. 18. *Loxoplocus* (*Lophospira*) sp. A, USNM 169482, Beechhill Cove Fm., silicon rubber impression,  $\times 3$ .

Fig. 20. Undetermined trochinid species. USNM 169486, Beechhill Cove Fm., silicon rubber impression,  $\times 2$ .

Figs. 21, 22. *Longstaffia* sp. USNM 169487, Beechhill Cove Fm., silicon rubber impression showing selenizone,  $\times 2$ .

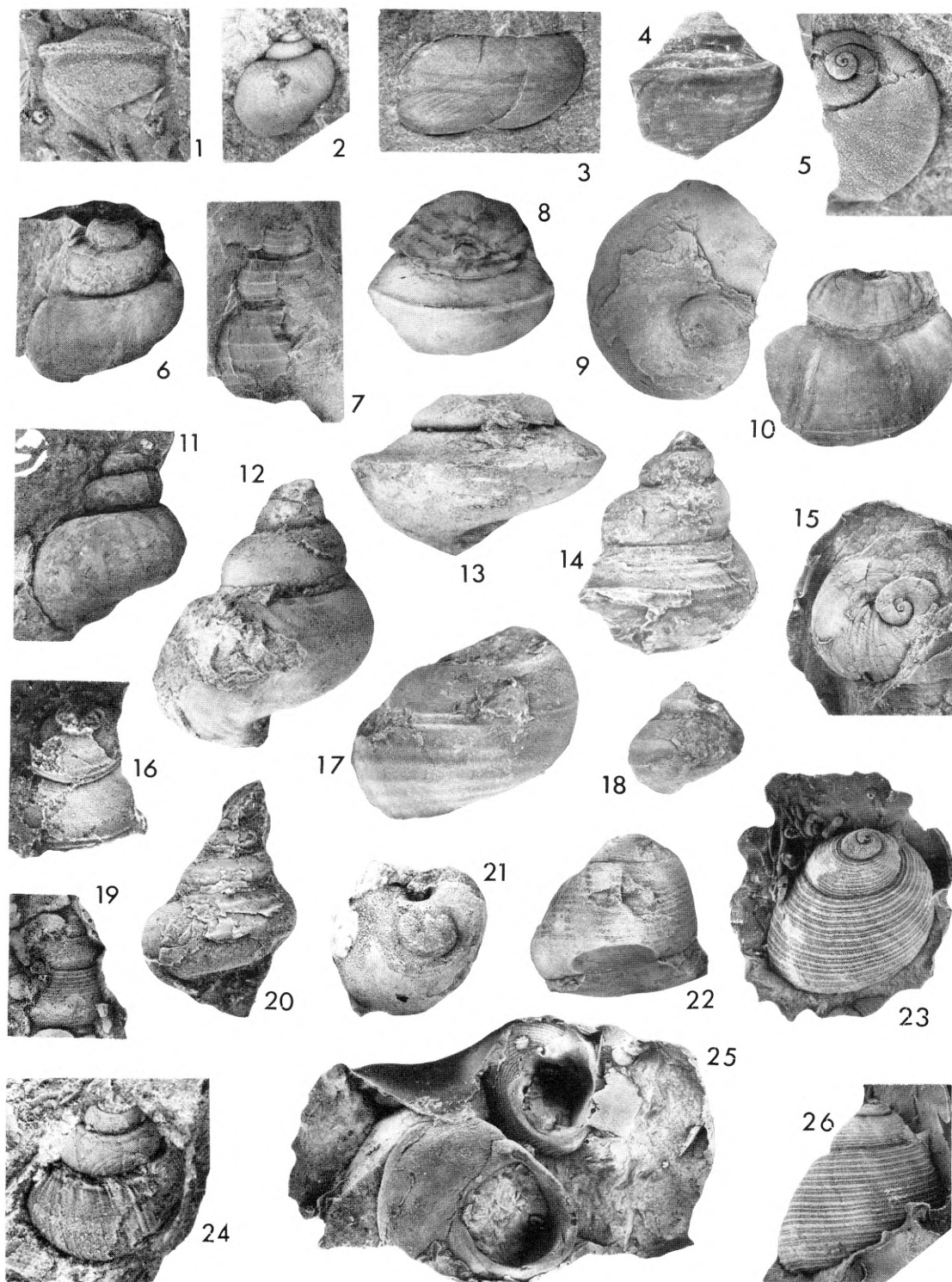
Fig. 23. *Loxoplocus* (*Lophospira*) *sedgwicki* (DONALD, 1906). USNM 169481, Beechhill Cove Fm., silicon rubber impression,  $\times 4$ .



## PLATE 3

- Fig. 1. *Loxoplocus (Lophospira)* sp. B. USNM 169485, Beechhill Cove Fm., silicon rubber impression,  $\times 3$ .
- Fig. 2. *Naticopsis trevorpatriciorum* PEEL, 1975c. YPM 28332, Moydart Fm.,  $\times 4$ .
- Fig. 3. *Murchisonia (Hormotoma)* sp. B. YPM 28340, Upper McAdam Brook Fm.,  $\times 2$ .
- Fig. 4. *Longstaffia centervillensis* (FOERSTE, 1923). YPM 28349, Middle Ross Brook Fm.,  $\times 2$ .
- Fig. 5. *Platyceras (Platystoma)* cf. *P. (Pl.) humilis* (BILLINGS, 1866). USNM 169490, Middle Ross Brook Fm., silicon rubber impression,  $\times 1.5$ .
- Figs. 6, 11. *Holopea rossbrookiensis* n. sp. Upper Ross Brook Fm.,  $\times 2$ . 6, YPM 28334. 11, YPM 28333, holotype.
- Fig. 7. *Gyronema haliburtoni* (McLEARN, 1924). YPM 462B, holotype, Ross Brook Fm.,  $\times 3$ .
- Figs. 8, 13. *Eotomaria* sp. 8, YPM 76, Middle Ross Brook Fm.,  $\times 1$ . 13, USNM 169463, Glencoe Brook Fm.,  $\times 1.5$ .
- Figs. 9, 15, 21. *Platyceras (Platystoma) cornutum* (HISINGER, 1837). 9, GSC 5657, upper Stonehouse Fm., holotype of McLEARN's variety *arisaigensis*,  $\times 1.5$ . 15, USNM 188522, French River Fm., latex impression,  $\times 1$ . 21, USNM 192117, Moydart Fm., oblique lateral view of internal mould showing circular muscle scar,  $\times 2$ .
- Fig. 10. Undetermined holopeid species. YPM 28336, Middle Ross Brook Fm.,  $\times 2$ .
- Figs. 12, 14, 16–18. *Seelya moydartensis* McLEARN, 1924. Moydart Fm. 12, YPM 464A, internal mould,  $\times 1$ . 14, GSC 33270, internal mould,  $\times 1$ . 16, GSC 33274, silicon rubber impression,  $\times 1.5$ . 17, YPM 464, holotype, internal mould,  $\times 1$ . 18, YPM 28331, internal mould,  $\times 1$ .
- Fig. 19. Undetermined gyronematid species. YPM 28346, Moydart Fm., silicon rubber impression,  $\times 3$ .
- Fig. 20. Undetermined trochonematid species. USNM 192115, upper Stonehouse Fm., internal mould,  $\times 3$ .
- Figs. 22, 23, 25, 26. *Cyclonema (C.) parvimedium* McLEARN, 1924. Beechhill Cove Fm.,  $\times 1$ . 22, GSC 5655, holotype, abraded. 23, 26, USNM 169473, silicon rubber impression. 25, USNM 169476 and 169477 (smaller specimen) oblique apertural views of silicon rubber impression showing thickened columellar lip and opercular groove.
- Fig. 24. *Haplospira sibeluxeni* PEEL, 1975c. USNM 192116, holotype, upper Stonehouse Fm.,  $\times 4$ .





## PLATE 4

Figs. 1–3. *Murchisonia (M.) aciculata* HALL, 1860. Upper Stonehouse Fm. 1, GSC 5650, internal mould, × 2. 2, AMNH 1649, holotype, internal mould, × 3. 3, GSC 5651, lateral view, × 4.

Figs. 4, 12, 13. *Murchisonia (M.) amii* (McLEARN, 1924). Upper Stonehouse Fm. 4, GSC 5652, partly exfoliated holotype, spiral cords of selenizone lacking, × 3. 12, YPM 28337B, silicon rubber impression showing two spiral cords within the selenizone, × 5. 13, USNM 192121, × 5.

Fig. 5. *Morania* (?) sp. YPM 28342, Lower McAdam Brook Fm., × 6.5.

Fig. 6. *Murchisonia (Sinuspira)* cf. *M. (S.) tenera* (PERNER, 1907). YPM 28338, Lower McAdam Brook Fm., × 2.5.

Figs. 7–9, 26. *Murchisonia (?Hormotoma) arisaigensis* (HALL, 1860). Upper Stonehouse Fm. 7, AMNH 1650, lectotype, internal mould, × 2.1. 8, USNM 192119, internal mould, × 1.5. 9, AMNH 1650, paralectotype, internal mould, × 2.1. 26, USNM 192118, juvenile with obscure band at midwhorl, × 4.

Fig. 10. *Loxonema sinuosum* (SOWERBY in MURCHISON, 1839). YPM 28337A, upper Stonehouse Fm., × 3.

Fig. 11. *Loxonema* sp. A. GSC 33269, McAdam Brook Fm., × 2.

Fig. 14. *Loxonema* sp. B. YPM 28341, Upper Ross Brook Fm., × 1.5.

Fig. 15. *Morania* (?) *boltoni* PEEL, 1975c. USNM 192120, holotype, upper Stonehouse Fm., × 2.

Fig. 16. *Auripygma* sp. YPM 28344, upper Stonehouse Fm., × 2.

Fig. 17. Undetermined gastropod sp. B, GSC 33278, Upper Ross Brook Fm., internal mould, × 2.

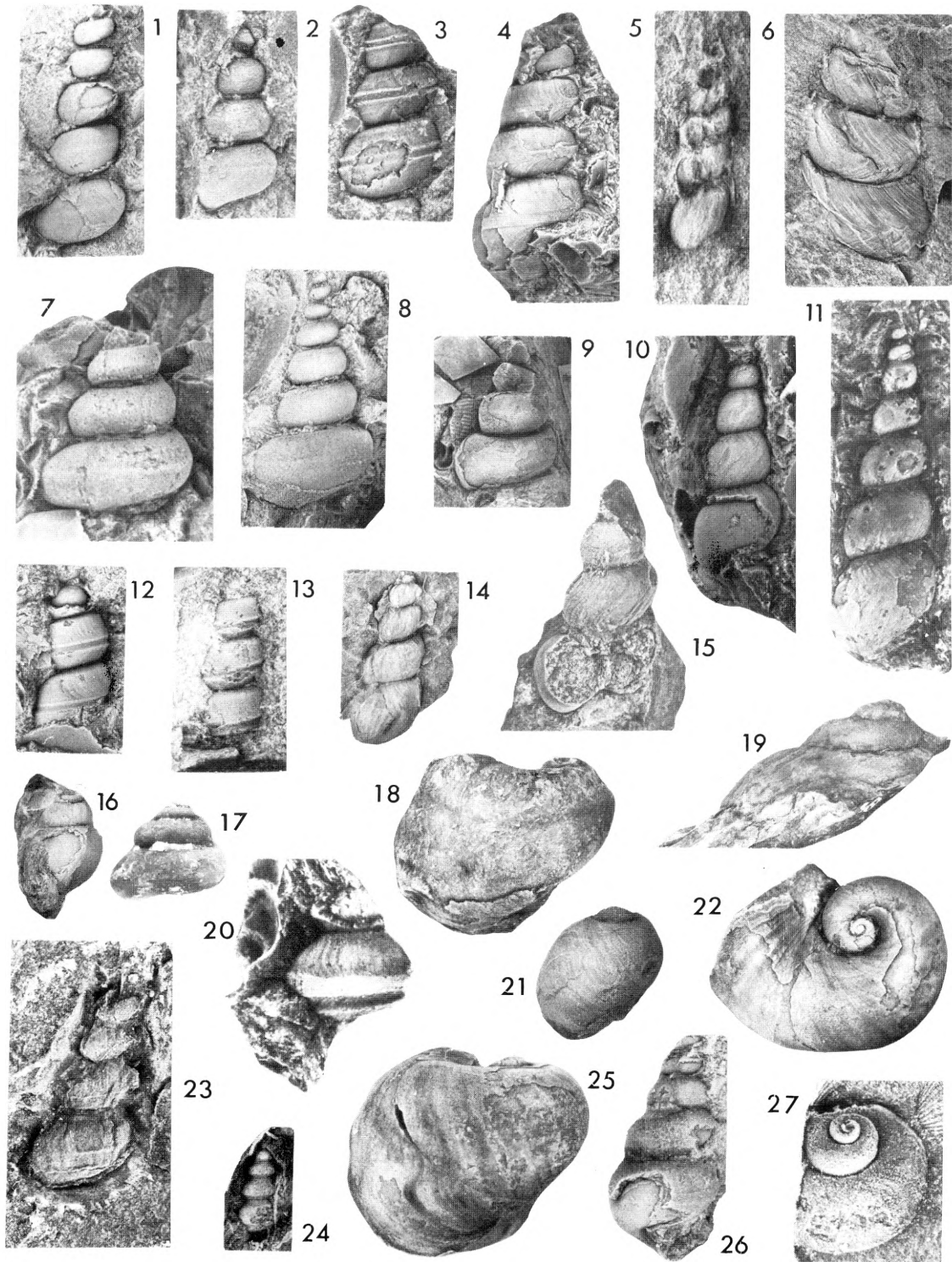
Figs. 18, 21, 22, 25. *Platyceras (Platyostoma) cornutum* (HISINGER, 1837). 18, GSC 33273, Moydart Fm., × 2. 21, GSC 5656, upper Stonehouse Fm., holotype of *Holopea caecistriata* McLEARN, 1924, × 2. 22, 25, GSC 33272, Moydart Fm., × 2.

Fig. 19. *Platyconus* (?) sp. GSC 32783, upper Stonehouse Fm., × 1.

Figs. 20, 24. *Murchisonia (s. l.) antigonishensis* n. sp. Moydart Fm. 20, USNM 169470, lateral view of holotype showing growth ornamentation and selenizone, × 8.5. 24, YPM 28345, silicone rubber impression, × 3.5.

Fig. 23. *Murchisonia (Hormotoma)* sp. A. YPM 28339, Upper Ross Brook Fm., × 5.

Fig. 27. *Naticonema kauffmani* PEEL, 1975c. YPM 462A, holotype, Beechhill Cove Fm., × 3.





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