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BULLETIN 321

CONTRIBUTIONS TO CANADIAN PALEONTOLOGY (three papers)

T.E. Bolton, G.S. Nowlan, H.J. Hofmann and R.A. Fortey



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Preface

This bulletin, under the general title "Contributions to Canadian Paleontology", contains three papers that describe corals, conodonts, trilobites and traces of the activity of worms and arthropods on the seafloor of an early Paleozoic sea.

These studies indicate depositional environments and provide a basis for precise paleontological correlations that are necessary for accurate dating and stratigraphic and economic analyses of rocks forming the sedimentary basins of eastern Canada.

> D.J. McLaren Director General Geological Survey of Canada

Ottawa, April 1979

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GEOLOGICAL SURVEY BULLETIN 321

CONTRIBUTIONS TO CANADIAN PALEONTOLOGY (three papers)

T.E. Bolton, G.S. Nowlan, H.J. Hofmann and R.A. Fortey

A LATE ORDOVICIAN FOSSIL ASSEMBLAGE FROM AN OUTLIER NORTH OF ABERDEEN LAKE, DISTRICT OF KEEWATIN

Thomas E. Bolton and Godfrey S. Nowlan

Abstract

A Late Ordovician fossil assemblage is described from limestone of an outlier on the Canadian Shield, north of Aberdeen Lake, District of Keewatin. The megafaunal assemblage includes the coral genera Palaeophyllum, Lobocorallium, Bighornia, Grewingkia, Saffordophyllum, Trabeculites, Calapoecia, Protrochiscolithus, Paleofavosites, Tollina, and Troedssonites, and a new species of the cephalopod Armenoceras. Most of the coral species are characteristic of the Churchill River Group of the Hudson Bay area. The conodont fauna includes the biostratigraphically diagnostic species Plegagnathus dartoni s.f., P. nelsoni s.f. and Belodina profunda, indicating a late Maysvillian to Richmondian age. Three new species of Panderodus are described, but not named formally, and a species of Walliserodus similar to Silurian forms is described and discussed.

Résumé

Dans le présent rapport, on décrit un assemblage de fossiles d'âge ordovicien supérieur, découverts dans les terrains calcaires d'une avant-butte du Bouclier canadien, au nord du lac Aberdeen dans le district de Keewatin. L'assemblage mégafaunique comprend les genres de coraux: Palaeophyllum, Lobocorallium, Bighornia, Grewingkia, Saffordophyllum, Trabeculites, Calapoecia, Protrochiscolithus, Paleofavosites, Tollina et Troedssonites, et une nouvelle espèce de céphalopode appartenant au genre Armenoceras. La plupart des espèces de coraux sont caractéristiques du groupe de Churchill River de la région de la baie d'Hudson. La faune à conodontes comprend les espèces de diagnostic biostratigraphique Plegaganthus dartoni s.f., P. nelsoni s.f. et Belodina profunda, qui indiquent un âge compris entre le Maysvillien supérieur et la Richmondien. On décrit trois nouvelles espèces de Panderodus, mais on ne leur a pas attribué de nom précis; on décrit aussi une espèce de Walliserodus semblage aux formes siluriennes.

INTRODUCTION

Outliers of Paleozoic rocks are known from widely separated localities on the Canadian Shield (Caley and Liberty, 1957; Ambrose, 1964; Bird, 1972, fig. 10-1). Most of these have been assigned an Ordovician age. Definite Silurian fossils have been identified only from the Lake Timiskaming area, Ontario and Quebec. Few of the fossil collections have been studied in detail, they are mainly the subject of cursory examinations for listing in more regional geological reports.

Recent systematic studies of either a portion or all of these fossils gathered from Paleozoic outliers include those on the Middle Ordovician ostracodes (Copeland, 1965) and corals (Sinclair, 1961; Bolton, 1977), and Silurian fauna (Bolton and Copeland, 1972) of the Lake Timiskaming outlier, Ontario and Quebec, Middle or early late Ordovician fauna (Walters et al., 1976) of Lake Waswanipi, Quebec, and Middle Ordovician corals (Bolton, 1965) of Lake Manicouagan, Quebec. Related paleontological studies include those of the Late Ordovician fauna of northern Manitoba (Nelson, 1963), late Middle and Late Ordovician assemblages from Southampton Island, Hudson Bay (Bolton, in prep.), Akpatok Island, Ungava Bay (Workum et al., 1976), and Silliman's Fossil Mount and Foxe Lowland, southern Baffin Island, and Melville Peninsula, District of Franklin (Bolton, 1977; Copeland, 1977; Barnes, 1977).

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Geological Survey of Canada, Bulletin 321, 1979.

Fossils collected by J.A. Donaldson in 1963 (GSC locality 57572) and M.R. Michaud of Western Mines Limited in 1977 (GSC locality 95286) from an outlier about 35 km north of Aberdeen Lake (65°57'N, 98°50'W), which is at least 500 km west of Hudson Bay, form the basis of the present study. The megafauna were determined by Bolton and the microfauna (conodonts) by Nowlan. Permission to examine and describe the material collected by Western Mines Limited, Toronto, is much appreciated. All illustrated fossils have been assigned to the National Type Collection of Invertebrate and Plant Fossils, Geological Survey of Canada (GSC), Ottawa.

GEOLOGICAL SETTING

The Aberdeen Lake outlier covers about 38 ${\rm km}^2$ and is indicated by two outcrops and rubble of Paleozoic carbonate rocks, resulting from frost heave, strewn over the area (Fig. 1, 2). Tts presence was first postulated by Wright (1955, p. 11). Subsequent mapping by Donaldson (1965; 1969) disclosed an outcrop of flatlying flaggy limestone exposed for more than 275 m along a stream valley (Fig. 3, 4) and abundant limestone rubble scattered within an oval-shaped area about 8 km long and 4.8 km wide. The rocks "are grey, buff- to grey weathering, finely crystalline limestone that characteristically are soft and friable" (Donaldson, 1965, p. 7), the bedding undulatory to irregular.



Figure 1. Area underlain by Ordovician carbonate showing location of sections 1 and 2. (NAPL A15329-126)

성수상 모님 전쟁을 통하는 것이다. 이상은 것님은 간식한 귀찮을 것이는 것 못했



Figure 2. Shaded area underlain by Paleozoic outlier north of Aberdeen Lake, District of Keewatin, and location of major (1) and minor (2) sections.



Figure 3. Major section Upper Ordovician limestone north of Aberdeen Lake, District of Keewatin; locality 1 on Figure 2. (GSC 119591, J.A. Donaldson, 1965)



Figure 4. Closer view of limestone, right-centre of Figure 3. (GSC 119592, J.A. Donaldson, 1965)

According to M.R. Michaud (letter December 9, 1977), during the course of the 1977 Dubawnt Project of Western Mines Limited, another small limestone outcrop was discovered approximately 4.8 km southeast of the outcrop of Donaldson. Both outcrops consist of flatlying, highly fractured, finely crystalline, grey fossiliferous limestone, weathered buff to grey. More than 3 m of limestone are exposed for about 500 m along the stream valley in the larger outcrop and 0.9 m for 6 m in the second, smaller outcrop. Fossils were found throughout the limestone rubble area, with the heaviest concentration in the southern half.

PALEONTOLOGY

Megafauna

The megafossils recognized in the Donaldson (GSC loc. 57572) and Michaud (GSC loc. 95286) collections are listed in Table 1. The completeness and preservation of the fossils and angular nature of the associated rubble all indicate that little if any transport has occurred.

Large, complete coral colonies and specimens of one large cephalopod species predominate. The rugose coral combination of *Lobocorallium-Bighornia-Grewingkia-Deiracorallium* is a typical North American Late Ordovician association, as is the tabulate coral assemblage *Troedssonites-Tollina-Calapoecia-Saffordophyllum-Paleofavosites*. All coral species recognized in the Aberdeen Lake outlier, except *Troedssonites flexibilis* Sololov, are common to the Churchill River Group, farther east in the Hudson Bay area (Nelson, 1963). Both Nelson (1963) and Barnes (1974) assigned a late Maysvillian to Richmondian age, probably Richmondian, to the Churchill River limestone of northern Manitoba and Southampton Island.

Some of the Aberdeen Lake corals, including *Protrochiscolithus cummingi* Bolton, are also common elements to the northeast within the Upper Ordovician portion of Lang River Formation on Somerset Island, District of Franklin (Dixon, 1975). To the west, an equivalent coral assemblage, characteristic of the Late Ordovician *Bighornia-Thaerodonta* fauna, is present in the lower and middle members of the Mount Kindle Formation, southern Franklin Mountains, District of Mackenzie (Norford and Macqueen, 1975).

The fossils collected by Donaldson from the Aberdeen Lake outlier (Sinclair, GSC Fossil Report 2-1964-GWS; in Donaldson, 1965, p. 7), despite some perplexing differences such as the absence of the usually abundant gastropod Maclurites, were regarded as nearly the same age as those from the Nicholson Lake outlier (62°40'N, 102°50'W), some 300 km southwest. Those Nicholson Lake collections were considered by Sinclair (ibid.) to be representative of the Red River fauna of Manitoba, and of late Middle Ordovician age. The new collections from Aberdeen Lake chronologically separate this outlier from all other outliers on the Canadian Shield, defining a late Upper Ordovician rather than the more prevalent late Middle or early Upper Ordovician age.

Table 1.

Ordovician megafauna from north of Aberdeen Lake, District of Keewatin

Megafauna	GSC collecting localities	
	57572	95286
ALGAE		
Cyclocrinites sp.		x
STROMATOPOROIDEA		
Cystostroma sp.		x
ANTHOZOA		
*Palaeophyllum raduguini Nelson var.		x
*Bighornia bottei Nelson	Х	х
Deiracorallium giganteum Nelson		х
*Grewingkia sp.	Х	
*Lobocorallium major Nelson		х
*Nyctopora sp.	X	
*Saffordophyllum churchillensis (Nelson)	x	
*Trabeculites manitobensis (Nelson)		x
*Calapoecia ungava Cox	X	ĺ
*Protrochiscolithus cummingi Bolton	х	
*Paleofavosites sp.		x
Catenipora sp.		х
*Tollina irregularis (Teichert)		х
*Tollina sp. aff. T. feildeni (Etheridge)		х
*Troedssonites flexibilis Sokolov		x
ÉCHINODERMATA		
Columnal debris, both round and pentagonal	х	x
BRACHIOPODA		
Plaesiomyid - Dinorthis(?) sp.		х
*Rafinesquinid		х
GASTROPODA		
<i>Trochonem</i> a sp. cf. <i>T. coxi</i> Wilson	х	x
CEPHALOPODA-NAUTILOIDEA		
Cyclendoceras sp. indet.		х
*Armenoceras michaudae n. sp.	Х	Х
Diestoceras sp. indet.	Х	X
TRILOBITA		
Fragments indet.	Х	Х
OSTRACODA		
Smooth tiny form, indet.		Х
*Species illustrated		

Microfauna

About 1800 g of rock were dissolved from GSC locality 57572 and about 1200 g from GSC locality 95286. One hundred and nineteen conodont elements were recovered. The localities and conodont specimens found in the samples are shown in Table 2.

The fauna is dominated by simple and denticulate cones and is typical of Midcontinent Province (Barnes et al., 1973) with the exception of Amorphognathus sp. The fauna indicates a Late Ordovician, upper Maysvillian to Richmondian age.

Plegagnathus dartoni (Stone and Furnish) and P. nelsoni Ethington and Furnish have been reported from loose blocks of 'Shamattawa limestone' of northern Manitoba (Ethington and Furnish, 1959), the upper part of the Bighorn Formation of Wyoming (Stone and Furnish, 1959), and the Stony Mountain Formation of southern Manitoba (Ethington and Furnish, 1960), all considered to be Richmondian in age. These species have also been reported from the Irene Bay Formation of the Canadian Arctic Islands (Weyant, 1968; Barnes, 1974) believed Maysvillian in age. Plegagnathus, considered indicative of Fauna 12 (Sweet et al., 1971) ranges from late Maysvillian through Richmondian (Sweet and Bergström, 1976). Fauna 12 is also known in this region from strata of the Churchill River Group on Southampton Island, northern Hudson Bay (Barnes, 1974).

Belodina profunda (Branson and Mehl) also indicates a late Maysvillian to Richmondian age, being known from upper Fauna 11 and Fauna 12. Panderodus breviusculus Barnes is here reported for the second time, being previously known only from the older Bad Cache Rapids Formation, Melville Peninsula, District of Franklin (Barnes, 1977). Nondiagnostic simple cones (e.g. Panderodus gracilis (Branson and Mehl) and Drepanoistodus suberectus (Branson and Mehl)) numerically dominate the fauna. A few previously undescribed species of Panderodus Ethington are also present and may prove stratigraphically useful in the future.

The occurrence of Walliserodus cf. W. curvatus (Branson and Branson) is of considerable interest. This species closely resembles the Silurian species from the Brassfield Formation of Ohio (Cooper, 1975) with which it is compared.

In a study of the Ordovician-Silurian boundary in eastern Missouri, Thompson and Satterfield (1975, p. 70) used the occurrence of *Paltodus dyscritus* Rexroad s.f. (a constituent of multielement *W. curvatus*) to indicate Early Silurian age. In several sections, they recovered specimens of *P. dyscritus* s.f. in association with *Amorphognathus ordovicicus* Branson and Mehl, and regarded specimens of the latter as reworked. The occurrence of *W. cf. W. curvatus* in the Aberdeen Lake outlier of undoubted Ordovician age suggests that the mixed faunas of Thompson and Satterfield (1975) might be of Ordovician age.

Table 2

Conodonts and *incertae sedis* from north of Aberdeen Lake, District of Keewatin

Microfauna	GSC collecting localities	
-	57572	95286
Acodus sp. s.f.	3	_
Amorphognathus sp.		
ramiform	3	-
holodontiform	1	-
ambalodiform	1	-
platform	1	-
<i>Belodina compressa</i> (Branson and Mehl)	-	1
<i>B. profunda</i> (Branson and Mehl)	1	1
Drepanoistodus suberectus (Branson and Mehl)		
homocurvatiform	4	2
oistodiform	-	1
Panderodus breviusculus Barnes	5	1
P. feulneri (Glenister) s.f.	-	3
P. gracilis (Branson and Mehl)		
compressiform	4	5
graciliform	11	27
P. panderi (Stauffer)	2	1
P. n. sp. A s.f.	3	-
P. n. sp. B s.f.		
asymmetrical	11	-
subsymmetrical	5	-
P. n. sp. C s.f.	2	1
Plegagnathus dartoni (Stone and Furnish) s.f.	2	1
P. nelsoni Ethington and Furnish s.f.	l	-
Walliserodus cf. W. curvatus (Branson and Branson)		
acodontiform	4	1
acodiform	2	2
distacodiform	3	1
acontiodiform	2	
TOTAL	71	48
Incertae sedis		
Milaculum ethinclarki Müller	2	-
Phosphannulus universalis Müller Nogami and Lenz	1	-
Form A	1	-
Form B	6	-

SYSTEMATIC PALEONTOLOGY

Megafauna (T.E. Bolton)

Anthozoa, Rugosa

Palaeophyllum raduguini Nelson var.

Plate 3, figures 1, 2, 5

Coralla from Aberdeen Lake fragmentary, phaceloid, but one corallum 17 mm wide and 16 mm high; in transverse section, corallites in cateniform arrangement, diameters ranging from 2.3 to 3.5 mm in hypotype 57695 and 3.4 to 4.4 mm in hypotype 57694, 11 to 14 major septa, usually 13, some of which extend to the centre and just unite although two or three may unite prior to reaching the centre, minor septa very short, either embedded in the thick walls or extending only a short distance beyond; in transverse section, corallites variable in width, increasing through lateral budding, tabulae arched, 5 1/2 to 6 in 5 mm length or 2 per 2.1 mm diameter, crowded in narrower corallites to 15 or 16 in 5 mm length.

<u>Remarks</u>. In corallite diameter and number of major septa, these specimens closely resemble *P. gracile* Flower from the Second Value Formation, Montoya Group, of Texas but that species has a small central region free of septa. *P. pasense* Stearn from the Stonewall Formation of southern Manitoba has corallites 3.0 to 4.5 mm in diameter but again the 15 major septa are not quite joined at the centre. *P. raduguini* Nelson from the Churchill River Group of northern Manitoba is identical with the Aberdeen Lake specimens except that the type specimens have 16 to 18 major septa.

Types. Hypotypes, GSC 57694, 57695.

Bighornia bottei Nelson

Plate 1, figures 5-7

Bighornia bottei Nelson, 1963, p. 41, Pl. 5, fig. 6; Pl. 9, fig. 5, 6; Pl. 11, fig. 5-8; Pl. 12, fig. 1-4

Solitary streptelasmatid corals from Aberdeen Lake with trochoid to ceratoid corallite, length and diameter ranging from 37 by 37 mm (hypotype 57696) to 70 by 40 mm (hypotype 57697), apex slightly flattened in plane of alar septa, mainly circular throughout remainder of corallite; in transverse section, cardinal septum and fossula on concave side, 50 thin major septa at 35 mm from apex, tips merging to form broad simple axial complex with solid "palicolumella", minor septa 3.0-4.0 mm long generally confined to stereozone; in longitudinal section, cystose tabulae numerous.

<u>Remarks</u>. This species is characteristic of the <u>Upper Ordovician Surprise Creek Formation</u>, Churchill River Group of northern Manitoba.

Types. Hypotypes, GSC 57696, 57697.

Grewingkia sp.

Plate 1, figures 1, 3, 4

Solitary streptelasmatid coral with ceratoid corallite 85 mm long and a maximum diameter of 40 mm; in transverse section, cardinal fossula on convex side, 46 trabeculate major septa at 55 and 70 mm from apex twisting to form a finely vermiform axial complex from one third to one half the diameter of the corallum, secondary septa 6.0 mm long embedded in a 5.0 mm thick stereozone; in longitudinal section tabulae slightly arched.

Remarks. The more widespread *Grewingkia robusta* (Whiteaves) is a larger species with 60 to 80 major septa and a wider, more complex axial structure.

Type. Figured specimen, GSC 57698.

Plate l

Figures 1, 3, 4. *Grewingkia* sp. All X2, fig. spec., GSC 57698, GSC loc. 57572. (1, 3) Transverse sections, 55 and 77 mm from apex, showing finely vermiform axial complex. (6) Longitudinal section showing slightly arched tabulae.

Figure 2. Lobocorallium major Nelson. Transverse section, 80 mm from apex, X1; hypotype, GSC 57699; GSC loc. 95286.

Figures 5-7. *Bighornia bottei* Nelson. (5, 6) Oblique transverse and alar longitudinal sections, X1; hypotype, GSC 57696; GSC loc. 95286. (7) Transverse section, 35 mm from apex, X2; hypotype, GSC 57697; GSC loc. 57572.

Figures 8-10. Trabeculites manitobensis (Nelson). Transverse and longitudinal sections, X5 and enlarged transverse, X10, showing round wall expansions; hypotype, GSC 57702; GSC loc. 95286.



Nyctopora sp.

Plate 2, figures 3, 4

Small laminar corallum 13 mm high; in transverse section, corallites polygonal, 5- to 6-sided, 2.0-2.2 mm in diameter but ranging from 1.9 to 2.6 mm, walls thick, straight, short wedgeshaped septa; in longitudinal section, corallite diameters range between 1.8 to 2.2 mm, tabulae transverse, 7 to 8 in 5 mm length.

<u>Remarks</u>. The large corallites distinguish this example of *Nyctopora* from most described species. *N. mackenziensis* Nelson from the Bad Cache Rapids Group of northern Manitoba has even larger corallites, 3.0 to 3.5 mm in diameter.

Type. Figured specimen, GSC 57700.

Saffordophyllum churchillensis (Nelson)

Plate 2, figures 1, 2

Lyopora churchillensis Nelson, 1963, p. 47, Pl. 6, fig. 4, a, b

Incomplete corallum from Aberdeen Lake at least 170 mm long and 50 mm high; in transverse section, corallites irregularly polygonal, 5- to 6-sided, mainly 2.0 to 2.1 mm in diameter but ranging from 1.7 to 2.5 mm, fibrous walls thin, lightly crenulate, septal ridges with short septa alternately developed, rarely paired, mural pores few, located both close to corners and in walls, few tubules of two sizes; in longitudinal section, corallite diameters range from 1.0 to 1.7 mm, tabulae complete to locally incomplete, mainly concave, 14 to 16 in 5 mm length.

Remarks. Saffordophyllum churchillensis (Nelson) from the Upper Ordovician Chasm Creek Formation, Churchill River Group of southern Hudson Bay is similar to S. newcombae Flower from the Middle Ordovician Second Value Formation, Montoya Group of Texas and S. troedssoni Scrutton from the Upper Ordovician Cantrum Formation of northeastern Greenland and Cape Calhoun Formation of northwestern Greenland in corallite diameter and average tabulae spacing, but differs from both species in greater septal and irregular mural pore development. Trabeculites manitobensis (Nelson)

Plate 1, figures 8-10

Lyopora manitobensis Nelson, 1963, p. 47, P1. 5, fig. 3a, b, 5a, b

Incomplete corallum from Aberdeen Lake hemispherical, cerioid, 220 mm wide and 70 mm high; in transverse section, corallites polygonal, irregularly 5- to 6-sided, ranging from 2.0 to 2.7 mm in diameter, walls thin composed of alternating thin and thick regions, thickened sections frequently distinctly circular, weakly developed Saffordophyllum-like crenulations in some normal walls, septal spines short, usually associated with swollen trabeculae but never abundant, no mural pores identified, few such features present more likely the result of fracturing of corallite wall (Pl. 1, fig. 10, upper right corner); in longitudinal section, corallites maximum diameter of 2.1 mm, tabulae transverse, complete to rarely incomplete, mainly 14 but ranging from 11 to 17 in 5 mm length.

Remarks. Trabeculites manitobensis (Nelson) from the Upper Ordovician Chasm Creek Formation, Churchill River Group, of northern Manitoba differs only in that the corallites average about 1.5 mm in diameter. In turn, T. manitobensis resembles T. maculatus Flower from Upper Ordovician rocks of Akpatok Island in corallite diameter but differs in the greater number of uniform tabulae per 5 mm length. The general dimensions of *T. manitobensis* are consistent with Saffordophyllum newcombae Flower from the Montoya Group and S. troedssoni Scrutton from the Centrum and Cape Calhoun formations. Its relationship to Favistella franklini Salter, 1852 is still uncertain; Flower (1961) suggested Salter's species might be assignable to Trabeculites and Scrutton (1975) confirmed that it was not a species of Saffordophyllum.

The circular structures in the walls are formed in this species as a result of round swellings and not of septal bending and union as suggested by Bassler (1950, p. 264) for *Lyopora*. Similar circular wall structures are present in *Nyctopora gunguensis* Preobrazhensky (1977, p. 57) from the Late Ordovician of northeastern Siberia.

Type. Hypotype, GSC 57702.

Type. Hypotype, GSC 57701.

Plate 2

Figures 1, 2. Saffordophyllum churchillensis (Nelson). Transverse and longitudinal sections, showing abundant short septa and a mural pore in corallite corner, bottom of transverse and lower right of longitudinal views, X10; hypotype, GSC 57701; GSC loc. 57572.

Figures 3, 4. Nyctopora sp. Transverse and longitudinal sections, X10; fig. spec., GSC 57700; GSC loc. 57572.

Figures 5, 6. *Paleofavosites* sp. Longitudinal and transverse sections, X5; fig. spec., GSC 57706; GSC loc. 95286.



Plate 5, figures 1-3, 6

Calapoecia canadensis var. ungava Cox, 1936, p. 12, Pl. 3, fig. 2

Calapoecia sp. cf. C. ungava Cox. Workum, Bolton and Barnes, 1976, p. 170

Calapoecia ungava Cox. Jull, 1976, p. 464, Pl. 4, fig. 1-4

Coralla from Aberdeen Lake elongated mounds 95 to 130 mm long and 50 mm high; in transverse section, corallites 9.0 mm below corallum surface, circular, 3.0 to 3.7 mm and 3.5 to 4.0 in diameter, some nearly touching whereas others separated by a thin coenenchyme, centres 4.5 mm apart with some spaced 3.4 to 3.7 mm apart, walls thin and porous to thick, at least 20 septae per corallite ranging from stubby triangles to short slightly hooked spines; in longitudinal section, corallite diameters range from 3.0 to 3.2 and 3.0 to 4.5 mm, tabulae irregular, many incomplete or sagging, varying from 6-7 to 9-11 in 5 mm length.

Remarks. The species C. ungava, based on specimens from the Toronto area, Ontario and Akpatok Island, Ungava Bay, District of Franklin, was erected by Cox for forms intermediate between typical C. canadensis Billings in which the polygonal to circular corallites (diameters 1.5 to 3.0 mm) are in contact and C. anticostiensis Billings in which the circular corallites (diameters 2.5 to 3.3 mm) are separated by wide zones of coenenchyme (Pl. 5, fig. 5, 8), displaying in different parts of a colony features characteristic of both species. Flower (1961, p. 67) differentiated within the Akpatok Island material two different types of colonies. In one group corallite diameters varied between 3.0 and 3.5 mm and in the other between 3.5 and 4.0 mm. The corallite centres ranged between 3.5 and 4.5 mm, rarely 5.0 mm, apart and 9 to 11 tabulae were present in 5 mm length. Jull (1976) restricted the species name to the Ontario material with corallite diameters commonly 1.8 to 2.0 mm and centres 2.0 to 3.0 mm or more apart. The Akpatok Island specimens of Cox (Jull, 1976, Pl. 4, fig. la, b) were considered conspecific with Richmondian specimens of C. huronensis Billings from Ohio and Kentucky (Pl. 5, fig. 4, 7).

Specimens from the Aberdeen Lake area and Akpatok Island (Pl. 5, fig. 6) herein assigned to *c. ungava* display all the intermediate characteristics stressed by Cox, but consistently having the grouping of larger corallite diameters recognized by Flower. They differ from the small, type specimens of *C. ungava* as recognized by Jull only in these consistently larger corallite diameters. In *C. huronensis*, the corallites mainly are in contact, with thin coenenchyme rarely present.

The specimen *Calapoecia* sp. figured by Oliver et al. (1975, Pl. 4, fig. 1, 2) from the Fairbanks-Rampart area of central Alaska appears conspecific with the Aberdeen Lake forms.

Types. Hypotypes, GSC 57703, 57704.

Protrochiscolithus cummingi Bolton

Plate 3, figures 3, 4

Protrochiscolithus cummingi Bolton, 1977, p. 29, Pl. 4, fig. 5-8; Pl. 5, fig. 1-3 (for complete synonymy)

<u>Remarks</u>. This species is based on the Aberdeen Lake area specimen and five others from the Churchill River Group of Churchill River, South Knife River, and Herriot Creek, northern Manitoba. It is also present in the upper part of the Lang River Formation of Somerset Island (*P. kiaeri* Troedsson of Dixon, 1975).

All these forms display thin common walls, narrow septa, and a solid columella. The Late Ordovician *P. kiaeri* from northeastern Greenland has thin common walls and narrow septa but a vesicular columella whereas, in contrast, the older *P. magnus* (Whiteaves) from the Red River Formation of southern Manitoba has a solid columella but thick common walls and broad septa.

Types. Hypotypes, GSC 57703, 57704.

Paleofavosites sp.

Plate 2, figures 5, 6

Incomplete corallum 130 mm long and 35 mm high; in transverse section, corallites polygonal with variable diameters ranging from 2.0 to 5.1 mm, generally 4.0 to 4.3 mm, walls thick with a few small mural pores in or near corners, no septal spines evident; in longitudinal section, corallite diameters range from 2.5 to 5.5 mm, tabulae complete, convex, abruptly upturned or downturned at margins, 7 to 8 in 5 mm length.

Plate 3

Figures 1, 2, 5. Palaeophyllum raduguini Nelson var. Transverse and longitudinal sections, X10; hypotypes, GSC 57694 (fig. 1, 2), 57695; GSC loc. 95286.

Figures 3, 4. Protrochiscolithus cummingi Bolton. Transverse and longitudinal sections, X10; paratype, GSC 42926; GSC loc. 57572.

Figure 6. Rafinesquinid brachiopod. Brachial valve with concentric rugae, geniculate, X2; fig. spec., GSC 57715; GSC loc. 95286.



Remarks. P. okulitchi Stearn from late Upper Ordovician rocks of southern Manitoba and Melville Peninsula (Bolton, 1977) has smaller corallites and mural pores both at corners and in the curving walls. P. cowei Scrutton from the Centrum Formation of northeastern Greenland is characterized by mural pores predominantly in the corallite walls rather than the corners, smaller corallites and well developed septal spines.

Type. Figured specimen, GSC 57706.

Tollina irregularis (Teichert)

Plate 4, figure 2

Halysites irregularis Teichert, 1937, p. 132, Pl. 7, fig. 4, 5; Pl. 8, fig. 3

Manipora irregularis (Teichert). Nelson, 1963, p. 60, Pl. 14, fig. 13

Colony turbinate, 170 mm wide and 110 mm high, corallites radiating from corallum origin, in close irregularly meandering ranks some of which are discontinuous, lacunae small surrounded by ranks of 1 or 2 up to 5 or 6 corallites; in transverse section, corallites basically arranged in single rows, with clustering of 4 or 6 corallites mainly at junctions, varying in shape from oval to subquadrate in agglutinative patches, diameters varying from 1.5 mm in oval to 1.7 by 1.4 mm in subquadrate forms, walls thick, outer walls gently curved with a few short septal spines preserved, common walls crenulate with convexities thickened into short septal ridges, never more than 3 on one side, and rare pore at angles; in longitudinal section, tabulae thin, predominantly transverse, complete, 9 to 10 in 5 mm length.

Remarks. This specimen closely resembles that described by Nelson (1963) from rubble of the Chasm Creek Formation, Churchill River Group (hypotype 10894); both differ from the older Portage Chute Formation form also assigned to this species by Nelson. The corallites of the Aberdeen Lake area specimen are slightly larger but the colony itself is a much greater size.

Type. Hypotype, GSC 57707.

Tollina sp. aff. T. feildeni (Etheridge)

Plate 4, figures 1, 4, 5

"Tollina feildeni" (Etheridge). Bolton, 1965, Pl. 9, fig. 2, 3

Colony domed, 260 mm long and 90 mm high; in transverse section, corallites essentially in monoserial ranks, lacunae meandering, very irregular in shape surrounded by 1 to 4 corallites at least, 3 to 4 1/2 in 5 mm length, corallites subquadrangular to quadrangular with outer walls straight or only slightly convex, 1.0 to 1.3 mm long and 0.8 to 1.2 mm at midwidth, some grouping of hexagonal corallites in which connecting walls either straight or vaguely crenulated with rare septal spines, minute pores at angles; in longitudinal section, corallite diameters range from 0.9 to 1.2 mm, tabulae thin, transverse, complete, 8 to 10 in 5 mm length.

Remarks. According to Flower (1961, p. 43) the forms illustrated by Troedsson as Halysites fieldeni Etheridge contain two different species. One is a massive coral, mainly cerioid with small lacunae rather than properly cateniform, and corallites with a very narrow contact wall (Troedsson, 1929b, Pl. 41, fig. 3a, b; Pl. 42, fig. 1a, b). Many parts of the Aberdeen Lake area colony are similar to this form which Flower suggests conforms with the original description of the species. The second form with distinct ranks, each one corallite wide (Troedsson, 1929b, Pl. 41, fig. 2; Pl. 43, fig. 1a, b) in overall aspect is considered very close to *T. magna* (Flower).

Type. Hypotype, GSC 57708.

Plate 4

(All X10, GSC loc. 92586)

Figures 1, 4, 5. *Tollina* sp. aff. *T. feildeni* (Etheridge). Tranverse and longitudinal sections showing irregular lacunae and grouping of hexagonal corallites with vaguely crenulated common walls and rare septal spine; hypotype, GSC 57708.

Figure 2. Tollina irregularis (Teichert). Transverse section, showing crenulated common corallite walls and short septal spines; hypotype, GSC 57707.

Figures 3, 6, 7. Troedssonites flexibilis Sokolov. (3) Transverse section, showing more angulate corallites; hypotype, GSC 57709. (6, 7) Transverse and longitudinal sections, showing the more normal circular corallites and abundant connecting hollow tubules; hypotype, GSC 57710.



Plate 4, figures 3, 6, 7

Syringopora? conspirata Troedsson. Miller and Youngquist, 1947, p. 5, Pl. 2, fig. 3

Troedssonites flexibilis Sokolov, 1949, p. 91, fig. 15, 16

Troedssonites flexibilis Sokolov. Sokolov and Tesakov, 1963, p. 134, Pl. 28, fig. 7, 8

Fasciculate, compact, domed colony, 300 mm long and 120 mm high; in transverse section, corallites phacelloid, circular to angular particularly when united, 0.9 to 1.2 mm in diameter, centres 1.2 to 1.4 mm apart, walls thick, short pointed septal spines rare, individual corallites may be connected at one to three corners by short hollow tubules to form short cateniporid chains separated by narrow lacunae; in longitudinal section, tabulae thin, flat complete to curved incomplete, 0.2 to 0.4 mm apart, 8 to 10 in 5 mm length, abundant horizontal hollow oval tubules connect cylindrical corallites, 0.2 to 0.4 in diameter, cut end of tubules and/or interspaces form vertical rows of 'pores' 0.3 to 0.6 mm in diameter, rare tabulae extending through tube into adjoining corallite.

Remarks. The corallites of this species, originally described from eastern Siberia (Sokolov and Tesakov, 1963), are smaller and much closer together than in the type species T. conspiratus (Troedsson) from the Cape Calhoun Formation of northeastern Greenland and late Ordovician of Ellesmere Island (Bolton, 1965). The Sutton Island form described by Miller and Youngquist (1947) is here assigned to T. flexibilis because the closely spaced cylindrical corallites are about 1 mm in diameter. T. pacificus Preobrazhensky has slightly smaller corallites (0.7-0.8 mm) that are spaced farther apart. In both T. wonghsiangensis Chen and T. multitabulatus Chen the corallites are close together but the diameters are 1.4 to 1.9 mm and 2.0 to 2.5 respectively.

Types. Hypotypes, GSC 57709, 57710.

Cephalopoda-Nautiloidea

Armenoceras michaudae n. sp.

Plate 6, figures 1-5

Incomplete orthoconic phragmacone 240 mm long, elliptical in cross-section, enlarging from a lateral diameter of about 93 mm near the posterior end to 128 mm at the anterior; siphuncle maximum diameter a constant 54 mm throughout length, filling much of the conch, nearly touching at posterior but 8 mm away from ventral wall at anterior, 3.75 segments in a length equal to its diameter; eccentric narrow meandering central tube or axial cavity with abundant radiating endosiphuncular structures (radial lamellae); septa strongly concave, 13 mm apart, sutures apparently directly transverse (Pl. 6, fig. 4).

A second specimen (Pl. 6, fig. 3) consists of 3.5 siphuncular segments, 54 mm in maximum diameter, 3.5 segments in a length equal to this diameter. A third (paratype, GSC 57714), badly weathered one half of a siphuncle consists of 7+ segments, 57 mm in maximum diameter, 3 segments in a length equal to its diameter; a fourth siphuncle, 300 mm long and at least 57 mm in maximum diameter, was sectioned (Pl. 6, fig. 1, 2, 5).

Remarks. This species is closest to the Armenoceras sp. siphuncle (diameter 45 mm, 3.5 segments per diameter) described by Troedsson (1929a, p. 62) from the Cape Calhoun Formation of Greenland and Armenoceras sp. siphuncle (diameter 49+ mm, 3.5± segments per diameter) described by Miller and Youngquist (1947, p. 16, Pl. 5, fig. 1-3) from Sutton Island, District of Franklin. A. magnum (Parks) from the Shamattawa limestone (Churchill River Group) of Shamattawa (Gods) River, Manitoba (Foerste and Savage, 1927, p. 64) has a siphuncle 55 mm in diameter but about 6.5 segments occur in a length equal to the diameter whereas A. saxosum Foerste from the Stony Mountain Formation of southern Manitoba has a diameter of 66 to 72 mm with 3+ segments per diameter length. All other Ordovician species of Armenoceras have much smaller siphuncles.

Types. Holotype, GSC 57711; paratypes, GSC 57712-57714.

Plate 5

Figures 1-3, 6. *Calapoecia ungava* Cox. (1, 3) Longitudinal and transverse sections, showing variation in coenenchyme thickness, X5; hypotype, GSC 57703; GSC loc. 57572. (2) Longitudinal section, showing continuation of corallite-coenenchyme connections, X5; hypotype, GSC 57704; GSC loc. 57572. (6) Longitudinal section, showing most corallites close together, X5; hypotype, GSC 41200; early Upper Ordovician, section II, 420' above sea-level, immediately east of Premium Homestead Akpatok L-26 drill hole, west-central coast Akpatok Island, District of Franklin.

Figures 4, 7. Calapoecia huronensis Billings. Transverse and longitudinal sections, showing corallites in contact and scattered small circular tubes, X5; hypotype, GSC 57705; Bardstown Member, Drakes Formation, Upper Ordovician, road cut along southwest side of U.S. Highway 150, about 1 mile northwest of Fredericktown, Kentucky, U.S.A.

Figures 5, 8. *Calapoecia anticostiensis* Billings. Longitudinal and transverse sections, showing corallites well apart, X5; holotype, GSC 2267c, b; Ellis Bay Formation, Upper Ordovician, west side of Ellis Bay, Anticosti Island, Québec.



Microfauna (G.S. Nowlan)

In the following descriptions multielement taxonomy is used wherever possible; residual form taxa are designated with the suffix s.f. (sensu formo).

Genus Acodus Pander, 1856 s.f.

Type species. A. erectus Pander, 1856

Acodus sp. s.f.

Plate 8, figures 3-5

Description. An extremely laterally compressed simple cone. Aboral outline is straight. Base is high, but the basal cavity is shallow and without a discernible apex. Oral edge is sharp and curves evenly into sharp posterior edge. Anterior edge of base is sharp and straight in lateral view. Cusp is proclined, compressed and filled with white matter near tip of cusp. An exceedingly thin and sharp lateral costa runs from the base to the tip of the cusp, situated within the posterior half of the base and at about midline of cusp. It is very thinwalled and translucent.

Remarks. One element is distacodiform with a costa developed on both sides; this form has a slightly deeper basal cavity. This species is similar in some ways to Acodus mutatus (Branson and Mehl) s.f., but it lacks much posterior extension of the base; the base is higher in this species and it is much more laterally compressed. The association of acodiform and distacodiform elements is analogous to the association of A. mutatus and Distacodus procerus Ethington (e.g. Webers, 1966). Barnes and Poplawski (1973) suggested that A. mutatus may be associated with O. venustus Stauffer s.f. in a species that would be referrable to Paroistodus Lindström, however no oistodiform elements were recovered with the sparse Aberdeen Lake material. Barnes (1977) treated associations of acodiform and distacodiform elements as a multielement taxon A. mutatus, but it is felt by this author that uncertainty about the generic affinity and apparatus structure of these Late Ordovician forms requires treatment of them in open taxonomy. Furthermore, the nature of the type species of Acodus s.f. has not been established and use of the generic name for multielement taxa is probably unwise.

Types. Figured specimens, GSC 57716, 57717.

Genus Amorphognathus Branson and Mehl, 1933

Type species. A. ordovicicus Branson and Mehl, 1933

Amorphognathus sp.

Plate 8, figures 11-18

A single nonblade (sinistral) Remarks. amorphognathiform element has been recovered which closely resembles those associated with A. ordovicicus. In addition, three elements of the ramiform complex (eoligonodiniform, cladognathiform, and trichonodelliform) are present. A small broken holodontiform element is indeterminate; only the cusp and parts of the posterior and inner lateral processes are preserved. The recovery of an unusual ambalodiform element precludes placement of these elements in A. ordovicicus. The posterior and anterior processes of the ambalodiform element are strongly denticulated and virtually parallel, such that the inner lateral face is almost flat. The posterior process is broad with a row of laterally compressed, closely spaces denticles that are fused for most of their length. The denticles are situated on the inner lateral margin of the process. The anterior process is compressed and bears irregular denticles, similar to hindeodellid denticulation. The lateral process is broad with three discrete denticles. The cusp is broad with sharp edges and an outer lateral costa; it is much higher than the denticles. The style of denticulation and marked lateral compression of the anterior process serve to distinguish this specimen from the ambalodiform element of A. ordovicicus.

Types. Figured specimens, GSC 57718-57723.

Genus Belodina Ethington, 1959

Type species. Belodus compressus Branson and Mehl, 1933

Belodina compressa (Branson and Mehl)

Plate 8, figure 6

Belodus compressus Branson and Mehl, 1933, p. 114, Pl. 9, fig. 15, 16

Belodina compressa (Branson and Mehl). Barnes, 1977, p. 105, Pl. 4, fig. 16-18 (includes synonymy through 1976)

Remarks. A single, diminutive, grandiform element has been recovered.

Type. Hypotype, GSC 57724.

Plate 6

(All from GSC loc. 95286)

Figures 1-5. Armenoceras michaudae n. sp. (1, 2, 5) Longitudinal and transverse thin sections of a siphuncle, showing the eccentric central tube and abundant radial lamellae, and traces of connecting rings (upper left corner of fig. 5 and enlargement, fig. 1), X10 and X2; paratype, GSC 57712. (3, 4) Natural weathered sections, showing siphuncles and strongly curved septa, X1; paratype, GSC 57713; holotype, GSC 57711.



Belodina profunda (Branson and Mehl)

Plate 8, figures 8, 9

Belodus profundus Branson and Mehl, 1933, p. 125, Pl. 10, fig. 25

Belodina profunda (Branson and Mehl). Barnes, 1977, p. 105, Pl. 4, fig. 11 (includes synonymy through 1976)

<u>Remarks</u>. One specimen with three denticles and one poorly preserved specimen with two denticles were recovered.

Type. Hypotype, GSC 57725.

Genus Drepanoistodus Lindström, 1971

Type species. Oistodus forceps Lindström, 1955

Drepanoistodus suberectus (Branson and Mehl) Plate 7, figures 11, 15, 16

Oistodus suberectus Branson and Mehl, 1933, p. 111, Pl. 9, fig. 7

Drepanoistodus suberectus (Branson and Mehl). Barnes, 1977, p. 106, Pl. 3, fig. 18-20 (includes synonymy through 1976)

Remarks. All specimens from these samples have well developed white matter in the cusp. No suberectiform elements were recovered.

Types. Hypotypes, GSC 57726-57728.

Genus Panderodus Ethington, 1959

Type species. Paltodus unicostatus Branson and Mehl, 1933

Panderodus breviusculus Barnes

Plate 7, figures 8, 12

P. breviusculus Barnes, 1977, p. 106, Pl. 3, fig. 13-17

Remarks. The specimens recovered most closely resemble the younger forms described by Barnes (1977, p. 106).

Types. Hypotypes, GSC 57729, 57730.

Panderodus feulneri (Glenister) s.f.

Plate 7, figures 5, 6

Paltodus feulneri Glenister, 1957, p. 728, Pl. 85, fig. 11

Panderodus feulneri (Glenister). Ethington, 1959, p. 284, 285, Pl. 30, fig. 2; Barnes, 1977, p. 107, Pl. 3, fig. 11, 12 (includes synonymy through 1976)

<u>Remarks</u>. This form species has been considered part of *P. gracilis* (Bergström and Sweet, 1966) or as a separate multielement species (Barnes, 1977). As only a few specimens have been recovered in this study, the species is considered as a form taxon.

Type. Hypotype, GSC 57731.

Plate 7

Figures 1, 2. Panderodus n. sp. A. s.f. Lateral views, x90; fig. spec., GSC 57737; GSC loc. 57572.

Figures 3, 4, 7. Panderodus panderi (Stauffer). (3) Lateral view, x90; hypotype, GSC 57735; GSC loc. 95286. (4, 7). Lateral views, x65 and x70; hypotype, GSC 57736; GSC loc. 57572.

Figures 5, 6. Panderodus feulneri (Glenister) s.f. Lateral views, x65; hypotype, GSC 57731; GSC loc. 95286.

Figures 8, 12. Panderodus breviusculus Barnes. (8) Lateral view, x45; hypotype, GSC 57729; GSC loc. 57572. (12) Lateral view, x70; hypotype, GSC 57730; GSC loc. 57572.

Figures 9, 10, 13, 14. *Panderodus* n. sp. B. s.f. (9, 10) Inner and outer lateral views, x55; asymmetrical element, fig. spec., GSC 57738; GSC loc. 57572. (13, 14) Lateral views, x50; subsymmetrical element, fig. spec., GSC 57739; GSC loc. 57572.

Figures 11, 15, 16. Drepanoistodus suberectus (Branson and Mehl). (11) Lateral view, x50; homocurvatiform element, hypotype, GSC 57726; GSC loc. 57572. (15) Lateral view, x65; oistodiform element, hypotype, GSC 57727; GSC loc. 95286. (16) Lateral view, x50; homocurvatiform element, hypotype, GSC 57728; GSC loc. 95286.

Figures 17, 18. Panderodus n. sp. C. s.f. Lateral views, x60; fig. spec., GSC 57740; GSC loc. 57572.

Figures 19, 21-23. Panderodus gracilis (Branson and Mehl). (19) Lateral view, x65; asymmetrical graciliform element, hypotype, GSC 57734; GSC loc. 57572. (21, 22) Lateral views, x65; compressiform element, hypotype, GSC 57732; GSC loc. 57572. (23) Lateral view, x65; symmetrical graciliform element, hypotype, GSC 57733; GSC loc. 57572.

Figures 20, 24. Form B. Lateral views, x65; fig. specs. 57754 and 57755; GSC loc. 57572.



Panderodus gracilis (Branson and Mehl)

Plate 7, figures 19, 21-23

Paltodus gracilis Branson and Mehl, 1933, p. 108, Pl. 8, fig. 20, 21

Panderodus gracilis (Branson and Mehl). Barnes, 1977, p. 107, Pl. 3, fig. 6, 7 (includes synonymy through 1976)

Types. Hypotypes, GSC 57732-57734.

Panderodus panderi (Stauffer)

Plate 7, figures 3, 4, 7

Paltodus panderi Stauffer, 1940, p. 427, Pl. 60, fig. 8, 9

Panderodus panderi (Stauffer). Barnes, 1977, p. 107, P1. 3, fig. 21, 22 (includes synonymy through 1976)

Types. Hypotypes, GSC 57735, 57736.

Panderodus n. sp. A s.f. Plate 7, figures 1, 2

Description. Aboral outline is straight. Base is low and posteriorly extended. Oral edge is sharply rounded. Anterior margin of the base is rounded and broad. Basal cavity is asymmetrically conical with its apex close to the anterior margin. Cusp is erect to slightly proclined and filled with white matter above the apex of the basal cavity. Anterior margin of the cusp is sharply rounded and the posterior margin is broadly rounded. Each side bears a thin costa near the anterior margin which extends along the midline of the cusp. A groove is developed posteriorly to each costa and they are markedly different on each face. On one side the groove is very broad with a narrow axial depression and on the other there is merely a shallow groove immediately posterior to the costa. On the broadly grooved side, there is a slight shoulder close to the oral edge which extends up the cusp as a weak postero-lateral costa. The posterior portion of the base is compressed, resulting in a basal cross-section that is roughly keyhole-shaped.

Remarks. See Panderodus n. sp. B s.f.

Type. Figured specimen, GSC 57737.

Panderodus n. sp. B s.f. Plate 7, figures 9, 10, 13, 14

Description. Two morphotypes, asymmetrical and subsymmetrical, comprise this species.

Asymmetrical element. Aboral outline is straight. Base is high with a deep conical basal cavity. Longitudinal striations are visible on the lower portion of the base. Cusp is proclined and filled with white matter above the tip of the basal cavity. Anterior margin is asymmetrically rounded, terminating in a lateral costa on the inner side. Inner lateral face is broadly rounded with a shallow, narrow groove immediately posterior to the anterolateral costa. Oral margin is narrowly rounded near the aboral margin to flattened near the point of curvature. A shallow groove is present on the flattened area, flanked by weak posteriorly directed ridges. The ridge on the outer side is more strongly developed. The outer face bears a deep median furrow, flanked by low ridges or costae. The anterior margin of the furrow is broadly rounded whereas the posterior margin is more angular. The base is notched at the furrow.

Subsymmetrical element. More slender element with rounded anterior margin. Lateral costae posteriorly directed. Posterior margin and oral edge sharp. A costa is situated posteriorly to one side of the posterior edge. Lateral furrows are more equally developed, although asymmetrical.

<u>Remarks</u>. This species may be related to <u>Panderodus</u> n. sp. A s.f. because of the general similarity of the position and nature of the grooves and costae. The two forms may be associated in an apparatus similar in structure to that of *P. gracilis* with *P.* n. sp. A homologous with the compressiform element and *P.* n. sp. B with the graciliform elements (asymmetrical and subsymmetrical).

Types. Figured specimens, GSC 57738, 57739.

Panderodus n. sp. C s.f.

Plate 7, figures 17, 18

Description. A long slender cone with a high base and unusual apically broadening cusp. Anterior margin rounded on the base to sharp on the cusp. Oral edge sharply rounded curving smoothly into sharp posterior edge. One lateral face is broadly convex with a faint costa near crest of convexity. A shallow groove is situated posterior of the costa. A more pronounced groove is developed on the other side which extends from a basal notch all the way up the cusp. Cusp is proclined and filled with white matter above apex of basal cavity. It is slender at point of curvature, broadens apically, and is broken near the tip.

<u>Remarks</u>. The cusp of this species is much longer than that of *Panderodus* n. sp. B which it most closely resembles and its grooves are much less pronounced. The curious apical broadening of the cusp is similar to that of one of the elements described as *P. arcuatus* Stauffer by Barnes (1977, p. 106, Pl. 3, fig. 24) but the pronounced costae of that specimen are absent from the Aberdeen Lake material.

Type. Figured specimen, GSC 57740.

Genus Plegagnathus Ethington and Furnish, 1959 Type species. P. nelsoni Ethington and Furnish, 1959

Plegagnathus dartoni (Stone and Furnish) s.f.

Plate 8, figures 2, 7

Belodus dartoni Stone and Furnish, 1959, p. 220, Pl. 31, fig. 15

Plegagnathus dartoni (Stone and Furnish). Ethington and Furnish, 1959, p. 545, Pl. 73, fig. 6, 7; ?Kohut and Sweet, 1968, p. 1472, Pl. 186, fig. 9-11; Weyant, 1968, p. 59, Pl. 4, fig. 6, 7; Barnes, 1974, Pl. 7, fig. 27

<u>Remarks</u>. This form species probably goes together with *Plegagnathus nelsoni* in a multielement association in which *P. dartoni* is an erect element and *P. nelsoni* a more reclined element. Specimens of the two taxa are similar and co-occur commonly but not consistently.

Two variants are illustrated: a large specimen (Pl. 8, fig. 2) which most closely resembles the holotype, and a smaller specimen (Pl. 8, fig. 7) which is more delicate and has fewer denticles. The specimen illustrated by Kohut and Sweet (1968) appears to be more readily placed in *Belodina*; similar specimens are known to the author from the Vauréal Formation, Anticosti Island, Québec, where they are associated with *Belodina profunda* (Branson and Mehl).

Types. Hypotypes, GSC 57741, 57742.

Plegagnathus nelsoni Ethington and Furnish s.f. Plate 8, figure 1

Plegagnathus nelsoni Ethington and Furnish, 1959, p. 544, 545, Pl. 73, fig. 2, 3; Ethington and Furnish, 1960, p. 272, Pl. 38, fig. 1; Weyant, 1968, p. 59, 60, Pl. 4, fig. 8

Remarks. See P. dartoni.

Type. Hypotype, GSC 57743.

Genus Walliserodus Serpagli, 1967

Type species. Acodus curvatus Branson and Branson, 1947

<u>Remarks</u>. Cooper (1975) has revised Serpagli's (1967) original description of this genus to a multielement status. The type species has been changed from *Paltodus debolti* Rexroad to *Acodus curvatus* Branson and Branson because of the inclusion of the latter element in the multielement species by Cooper (1975).

Walliserodus cf. W. curvatus (Branson and Branson) Plate 8, figures 19-32

Acodus curvatus Branson and Branson, 1947, p. 554, P1. 81, fig. 20

- cf. Walliserodus curvatus (Branson and Branson). Cooper, 1975, p. 995, 996, Pl. 1, fig. 10, 11, 16-21 (includes synonymy to 1975)
- Walliserodus debolti (Rexroad). Serpagli, 1967, p. 104-106, Pl. 31, fig. 1, 6, 9, 11; ?Pl. 31, fig. 2-5, 7, 8, 10, 12, 13
- Drepanodus amplissimus Serpagli, 1967, p. 66, Pl. 15, fig. 1a-5b
- *?Scandodus zermulaensis* Serpagli, 1967, p. 96, 97, Pl. 27, fig. 4a-6d
- ?Paltodus dyscritus Rexroad. Thompson and Satterfield, 1975, p. 70, fig. 5D

Remarks. The elements assigned to this species are being described and discussed in detail in a study of conodonts from the Vauréal Formation, Anticosti Island (Nowlan and Barnes, in prep.) where the species is much more abundant. Elements homologous with and similar to the acodontiform (Acodus unicostatus Branson and Branson) and costate elements described by Cooper (1975) for W. curvatus have been recovered. The acodontiform element of this study is conspecific with Drepanodus amplissimus Serpagli, and a transition series of costate elements, acodiform (cf. Acodus curvatus Branson and Branson), distacodiform-paltodiform (cf. Paltodus migratus Rexroad), and acontiodiform (cf. Paltodus dyscritus Rexroad) have also been recovered.

The acodontiform element differs from that of *W. curvatus* in that it is laterally carinate and more variable. The number of secondary costae illustrated by Rexroad (1967, fig. 4) for some of the constituent form species of *W. curvatus* are not present on specimens in this material. In addition, the anterior face of the acontiodiform element is flat rather than convex as shown for *Paltodus dyscritus* Rexroad s.f. In this material an additional costa may be present on the anterior face of the acontiodiform element close to one of the antero-lateral costae giving the appearance of a split antero-lateral costa.

Thompson and Satterfield (1975) illustrated but did not describe a specimen they referred to Paltodus dyscritus Rexroad from the Bowling Green Dolomite of Missouri. Their 'Paltodus dyscritus' fauna (1975, p. 70) included Acodus curvatus and A. unicostatus and they considered it to represent earliest Silurian, although it co-occurs with Amorphognathus ordovicicus Branson and Mehl in its oldest occurrence in a number of areas. The coexisting Ordovician forms were considered reworked from the Maquoketa Shale (Thompson and Satterfield, 1975, p. 70). This occurrence of similar elements in undoubted Ordovician strata may suggest that the oldest parts of their Silurian sequence are in fact Ordovician.

Types. Hypotypes, GSC 57744-57750.

Plate 8

Figure 1. Plegagnathus nelsoni Ethington and Furnish s.f. Lateral view, x45; hypotype, GSC 57743; GSC loc. 57572.

Figures 2, 7. *Plegagnathus dartoni* (Stone and Furnish) s.f. (2) Lateral view, x50; large specimen, hypotype, GSC 57741; GSC loc. 57572. (7) Lateral view, x65; small specimen, hypotype, GSC 57742; GSC loc. 57572.

Figures 3-5. Acodus sp. s.f. (3, 4) Lateral views, x90; distacodiform element, fig. spec., GSC 57717; GSC loc. 57572. (5) Lateral view, x90; acodiform element, fig. spec., GSC 57716; GSC loc. 57572.

Figure 6. Belodina compressa (Branson and Mehl). Lateral view, x85; hypotype, GSC 57724; GSC loc. 95286.

Figures 8, 9. Belodina profunda (Branson and Mehl). Lateral views, x80; hypotype, GSC 57725; GSC loc. 57572.

Figure 10. Form A. Posterior view, x75; fig. spec., GSC 57753; GSC loc. 57572.

Figures 11-18. Amorphognathus sp. (11) Inner lateral view, x65; eoligonodiniform element, fig. spec., GSC 57718. (12) Lateral view, x65; cladognathiform element, fig. spec., GSC 57719. (13) Lateral view, x50; trichonodelliform element, fig. spec., GSC 57720. (14) Posterolateral view, x75; fragmentary holodontiform element, fig. spec., GSC 57721. (15, 16) Outer and inner lateral views, x60; ambalodiform element, fig. spec., GSC 57722. (17, 18) Lower and upper views, x45; platform element, fig. spec., GSC 57723; all specimens from GSC loc. 57572.

Figures 19-32. Walliserodus cf. W. curvatus (Branson and Branson). All specimens x55. (19, 20) Outer and inner lateral views; acodontiform element, hypotype, GSC 57744; GSC loc. 57572. (21, 22) Inner and outer lateral views; 'acodiform' element which lacks prominent inner costa, ' hypotype, GSC 57747; GSC loc. 57572. (23-25) Lateral, posterior and lateral views; acontiodiform element, hypotype, GSC 57745; GSC loc. 57572. (26, 27) Outer and inner lateral views; acodiform element, hypotype, GSC 57748; GSC loc. 95286. (28) Outer lateral view; carinate element, hypotype, GSC 57750; GSC loc. 57572. (29, 30) Outer and inner lateral views; acodiform element, hypotype, GSC 57749; GSC loc. 95286. (31, 32) Lateral views; distacodiform element, hypotype, GSC 57746; GSC loc. 57572.

Figure 33. Phosphannulus universalis Müller, Nogami and Lenz. Upper view, x75; hypotype, GSC 57752; GSC loc. 57572.

Figure 34. Milaculum ethinclarki Müller. Upper view, x50; hypotype, GSC 57751; GSC loc. 57572.



Incertae sedis

Genus Milaculum Müller, 1973

Type species. M. rutteri Müller, 1973

Milaculum ethinclarki Müller

Plate 8, figure 34

Milaculum ethinclarki Müller, 1973, p. 223, Pl. 34, fig. 5, 6, 8

Type. Hypotype, GSC 57751.

Genus Phosphannulus Müller, Nogami and Lenz, 1974 Type species. P. universalis Müller, Nogami and Lenz, 1974

Phosphannulus universalis Müller, Nogami and Lenz

Plate 8, figure 33

Phosphannulus universalis Müller, Nogami and Lenz, 1974, p. 89, Pl. 18, fig. 1-12; Pl. 19, fig. 1-13; Pl. 20, fig. 1-7; Pl. 21, fig. 1-9

Type. Hypotype, GSC 57752.

Form A

Plate 8, figure 10

Description. A simple, phosphatic, conical form with a sharp lateral flange. The posterior edge of the base is even, but anteriorly the basal edge is extended asymmetrically downwards and a notch is developed on the flanged side. The cone is subcircular in cross-section. The flange is developed on one side and extends from the base about two thirds up the cone. It is broadest near the base and narrows apically. A large cavity fills most of the

cone and the form is opaque around the cavity. The flange and tip of the cone are translucent. The cone is moderately recurved posteriorly; its surface is horizontally striated and these striations may represent growth lines.

<u>Remarks</u>. This form resembles a conodont in several ways (e.g. cone shape, basal cavity) but the horizontal striations may suggest another phylum.

Type. Figured specimen, GSC 57753.

Form B

Plate 7, figures 20, 24

Description. A simple conical form with a triangular cross-section. Lateral faces are smooth and flat, meeting in a sharp (posterior) edge, which is virtually straight in lateral view. The anterior face is flat, broadest at the base tapering to the tip of the cone. The anterolateral edges are sharply rounded. In lateral view, the anterior margin has a characteristic narrowing at about mid-height. A deep cavity fills most of the cone, extending almost to the tip. It is restricted to the anterior five sixths of the cone. The posterior one fifth of the cone is translucent.

<u>Remarks</u>. This form is known to the author from the late Ordovician Vauréal Formation of Anticosti Island, Québec. Its affinities are uncertain, but it may be a conodont. The closest genus is *Pseudooneotodus* Drygant, but that form contains short conical units, rather than the long elements described here.

Types. Figured specimens, GSC 57754, 57755.

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CHAZY (MIDDLE ORDOVICIAN) TRACE FOSSILS IN THE OTTAWA - ST. LAWRENCE LOWLANDS

H.J. Hofmann

Abstract

Trace fossils are abundant in terrigenous, shallow marine clastic rocks in the lower part of the Laval Formation (Chazy Group) of the St. Lawrence Lowlands, and equivalent rocks (Rockcliffe Formation) in the Ottawa Valley. Most prevalent are crawling traces (Repichnia) and feeding burrows (Fodinichnia), followed by resting traces (Cubichnia) and dwelling burrows (Domichnia); systematic feeding traces (Pascichnia) are absent. The following 17 ichnogenera are reported from the terrigenous beds: Arthraria, Chondrites, Conostichus, Cruziana, Diplichnites, Diplocraterion, Isopodichnus, Palaeophycus, Petalichnus, Phycodes, Planolites, Rhizocorallum?, Rusophycus, Skolithos, Teichichnus, Walcottia?, and the new ichnogenus Caugichnus. Two of these, Teichichnus and Phycodes, occur as integral structures made by a single species of organism. Also present are 3 genera of borings: Trypanites, on a hardground developed on a calcarenite in the upper part of the Laval Formation, and Ropalonaria and Vermiforichnus, perforating valves of the orthid brachiopod Mimella imperator Billings in the Rockcliffe Formation. Two overlapping shallow water facies are recognized: Seilacher's Skolithos facies (in the west), and the Cruziana facies to the east; the latter is subdivided into a Rusophycus subfacies (in the middle of the study area), and a Phycodes subfacies in the east.

INTRODUCTION

A variety of fossil tracks, trails, and burrows of invertebrate animals occurs in the Chazy Group of eastern Ontario, southern Quebec, and northern New York State, but only a few brief, older and widely scattered reports have been published. These include papers by Hall (1847), Billings (1862, 1865), Dawson (1864, 1890), Ami (1887), Raymond (1910), and Wilson (1932); the last three have not been incorporated in major modern bibliographic compilations (Häntzschel, 1965, 1975).

This paper describes, illustrates, and interprets this ichnofauna and summarizes information on the taxonomy and the stratigraphic and geographic distribution of 23 identified ichnotaxa (Fig. 5). Type and reference specimens are deposited in the National Type Fossil collection, Geological Survey of Canada (GSC), Ottawa (GSC catalogue nos. 54182-54227).

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Résumé

Les traces fossiles sont abondantes dans les sédiments marins terrigènes de la partie inférieure de la Formation de Laval (Groupe de Chazy) des Basses Terres du St-Laurent, et dans les unités équivalentes (Formation de Rockcliffe) de la vallée de l'Outaouais. Les types les plus abondants sont les traces de locomotion (Repichnia) et les structures de nutrition (Fodinichnia), suivis par les traces de station (Cubichnia) et les structures d'habitation (Domichnia); les traces systématiques de nutrition (Pascichnia) sont absentes. Les 17 ichnogenres suivants sont reportés: Arthraria, Chondrites, Conostichus, Cruziana, Diplichnites, Diplocraterion, Isopodichnus, Palaeophycus, Petalichnus, Phycodes, Planolites, Rhizocorallum?, Rusophycus, Skolithos, Teichichnus, Walcottia? et le nouveau ichnogenre Caugichnus; deux de ceux-ci (Teichichnus et Phycodes) forment des structures intégrales, construites par une seule espèce d'organisme. Trois genres additionnels de perforations sont également présents: Trypanites, dans un hardground développé sur une calcarénite dans la partie supérieure de la Formation de Laval, et Ropalonaria et Vermiforichnus dans les coquilles du Brachiopode Mimella imperator Billings. On reconnait deux des ichnofacies de Seilacher: le faciès à Skolithos à l'Ouest, et le faciès à Cruziana à l'Est; le dernier est divisé en un sous-faciès à Rusophycus au centre de la région étudiée et un sous-faciès à Phycodes à l'Est.

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GENERAL GEOLOGICAL SETTING

The Chazy Group is an early Middle Ordovician sequence of shallow marine sandstone, shale, and limestone with a peculiarly provincial fauna. It overlies, without structural discordance, lagoonal, intertidal, and evaporitic,



Figure 5. Synopsis of Chazy ichnofauna in Ottawa-St. Lawerence Lowlands. For definitions of terms referring to ethologic and toponomic classification see Hantzschel (1975, p. W19-W21).

supratidal dolomite and minor shale of the Beekmantown Group. In its type area in the Lake Champlain Valley the Chazy Group is up to 270 m thick (Fig. 6A) and comprises mainly diverse types of limestone, but with several tens of metres of basal terrigenous clastic rocks containing trace fossils (Head and Wait members of the Day Point Formation; Oxley and Kay, 1959).

The Chazy Group thins northward towards Montreal, where it is only about 100 m thick and is known as the Laval Formation; the lower, trace fossil-bearing greenish grey shale and sandstone beds comprise the Sainte Thérèse Member (Clark, 1952; 1972). The carbonate lithologies in the middle and upper parts include crossbedded pelmatozoan calcarenite, lumpy bedded calcisiltite, and shaly limestone, all interpreted as very shallow water deposits. Some of the earliest known coral bioherms are found in the limestone units in a narrow belt extending from northwest of Montreal to the Champlain Valley. Facies changes are frequent, and individual beds commonly cannot be traced from quarry to quarry. The shale and sandstone beds are generally equally variable in thickness and occurrence. Mud cracks are common in facies in which shale and sandstone are intimately intercalated, and channeling is evident, suggesting accumulation on the lower intertidal mud and sand flats.

The thinning trend of the Chazy rocks continues westward, accompanied by the progressive elimination of the carbonate facies, so that the section at Ottawa (Rockcliffe Formation; Wilson, 1946) is about 50 m thick and almost entirely comprises greenish grey and grey, ripple marked and cross laminated sandstone with mud-cracked shale laminae. Farther west near Fitzroy Harbour, the sediments are reddish coloured. For a detailed discussion of the stratigraphy and paleogeography the reader is referred to Hofmann (1963).

The Chazy Group of the Ottawa-St. Lawrence Lowlands can best be interpreted as a complex of estuarine or deltaic deposits prograding eastward into a marine embayment that was localized in the same general area as the present lowlands (Fig. 6B). The influx of detritus from the west was a result of renewed tectonic activity, uplifts that followed a long period of quiescence ending with a widespread dolomite deposition on sabkhas and in shallow platform basins during the Early Ordovician. Subsidence in the east brought more open marine conditions to the eastern portion of the area, permitting an invasion of a diverse marine fauna dominated by brachiopods and echinoderms, but containing calcareous algae, trilobites, ostracodes, molluscs, and, for the first time in the area, scyphozoans, anthozoans, and bryozoans. The debris derived from the skeletons of these various animals accumulated to form the various limestone facies of the middle and upper parts of the Laval Formation, the character of the lithology depending on the relative contribution of the dominant taxa. Trace fossils are not very evident in the carbonate beds, although a general bioturbation is sometimes discernible.



- A. Stratigraphic section of the Chazy Group, showing terrigenous units with trace fossils (stippled pattern).
- B. Sketch map of area in Figure 5, illustrating inferred ichnofacies distribution. Boundaries between facies are highly schematic, and overlap may be more extensive than shown.

Figure 6.

The ichnofossil assemblage here described is predominantly localized in the terrigenous units, particularly where alternating soft shale and hard sandstone are present. The alternating conditions of fine and coarser sedimentation provided the contrast necessary for enhancing the production (in shale) and preservation (by casting in sand) of such structures. The trace fossils are thus found throughout the whole Chazy section in the Ottawa area, but are essentially confined to its lower portion in the Montreal and Lake Champlain areas.

CHARACTER OF THE TRACE FOSSIL ASSEMBLAGE

Figure 5 shows the dominance of crawling traces (Repichnia) and feeding burrows (Fodinichnia) in the assemblage, with *Planolites* sp. being ubiquitous; systematic feeding traces (Pascichnia) are absent. The structures can be assigned to Seilacher's (1967) Skolithos and Cruziana facies. The Skolithos facies is in the west, and the Cruziana facies is divided into two subfacies or assemblages, a Rusophycus subfacies in the centre of the study area, and a Phycodes subfacies in the east (Fig. 6B), reflecting a general bathymetric zonation (Seilacher, 1967; Häntzschel, 1975, p. W32-33), with increasing depth to the east. These facies overlap, and, because of the lateral shifting of lithotopes with time, the geographic positions of each facies varies with stratigraphic position within the Chazy Group.
The Skolithos facies is developed in sandstone rich in lingulid fragments that accumulated in high energy conditions, under the influence of waves and tides and periodic exposure, such as found on wide beaches or tidal flats. Interlaminated sand and shale, sometimes mud cracked and channeled, and containing the Rusophycus assemblage indicate accumulation on more protected lower intertidal flats and in shallow subtidal environments, whereas the Phycodes subfacies may represent slightly deeper waters found in interdistributary bays or depressions.

The provincial aspect of the shelly Chazy fauna suggests considerable isolation of the former embayment, and the belt of coralbryozoan reef from Montreal to the Champlain valley may have been near the general eastern limit of this embayment. Farther east, in the Appalachian area, dark shale accumulated in a deep water basin. Vagrant worms, trilobites, and other animals populated the shallow embayment in addition to the limestoneproducing benthos, but it was generally only on the terrigenous lithotopes where suitable conditions existed for the animals to leave behind a visible record of their activity on and in the seabed.

TABLE 3

Nonboring Chazy ichnogenera and their occurrence in other ichnofaunas

Chazy Group (Middle Ordovician)	Bell Island and Wabana groups (Early Ordovician)	Medina and Clinton groups (Early and Middle Silurian)
Arthraria	Х	х
Caugichnus		
Chondrites		х
Conostichus		х
Cruziana	Х	х
Diplichnites	Х	х
Diplocraterion	Х	х
Isopodichnus	Х	х
Palaeophycus		х
Petalichnus		Х
Phycodes	Х	х
Planolites		
Rhizocorallium?		х
Rusophycus	Х	х
Skolithos	Х	
Teichichnus	Х	
Walcottia?		
17	9	12

The phylogenetic affinities of the originators of the traces lie predominantly with worms and trilobites (Fig. 5); a coelenterate is possibly responsible for one ichnogenus, and a bryozoan for another. From a toponomic point of view, the taxa are chiefly hypichnia (on the underside of sandstone beds), (Martinsson 1965, p. 203; Häntzschel, 1975, p. W19), followed by endichnia (within sandstone beds). Epichnial (on top of sandstone beds) and exichnial (in shale between sandstone beds) taxa are not numerous, however, the exichnial taxon *Planolites* is the most widespread and common trace fossil in the assemblage; it possibly represents several species of originators.

The assemblage can be compared with others representing similar environments (Billings, 1872, 1874; Nautiyal, 1966; Seilacher and Crimes, 1969; Bergström, 1976). The slightly older (Early Ordovician) Bell Island-Wabana assemblage in Conception Bay, Newfoundland appears to be dominated by trilobite traces of the Cruziana facies; at least 9 ichnogenera are in common with the Chazy ichnofauna (Table 3). However, the similarity is greater with the ichofauna of the Medina and Clinton groups (Early and Middle Silurian) of New York State; at least 12 of 17 nonboring ichnotaxa are common to both (Hall, 1843, 1850, 1852; Osgood and Drennen, 1975). It is possible that the similarities among the three ichnofaunas may be even greater, considering that recent publications (Osgood and Drennen, 1975; Bergström, 1976) have concentrated only on the trilobite trace fossils. Planolites burrows should certainly be expected in the other two assemblages, as should Palaeophycus in the Bell Island-Wabana sequence, and Teichichnus, or its analogue, in the Medina-Clinton sequence.

DESCRIPTION OF TRACE FOSSILS

Rusophycus carleyi (James), 1885

Plate 9, Text-figure 7

Cruziana Carleyi James, 1885, p. 155, Pl. 8, fig. 1 Isotelus arenicola Raymond, 1910 (partim), p. 130-132, Pl. 2, fig. 5

Cruziana carleyi Seilacher, 1970, p. 474, fig. 11b Rusophycus carleyi Osgood, 1970, p. 306, 307, P1. 57, fig. 1; P1. 58, fig. 7, 8; P1. 59, fig. 6; P1. 71, fig. 1; Text-fig. 29b

Raymond (1910) described and illustrated "a rather remarkable specimen" from the Rockcliffe Sandstone of the Britannia Bay area in the western part of the City of Ottawa. This spectacular, though abraded specimen is on the upper surface of a sandstone bed (epirelief) showing shallow depressions excavated in ripple marked and crosslaminated medium to fine grained sandstone, and made by 3 different parts of the appendages of what is most likely a species of *Isotelus*.

The impression is preserved as a subelliptical outline approximately 31 by 21 cm, and is thus somewhat larger than the largest known specimen of *Rusophycus* reported by Osgood (1970, p. 307). It comprises an oval, posteriorly



Figure 7. Rusophycus carleyi (James). Line drawing of specimen in Plate 9, showing the various types of markings.



Plate 9

Rusophycus carleyi (James). Epirelief on crosslaminated sandstone, described by Raymond (1910), and attributed by him to *Isofelus arenicola* Raymond. Rockcliffe Formation, south shore of Ottawa River, Britannia Bay section, Ottawa, Ontario. GSC 4328. (GSC photo 202242-T)

pointed central portion of about 13 by 7 cm, containing an axial ridge flanked by 2 longitudinal series of paired impressions of the proximal portions of the legs, 8 large pairs on the thorax, and at least 4 smaller pairs of impressions at the anterior part of the pygidium. The central portion is surrounded by 2 wide, lateral, crescentric lobes with fine scratch marks. The axial ridge is 7 mm wide at the anterior end and tapers to 3 mm wide at the junction of thorax and pygidium. The inner, coxal impressions are transversely elongate and about 15 to 18 mm by 12 mm. The outer longitudinal series of 5 by 10 mm wide impressions (endopodial?) in the central portion is less well preserved; it is contiguous with the inner series, but offset from it, being in advance of the coxal impressions one third to one half the distance between articulations of the pleurae, much like a specimen shown by Osgood (1970, Pl. 57, fig. 1).

The outer portion of the trace fossil, which Raymond (1910, p. 132) did not consider a part of the specimen, comprises 2 flat lateral lobes, each about 6 cm wide, representing the impressions of the distal portions of the limbs. In the anterior portions faint short outwardly and posteriorly directed scratches (of expodia?) are visible.

A faint impression of the posterior part of the hypostoma appears in the cephalic region, marked by 2 symmetrically placed, anteriorly converging ridges and flanking depressions 2 cm long, that join the sides of a trapezium 4.5 cm wide at the back and 2.5 cm wide at the front. The nomenclature of the bilobate traces of trilobites, *Cruziana* and *Rusophycus*, is problematic because these two ichnogenera have been regarded as synonymous and as distinct at various times (Seilacher, 1970; Osgood, 1970; Crimes, 1975; Häntzschel, 1975). I here follow the latter three authors in maintaining separate ichnogenera for short and for long traces, assigning short resting excavations to *Rusophycus* Hall, and longer traces evidencing forward motion to *Cruziana* d'Orbigny.

Rusophycus grenvillense Billings, 1892

Plate 10, A-D

Rusophycus Grenvillensis Billings, 1862, p. 101, 102; 1865, p. 101

Rusophycus grenvillensis Dawson, 1864, p. 363, 458 Rusichnites grenvillensis Dawson, 1890, p. 597, fig. 1 Cruziana grenvillensis Seilacher, 1970, p. 459, 460

Structures assigned to this ichnospecies are found as hypichnial casts in the form of oblong-ovate, bilobate hemispheroidal masses, with a longitudinal median furrow and transverse wrinkles on the lobes, as well as crescentic grooves on the steep sides. The bodies are generally from 5 to 10 cm in length and from 5 to 8 cm in width, but much larger specimens have also been observed. All are composed of medium to coarse grained quartz sandstone without any particular internal structure (Pl. 10, D). They are surrounded by green shale, and represent rapid filling of a biologic excavation in mud. In most specimens the steep flanks converge only very slightly. In more ornate samples (Pl. 10, B)

Plate 10

A-D. Rusophycus grenvillense Billings. A. Stereoscopic view of specimen illustrated by Dawson (1890); anterior at top. Note Diplichnites-like tracks behind distal end, which Dawson considered to have been made by the same animal that made the burrow. (Compare with Bergström, 1976, Fig. 19C). Rockcliffe Formation, Grenville, Quebec. Redpath Museum 592.

B. Side view of burrow with curved lateral markings made by carapace. Anterior at right. Rockcliffe Formation, creek west of Greece's Point, 7 km east-southeast of Grenville, Quebec. GSC 54182.

C. Bottom view of same specimen as B; anterior at top.

D. Transverse section, showing coarse terrigenous fill and greenish grey shale of underlying bed adhering to burrow fill in medial furrow between the two lobes. Same locality as B. GSC 54183.

E. *Petalichnus* sp. Epirelief. Two sets of pit-and-mound imprints of appendages. Lower half of Laval Formation, in interval 11.6-8.9 m below top of Lagacé Quarry, Laval, Quebec. GSC 54184.

F. Walcottia? sp. Convex relief of portion of curved trail in crosslaminated micaceous sandstone with shale partings. Rockcliffe Formation, loose from rubble 65 m west of entrance to filtration plant at Britannia, near Ottawa, Ontario. GSC 54185.

G. *Cruziana? dilatata* Seilacher. Unique specimen preserved in greenish grey shale. Longitudinal markings grouped in lobes over broad area. Lower half of Laval Formation, in interval 31-18 m below top of Lagacé Quarry, Laval, Quebec. GSC 54186.



upward pointing crescentic ridges are visible on the sides, whereas the surfaces of the two convex lobes on either side of the median furrow are sculptured with closely spaced transverse wrinkles that become finer towards the slightly narrower end.

The bodies are best developed and most abundant in the interbedded sandstone and green shale of the Rockcliffe Formation in the Ottawa Valley near Grenville, Quebec and Hawkesbury, Ontario. Those from the Montreal area are not as well formed, and occur sporadically in the lower Laval sandy quartz beds and green shale exposed in the lower part of the Lagacé Quarry, Laval, and in the quarries in the Caughnawaga area.

R. grenvillense has a close resemblance to the more elongate forms from the Silurian of New York which Hall (1852) named *R. bilobatus*. Hall and Billings originally ascribed an algal origin to these bilobites. Dawson (1864) was the first to conclude that the markings are the casts of burrows and tracks of marine animals, probably of trilobites, and he (1890) proposed a new generic name, *Rusichnites*, to emphasize their ichnological origin. However, according to nomenclatorial rules, *Rusophycus* is the valid name.

Seilacher (1960, p. 43) has shown that rusophycoid structures can be produced by polychaetes, gastropods, phyllopods, and trilobites. Each of these is distinct, and, considering their size and morphology, only trilobites are likely originators for the Chazy forms. Dawson's original interpretation of the structures as trilobite burrows is valid. Osgood (1970) has been able to distinguish several morphologic and genetic types of rusophycids, and attributed them to Isotelus, Flexicalymene, and Cryptolithus. The Chazy rocks have not yet yielded specimens with the trilobite preserved, but from comparison with the Cincinnatian material, and a study of the rather poorly preserved Chazy trilobites from southern Quebec, it seems likely that they were made by some asaphids, probably Isotelus.

Cruziana? dilatata Seilacher, 1970

Plate 10, G

Cruziana dilatata Seilacher, 1970, p. 474

A simple, delicate trace is preserved in very fragile green shale interbedded with siltstone laminae. It occupies an oval area 8 by 10 cm, and consists of a series of parallel curvilinear striae 5 to 10 mm long, spaced 0.9 mm apart, and grouped into successive bundles with a maximum of 7 or 8 striae each. The bundles are separated by oblique furrows. The slab shows 2 series of diverging bundles which are concave towards an axial region.

The structure pictured here is interpreted as an incompletely preserved *Cruziana* trail. It probably originated from the activity of an asaphid trilobite. The elaborate appendages, in particular the spiny telepodite segments, brushed against the mud during successive strokes as the animal moved across the sea floor. Although superficially resembling the grazing trail *Dimorphichnus*, it lacks the distinct sigmoidal groove pattern, the pre-tarsal impressions, and the morphological asymmetry of the markings.

The unique specimen was collected loose in a crushed stone pile in the Lagacé Quarry, but comes from the interval 13 to 31 m below the top of the quarry, which is in the lower part of the Laval Formation.

Cruziana sp., cf. C. quadrata Seilacher, 1970

Plate 11, B

Cruziana quadrata Seilacher, 1970, p. 470, Text-fig. 7, ° no. 24

Cruziana cf. C. quadrata Osgood and Drennen, 1975, p. 319, Pl. 4, fig. 1, 3

These structures, preserved as sinuous, crisscrossing convexities on the bottom surfaces of sandstone beds (hyporeliefs), 8-14 mm wide and up to 30 cm long, are attributed to the foraging of small trilobites. Two parallel ridges (casts of endopodial excavations) lie along an axial groove, and each ridge is paralleled on the outside by a lower, but equally wide band made by exopodia or by dragging of the pleurae. Faint transverse to oblique scratch marks are visible in places. The morphology is variable, mainly because of weathering and abrasion due to quarrying. Similar specimens from an unknown locality but probably from the Rockcliffe Formation of the Hawkesbury-Grenville area are deposited in the type collections of the Geological Survey of Canada (GSC 54227 a, b).

The structures illustrated in Plate 11, B occur on the bottoms of large sandstone slabs in the middle of the abandoned quarry on Highway 17, 4.3 km west of Cumberland, Ontario, and are from the lower part of the Rockcliffe Formation. They are remarkably similar in size and form to specimens of *Cruziana* illustrated by Osgood and Drennen (1975, Pl. 4, fig. 1) from Clinton rocks (Middle Silurian) of east-central New York State.

Isopodichnus sp.

Plate 11, C

On the bottom surface of another large slab at the same locality as the quadrilobate *Cruziana* sp., cf. *C.* quadrata illustrated in Plate 11, B, there occur sinuous, bilobate trails (hypichnia), up to several decimetres long, and uniformly between 5 and 7 mm wide. The trails are winding, but not meandering, and cross over themselves and other trails. Some portions of the trails were excavated more deeply, leaving nodes that resemble small forms of *Rusophycus*. The structures were probably made by small arthropods.

The generic assignment of the trails is problematic. Basically, the structures are like very small *Cruziana* or *Crossopodia*, but the scratch markings are not well preserved and appear more transverse than oblique. They do



A. *Diplichnites* sp. Hypichnial trackway, originally illustrated by Raymond (1910, Pl. 2, fig. 4). Illumination from top right. Rockcliffe Formation at Deschênes, Quebec. GSC 7383. GSC photo 202989-E.

B. Cruziana sp., cf. C. quadrata Seilacher. Sinuous, quadrilobate, hypichnial tracks of foraging trilobites in large block from lower part of Rockcliffe Formation, in road cut on Highway 17, 4.3 km west of Cumberland, Ontario. GSC 54187.

C. *Isopodichnus* sp. Long, narrow bilobate hypichnia. Tracks near middle of photo show short *Rusophycus*-like nodes. Large sandstone block from basal part of Rockcliffe sandstone in road cut on Highway 17, 4.3 km west of Cumberland, Ontario. GSC 54188 is fragment from left portion of block.

not seem to be significantly different from trails designated as *Isopodichnus* in the Treatise (Häntzschel, 1975, p. W74), although this generic name has also been used for small *Rusophycus*-like impressions (e.g., <u>see</u> Osgood, 1970, p. 303). I here follow the Treatise and place these small *Cruziana*-like trails in *Isopodichnus* Bornemann.

Petalichnus sp.

Plate 10, E

A single specimen was found on a fine grained sandstone fragment from the lower part of the Laval Formation in the Lagacé Quarry. The trace comprises two converging, slightly curved rows of 8 pits and adjoining mounds approximately 1 mm² in area. Successive pits in the same row are spaced 4 mm apart. The mounds are made of material excavated from the pits, which bear faint trifid irregularities anteriorly. The trace is interpreted as two successive series of steps of the right half of a trackway of a trilobite with 8 pairs of legs with tripartite pretarsal claws (Isotelus?). The structure resembles a portion of P. multipartitum Miller, 1880, illustrated by Osgood (1970, Text-fig. 22A, Pl. 22, fig. 5).

Diplichnites sp.

Plate 11, A

Trails, Raymond, 1910, p. 133, Text-fig. 3, Pl. 2, fig. 4

Raymond (1910) described and illustrated some tracks which can be assigned to *Diplichnites* Dawson, 1873; he attributed their formation to the gnathobases of *Isotelus*. One of the structures, here reillustrated in Plate 11, A, is a trackway, 10 cm long, comprising two series of straight, oblong, paired hypichnial ridges each about 1 cm long, and making an angle between 30° and 80° with the axis of the track; a 3-5 mm wide band separates the two series of ridges. Plate 11, A also illustrates a second trackway, crossing the first at an angle of about 70°. It is composed of two parallel rows of pointed, crescentic hypichnial ridges about 1 cm long, and 2 mm wide near the middle. The two rows are spaced more widely (10-12 mm) than in the first trackway, and one of the rows has double the number of imprints of the other row, suggesting a different origin. In comparison to the first trackway the second trackway could have been made by more distal portions of trilobite legs, with the organism in a tilted position. The third trackway of Raymond (1910, Text-fig. 3) is similar to the first.

Raymond's slab bearing the three specimens (GSC 7383) as well as other indistinct markings, comes from the Rockcliffe Formation at Deschênes, Quebec across the Ottawa River from Ottawa, Ontario.

Walcottia? sp.

Plate 10, F

A specimen questionably assignable to *Walcottia* Miller and Dyer, 1878 is illustrated in Plate 10, F. It comprises an incomplete, curved, slightly tapering convex hyporelief, up to 9 mm wide, and possessing 2 paired rows of closely spaced, oblique lanceolate lobes; the two rows are separated by a medial longitudinal depression. The lobes have dimensions averaging 3 by 1.5 mm, and a maximum relief of about 0.5 mm; they are paired and make obtuse angles of about 135°. The portion of the trace with the paired lobes is 2 cm long and merges, in the direction of the apices made by the lobes, with an indistinct, narrow appendage 3-5 mm wide and of indeterminate length.

The origin of structures assigned to Walcottia is problematic (Osgood, 1970, p. 379; Häntzschel, 1975, p. W189). The present specimen is not too well preserved and there is no further evidence to clearly demonstrate either an annelid or arthropod origin. The structure could be a *Cruziana*-like trail made by proximal portions of trilobite legs, such as suggested by Raymond (1910, p. 133) for *Diplichnites* sp.

Plate 12

A. Planolites sp. Exichnial burrow fillings; view from below. Ste. Thérèse Member, Laval Formation, Rivermont Quarry, Caughnawaga, Quebec. (Quarry E-7 in Clark, 1972, Map 1737. Interval between Unit C_{23} and C_{28} in Hofmann, 1972, Fig. 9). GSC 54189a.

B. Planolites sp. Vertical section of same specimen as A.

C. *Planolites* sp. Sinuous exichnial burrow fill. Specimen considerably more flattened than those in A-C. In reddish micaceous shaly sandstone of Rockcliffe Formation; just north of bridge over Carp River, Fitzroy Harbour, Ontario. GSC 54190.

D-H. Palaeophycus tubulare Hall. Burrow fillings from lower half of the Laval Formation interval 23.6-31.3 m below top of Lagacé Quarry, Laval, Quebec. (Quarry C-5a in Clark 1972, Map 1737). D and E are cross sections; location of E shown by markers in F. Note faint scratch marks at bottom of F, reminiscent of *Trichophycus*. GSC 54191 (D), 54192 (E-F), 54193 (G), 54194 (H).



The specimen was collected 65 m west of the entrance at the east end of Cassels Street from loose rubble excavated during the construction of the water filtration plant at Britannia, in the west end of Ottawa. It is preserved in grey fine grained, cross laminated and ripple-marked micaceous sandstone with greenish grey shaly partings, which occurs with interbedded mudcracked shale and shalechip conglomerate lenses. Associated trace fossils are *Planolites*, and arthropod scratch marks.

Palaeophycus tubulare Hall, 1847

Plate 12, D-H

Palaeophycus tubularis Hall, 1847, p. 7, 8, Pl. 2, fig. 1, 2, 4, 5

Palaeophycus tubulare Osgood, 1970, p. 373, 374, Pl. 76, fig. 8; Pl. 77, fig. 1, 4, 7 (see this reference for extensive synonymy)

These burrow casts are found in the lower terrigenous part of the Laval Formation as straight to gently curved, flattened horizontal cylinders of fine grained calcareous sandstone, 6-13 mm wide, 2-12 mm thick, and up to 10 cm long. The pipes have elliptical to semicircular cross sections, and their lower surface, where in contact with underlying dark greenish grey shale, is sculptured with low irregular swellings and annular corrugations which are oblique to the longitudinal axis. Some specimens (Pl. 12, F, H) have faint delicate markings preserved similar to those found on Trichophycus and are suggestive of arthropod or annelid scrapings (compare with fig. 11 in Seilacher and Meischner, 1964). The rods have

blunt, round, upturned ends, and some show apparent branching at very acute angles. The structures are not preserved well. Compaction and diagenetic alteration by overgrowth of pyrite crystals on the lower surfaces has partly obliterated the delicate markings.

Osgood (1970, p. 375-376) has discussed possible ways of distinguishing *Planolites* from the morphologically similar *Palaeophycus*, namely on whether the lithology of the burrow filling is essentially the same as that of the host rock (*Palaeophycus*) or markedly different (in *Planolites*), and whether the material of the filling has passed through the gut (*Planolites*) or is a passive filling (*Palaeophycus*). Alternatively, Alpert (1975, p. 512) distinguished the two ichnogenera by the presence (in *Palaeophycus*) or absence (in *Planolites*) of true branching.

The problem is further complicated in the present material because the sand-filled structures sometimes occur along the shalesandstone interface, and may pass entirely into one or the other host lithology. They thus might be assigned to either ichnogenus at the same time, because the upper portion of the horizontal cylinder may be in a sandstone and the lower in a shale host rock. The structures best fit the description for Hall's *Palaeophycus tubulare* and are here assigned to Hall's taxon.

The cylinders are thought to be crawling or feeding burrows of arthropods or worms.

Specimens were found in the lower half of the Lagacé Quarry in Laval, and in the Rivermont Quarry at Caughnawaga 4-6 m below the top of the quarry.

Plate 13

A. ?Rhizocorallium auriforme (Hall). Worm's eye view of horseshoe-shaped exichnial burrow casts. Arrow indicates possible spreite. Hawkesbury, Ontario, 40 m south of corner of Portelance Avenue and Taché Boulevard. GSC 54195a.

B. *Diplocraterion parallelum* Torell. View from above, showing cross sections of specimens with protrusive spreiten. Black line indicates section shown in D. Same locality as A. GSC 54196a.

C. Same specimen as B, seen from below. Black line indicates section shown in D.

D. Vertical section of specimen in B, C, showing spreite in longitudinal section.

E. Vertical section of specimen in B, C, along left margin of B and right margin of C.

F-H. Arthraria antiquata Billings. Three convex hyporeliefs from Rivermont Quarry, Caughnawaga, Quebec, interval 17.0-19.2 m above base of Laval Formation. GSC 54197 (F), 54198 (G), 54199 (H).



Planolites sp.

Plate 12, A-C

?Scolithus sp. Ami, 1887, p. 304-306 Worm burrows? Wilson, 1932, p. 378, Pl. 1, fig. 3, 4 For extensive synonymy see Alpert, 1975, p. 512

Perhaps the most abundant, yet also most nondescript type of trace fossil in the Chazy Group are horizontal curved exichnial burrow fillings between 0.5 and 5 mm across, and up to a decimeter or more long. They occur in a criss-crossing, often spaghetti-like network, whose unsystematic pattern permeates dark greenish grey shale beds and laminae. Through compaction of original mud, the more rigid, fine grained calcareous burrow fillings became pressed and slightly deformed by juxtaposed burrow fills, giving them a somewhat irregular appearance. Where shale layers between sandstone layers are thick (Pl. 12, A, B) the cross sections are subcircular, but where thin, the cross sections are strongly flattened ellipses (Pl. 12, C).

On the basis of the contrasting host and burrow lithologies and the absence of branching (Pl. 12, B) the structures are assigned to *Planolites* Nicholson. They probably represent the former activity of small marine worms.

The burrows occur throughout the terrigenous part of the Chazy Group, between Fitzroy Harbour, Ontario, in the west (A, Text-fig. 5) and La Carrière-St. Pie Hill in the east (V, W, Text-fig. 5); they are particularly abundant in certain units in the Montreal area.

?Rhizocorallium auriforme (Hall), 1843

Plate 13, A

Fucoides auriformis Hall, 1843, p. 47, Pl. 1, fig. 2; 1852, p. 7, Pl. 3, fig. 4

Included here are small, unbranched, C-, G-, J-, S-, and U- shaped exichnial burrow casts, with a plane of curvature essentially parallel. to bedding, and upturned ends. The most common form is that of a miniature horseshoe. The casts are 0.8-2.5 mm thick, have spans of 4-15 mm and are composed of fine sand- or siltsized particles; they are imbedded in greenish shale layers in the lower terrigenous portions of the Chazy Group, particularly at levels where shale and fine grained sandstone are intimately interlaminated. Some of the larger specimens show faint annulations or irregularities. The structures resemble short burrows of Rhizocorallium, but the spreiten are not evident, and they exhibit configurations other than those of the letters U or C. The appearance is similar to structures shown by Hall (1843, 1852) under the name Fucoides auriformis which, however, are more sharply defined, and cast in coarser material. I have re-examined Hall's material, and consider it to represent burrows with protrusive spreiten. However, because the spreiten are not evident in the present material, the Chazy burrows are questionably referred to Rhizocorallium auriforme.

The diameters of the Chazy tube casts are in the range of those for *Planolites* sp. illustrated in Plate 12, A-C, and it is possible that both could have been made by the same species of worm, but that they represent different behaviours.

The horseshoe shaped casts were found at Hawkesbury, Ontario about 40 m south of the intersection of Portelance Avenue and Taché Boulevard, and in the lower half of the Lagacé Quarry near Montreal, Quebec.

Diplocraterion parallelum Torell, 1870

Plate 13, B-E

Diplocraterion parallelum Torell, 1870, p. 13 Diplocraterion parallelum Fürsich, 1974, v. 48, no. 5, p. 958, 959 (see this reference for extensive synonymy)

Vertical, spreite-bearing U-tubes are abundant in certain shaly sandstone beds in Hawkesbury and near Cumberland, Ontario. They are 2-5 cm wide, with arms 4-8 mm thick, and are relatively shallow (less than about 2 cm deep), being truncated by diastems and other burrows. The base of the U is flattened, presenting a subangulate outline of the U in vertical section, possibly in part due to compaction of intercalated shale laminae; spreiten are both retrusive and protrusive.

The structures are generally seen as randomly oriented, elongate convex hyporeliefs similar to those illustrated by Hall (1852, Pl. 9, fig. 4) from the Clinton Group (Silurian) of New York. In transverse sections they are dumbbell shaped, with smooth transitions between cross-bar and the two ends, in contrast to the abrupt contacts exhibited in bedding plane views of *Arthraria antiquata*. The Chazy forms are classified as *D. parallelum* according to the criteria set out by Fürsich (1974). They are interpreted as dwelling burrows of marine worms living in an environment experiencing pronounced variations in sedimentation and erosion.

Arthraria antiquata Billings, 1872

Plate 13, F-H

?Root of marine plant, Hall, 1852, p. 25, Pl. 10, fig. 6

Arthraria antiquata Billings, 1872, p. 467, fig. 2; 1874, p. 66, fig. 33

?Arthraria rogersensis Foerste, 1924, p. 79, P1. 4, fig. 5

Arthraria antiquata Bergström, 1976, p. 1630

Included here are dumbbell shaped hypichnia, about 2-2.5 cm long, composed of discoid to oblate spheroidal extremities 3-6.5 mm in diameter, and connected by an 8-12 mm long stem 2-3 mm across. Some individuals (Pl. 13, F, G) show that tubes, filled with the same material and diameter as the connecting stem, extend upward from the bulbous extremities for a short distance. The dumbbell is thus the bottom end of a U-tube.



Conostichus sp. A-C. Side, top, and bottom views of incomplete specimen from lower half of Laval Formation, in sandstone interval 12-13 m below top of section in Bédard Quarry, Caughnawaga, Quebec (Quarry E-8 in Clark, 1972, Map 1737). GSC 54200a-d.

D, E. Vertical and horizontal polished sections of sandstone exhibiting the characteristic funnel-in-funnel structure. Specimens from about 19.5 m below top of former Cap St. Martin Quarry, Laval, Quebec (Quarry B-6 in Clark, 1972, Map 1737), just west of intersection of Hwy 117 and Côte St. Elzéar. GSC 54201a (D), and 54202a (E).

F, G. Axial thin sections of two specimens showing detail of the dark argillaceous and somewhat bituminous laminae in the calcareous sandstone. Same locality as D, E. Rectangle in F is outline of field in H. GSC 54203a (F), and 54204a (G).

H. Enlargement of rectangle in F.

Osgood (1970, p. 323) attributed Arthraria antiquata Billings to Corophioides, and Bergström (1976, p. 1630, 1632) considered Arthraria a junior synonym of Diplocraterion; both genera have spreiten. Dumbbell structures are also described under the name Bifungites Desio, possibly a junior synonym of Billings' taxon. Gutschick and Lamborn (1975) and Osgood (pers. comm., Aug. 1977) consider Bifungites to be without spreiten, and therefore a distinct genus. The specimens in the present collection are preserved in very thin layers, separated by diastems; the upper portions of the tubes are not present. It is thus not possible to determine whether they are burrows with spreiten of Diplocraterion biclavatum type, or simple burrows without spreiten of *Bifungites* type. Therefore, the dumbbells are assigned to Arthraria antiquata Billings, with which description they accord best.

The structures are found in interlaminated fine grained calcareous sandstone and dark greenish grey shale of the lower part of the Laval Formation in the Rivermont Quarry at Caughnawaga, Quebec, in the interval 17-19.2 m above the base of the Laval Formation.

Conostichus sp.

Plate 14, A-H

These endichnial structures are fluted cones or pear-shaped bodies composed of fine grained sandstone, 5 to 10 cm across at the top, tapering downward to a diameter of 3 or 4 cm. The top surface is convex and smooth, and bears

faint concentric wrinkles and a shallow central depression. Specimens generally break into oblate or top-shaped bodies, the undersides of which bear straight, curved, or branching crenulations that extend upward and outward. Thin and polished sections of axial planes exhibit a characteristic funnel-in-funnel structure, produced by alternating curved, conical laminae of argillaceous and fine arenaceous materials which are continuous with and pass into horizontal bedding planes. Transverse sections show the stacked tunnels as wrinkled concentric bands. Specimens of this type were found in the quartz-sandy beds of the lower part of the Laval Formation in quarries of the Cap St. Martin area, and in the Bédard Quarry at Caughnawaga, Quebec.

The structures are assigned to Conostichus Lesquereux on the basis of their general resemblance to Pennsylvanian forms described by Branson (1960, 1961, 1962), Pfefferkorn (1971), and Chamberlain (1971). The main distinction is in the ornamentation on the lower surfaces. None of the specimens from the Chazy displays the duodecimal starlike pattern on the basal surface. However, the differences in ornamentation may be due to the fact that complete specimens were not obtained, or the result of different morphology of the originator. At least 10 species of Conostichus have been named, but as Branson (1960, p. 195) suggested, the specific names reflect stratigraphic and geographic position more than they do morphology. The Chazy specimens most closely resemble C. broadheadi illustrated by Pfefferkorn (1971, Pl. 101).

Plate 15

A-E. *Skolithos gyratus* n. sp. Specimens from abandoned railway cut 40 m north of intersection of Howe Street and Poulin Avenue, Ottawa, Ontario.

A. Weathered longitudinal section, showing corkscrew-like sand filling inside weathered-out argillaceous lining. Holotype, GSC 54205.

B. Another weathered longitudinal section. GSC photo 200446-E. Paratype, GSC 54206.

C. Polished longitudinal section showing axial sand filling inside light greenish grey argillaceous lining, surrounded by slightly darker envelope representing altered, more irregular contact zone with host sediment. Paratype, GSC 54207a.

D. Polished transverse section of several tubes, showing concentric arrangement of fillings reminiscent of *Monocraterion*. Paratype, GSC 54207a.

E. Longitudinal section of specimen with pink calcite (light grey in photo) filling tube inside sandstone, which itself is within argillaceous lining. Sand was prevented from filling part of tube (organism died in place?). Paratype, GSC 54208.

F. Chondrites antiquatus (Hall). Specimen of "Bythotrephis? chazyensis" described by Wilson (1932, Pl. 1, fig. 1). Shore of St. Lawrence River near Cornwall, Ontario. GSC 6521a. GSC photo 201556-W. (Original photo in Wilson is GSC photo 72170).

G. Chondrites antiquatus (Hall). Bedding plane view (portion of base of specimen in H). Abandoned railway cut 40 m north of intersection of Howe Street and Poulin Avenue, Ottawa, Ontario. GSC 54209.

H. Same specimen as in G; vertical section.



Forms assignable to *Conostichus* have been reported from the Middle Silurian of central New York State (Hall, 1852, p. 21, 22, Pl. 7, fig. 2a-2c; Pl. 10, fig. 4?, 9a, b, 10), the Lower Devonian of Bolivia (King, 1955, p. 159), and the Lower Cretaceous of Alaska (Imlay, 1961, p. 39, Pl. 1, fig. 1, 2, 9, 10).

The specimens from the Pennsylvanian have been variously interpreted as algal structures, sponges, trace fossils, plants, and scyphomedusan casts (see Pfefferkorn 1971, p. 888). Hall (1852, p. 21, 22) has interpreted the Silurian forms as seaweed swirls or root impressions. As the patterns of the Chazy specimens are irregular, little can be said about the morphology of their originator. The structures are not body fossils inasmuch as the argillaceous laminations transect them. The laminae record successive upwardly displaced positions of the animal as it kept pace with the increments of accumulating fine sand to prevent excessive burial.

The method of construction may be as Chamberlain (1971) has inferred, or by periodic movements such as Schäfer (1972, p. 369) has described for modern sea anemones living in sediment. The Chazy fossils are here interpreted as retrusive conical dwelling burrows of coelenterates or worms.

Skolithos gyratus n. sp.

Plate 15, A-E

?Scolithus Ami, 1887, p. 305

Peculiar isolated, slender cylindrical burrows occur in the lower medium grained sandstone of the Ottawa area. The structures are straight and unbranched, 2.5-4 mm across, up to at least 10 cm long, and contain a greenish argillaceous lining which in turn surrounds a twisted, screwlike filling of sand indistinguishable from that of the host rock; the inner screw may itself contain an axial filling of pink calcite, perhaps the replacement of the original softbodied invertebrate that inhabited the burrow, and whose body may have prevented the infiltration of sand. On weathered surfaces the argillaceous lining has disappeared, bringing out the distinct and characteristic screw-like filling which has a pitch of 1.5-2 mm. None of the specimens obtained show the upper or the lower termini, leaving the full morphology of this trace fossil undisclosed.

The structures may have been made by worms. They resemble *skolithos*, *Tigillites*, and *Monocraterion* in occurrence and morphology. According to Alpert (1974) and Häntzschel (1975), *skolithos* tubes may be finely annulated, *Tigillites* can be annulated but without special lining, and *Monocraterion* has funnel-shaped tops and no annulations. The present structures are assigned to *Skolithos*, but differ somewhat from previously described species by their characteristic and prominent twisted axial filling and argillaceous lining. They are thus distinct and are here assigned to a new ichnospecies, *Skolithos gyratus*. Ami (1887, p. 305) reported finding a species of "Scolithus" in the same rocks in the same general area as the new taxon, but because he did not mention any readily apparent twisted structures, it is unknown whether he dealt with the same structures. No collection is available for restudy of his material. He may have found burrows that could now be attributed to Chondrites, also common in these rocks.

Diagnosis of ichnospecies: Isolated, slender, erect, unbranched cylindrical endichnial burrow in sandstone, with millimetric diameter, centimetric to decimetric length, and containing an argillaceous lining which surrounds a screw-like or annulated axial filling of 2/3 to 3/4 the outer diameter of the burrow. Outside diameter 2.5-4 mm, pitch (distance between two successive threads of screw) 1.5-2 mm.

Type specimens: Holotype, GSC 54205; Paratypes, GSC 54206-54208.

Type locality: Abandoned railroad cut 40 m north of the intersection of Howe Street and Poulin Avenue near Britannia Bay in the western end of Ottawa, Ontario (45°22'02"N, 75°47'38"W).

Type horizon: Rockcliffe Formation.

Type lithofacies: Brownish to greenish grey, ripple marked, medium grained, thin bedded, phosphatic, noncalcareous quartz sandstone.

Name: The name is given in reference to the twisted axial filling (L.gyro = turn around).

Caugichnus caughnawagensis n. gen. et n. sp.

Plates 16, 17; Text-figure 8

Phycodes Hofmann, 1972, p. 23; Clark <u>et al.</u>, 1972, p. 31

A very characteristic yet enigmatic type of trace fossil occurs in the basal massive, bioturbated sandstone of the Ste. Therese member of the Laval Formation in the Rivermont Quarry at Caughnawaga, Quebec. The structures



Figure 8. Line drawing of *Caugichnus caughnawagensis* n. gen. et n. sp.

are best seen on sandstone-shale interfaces at several horizons, and are particularly noticeable at the Chazy-Beekmantown contact. Blocks of massive sandstone with surfaces showing the structures are used to fence the ramps in the quarry.

The traces occur as variably oriented, lanceolate or canoe-shaped convex hyporeliefs 5-10 cm long, 0.5-1.5 cm wide, and 0.5-2.5 cm relief. Each structure is a composite "system" of shallow, bundled vertically oriented arcuate burrows, 1-3 mm across, which diverge laterally and upward in a manner that superficially is suggestive of a double-ended Phycodes flabellum. The burrows become endichnial, extending into the overlying sandstone, which is so heavily churned up that bedding is no longer recognizable. Their upward extent, however, is very limited, inasmuch as the individual hypichnial convexities (Pl. 17, A) are no longer identifiable in a horizontal section 2-4 cm higher up (P1. 17, B). The lanceolate convexities are closely spaced and distributed fairly uniformly, with local preferred orientation (Pl. 16, B), and there is little crossing of individual "systems". Internally, each structure looks different; there is no uniformity, and the external structure poorly reflects the detail of the unsystematic, but well aligned interior arrangement of the composing individual tubes in the "system" (Text-fig. 8). Whereas endichnial U-shaped systems apparently made by the same type of organisms slightly higher in the sandstone bed exhibit spreiten, both retrusive and protrusive (P1. 17, F), the shallow bottoms of the U-tubes that form the canoe-shaped hyporeliefs are both with and without spreiten. This, together with the presence of tubes of different diameters, indicates multiple entry and more than one organism, and aids in distinguishing these structures from Phycodes.

Whereas the individual 1-3 mm arcuate burrows could be alternatively assigned to Arenicolites and to Diplocraterion, depending on whether they possess spreiten, a bundled multiple entry arrangement such as here illustrated has not, as far as I know, been described heretofore. Inasmuch as this trace fossil is abundant and a characteristic constituent in the basal 10 m of the Chazy rocks at Caughnawaga, and in view of Osgood's (1970, p. 295) and Häntzschel's (1975, p. W24) comments on the potential loss in the literature of forms that remain unnamed, it seems useful to endow it with its own name. I would like to reiterate that this is a compound structure, whose external morphology is no index of internal consistency, and only in a general way reflects its interior organization. The patterns were probably made by worm-like organisms burrowing in the sand, and more than one individual could be involved in the formation of one structure. The localization of the first entry may have been more or less random, but subsequent visits could have been influenced or guided by the existing burrows.

Diagnosis of new ichnogenus: Centimetric canoe-shaped hypichnia; composite, multipleentry system of bundled shallow, subparallel to cross cutting, upright, arcuate burrow fills; structure externally projecting an appearance of organization, but disorganized internally. Individual burrows smooth, of millimetric diameter and with or without spreiten.

Type ichnospecies: Caugichnus caughnawagensis (monotypic).

Type specimens: Holotype, GSC 54210; paratype, GSC 54211 a-e.

Type locality: Rivermont Quarry, Caughnawaga, Quebec.

<u>Type horizon</u>: Ste. Thérèse Member, Laval Formation. Base of Unit C₁ of Hofmann (1972, p. 22).

Type lithology: Medium grained, massive grey sandstone, in contact with brownish black dolomitic shale.

Diagnosis of ichnospecies: As for ichnogenus.

Name: The generic name is a combination of the first syllable of Caughnawaga and the suffix-*ichnus*, designating a trace fossil. The specific name indicates its occurrence at Caughnawaga. (Caughnawaga = "village of the rapids" in Iroquois).

Chondrites antiquatus (Hall), 1847

Plate 15, F-H

Buthotrephis antiquata Hall, 1847, p. 8, Pl. 2, fig. 6 ?Scolithus Ami, 1887, p. 305 Bythotrephis? chazyensis Wilson, 1932, p. 377, 378, Pl. 1, fig. 1, 2

From the Rockcliffe Formation in the Cornwall, Ontario area, Wilson (1932) described and illustrated branching, flattened cylindrical structures which she interpreted as algae. The present collections include material from the same formation in the Ottawa and Hawkesbury areas.

The structures comprise greenish, mudfilled burrow systems in grey sandstone, with horizontal, oblique, and vertical shafts 0.8-1.6 mm across. Segments between branches are 4-11 mm long, and the angle of branching is generally of the order of 45-75°. The socalled discs reported by Wilson, 1-1.5 mm in diameter, are not floats or sporangia, but cross-sections of inclined burrows which can be seen to pass across the bedding. The burrows are not distinctly different from those described by Hall from the Beekmantown or Chazy in northern New York State, and are therefore placed in synonymy with Hall's ichnospecies. They are probable feeding burrows of worms.



A. Caugichnus caughnawagensis n. gen. et n. sp. Convex, canoe-shaped hypichnia at the Beekmantown-Chazy groups contact. Large block in Rivermont Quarry, Caughnawaga, Quebec. Base of unit C_1 in Hofmann, 1972, Fig. 9. The slight preferred orientations of specimens on this slab is given in B.

B. Analysis of orientation of hypichnia shown in A. Rose diagram at centre gives overall orientation of 283 specimens; roses at corners show orientations in each quadrant of A.

Plate 17

Caugichnus caughnawagensis n. gen. et n. sp. Burrows in basal quartz sandstone of Ste. Thérèse Member, Laval Formation; Rivermont Quarry, Caughnawaga, Quebec (Quarry E-7 of Clark, 1972, Map 1737; Base of Unit C₁ in Hofmann, 1972, Fig. 9).

A. Bottom view of Chazy-Beekmantown groups contact, showing bundled, canoe-shaped hyporeliefs of shallow U-tubes protruding from basal bed of St. Thérèse sandstone. Holotype, GSC 54210a.

B. Polished surface parallel to bedding at level indicated in F, showing the pervasive bioturbation at a level 2-4 cm above the formational contact. Holotype, GSC 54210b.

C-E. Polished horizontal sections, showing disorganized interior a few millimetres above base of hypichnia. Paratype, GSC 542lla (C); 542llb (D); 542llc (E).

F. Vertical section along top of view in A. Triangular marks indicate level of section B. Base of specimen is Chazy-Beekmantown contact. Some exhibit spreiten (s).



Teichichnus sp.

Plates 18, 19; Text-figure 9 (partim)

Criss-crossing, mostly rectilinear, horizontal burrows with retrusive spreiten occur in shale and on the bottom surfaces of the sandstone layers in the eastern part of the Ottawa-St. Lawrence Lowland. They are preserved as sandstone rods 3-5 mm across, up to 12 mm high, and up to 15 cm long, with longitudinal striations where the retrusive spreiten intersect the lateral margins. Local flexures occur where one burrow overlies another, due to draping which is the result of differential compaction of the sandstone filling and the enclosing shale (Pl. 19, I). On a few rods delicate, transverse to oblique, chevron-like striations are preserved (P1. 19, K), spaced a millemetre or less apart. The cross-section of the uppermost and last burrow in the system is generally circular (P1. 19, C), suggesting a worm-like originator.

The structures are found association with *Phycodes reniforme* n. sp. Indeed, some burrows which would be referred to *Teichichnus* sp. if found isolated, can be traced directly into the kidney-shaped swellings of *Phycodes reniforme*. These are discussed further under that name.

Phycodes reniforme n. sp.

Plates 18, B, 19, A-D; Text-figure 9 (partim)

On certain bedding planes in the lower terrigenous parts of the Laval Formation there occur peculiar burrow systems (convex hyporeliefs), showing a tripartite organization that includes as its elements the ichnogenera Teichichnus Seilacher and Phycodes Reinhard Richter, as well as a terminal portion for which no formal name exists. The structures comprise randomly oriented burrow systems, each composed of a rectilinear, horizontal, retrusive burrow indistinguishable from Teichichnus sp., which passes at one end into an anchor-like phycodean portion, which, in turn, merges distally with a large crescentic or kidney-shaped terminus that is composed of closely crowded (nested) disc-like or lenticular bodies. Such distal crescentic swellings and lenticular structures do not appear to have been recorded heretofore.



Figure 9. Line drawing of *Phycodes reniforme* n. sp. and *Teichichnus* sp.

The teichichnian elements of the system vary from 3-5 mm in width, and are up to 12 mm high. These dimensions are the same as those of *Teichichnus* sp.; they attain, however, lengths of up to 30 cm and are thus more complete structures. The phycodean element to which they connect is relatively short, several centimetres at the most. The distal crescentic swelling is of the order of 8-14 cm by 5-8 cm. The nested lenticular bodies at the termini of individual burrows are 5-12 mm across.

It is evident that the burrows under discussion form a complex system composed of 3 distinct parts, two of which have formal names, yet each presumably made by the same organism. A comparable situation has been reported for a Jurassic assemblage of Teichichnus-Phycodes (Häntzschel and Reineck, 1968, p. 26). A nomenclatorial problem thus exists: to which ichnotaxon should these structures be assigned? Personal choice favours assignment to Phycodes, which has priority, with the concomitant erection of a new ichnospecies to express and accommodate the complex ethologic and morphologic character of the burrow system. Isolated teichichnian burrows without distal phycodean elements are referred to Teichichnus sp.

Plate 18

A. Teichichnus sp. Criss-crossing hypichnia, Laval Formation, lower part of Lagacé Quarry, Laval, Quebec.

B. *Phycodes reniforme* n. sp. General view of lower surface of large block, showing variable orientation of more than a dozen specimens. The structures are tripartite hyporeliefs, composed of 1) more or less rectilinear teichichnian burrows, 2) bundled, anchor-like subterminal bifurcations, and 3) nested terminal crescentic swellings. The specimens labelled a, c, and d are illustrated in greater detail in Plate 19A, C, and D. Loose block of interbedded sandstone and shale in lower half of Laval Formation from lower part of Bédard Quarry, Caughnawaga, Quebec (Quarry E-8 of Clark, 1972, Map 1737). Holotype, GSC 54213; paratypes, GSC 54215a, 54216b.



Phycodes reniforme n. sp. and Teichichnus sp. from lower half of Laval Formation of the Montreal area. Bédard Quarry, Caughnawaga (A-D, K) and Lagacé Quarry, Laval, Quebec (E-J, L).

A. *Phycodes reniforme* n. sp. Convex hyporelief of body outlined in upper right of Plate 18, B, showing the tripartite arrangement of the terminal portion of teichichnian burrow with phycodean branching pattern and kidney-shaped burrow system of closely packed, disk-like bodies. GSC 54213

B. Phycodes reniforme n. sp. Another, smaller convex hyporelief with more pronounced disc-like termini on diverging branches. GSC 54214.

C. *Phycodes reniforme* n. sp. Vertical section of specimen outlined at the bottom of Plate 18, B, illustrating cross section of disk-like termini, and crossed by a later, retrusive teichichnian burrow. GSC 54215a

D. *Phycodes reniforme* n. sp. Vertical section across diverging, retrusive branches in specimen shown in Plate 18, B to the left of centre. GSC 54216b

E-J. Side views of short portions of *Teichichnus* sp. From interval 31-33 m below top of Lagacé Quarry, Laval, Quebec. GSC 54217a-f.

K. Bottom view of teichichnian burrow with fine, oblique, lateral corrugations. Lagacé Quarry, Laval, Quebec. GSC 54218.

L. Polished vertical section of block replete with *Teichichnus* sp. GSC 54219



to permit definite conclusions concerning the taxonomic position of the originators, although circular cross section, size, striae, regularly curving branches and habitat would make marine worms likely contenders. The systems are interpreted as feeding burrows.

Diagnosis of new ichnospecies: Phycodes with distal, kidney-shaped swelling containing disc-like or lenticular terminal enlargements of individual branches of a tunnel system emanating from a proximal, rectilinear teichichnian burrow.

Type specimens: Holotype, GSC 54213; paratypes, GSC 54212, 54214, 54215, 54216.

Type locality: Lower half of Bédard Quarry, Caughnawaga, Quebec.

Type horizon: Lower half of Laval Formation.

Type lithology: Interbedded greenish grey shale and medium to fine grained sandstone and siltstone.

Name: In reference to the presence of the kidney-shaped swelling (L. ren = kidney).

Phycodes sp.

Plate 20

Included in this category are fan-shaped feeding burrows (probably of worms) comprising slightly curved, but distally nearly straight, bundled, diverging horizontal burrows 2-3 mm wide. The burrows are smooth, emanate from a proximal teichichnian portion, branch repeatedly at very acute angles, and are preserved as convex hyporeliefs in sandstone. Terminal portions of individual cylinders are blunt, sometimes slightly swollen with respect to more proximal portions. The fan-like arrangement has a radius of about 8-12 cm.

This taxon is morphologically distinct from P. reniformen. sp., which differs by its shorter, more anchor-like branches and the presence of the large kidney-shaped terminus.

Not enough evidence is available at present It more closely resembles structures from the Cambrian and Jurassic illustrated by Seilacher (1955, Pl. 23, fig. 3, 4), which were compared by him to Buthotrephis palmata Hall, 1852 and considered to belong to Phycodes. P. palmatum from the Silurian of New York State, however, has much larger burrows reaching 2 cm in diameter (Osgood, 1970, p. 342).

> The structures have been found only at one locality, as loose fragments from an undetermined interval in the lower half of the Lagacé Quarry, Laval, Quebec.

Trypanites sp.

Plate 21, A-E

The fossils described under this name are borings, made after lithification of the sediment, and hence are distinct from burrows which originated in unconsolidated sediment. Although some geologists would not consider borings as trace fossils for this reason, it is expedient to include them here, for they provide useful information about paleoenvironments. In particular, they show that sufficient time elapsed, for diagenesis to proceed, resulting in the consolidation of the sediment (development of hardground) before the formation of the etching traces. The structures may record the presence of a disconformity (Bromley, 1975).

The borings in question are cylindrical, unbranched tubes in coarse calcarenite, filled with argillaceous dolomitic siltstone containing dark phosphatic grains. With circular apertures of 0.8-1.0 mm at the top, they cut sharply across grains, and extend downwards vertically or obliquely for up to 1 cm depth, enlarging gradually to sac-like endings 1.5 mm across. A multitude of these tubes, about 20-35 tubes/ cm² penetrate the upper surface of the St. Martin calcarenite unit in the St. Vincent de Paul Quarry (at the 18.0 foot level in Fig. 8 of Hofmann, 1963, p. 288)



Phycodes sp. Hyporelief from lower half of Lagacé Quarry, Laval, Quebec. GSC 54220a.

The clean, cutting relationship with grains of the matrix, their morphology, and their extreme abundance in a single upper bed surface leave little doubt that they are etching traces made after consolidation of the skeletal lime sand. The borings were later filled with terrigenous, dolomitic and phosphatic material. The relationship shown on Plate 22, E suggests that the borings were produced by solution rather than by biomechanical abrasion.

Perkins (1966, p. 631), who suggests that such borings in carbonate sequences imply breaks with histories of emergence, lithification, and resubmergence, distinguished several types of borings, namely those made by molluscs, sponges, worms, barnacles, and isopods. The producers of the Chazy borings are not known though worms seem a reasonable choice, considering their size and shape.

Vermiforichnus sp.

Plate 22, A-F

Small, straight to slightly curved, distally enlarging sac-like cylindrical borings with circular cross section (Vermiforichnus Cameron, 1969) are abundant in valves of the large brachiopod Mimella imperator (Billings), 1859. They are preferentially developed in the posterior, thickest part of the valves, and have their apertures on the interior as well as on the exterior surface of the shell. The shells in which the borings are developed are disarticulated but not very abraded, and are preserved in olive green, parallel-laminated shaly sandstone of the Rockcliffe Formation, commonly with their convex side up. Differential chemical weathering has left moulds of the interior and exterior of the valves, and exposed the casts of the borings as well as the borings of other organisms (see under *Ropalonaria* sp.). The *Vermiforichnus* borings are perpendicuhar, oblique, and parallel to the valve surface, and are generally between 0.2 and 1 mm in diameter, although sac-like endings may be slightly wider (Pl. 22, C); they are up to 11 mm long.

These borings have been found only in the Rockcliffe Formation, at the northeast corner of the intersection of Highways 17 and 34, at Hawkesbury, Ontario.

It is interesting to speculate as to why the borings are concentrated in the thickened regions of the brachiopod shells. Did the borers that made Vermiforichnus (probably worms) have the capacity to sense the general region of greatest thickness of the valves to maximize their chances for continued existence, were they sensitive to slight differences in chemical or mineralogical composition of the shell material in the area of the muscle cavities that facilitated penetration, or is this concentration of borings a reflection of the shape of the substrate (made at the lowest point on the shell surface if made in the concave-up position, or the highest if made on the inside of disarticulated, convex-up shells)?

Plate 21

Trypanites sp. A. Outcrop view of hardground with Trypanites sp., developed in uppermost calcarenite bed of Laval Formation in the Laval Nature Centre, Laval, Quebec, formerly the quarry of the Montreal Crushed Stone Company (Quarry B-11 in Clark, 1972, map 1737). This section, photographed in 1960 and now no longer exposed, is located approximately between Stations D and E in Figure 3 of Hofmann (1972); the arrow identifies the hardground at the 18.0 foot level in Figure 8 of Hofmann, 1963, and top of Bed 1 in Hofmann, 1972, Figure 4. Metre-stick gives scale.

B. Polished vertical section of bored calcarenite. GSC 54221a.

C. Plan view of hardground surface, showing subcircular apertures of borings. Same specimen as B.

D. Thin section of specimen in B in unpolarized light, showing truncated shell fragments (chiefly of the brachiopod *Rostricellula plena*), and fillings of limonite-stained dolomite mudstone. Note intersection of borings left of centre. GSC 54221c.

E. Distal end of mud-filled borings, showing platy, phosphatic fragment protruding into boring; the relationship suggests that the boring was produced chemically, rather than mechanically, the animal having greater facility for dissolving carbonate than for the phosphate. The large opaque grain penetrating the boring from the left is diagenetic pyrite. Same thin section as D.



The disarticulated nature of the valves with borings, the predominance of the convexup position, and the characteristics of the associated terrigenous sediment indicate that the shells are allochthonous and came to rest in a position that was stable in fairly strong currents. Their generally well preserved exteriors suggest that transport and abrasion were minimal; the shells make only a small volumetric contribution to the shaly sandstone bed in which they occur, and they were not abundant enough to be knocked against one another.

A scenario leading to the observed relationship is as follows: 1) Mimella imperator established colonies in shallow subtidal interdistributary bays in a spreading deltaic complex; 2) brachiopods died, valves disarticulated and accumulated with convex as well as concave sides up; 3) borers infested surfaces of valves, localizing themselves in thickest portions; 4) storm waves eroded and transported shells to nearby subtidal sand banks or shoals, or onto the lower tidal flat where they then became stabilized in the convex-down position, were buried, and entered the fossil record.

Ropalonaria sp.

Plate 22, C, E, F

Delicate creeping excavations of Ropalonaria Ulrich, 1879, occur on both surfaces of the same disarticulated valves of Mimella imperator (Billings, 1859) as those that also contain Vermiforichnus sp.; they are preserved as mudcasts of the original boring organisms, bryozoans. When present, the extensively anastomosing network of stolons commonly crisscrosses the entire valve area within 0.2-0.3 mm of the interior surface. Stolons are 0.07-0.1 mm wide, expanding to ellipsoidal or fusiform zooecial casts 0.2 mm wide at more or less regular intervals, about 2 stolons/mm. In some specimens the creeping stolon casts follow the contour of casts of Vermiforichnus sp., indicating that they postdate the excavations of Vermiforichnus, but generally the Vermiforichnus casts are unornamented by casts of Ropalonaria.

As with Vermiforichnus sp., Ropalonaria sp. was found at only one locality, the Rockcliffe Formation at the northeast corner of the intersection of Highways 17 and 34 at Hawkesbury, Ontario.



A-F. Borings in values of *Mimella imperator* Billings. The casts of the larger cylindrical borings are *Vermiforichnus* sp., attributed to annelids; the delicate network with ellipsoidal and fusiform enlargements represents casts of bryozoan borings, *Ropalonaria* sp. Northeast corner of intersection of Highways 17 and 34, Hawkesbury, Ontario. GSC 54222 (A), 54223 (B), 54224 (C), 54225 (D), 54226 (E, F).

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EARLY ORDOVICIAN TRILOBITES FROM THE CATOCHE FORMATION (ST. GEORGE GROUP), WESTERN NEWFOUNDLAND

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Abstract

This paper describes the trilobite fauna from the type section of the Catoche Formation at Port au Choix. western Newfoundland, and includes the species described by Billings in 1865 from the St. George Group. Correlation of part of the section with zone H of Utah and Nevada is demonstrated, and an early Arenigian age is suggested. There is a hiatus between this fauna and that of the overlying Table Head Group. Species described and figured include: Carolinites genacinaca nevadensis Hintze, Opipeuter cf. angularis (Young), Isoteloides peri sp. nov., I. latimarginatus sp. nov., Bathyurina timon (Billings), Bolbocephalus convexus (Billings), Catochia ornata gen. et sp. nov., C. glabra sp. nov., Petigurus nero (Billings), Strigigenalis caudata (Billings), Bathyurellus abruptus (Billings), B. platypus sp. nov., Punka flabelliformis gen. et sp. nov., Punka? sp. indet., Uromystrum cf. affine (Poulsen), Benthamaspis gibberula (Billings), B. conica sp. nov., Ischyrotoma anataphra sp. nov. and Strotactinus insularis (Billings). Revision of the type species of Bathyurellus considerably restricts the scope of this genus; many of the species previously assigned to Bathyurellus are referred to Punka gen. nov. Identification of the pygidium of Strigigenalis indicates that this genus is a typical bathyurid. A new pliomerid subfamily (Cybelopsinae) is proposed to include genera with characteristic pygidial structure (Cybelopsis, Strotactinus, Pseudocybele and Canningella), to which the previously problematic genus Ectenonotus is assigned.

The Catoche fauna is a typical shallow water assemblage of the Bathyurid Province, representing a short-lived deepening event in the early Ordovician history of western Newfoundland. With the exception of *Carolinites* and *Opipeuter*, all the species were benthic, and included sluggish forms that ploughed the sediment surface (*Punka*), more active species that were capable of partially burying themselves (*Catochia*), and possible algal grazers (*Benthamaspis*).

Résumé

Dans cette étude, on décrit la faune à trilobites provenant du profil type de la formation de Catoche, qui se situe à Port au Choix dans l'ouest de Terre-Neuve; cette faune inclutles espèces trouvée dans le groupe de Saint-George, que Billings a décrite en 1865. On a démontré qu'il était possible d'établir une corrélation entre une partie de ce profil et la zone H définie pour l'Utah et le Nevada, et on propose qu'il soit de l'Arénigien inférieur. On a constaté l'existence d'une lacune stratigraphique entre le niveau où apparait cette faune, et le groupe sus-jacent de Table Head. Les espèces décrites et représentées sont: Carolinites genacinaca nevadensis Hintze, Opipeuter cf. angularis (Young), Isoteloides peri sp. nov., I. latimarginatus sp. nov., Bathyurina timon (Billings), Bolbocephalus convexus (Billings), Catochia ornata gen. et sp. nov., C. glabra sp. nov., Petigurus nero (Billings), Strigigenalis caudata (Billings), Bathyurellus abruptus (Billings), B. platypus sp. nov., Punka flabelliformis gen. et sp. nov., Punka? sp. indet., Uromystrum cf. affine (Poulsen), Benthamaspis gibberula (Billings), B. conica sp. nov., Ischyrotoma anataphra sp. nov. et Strotactinus insularis (Billings). On a révisé la classification de l'espèce type de Bathyurellus, et le genre se trouve de ce fait considérablement réduit; un grand nombre des espèces autrefois attribuées au genre Bathyurellus font maintenant partie de Punka gen. nov. L'examen du pygidium de Strigigenalis indique qu'il s'agit d'un bathyuride typique. On propose une nouvelle sous-famille de Pliomerides (Cybelopsinae), qui incluerait certains genres possédant une structure pygidiale caractéristique (Cybelopsis, Strotactinus, Pseudocybele et Canningella); on rattache maintenant à cette sous-famille le genre Ectenonotus autrefois considéré comme énigmatique.

La faune de Catoche représente un assemblage typique de la province à Bathyurides, qui s'est formé en eau peu profonde pendant un court épisode de subsidence, durant la période de histoire qui a caractérisé l'Ordovicien inférieur de l'ouest de Terre-Neuve. A l'exception de *Carolinites* et *Opipeuter*, toutes les espèces sont benthiques et comprennent des formes peu actives, qui exploraient la surface des sédiments (*Punka*), ainsi que des espèces plus actives, capables de s'enfouir partiellement dans les sédiments (*Catochia*), et peut-être même des brouteurs d'algues marines (*Benthamaspis*).

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INTRODUCTION

Billings (1865) is one of the landmarks in Early Paleozoic studies, and is remarkable for the precision of its observations. The collections from the western coast of Newfoundland form an important part of Billings' work, and the trilobites, perhaps more than any other group, are unusual in their diversity and the excellence of their preservation. Whittington (1963, 1965) has given outstanding accounts of the trilobite faunas from the Table Head Group, and the allochthonous boulder at Lower Head. The purpose of this paper is to describe the fauna of the underlying St. George Group, and particularly to revise Billings' species.

The fauna of the St. George Group is regarded as typical of the later Canadian, but surprisingly little attention has been given to the redescription of the fossils. Raymond (1905, 1913) and Whittington (1953) reconsidered a few forms. Kindle and Whittington recollected the sections from which J. Richardson obtained the specimens later described by Billings. Their faunal lists (Whittington and Kindle, 1969) added preliminary identifications of several genera additional to those known to Billings. Recent mapping in the Boat Harbour area, near Cape Norman (Fig. 10) by the



Figure 10. Localities in Newfoundland with early Ordovician trilobites described in the text. Inset: Port au Choix Peninsula, showing location of section in Figure 11, between southwest end of Barbace Cove and Laignet Point.

Newfoundland Department of Mines and Energy (Knight, 1977) has shown the presence of earlier Canadian faunas in the St. George Group. These are not included here; they are being studied by W.D. Boyce of the Memorial University of Newfoundland. Flower (1978) has presented a summary of cephalopod distribution through the St. George Group and Table Head Formation.

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STRATIGRAPHY

Stratigraphic terminology

The type section of the St. George Group is along the southern shore of Port au Port Peninsula (Schuchert and Dunbar, 1934). The early Ordovician carbonate rocks were first grouped as a single formation, a usage that has continued until recently (Whittington and Kindle, 1969). The trilobites described by Billings came from the Port au Choix area (Fig. 10), and were localized according to the alphabetic (F, G, H, I) divisions of the St. George strata described by Richardson (in Logan, 1863). For this reason it is this area that has been recollected again for the present study. Kluyver (1975) remapped the Port au Choix Peninsula, and divided the St. George rocks into three formations: in succeeding order, Barbace Point, Catoche, and Port au Choix. This elevated the St. George sequence to group status. Mapping in the area south of Cape Norman (Knight, 1977), and in the type area on the Port au Port Peninsula (N. James, R. Levesque, pers. comm., 1978) also indicated that the St. George rocks may be divided into three stratigraphic units for which formational terminology is appropriate; the St. George therefore is considered as a group in the present account.

All the fossils collected for the present study came from the Catoche Formation of Kluyver (1975), the probable equivalent of Logan's (1863) division H. There are some problems with Kluyver's divisions, which should be mentioned here. Kluyver (1975, Fig. 1) indicated the presence of two faults which delimit a small cove (Barbace Cove) on the northwest coast of Port au Choix Peninsula (Fig. 10), that are purported to bring the

Barbace Point Formation to the surface in "a small horst-like structure". N. James has indicated to me that this is probably simply a local dolomitized front. The base of the overlying Port au Choix Formation may be on a similar front. In view of these ambiguities we have concentrated our collecting on the unequivocally continuous section running along the shore from Catoche Point, on the southern end of Barbace Cove, to Laignet Point at the northern tip of Port au Choix harbour (section B-B' of Kluyver, 1975). This interval includes the beds with numerous trilobites, and embraces all the species described by Billings (1865). We found no younger faunas. The lower part of the St. George succession obviously needs clarification, and this will no doubt be forthcoming from the mapping in the Cape Norman area, where good continuous sections are exposed, and earlier Canadian faunas have now been proved.

Stratigraphic ranges of the trilobites

The section in the Catoche Formation is developed mainly in thin bedded and rubbly surfaced limestone, with many stylolite seams. Thin dolomite beds form recessive units less than half a metre thick at intervals through the section. More massive limestone, which caps small bluffs along the shore, contains numerous remains of gastropods, the shells of which have been much recrystallized and are best seen where the sea has polished the bedding planes. Massive limestone increases toward the top of the section, and is progressively more dolomitized. Elsewhere dolomitization occurs preferentially along numerous bifurcating "worm" trails, producing a mottled appearance on fresh rock surfaces.

Trilobites are most numerous in lenses of lime sand. Their remains are disarticulated, and broken in some beds. Such lenses are most easily discovered in the mid-part of the section, and general abundance of fossils decreases above and below. Samples at more or less regular intervals through the section have been secured to compile the range chart of trilobites shown on Figure 11.

Two faunas can be distinguished, which are distinct at their extremes but with a complex overlap of species in the middle part of the section. Where successive species of the same genus occur - as in *Catochia* gen. nov., *Bathyurellus*, *Isoteloides* and *Benthamaspis* - the



Figure 11. Stratigraphic ranges of the trilobites described in this paper within the measured section from the south end of Barbace Cove to Laignet Point, Port au Choix, Newfoundland. Stratigraphic positions of collections indicated by dots below the section.

change from the earlier to the later species is not synchronous in the several lines, such as would be expected if there was a disconformity of any magnitude in the section.

From the combination of species described by Billings (1865) it is reasonable to assume that Richardson obtained his collections from within the interval at the middle of the section, where the ranges of Billings' species overlap, and where trilobites are most abundant.

The lower fauna certainly continues in the strata on the north side of Catoche Cove, where Benthamaspis conica, Punka flabelliformis, and Uromystrum cf. affine occur.

Correlative fauna's in the St. George Group

Whittington and Kindle (1969) described other occurrences of the Catoche trilobite fauna over the considerable area of outcrop of the St. George Group. The same beds have yielded the Cassinoceras wortheni cephalopod fauna of Flower (1978). In the type area on Port au Port Peninsula trilobites so far have not been recovered in any abundance. The presence there of Petigurus nero, Bolbocephalus cf. convexus and Isoteloides sp. indicates that the Catoche Formation has equivalents in the type section of the St. George Group. To the north in the Boat Harbour area (Knight, 1977, p. 28) there are good exposures of the Catoche Formation. Examination of collections made by Whittington and Kindle from this area has revealed the presence of the following species: Isoteloides peri, Ischyrotoma anataphra, Punka flabelliformis, Bolbocephalus convexus, Bathyurellus abruptus, Bathyurina timon, Benthamaspis cf. B. gibberula, and Strotactinus insularis. I have not yet seen examples of the upper fauna.

Association of trilobite parts

One of the particular problems of working with the later Canadian trilobites is that of associating the correct cranidia, pygidia and free cheeks. Examples of the previous incorrect undetermined A" described by Demeter (1973) assignment of parts are cited frequently in the from zone G2 in western Utah; its range in systematic section of this paper. This is particularly so with Bathyuridae, in which a number of species of the same general type occur in the same beds. Almost all of the associations given in this work are made with confidence. The trilobite-bearing lenses often concentrate the remains of one species in preference to another; most of the associations were made initially from a single lens. The different stratigraphic ranges of species also help to avoid confusion. For example, the range of Bathyurellus sensu stricto extends beyond that of Punka gen. nov., hence the correct cephalic parts for Billings' pygidia of B. abruptus type could be determined. A second type of cranidium in the earlier fauna was therefore likely to be that of Punka.

Of morphological features, sculptural patterns are useful when assigning free cheeks to cranidia, as well as the "fit" of the facial sutures. Bathyurid species also demonstrate a similarity between the surface sculpture (or lack of it) on the glabella and the pygidial axis.

AGE AND CORRELATION OF THE FAUNAS

The fauna of Logan's division H of the St. George Group has long been recognized as late Canadian in age, and evidence supporting correlation with other areas has been well summarized by Whittington (1968, p. 52, 53). The purpose of the present report is to describe the correlations suggested by species-level comparisons with other faunas, based on the new descriptions and discoveries. The Catoche Formation records two faunas that completely intergrade with one another in the mid-part of the section. Most of the changes that occur between these faunas are at species-to-species level, and the comparisons are accordingly made with other species outside Newfoundland, rather than overall generic composition.

Comparison with zonations by Ross (1951) and Hintze (1953) from Utah and Nevada

The occurrence of the pelagic trilobite Carolinites genacinaca nevadensis in the middle part of the measured section of the Catoche Formation is important. This is a characteristic form of zone H of Utah and Nevada. In the zone H fauna described by Young (1973) from the Ibex area of Utah, C. nevadensis is accompanied by an Opipeuter species close to one from the Catoche Formation. I have also recognized Benthamaspis gibberula (Billings) in Young's collections and Bolbocephalus convexus (Billings) probably also occurs in that area. Other species in the same fauna are close to those from the Catoche Formation but with small specific differences examples are discussed below under Bathyurellus (which is restricted considerably in this paper), Strigigenalis, and Ischyrotoma. These similarities combine to support a correlation of much of the Catoche Formation with zone H of Utah and Nevada. The lowermost fauna thus probably equates with the upper part of zone G (zone G2). In this connection it should be noted that the pygidium of Strotactinus insularis (Billings, 1865) from the Catoche Formation is identical to that of "genus and species Newfoundland spans the upper and lower faunas.

In summary, species comparisons indicate that the Catoche Formation includes the equivalents of the upper part of zone G of Utah and Nevada and the overlying zone H. Because the ranges of the uppermost species (Figure 11) extend beyond any of the species diagnostic of zone H it is perfectly possible that the upper part of the Catoche Formation extends upwards into zone I. A correlation of the Catoche cephalopod fauna characterized by Cassinoceras wortheni with zone I of Utah and Nevada was suggested by Flower (1978, p. 223).

Correlation with standard Ordovician series via graphlolitic facies

Benthamaspis conica sp. nov., a species of the lower fauna in the Catoche Formation, occurs with graptolites of Berry's zone 4 (Tetragraptus fruticosus 4-branched) in the Marathon region, Texas. Fortey (1976) has shown that the range

of Carolinites genacinaca nevadensis extends into Berry's (1960) zone 5 (Tetragraptus fruticosus 3and 4-branched) in Spitsbergen, where a correlation of that zone with Ross's (1951) zone H was proposed. Cumming's (1967) report of Clonograptus flexilis from the Catoche Formation is also consistent with a zonal indication as late as Berry's zone 4 (Berry, 1960, p. 16). These few trilobites provide good links with the graptolitic sequence at the specific level. In Spitsbergen the fauna of the Nordporten Member of the Kirtonryggen Formation (Fortey and Bruton, 1973) includes several additional species in common with the Catoche Formation, and is succeeded by richly graptolitic shale of the Valhallfonna Formation, the lower part of which lies in Berry's zone 5. I conclude that deposition of the Catoche Formation was within a relatively short, early Arenig interval represented by the *T. fruticosus* zones, equivalent to the upper part of the Bendigonian Stage of the Australian standard.

This interval is generally correlated with the *Didymograptus deflexus* Zone of the British Arenig Series. The presence of the underlying Zone of *Tetragraptus approximatus* has not yet been proved from the type Arenig in North Wales (Skevington, 1969), although this zone is often included in the Arenig rather than the Tremadoc. As far as correlation can proceed between such widely separated areas in the early Ordovician, the Catoche Formation thus appears to be coeval with the lower part of the Arenig in the type area. Kluyver (1975) was incorrect in assuming a late Arenig age for the Catoche Formation.

Correlative formations in platform facies

Poulsen (1951) and Whittington (1953, 1968) have noted the similarity of trilobite faunas distributed over the wide carbonate platform that extended during the Canadian from the southwestern United States through eastern Canada, western Newfoundland, East Greenland, and ultimately to Spitsbergen at 80°N. In early Ordovician times this belt lay near the equator. The same broad belt includes the Midcontinent conodont province (Fortey and Barnes, 1977), which extended on to the northeastern Siberian platform. Similar trilobite faunas in that area may be partly "hidden" in different taxonomies.

Formations that have yielded species close or identical to those from the Catoche Formation are briefly listed here. Many trilobites from the "Beekmantown" limestone strata are fragmentary, incompletely known, or inadequately described. Detailed discussions are given in the systematic part. Exact age relations to the Catoche Formation cannot be determined without revision of such species. Proceeding from north to south:

Northern Spitsbergen. The upper (Nordporten) member of the Kirtonryggen Formation includes a fauna closely comparable with that of the Catoche Formation. This fauna has yet to be described, but includes (Fortey and Bruton, 1973) similar or identical species of Bathyurina, Bathyurellus, Petigurus, Punka gen. nov., Bolbocephalus, and Benthamaspis.

Ellesmere Island, Arctic Canada. The fauna described by Poulsen (1946) includes a few fragmentary forms, but there is enough to indicate the presence of closely related species of *Isoteloides* and *Benthamaspis* to those of the Catoche Formation. *Bathyurina* also occurs there.

East Greenland. The lower part of the Cap Weber Formation (Poulsen, 1937; Cowie and Adams, 1957) includes a fauna with species in common with the Catoche fauna, or closely similar. Examples are discussed below under Bathyurina, Bathyurellus, Bolbocephalus, Petigurus, Uromystrum, and Punka gen. nov. Carolinites of genacinaca type also occurs in the black limestone interval within the Cap Weber Formation (Cowie and Adams, 1957).

Eastern Canada. The fauna of the Romaine Formation on the Mingan Islands, Quebec, is poorly known, but includes bathyurids ("Bathyurus" amplimarginatus Billings, "B." cybele) similar to those described from the Catoche Formation. To the west, the Oxford Formation of eastern Ontario (Ludvigsen, 1979) includes Strotactinus, Bathyurina, and Bolbocephalus species, but distinct (possibly younger) from those of the Catoche Formation.

Vermont, U.S.A. Whittington (1953) redescribed bathyurids from the Fort Cassin Formation, which include a *Strigigenalis* probably identical to *s*. *caudata* from Newfoundland. *Bolbocephalus* species from the same formation include one closely similar to that from the Catoche Formation.

Missouri-Arkansas-central Tennessee, U.S.A. The fauna of the Powell Formation (Cullison, 1944) includes species of *strigigenalis* and *Bathyurina* which are close to forms from Newfoundland. Further comparisons are hampered by the scanty material from the Powell Formation. Correlation with the Pogonip Group of Utah and Nevada has been discussed above.

Relation of Catoche Formation to younger rocks in Newfoundland

The middle Table Head Formation has been regarded by Whittington (1965, p. 294) as of early Llanvirn age. Discovery of graptolitic equivalents of the middle Table Head Formation on Port au Port Peninsula supports this interpretation, and indicates correlation with the upper part of the European zone of *Didymograptus bifidus* (<u>non Berry</u>, 1960). As several trilobite species (*Ectenonotus westoni*, *Nileus affinis*) range through both the lower and middle Table Head it is unlikely that the lower Table Head Formation is older than Llanvirn.

The youngest fauna in the Catoche Formation is of early Arenig age; the rest of the Arenig Series is therefore accommodated between this fauna and the base of the lower Table Head. Ruedemann's (1947, Pl. 55, fig. 22; Pl. 56, fig. 17) description of the long ranging graptolite *Didymograptus patulus* probably from within this interval, does not necessarily prove a horizon above that indicated by the younger Catoche fauna. Whittington and Kindle (1963; also Cumming, 1968) report a disconformity at the base of the Table Head Formation
at the type section; if this is the case then part of the upper Arenig may have been removed prior to the deposition of the Table Head Formation. Because the upper part of the St. George Group is largely dolomitic (partly cherty) it is also possible that diagenetic processes have destroyed the fossils of the upper part of the group. Recent mapping by the Newfoundland Department of Mines and Energy and others indicates that the thickness of the upper dolomite varies greatly regionally, and there is the possibility of a regional unconformity below the Table Head Formation (Flower, 1978). Whatever the nature of the contact with the lower Table Head Formation there is as yet no evidence of the upper part of the Arenig in the platform succession. In terms of the North American shelly succession, zone J of Ross (1951) and Hintze (1953) is absent, plus the "pre-Whiterock interval" occurring between those zones and typical Whiterock assemblages in Spitsbergen (Fortey, 1975a, p. 10; 1976, p. 273). There is as yet no evidence of faunas fitting in this gap being present in the boulders of the Cow Head Group (Whittington, 1968, p. 50). . Taken together, this is suggestive of a major period of nondeposition, or at least shallowing to a point where hypersalinity prevented trilobites from living, in the western part of Newfoundland through a large part of the Arenig Series. This is in accord with the work of Flower (1978) summarizing the distribution of cephalopod faunas, in which there is a similar gap in zonal succession beneath the Table Head Formation in the Port au Choix area.

ENVIRONMENTAL SETTING OF THE CATOCHE FORMATION

It is generally accepted that the St. George Group as a whole is a relatively shallow water carbonate succession. Within the St. George Group the Catoche Formation is the middle unit and is largely limestone, contrasting with highly dolomitic sequences above and below. In the lower units of the St. George Group there are abundant stromatolite beds, local erosional levels are common, and the associated sedimentary features (oolites, common mud flake conglomerates) all indicate accumulation in very shallow water, in part at least intertidal. Gastropods are probably the most common fossils in this part of the succession, with nautiloids at certain horizons. Trilobites are generally rare, although certain trilobite horizons have now been recognized in the north part of the outcrop area around Boat Harbour. This sedimentary regime can be widely recognized in the Canadian Series, and is typical of much of the Beekmantown Group and correlative units in platform North America, as far south as the El Paso Group of New Mexico. Outside North America closely similar sedimentological suites exist in the contemporaneous Ninmaroo Formation of central Queensland, Australia.

Few stromatolitic beds are present in the Catoche Formation, but in the lower part there are frequent intraformational conglomerate beds, sometimes with clasts stacked edgewise, and occasional oolitic lenses have been recognized. Thin dolomite beds occur at more or less regular intervals. The flood of trilobites that appears within the Catoche Formation indicates a change in conditions, but the general similarity of sedimentary features indicates that this change was not profound. Much of the sediment in the Catoche Formation was reworked, perhaps repeatedly, by soft bodied animals that have left dolomitized trails. Macluritid gastropods and nautiloids continue to be abundant. The concentration of the trilobites into lime sand lenses, and their complete disarticulation, often with breakage of the more delicate cephalic parts, indicates the activity of currents and/or tides was at least powerful enough to break, move, and "winnow" trilobite skeletal parts.

Between the lenses of concentrated trilobite fragments the greater thicknesses of more or less burrowed, often knobbly limestone also contain trilobites, but they are much easier to overlook than those in the lenses, and the fauna is relatively reduced. Of the fauna described below only the asaphids, Bolbocephalus and Petigurus, were collected from the main body of the limestone. In part the less fossiliferous nature of the limestone may be more apparent than real. Sectioning of some of these beds in the laboratory has shown the presence of Receptaculites, Calathium and ?Bryozoa, which may have been numerous enough to make small bioherms. The upper part of the Catoche Formation includes some apparently structureless mounds several metres in diameter.

The appearance of the pelagic trilobites Carolinites and Opipeuter in the section is significant because it indicates free connection with the open oceans of the time. Both genera were distributed as far away as Australia on the far side of the equatorial great circle in the early Ordovician (Legg, 1976). Cumming's (1967) description of Clonograptus from the Ca+oche Formation, and the occurrence of benthamaspis conica both in the Newfoundland sections and in the graptolitic sequence of Marathon, Texas, provide further evidence of connection with more oceanic facies.

It seems reasonable to explain the faunal and sedimentary changes briefly listed above as a response to a deepening event during the deposition of the Catoche Formation compared with the earlier part of the St. George Group. This allowed for a shelfward invasion of trilobite faunas, including forms that swam actively near the surface. As noted previously, because the lower Table Head Formation is probably of Llanvirn age (Whittington, 1968) the upper part of the Arenig Series is either accommodated within the unfossiliferous dolomite overlying the Catoche Formation, or is cut by a disconformity at the base of the Table Head Formation. It may be tempting to assume a return to extreme shallow water, "starved" conditions at the top of the Catoche Formation, but, as these dolomite strata are probably secondary (I. Knight, N. James, pers. comm. 1977) it is also possible that the subsequent faunas have been removed during diagenesis.

The deepening event that accompanied the Catoche trilobite faunas may have been more or less contemporaneous over a wide area. In Spitsbergen the drastic sedimentary and faunal change (also a deepening event) at the base of the Valhallfonna Formation (Fortey, 1976) occurs within the range of Carolinites genacinaca nevadensis, which is also reported in this paper. The same species is introduced in a dark limestone interval within the otherwise shallow water limestone sequence of the Cap Weber Formation, East Greenland (Cowie and Adams, 1957). In Utah the fauna from zone H described by Young (1973) includes a number of trilobite species either identical or close to forms from the Catoche Formation, including similar pelagic species. Accompanying these are species of genera like Shumardia and Geragnostus (Trinodus) which have been associated with Nileid ("upper slope") community type of Fortey (1975b). This event is approximately coincident with the base of the Arenig transgression in its type development in Wales, as far as correlation between the widely different faunas will permit.

If such contemporaneity can be further substantiated using other fossil groups, it may be necessary to invoke a world-wide sea level rise to account for its effects in what were separate plates in the earlier part of the Ordovician.

REMARKS ON THE LIFE HABITS OF THE TRILOBITES

A few general remarks on the life habits of the Catoche trilobites are given here. More detailed treatments of the functional morphology of Catochia gen. nov. and Punka gen. nov. are given after the systematic account of those genera.

The distribution of fauna in the stratigraphic comparison above and the systematic treatment below indicates that most of the genera were confined to shallow water platform carbonates of the Bathyurid Province. Two genera are exceptionally widely distributed, both geographically and across facies. These are Carolinites and Opipeuter, both of which were free-swimming, oceanic forms. The lines of evidence leading to this conclusion sp. nov. This was probably a sluggish about these trilobites has been given detailed treatment by Fortey (1974, 1975a). The rest of the fauna is either benthic or nektobenthic, closely tied to the limestone facies developed near the equator in the early Ordovician.

Several species had an exceptionally robust, thick, and tuberculate cuticle (Petigurus, Ischyrotoma). Whereas it would be tempting to associate this with protection in an environment subject to temporary exposure, they are accompanied by other species, such as Isoteloides and Punka, which are not unusual in this respect. Isoteloides is one of the few trilobites in the fauna that lacks dorsal surface sculpture. Both Isoteloides and Petigurus can be found as large "clasts" in intraformational conglomerates; I have also been shown pygidia of the former from the St. George Group of Port au Port Peninsula that are apparently in association with stromatolitic

bodies. Both genera seem to have been able to live in exceptionally shallow water conditions. Presumably both the high degree of effacement of Isoteloides and the exceptionally thick cuticle and coarse tuberculation of Petigurus were adaptations for life in shallow water. Deeper water asaphids, such as those of the nileid community type (Niobe, Gog) usually have fine dorsal terrace lines and/or distinct pygidial ribs.

Progressive effacement is a feature observed in three evolutionary, or at least morphological, series in the Catoche fauna (Catochia, Benthamaspis and Bathyurellus); the younger species are the more effaced dorsally. I believe that it would be an oversimplification to attribute this simply to a common adaptation to shallow water conditions, as in other respects these genera differ profoundly. The last two, for example, retain cephalic surface sculpture, and the genal and pygidial morphology of all three genera could scarcely be more different.

Stitt (1976), in a functional study of the inshore late Cambrian genus Stenopilus, described a broad and upward-flexed cephalic doublure as functioning as a "rasp" for algal grazing. We observe a similar structure on Benthamaspis, which also shares with Stenopilus narrow (trans.) free cheeks with rounded angles, and a globose pygidium with a short axis. Cranidial effacement in Benthamaspis is progressive in younger species and the main difference from a functional point of view resides in the larger eyes of the Ordovician genus and its dorsal bertillon pattern (unfortunately the thoracic structure is unknown). Stenopilus seems to provide the best comparison for Benthamaspis, and it is considered possible that their feeding habits were the same. Associated lithologies are similar. Other details were probably different, for example, the burial habit shown by Stitt (1976) was supported by a specific pattern of exoskeletal sculpture not present on the Newfoundland species.

A distinctive combination of morphological features, including a convex cephalon with long, triangular and backward-swept genal spines, and a relatively flat pygidium, has been interpreted below for Punka flabelliformis species, habitually resting on the sediment surface on its cephalic brim and using the genal spines as a plough to turn aside the sediment as it progressed forwards. Generally similar combinations of morphological features are shown by Bathyurellus and Uromystrum. The former has a shorter cephalic brim; anterior upthrust on the sediment surface in this genus may have been principally effected by the ventral concavity of the cephalic doublure.

More active habits are inferred for Catochia and the same general conclusions probably apply to Bathyurina, Ischyrotoma, and Strigigenalis. Catochia shows specialized features indicating that it was capable of partially burying itself, but the other genera differ in these same features. Both Bathyurina and Ischyrotoma have thick cuticles, and are coarsely tuberculate, in these respects resembling Petigurus.

SYSTEMATIC DESCRIPTIONS

Terminology. Terminology follows that in the Treatise (Moore, 1959), with the addition of a few terms given in Whittington (1965) and Öpik (1967). The glabella is regarded as including the occipital ring, unless specifically excluded in the descriptions by the term: "pre-occiptial glabella".

Systematic order. The order of the descriptions is by superfamily as used in the Treatise. Families, subfamilies and genera follow in alphabetical order. Species are treated in the order that keeps the text to a minimum. Where more than one species in a genus is described, the second is distinguished in a comparative discussion to obviate inessential repetition.

Names. Every attempt has been made to conserve the original specific nomenclature of Billings (1865). This has proved possible in all cases except "Bathyurellus" marginiatus, where the lectotype cranidium cannot be associated with pygidia This graptolite zone is early Arenigian, and of the type figured by Billings.

New names are arbitrary combinations of letters, except in the case of Catochia gen. nov., named after Catoche Point, Port au Choix, and Isoteloides peri sp. nov., which is named after P.E. Raymond.

Type and figured material. Type specimens are stored in the National Type Fossil Collection, Geological Survey of Canada (GSC), Ottawa, and the Sedgwick Museum (SM), Cambridge, England. Reference specimens are deposited in the British Museum (Natural History), London, England.

Species diagnoses. Most species described hereafter can be well characterized by "presence or absence" of morphological features, which are briefly summarized in the diagnoses. Exceptions are the Asaphidae, and satisfactory species definitions will probably require a statistical analysis of <u>all</u> species that have been referred to Isoteloides, which is beyond the scope of the present account.

Superfamily KOMASPIDACEA Kobayashi, 1935 Family TELEPHINIDAE Marek, 1952 Genus Carolinites Kobayashi, 1940 Type species Carolinites bulbosus Kobayashi, 1940

Carolinites genacinaca nevadensis Hintze, 1953

Plate 36, figures 14-17

Synonymy in Fortey (1975, p. 115)

Figured material. Cranidia, GSC 57756, 56794; pydigidum, GSC 56795; free cheek, GSC 56796.

Stratigraphic range. Catoche Formation, 11 to 35 m in measured section.

Discussion. This species has been described by Fortey (1975a) from the early Ordovician of Spitsbergen. It is of considerable importance in the long distance correlation of the St. George faunas, indicating the presence of zone H of Ross (1951) and Hintze (1953) in the Newfoundland sections.

Particular diagnostic characters of the subspecies are well shown by the present material. The free cheek (Pl. 36, fig. 17) has a well developed subocular ridge and a smaller eye than later species of the genus. On the cranidium (Pl. 36, fig. 15) the bacculae adjacent to the basal part of the glabella are smaller than is the case in C. genacinaca genacinaca, and do not indent the glabella. The pygidium has transverse axial furrows; only two axial rings are deeply defined, and the axial rings lack median tubercles.

Fortey (1975a, 1976) has demonstrated the stratigraphic importance of Carolinites in correlating between different facies in the earlier Ordovician, related to the inferred pelagic habits of the genus. C. genacinaca nevadensis occurs with graptolites of upper Tetragraptus fruticosus zone in Spitsbergen. probably equates with earliest Arenig strata of the type area in North Wales.

> Superfamily REMOPLEURIDACEA Hawle and Corda, 1847

Family OPIPEUTERIDAE Fortey, 1974

Genus Opipeuter Fortey, 1974

Type species Opipeuter inconnivus Fortey, 1974

Opipeuter cf. angularis (Young, 1973)

Plate 37, figures 13-15

Remopleuridiella angularis Young, 1973, p. 112-114, P1. 1, fig. 21, 22, 26, non fig. 25, 27

Figured material. Cranidia, GSC 56797, 56798.

Stratigraphic range. Catoche Formation, 47 m in measured section.

Discussion. Young (1973) figured a cranidium from a zone H fauna from Utah which he attributed to Remopleuridiella angularis. The cranidium clearly belongs to Opipeuter Fortey, 1974, which, although possibly with remopleuridacean ancestry, differs from remopleuridids in most features of the entire exoskeleton. Note that the free cheek assigned to this species by Young differs from that of Opipeuter, and has the subocular ridge characteristic of the free cheek of *Carolinites* genacinaca nevadensis, which occurs in the same fauna. The stratigraphically earliest cranidia attributed to the type species from Spitsbergen (e.g. Fortey, 1974, Pl. 13, fig. 6-8) may also be referable to 0. angularis. Two small Opipeuter cranidia have been obtained from the Newfoundland sections. Both differ from typical examples of the type species (Fortey, 1974, Pl. 13, fig. 2-5) in their broader (trans.) remnant fixigenal areas and wide anterior glabellar tongues. They resemble O. angularis more closely in these features, and in the relatively long posterior

taper of the glabella. *O. emanuelensis* Legg, 1976, from the Canning basin, western Australia, is more like the type species in the same characters. The present specimens differ from the type specimen of *O. angularis* in the sinuous course of the axial furrows, resulting in a rounded median expansion of the glabella, and on one specimen the IP glabellar furrow is particularly deep and wide at its outer edge (P1. 37, fig. 15).

With the limited data available on the Utah species it is not possible to be certain whether these differences are due to intraspecific variation or the silicified preservation of *O. angularis*, and the determination is accordingly tentative.

The occurrence of *Opipeuter* in the Newfoundland sections is further evidence of its wide distribution, consistent with inferred pelagic life habits. In Newfoundland it is associated with shallow shelf faunas, whereas in Spitsbergen it extends into the off-shelf olenid and nileid environments (Fortey, 1975b).

Superfamily ASAPHACEA Burmeister, 1843

Family ASAPHIDAE Burmeister, 1843 Subfamily Isotelinae Angelin, 1854 Genus *Isoteloides* Raymond, 1910

Type species Asaphus canalis Whitfield, 1886 (but see following)

Note on nomenclature. Raymond (1910, p. 35) specified the Upper Canadian species Asaphus canalis Whitfield as the type species of Isoteloides. The name canalis had been used previously by Hall (ex Conrad MS) in the first part of Paleontology of New York (1847, p. 25, Pl. 4 bis, fig. 17-19) applied to Isoteles (now Isotelus) canalis, represented by a hypostoma and a doublural fragment. Although Whitfield (1886) regarded his Asaphus canalis as conspecific with Hall's Isotelus canalis he did not refer it to the same genus. Raymond (1910, p. 37) further stated that the specimens figured by Hall might belong to "what is now known as Isotelus harrisi Raymond", a Chazy species redescribed by Shaw (1968). Raymond (1910, p. 36) separated specimens of Asaphus canalis described by Whitfield under the name Isoteloides whitfieldi, which species name has become the accepted type designation of Isoteloides. However there was no necessity for Raymond to propose a nom. nov. for Whitfield's material, as the latter had not referred his canalis to the same genus as Hall. In short, the type species of Isoteloides is I. canalis (Whitfield), of which I. whitfieldi is a junior objective synonym. Isotelus canalis Hall is presumably the senior synonym of I. harrisi Raymond. The name Isoteloides whitfieldi, however, is now entrenched in the literature, but its ratification will presumably require an ICZN decision. It is used again here, but with obvious reservations.

Discussion. Discrimination of isoteline genera can be difficult due to the general effacement of the dorsal exoskeletal surface. Two isoteline species occur in the St. George Group at Port au Choix, and both compare closely with Isoteloides whitfieldi (Whitfield, 1886, Pl. 34, fig. 1-8; Jaanusson in Moore, 1959, p. 340, fig. 251, 1). To these may be added I. polaris, Poulsen, 1927 (see also Hintze, 1953) and I. flexus, Hintze, 1953. All the species occur in the upper half of the Canadian Series. Characteristic features of the group are: relatively broad, flattened cranidial border which continues on to the free cheek with diminishing width to genal spine; preocular sutures subparallel to slightly divergent; postocular sutures distally curve sharply backwards producing a rounded extremity to the fixed cheeks; eyes just posterior to mid-length of cephalon and rather small; hypostoma deeply forked, the sides of the fork converging on the sagittal line at a low angle, its apex transverse; pygidial border well defined, pygidial axis narrow, pygidial doublure with inner margin slightly concave. The presence or absence of ribbing on the pygidial pleural fields appears to be a variable feature, even within a species.

Stegnopsis Whittington, 1965 (type species S. solitarius, Whittington, 1965) is a closely related, more convex (sag.) genus in which the eyes have migrated to a relatively posterior position, thereby defining narrower (exsag.) postocular cheeks. Preocular divergence of the facial sutures is greater on the type species than in *Isoteloides*, but not conspicuously so on *S. huttoni* (Billings, 1865) (Whittington, 1965, Pl. 22, fig. 3). The cephalic and pygidial doublure is similar on *Isoteloides* and *Stegnopsis*. *Isoteloides liangshanensis* Lu, 1957 (also Lu, 1975, p. 322, Pl. 9, fig. 6-10, Pl. 10, fig. 1-11) has an intermediate set of characters, but as it has somewhat acute postocular cheeks, should perhaps be referred to *Stegnospis*.

Isoteloides peri sp. nov.

Plate 23, figures 1-8

Holotype. Cranidium, GSC 56799.

Figured specimens. Cranidium, GSC 56800; pygidia, GSC 56801-56803; free cheek, GSC 56804; hypostoma, GSC 56805.

Stratigraphic range. Lower part of measured section of Catoche Formation, preceding I. latimarginatus sp. nov., from near the base of the section to about 7 m above the base.

<u>Diagnosis</u>. *Isoteloides* with anterior sections of facial sutures slightly divergent. Eyes small. Pygidium about two-thirds as long as wide, distinct border of moderate width.

Description. Fragmentary remains of this species are common in the lower part of the Catoche Formation where they often occur as "clasts" in intraformational conglomerate. *I. peri* evidently grew to a large size, and pieces of free cheeks more than 7 cm long have been seen, but the larger pieces are usually incomplete; they are very flat, indicating that the convexity of large individuals was extremely low. There is little relief even on small specimens.

Cranidium of sagittal length about 0.8 times the width across the posterior glabellar margin, gently sloping downwards anteriorly to flat border, postocular cheeks equally gently declined. Glabella poorly defined, discernable posteriorly, where there is a gentle anterior taper to a point close to the palpebral lobes, and at curved anterolateral corners. Glabellar furrows not visible. Border one-fifth to one-sixth total cranidial length, but proportion difficult to estimate exactly due to poor anterior definition of glabella. Palpebral lobes close to faint axial furrows, small, only about one-eighth cephalic length (exsag.), strongly curved outline. Fixed cheeks of transverse width slightly more than half the width of the base of the glabella; posterior border wide (exsag.) and faintly defined. Facial sutures strongly isoteliform, preocular divergence low, no more than 20° to sagittal line, and generally about 5°; postocular sutures gently sigmoidal, for the most part running outwards and backwards at 70-80° to sagittal line, distally curving rapidly posteriorly or even slightly recurved to cut posterior margin at approximate right angle. Cranidial surface without sculpture.

Hypostoma with inflated middle body (sag., trans.), scarcely longer than wide. Middle furrows short, deep, and directed slightly backwards, near posterolateral end of middle body. Maculae oval and smooth, at least dorsally. Anterior border depressed, arched slightly forwards medially, and continuing without a break into broad, sharply upwardflexed anterior wings. Lateral borders narrow adjacent to anterior part of middle body, gradually expanding in width until opposite posterior lobe of middle body, thence tapering backwards along sides of fork to rounded extremities. Fork deep, about half sagittal length of middle body, sides very gently converging forwards and inclined ventrally, apex rather sharply transverse. Sculpture of terrace lines strong on borders and running parallel to margins of hypostoma, weaker and approximately transverse over middle body.

Free cheek with distinct border, narrowing gradually backwards and continuing on to proximal part of robust and pointed genal spine. A few fine terrace lines appear on border, and on inner side of genal spine.

Pygidium of length between 0.6 and 0.7 times transverse width at anterior margin. Genal fields slightly convex, slope to border abrupt. Narrow axis not sharply defined, very gently tapering to border, up to ten obscurely defined axial rings on some specimens. Pleural fields generally unfurrowed, except behind facets, but can show up to seven shallow ribs on some specimens (Pl. 23, fig. 8). Articulating facet steeply downturned, extending adaxially beyond border. Border gently downward-inclined, generally of nearly equal width along its length, about one-fifth total pygidial length, or expanding very slightly posterolaterally; on small specimens narrow postaxially. Fine terrace lines slightly oblique to margin never extending far onto pleural fields. Inner margin of doublure gently concave, flat beneath border, inner margin sharply curved upwards. Fine terrace lines on doublure subparallel to inner margin, oblique to outer margin.

Discussion. I have examined the type collection of Asaphus canalis Whitfield in the American Museum of Natural History, New York, on which Raymond (1910) based I. whitfieldi. More than one species is present. A number of specimens are very different from *I peri*, having broad pygidial borders that gently merge with the pygidial pleural fields, and somewhat acute postocular cheeks (Whitfield, 1886, Pl. 34, fig. 7; 1889, Pl. 11, 12). However, one cranidium (Whitfield, 1886, Pl. 34, fig. 1) resembles that of I. peri, and a complete specimen of this type was used by Raymond (1910, Pl. 14, fig. 1-3) to illustrate I. whitfieldi. A recent figure of a pygidium attributed to I. whitfieldi and very similar to that of the Newfoundland species has been given by Welby (1962, Pl. 13, fig. 11). The final status of I. peri may depend on a complete study of the Vermont species, and particularly on which specimen from Whitfield's collection is chosen as lectotype of I. whitfieldi.

Plates 23 to 37

Specimens blackened with a thin coating of photographic opaque and whitened with ammonium chloride before photography. Except where otherwise mentioned orientation is in conventional dorsal view. Photography by the author.

Plate 23

Figures 1-8. Isoteloides peri sp. nov. (1) Free cheek, X3; paratype, GSC 56804; 2 m from base. (2) Cranidium, partly decorticated, X2; holotype, GSC 56799; same locality as figure 1. (3) Pygidium, prepared to show doublure on left, X3; paratype, GSC 56801; 6 m from base. (4) Latex cast of external mould of hypostoma, X6; paratype, GSC 56805; same locality as figure 3. (5, 6) Pygidium in dorsal, X3, and lateral, X4, views; paratype, GSC 56800; 2 m from base. (7) Small cranidium, X5; paratype, GSC 56800; 2 m from base. (8) Latex cast of external mould of pygidium photographed in oblique light to emphasize pleural furrows, X5; paratype, GSC 56803; 6 m from base.



I. flexus Hintze (1953, p. 172, Pl. 17, fig. 2c, 3-8) differs from I. peri in having larger eyes and narrower postocular cheeks; the small pygidia of I. flexus are identical to smaller specimens of I. peri. On cranidial characters alone it is impossible to distinguish I. peri from I. polaris Poulsen, 1927, as identified from Utah by Hintze (1953, p. 171, 172, Pl. 17, fig. 9-15). The palpebral lobes are smaller on *I. peri*, but, as Hintze notes, the length of the eyes decreases during ontogeny, and as Hintze's (Pl. 17, fig. 14) specimen is smaller than Newfoundland specimens retaining palpebral lobes the difference may be ontogenetic. The large specimen from northwest Greenland figured by Poulsen (1927, Pl. 19, fig. 14) has very small palpebral lobes, but on that specimen the postocular sutures curve backward to cut the posterior border at an acute angle, unlike any specimen of I peri. Poulsen's fragmentary free cheek (Pl. 19, fig. 13) shows that this acute postocular suture cuts the margin adjacent to the genal spine; I. peri invariably has a distinct posterior border on the free cheek. The free cheek attributed to I. polaris by Hintze (1953, Pl. 17, fig. 11) has a short and slender genal spine compared with that of I. peri. The largest pygidium assigned by Hintze to I. polaris is considerably more transverse than any in the population of I. peri from Newfoundland; on both large and small pygidia from Utah the articulating facets on the pygidia more closely approach the axial furrows. These differences combine to suggest that the name I. polaris cannot be applied to the species from the St. George Group, but lack of "presence or absence" characters makes the distinction a fine one. Both Greenland and Utah occurrences of I. polaris are from a stratigraphically younger horizon than that inferred for I. peri. Poulsen (1927, p. 296) mentions an additional possible occurrence of I. polaris from the Powell Formation of Missouri. Hypostomata of I. peri, I. polaris and I. flexus are all remarkably alike.

Differences between *I. peri* and the second species of *Isoteloides* from Newfoundland, *I. latimarginatus* sp. nov., are summarized below.

Isoteloides latimarginatus sp. nov. Plate 24, figures 1-9

Holotype. Pygidium, GSC 56806.

Figured material. Incomplete cranidium, GSC 56807; small cranidium, GSC 56808; pygidia, GSC 56809, 56811; free cheeks, GSC 56810, 56812; hypostoma, GSC 56813.

Stratigraphic range. Upper part of section through Catoche Formation, 24 to 57 m.

Diagnosis. Isoteloides with wide, flat pygidial border. Palpebral lobes of medium size. Hypostoma more deeply forked than other species of the genus.

Discussion. This *Isoteloides* species occurs in stratigraphically younger beds of the Catoche Formation than *I. peri*. The differences are summarized as follows:

- 1. The palpebral lobes are of greater length (exsag.) on comparably sized cranidia.
- 2. The divergence of the preocular sutures is about 30° to the sagittal line.
- 3. The width of the pygidial border is twice that of *I. peri*. The border widens posterolaterally, and on larger specimens is almost flat.
- The hypostoma has a longer, deeper fork, and the lateral borders flare out rapidly anteriorly.

The wide, flat border of the pygidium and the characters of the hypostoma make this a distinctive *Isoteloides* that cannot be confused with the intergrading series of forms discussed under *I. peri*.

A small cranidium (Pl. 24, fig. 3) is like that figured for *I. polaris* by Hintze (1953, Pl. 17, fig. 12), except that the basal pair of glabellar furrows are shallower. At this size the glabella is well defined, conspicuously wider in the occipital area. A posterior glabellar tubercle is prominent. Palpebral lobes are large, and the postocular cheeks correspondingly restricted.

Wide doublure of free cheek (Pl. 24, fig.8) much like that of *Stegnopsis* (Whittington, 1965, Pl. 20, fig. 7), with panderian opening in posterior, adaxial corner of doublure. Both *Ptyocephalus* and *Lachnostoma* have longitudinal ridges on the doublure of the free cheek (Ross, 1951, Pl. 22), and this indicates that neither of these is close to the evolving early to middle Ordovician plexus that includes *Isoteloides* and *Stegnopsis*.

Plate 24

Figures 1-9: Isoteloides latimarginatus sp. nov. (1) Incomplete large cranidium, X4; paratype, GSC 56807; 30 m from base. (2, 6) Latex cast of external mould of pygidium, in dorsal, X3, and lateral, X2.5, views; holotype, GSC 56806; 57 m from base. (3) Small cranidium, X8; paratype, GSC 56808; 35 m from base. (4) Free cheek, X6; paratype, GSC 56812; same bed as holotype. (5) Latex cast of external mould of hypostoma, X5; paratype, GSC 56813; same bed as holotype. (7) Latex cast of large pygidium, X1.5; paratype, GSC 56809; 30 m from base. (8) Doublure of free cheek showing panderian opening, X2; paratype, GSC 56810; 35 m from base. (9) Small pygidium, X6; paratype, GSC 56811; same bedding plane as previous specimen. Note that at this size, width of border is not different from *I. peri* sp. nov.



Superfamily BATHYURACEA Walcott, 1886 Family BATHYURIDAE Walcott, 1886

Remarks on the classification of the Bathyuridae

The last general review of the classification of the Bathyuridae was that by Whittington (1953). Several species described in this paper modify the generic concepts within the family, and a summary of the new information is given below. In defining genera the characters of the pygidium have proved as useful as cephalic features in the discrimination of monophyletic groups. This has resulted in the re-assignment of many of the previously described species, reported in the systematic treatment. The later Canadian and middle Ordovician genera are now well understood, but some of the earlier forms, particularly those described by Cullison (1944), are imperfectly known, and their revision is distinctive and appears to characterize a is a prerequisite before the phylogeny of the group can be appraised in any detail. What is clear is that the subfamilies Bathyurinae and Bathyurellinae are distinctly separate in late Canadian time.

- The type species of Bathyurellus is unlike (i) many species with fan-like pygidia that have been referred to that genus. These are now placed in the new genus Punka. Punka is more closely related both to Licnocephala and Uromystrum than to Bathyurellus in the strict sense. A11 four genera (probably with Grinellaspis) together constitute a related group of bathyurellines.
- (ii) Bathyurina is a valid genus with a distinctive, strongly-furrowed pygidium, with several species widely distributed in later Canadian occurrences.
- (iii) Association of the correct cephalic and pygidial parts shows that *Strigigenalis* is a typical bathyurid, again widely distributed in strata approximating to zone H of Ross (1951) and Hintze (1953). Strigigenalis has been previously assigned to the Lecanopygidae or Leiostegiidae.
- A new genus, Catochia is proposed. Although (iv) two species of the genus occur in the St. George Group, they cannot at present be compared with any bathyurid outside Newfoundland (one unnamed pygidium from East Greenland may belong here).

The functional morphology of Catochia and Punka is discussed below, perhaps representing the extremes of bathyurid anatomy.

For comparative purposes cephalic and pygidial reconstructions of some of the genera described in this paper are shown in Figure 12.

Subfamily BATHYURINAE Walcott, 1886

Genus Bathyurina Poulsen, 1937

Type species Bathyurina megalops Poulsen, 1937

Discussion. This genus has been incompletely understood, the type species, B. megalops Poulsen, 1937, from the early Ordovician of East Greenland, being represented by two cranidia. Cranidia closely similar to the type occur in the present faunas and there is no reason to doubt that they should also be referred to Bathyurina. The Newfoundland cranidia can be associated with the pygidium described by Billings (1865) as Bathyurus timon. While the cranidium is similar in some ways to that of the species of Goniotelina, notably in the large palpebral lobes, and tuberculate glabella lacking incised glabellar furrows, the pygidium group of species of Canadian age, suggesting that generic status is warranted.

The Bathyurina pygidium is elongate, its length three quarters or more its transverse width, with highly convex pleural fields with three pairs of deep pleural furrows, which stop abruptly at a distinct, flattened or sloping pygidial border. Pygidia of this type have been described from several localities under different generic names. Jeffersonia jennii Cullison, 1944, from the Cotter Dolomite of the Ozark Uplift, should be referred to Bathyurina (the border on the pygidium illustrated by Cullison, 1944, Pl. 35, fig. 21, 22 is incomplete). "Genus et sp. indet.II (bathyurid?) " from the early Ordovician of Ellesmere Island figured by Poulsen (1946, P1. 22, fig. 8-10) is a Bathyurina species apparently with a slight emargination of the posterior pygidial border. The pygidium attributed to Psalikilus paraspinosum Hintze from the Williston Basin, Montana (Lochman, 1966, Pl. 34, fig. 3, 5, 7) is probably referable here. There is an undescribed species in the Kirtonryggen Formation, northern Spitsbergen.

From a slightly younger (mid-Arenig) horizon than *B. timon*, Hintze (1953, Pl. 26, fig. 7-10) figured Goniotelus brevus, a species essentially similar to Bathyurina in cranidial and pygidial morphology, except for the development of a small median spine on the pygidial border, and reduced genal spines. Gonioteloides Kobayashi (type species G. monoceros Kobayashi, 1955, form the McKay Group of British Columbia) is also similar to Bathyurina in pygidial structure, but with a peculiar, produced axis. The validity of Gonioteloides cannot be finally assessed without more knowledge of the cephalic parts.

Figure 12. Reconstructions of cephalic and pygidial shields of some of the bathyurid genera described in this paper.

- A. Punka flabelliformis gen. et sp. nov. (X1.5).
- B. Catochia ornata gen. et sp. nov. in dorsal
- and lateral views (below) (approx. X3).
- C. The type species of Bathyurellus, B. abruptus Billings, 1865, for comparison with Punka (X1.5).
- D. Strigigenalis caudata (Billings, 1865) (approx. X2).
- E. Bathyurina timon (Billings, 1865) (X2).



Bathyurina timon (Billings, 1865)

Plate 25, figures 1-10; Figure 12

Bathyurus timon Billings, 1865, p. 261, fig. 244 "Bathyurus" timon Billings. Whittington and Kindle, 1969, p. 658

Holotype. Pygidium, GSC 636.

Figured material. Cranidia, GSC 56814, 56816; pygidia, GSC 56815, 56817; free cheeks, GSC 56818, 56819.

Stratigraphic range. Measured section, 30 to 47 m from base.

Diagnosis. Bathyurina with lateral lobes on occipital ring. Pygidium with broad, flat or slightly downsloping border almost without tubercules which cover rest of exoskeleton; median acumination lacking.

Description. Glabella parallel sided to slightly forward-expanding, front profile broadly rounded, maximum downward curvature on forward half. Glabella covered with depressed tubercles, except for smooth areas adjacent to axial furrows representing muscle insertion areas. Broad (trans.) oval area opposite posterior part of palpebral lobe extending about one quarter across width of glabella; smaller smooth patch opposite anterior limit of palpebral lobe. Occipital furrow deep, slightly shallower medially and curved forwards laterally. Occipital ring one-sixth or less total sagittal length of glabella in dorsal view, widening slightly laterally, where its distal extremes are cut off by narrow furrows into circular lobes (Pl. 25, fig. 2). Axial furrows deep, shallowing anteriorly around front of glabella. Dorsal tuberculation only faintly reflected on internal moulds. Palpebral lobes very large, length (exsag.) half or more that of preoccipital glabella in dorsal view, almost reaching axial furrows at both anterior and posterior extremities, tilted slightly downwards towards glabella. Outline comprising almost two thirds of a circle; narrow palpebral rims without tubercules follow same outline, defined by broad, shallow palpebral furrow. Surface of palpebral lobe tuberculate like glabella. Postocular fixed

cheeks narrow (exsag.) of transverse width slightly less than that of occipital ring; border furrow deep. Posterior border convex and tuberculate, adaxially with narrow, posterior articulating flange, laterally widening and curved slightly backwards. Preocular cheeks narrow (trans.), widening forwards, divided into a lateral, tuberculate area, and a slightly depressed, smooth adaxial area, merging with preglabellar field, which is absent medially. Border furrow narrow and shallow, setting off narrow, slightly convex anterior border, which widens medially, from steeply sloping preocular cheeks. Facial sutures hardly diverge in front of palpebral lobes, anteriorly curving adaxially to cut anterior border at an obtuse angle; posterior sections of sutures almost at right angles to sag. line for most of their course.

Free cheek with outline like a quarter circle when in life orientation, genal fields slightly convex outwards. The large, curved and outward-bulging eye is rather high dorsoventrally, and the lenses are so small and numerous that even slight recrystallization obliterates the individual lenses. Beneath the eye there is a deep groove, carrying scattered, minute granules, within which there is a narrow ridge-like eye socle following the ventral profile of the eye. Wide lateral border furrow shallows near genal angle, lacking tubercles; a smooth band parallel to the border furrow continues up on to genal field, which is otherwise tuberculate like the glabella. Lateral border convex. widening towards genal angle, bearing a series of raised ridges. Ridges continue on to relatively short, outward-directed genal spine.

Pygidium highly convex (particularly trans.), length about three-quarters maximum width at posterior end of articulating facets. Axis tapers gently posteriorly, extending to about four-fifths total pygidial length; terminal piece rounded posteriorly. Three axial rings of equal width (sag., exsag.) clearly defined across middle of axis; a fourth, incompletely defined by furrows on flanks of axis only, especially on internal moulds. Anterior ring shows tendency to develop lateral lobes like those on occipital ring. Three pairs of deep pleural furrows

Plate 25

Figures 1-10. Bathyurina timon (Billings, 1865). (1, 6) Cranidium, dorsal and anterior views, X6; GSC 56814; 40 m from base. (2, 4) Cranidium, internal mould, dorsal and lateral views, X6; GSC 56815; same bed as previous specimen. (3, 5) Pygidium (original of Billings, 1865, figure 244), dorsal and lateral views, X6; holotype, GSC 636. (7) Free cheek, lateral view, showing eye socle and surface sculpture, X6; GSC 56818; 42 m from base. (8) Detail of lateral view of pygidium preserving cuticle, to show furrow in articulating facet, X10; GSC 56816; same bed as figure 1. (9) Free cheek, dorsal view (eye incomplete), showing genal spine, X5; GSC 56819; same bed as figure 7. (10) Internal mould of pygidium, X6; GSC 56817; same bed as figure 1.

Figure 11. Bathyurina megalops Poulsen, 1937. Anterior view of cast of holotype cranidium, X2; original of Poulsen, 1937, Plate 6, figure 14; Cape Weber Formation, East Greenland. Note preglabellar field, and compare with figure 6.

PLATE 25



slope progressively backwards posteriorly and stop at the border; a slight widening of the deep axial furrows posteriorly may represent remnant of a fourth pair of furrows. Border flat, or slightly downward-declined, smooth except for a scattering of post-axial granules on some specimens, and a few raised ridges peripherally. Posterior margin rounded, or with suggestion of median point. Axial rings and pleural lobes tuberculate. Internal mould punctate, indicating a tuberculate inner cuticular surface. Facets strongly backwarddeflexed and steeply downsloping, bisected by a groove, presumably to receive the posterolateral tips of the preceding thoracia segment (Pl. 25, fig. 7).

Discussion. The cranidium of *B. timon* is very like that of the type species, *B. megalops* (Poulsen, 1937, Pl. 6, fig. 14, 15) in the form of the glabella and the size of the palpebral lobes. Examination of the type specimen of *B. megalops* (Pl. 25, fig. 11) has shown that this species has a short, almost vertical preglabellar field, which is not present on *B. timon*. Although Poulsen assigned no pygidium to *B. megalops*, a fragmentary specimen (*ibid.*, Pl. 8, fig. 4) is clearly of *Bathyurina* type, and may be that of *B. megalops*. Other species of *Bathyurina* are indicated in the generic discussion.

Bathyurina sp. indet.

Plate 28, figures 8, 10, 11

Figured material. Pygidium, GSC 56820; cranidium, GSC 56821.

Stratigraphic range. 57 m from base of Catoche Formation, measured section.

Discussion. A second, stratigraphically younger species of *Bathyurina* occurs in western Newfoundland, but the material available is not sufficient to formally propose a specific name for it.

The important differences are on the pygidium. Compared with *B. timon* the border is narrower, especially posterolaterally, more steeply sloping and more convex. The posterior acumination is accordingly more prominent. Distal parts of the extremely deep pleural furrows tend to curve posteriorly. No pygidium with dorsal exoskeleton is available for comparison with the sculpture of *B. timon*, but the tuberculation of the cranidia of the two species is similar. Further collecting may prove a transition between this species and the earlier *B. timon*. Examination of specimens of *Bathyurina jennii* (Cullison, 1944) in the Smithsonian Institution, Washington, has shown that this species may be conspecific with *Bathyurina* sp. indet. from the Catoche Formation. Because of the incomplete information on the Newfoundland form, and *B. jennii*, open nomenclature is preferable at the moment.

Genus Bolbocephalus Whitfield, 1890

Type species Bathyurus seelyi Whitfield, 1886

Bolbocephalus convexus (Billings, 1865)

Plate 26, figures 1-10; plate 28, figures 9, 12

Dolichometopus? convexus, Billings, 1865, p. 269, fig. 253

Holotype (by monotypy). Pygidium, GSC 718.

Figured material. Pygidium, GSC 56822; cranidia, GSC 56823-56825; free cheek, GSC 56826.

 $\frac{\text{Stratigraphic range. 23 to 57 m through the}{\text{Catoche Formation measured section.}}$

Diagnosis. Bolbocephalus with relatively short (sag.) glabella in dorsal view, which rapidly expands in width forwards, and is highly convex in the dorso-ventral plane. Pygidium generally effaced, without defined border, interpleural furrows almost obsolete.

Description. This species evidently attained a large size, the larger figured pygidium (GSC 56822) having a width approaching 4 cm, and even larger fragmentary specimens have been observed in the field.

Cranidium highly convex, both glabella and preocular cheeks following strong anterior downward flexure. Occipital ring and preoccipital glabella horizontal in lateral profile, downward flexure beginning a short distance in front of the occipital ring, and continuing with an almost semicircular profile to the front of the glabella, which protrudes considerably forward beyond the cranidial margin. Glabella tapers strongly forward at first, being narrowest pre-occipitally, then expands forward from a point opposite mid-length of palpebral lobes, this expansion being of a somewhat lesser degree than the taper in the occipital region. Maximum transverse width of glabella anteriorly in front of occipital ring only slightly less than sagittal cranidial length in dorsal view, and exceeded by transverse width of occipital ring at posterior margin. No glabellar furrows are defined. Occipital furrow narrow, transverse

Plate 26

Figures 1-10. Bolbocephalus convexus (Billings, 1865). (1, 4) Cranidium preserving cuticle, dorsal and lateral views, X6; GSC 56823; 23 m from base. (2, 5, 7) Internal mould of pygidium, dorsal, lateral and posterior views, X2; GSC 56822; 29 m from base. (3, 6) Large, poorly preserved cranidium, lateral and dorsal views, X1.5; GSC 56824; north side of Catoche Cove, coll. W.D. Boyce. (8) Pygidium (original of Billings, 1865, figure 253), X2.4; holotype, GSC 718. (9, 10) Free cheek, largely preserving cuticle, in anterior, X6, and dorsal, X4, views (note effacement of border furrow anteriorly); GSC 56826; 57 m from base.



or slightly forward-bowed medially. Flat occipital ring occupies slightly less than one quarter total cranidial length in dorsal view. Axial furrows narrow and distinct, except towards posterior margin of occipital ring, where there may be partial effacement.

Palpebral lobes gently curved, about onethird length of glabella (dorsal view), close to glabella especially at anterior limits, posterior limits opposite a point just in front of lateral end of occipital furrow. Palpebral furrows narrow and deep, following outer profile of palpebral lobes. Postocular cheeks narrow (exsag.) and slightly declined, incomplete on available material, but, from sutural outline preserved on free cheek, certainly of a transverse extent less than that of the occipital ring; posterior border furrow probably shallow. Preocular cheeks extremely narrow (trans.), curving around circular anterior margin of glabella; preglabellar field probably absent medially. The broadly curving anterior sections of the facial sutures defining preocular cheeks contrast with highly divergent posterior sections. Surface sculpture on cranidium of fine raised lines curving forward over preoccipital glabella, less strongly so on occipital ring, more or less transverse on preocular cheeks.

Small cranidium (Pl. 28, fig. 12) attributed to *B. convexus* is more typically bathyurine, with waisting of glabella less conspicuous, broader preocular cheeks and narrow preglabellar field. Palpebral lobes are relatively large and their outline more strongly curved.

A free cheek occurs above other specimens of the species but sculpture and morphology suggest that it is correctly referred here. Relatively narrow (trans.) compared with that of B. seelyi (Whittington, 1953, Pl. 66, fig. 6, 10) and lacking genal spine. Lateral border furrow obsolete anteriorly, deeper near rounded genal angle where it meets very short section of posterior border furrow. Lateral border widening backwards, convex, anteriorly curving downward and wrapping under the margin apparently without distinct break into doublure. Convex eye socle carries one or two ridges running along its length. Gently curved eye with lenses so minute as not to have survived slight recrystallization of cuticle. Raised lines as on glabella, anteriorly having character of true terrace ridges.

Pygidium convex, lacking any trace of border. Axis occupies about 0.4 times total pygidial width anteriorly, gently convex, and diminishing so posteriorly, where at about three-quarters pygidial length in dorsal view its truncate tip merges without a break into the postaxial field. Two or three pairs of pleural furrows on adaxial part of pleural fields of which first pair is by far the deepest. Faint indication of distal part of first two interpleural furrows near pygidial margin. Broad, downturned facet extends to about halfway across front margin of pleural field. Internal mould shows fine, scattered punctae, dorsal cuticular surface only preserved in small patches, apparently smooth.

Discussion. B. convexus differs from the type species (Whittington, 1953, p. 655-657, Pl. 66, fig. 1-10, 12-14, 17, 21, 22) in its greater cephalic convexity, so that a greater part of the glabella overhangs the cephalic border, accompanied by a more rapid anterior glabellar expansion; the Newfoundland species also has gently curved palpebral lobes, which are almost semicircular in B. seelyi. The pygidial effacement of B. convexus, and the lack of a pygidial border, at once distin-guishes our pygidium from the strongly furrowed pygidium of B. seelyi. There is no doubt that B. convexus should be referred to Bolbocephalus because of the hourglass glabellar structure, unique among bathyurids. The differences between B. seelyi and B. convexus are another example of effacement in bathyurid genera proven elsewhere in this paper.

The pygidium of Bolbocephalus truncatus Whitfield, 1890, has been illustrated by Whittington (1953, Pl. 69, fig. 23-25), but was assigned by him to Strigigenalis cassinensis. This assignment is incorrect (see generic discussion of Strigigenalis below), and B. truncatus is evidently a Bolbocephalus species extremely close to, and possibly identical with B. convexus, showing a similar degree of dorsal effacement. Another similar pygidium from northeast Siberia was figured by Maximova (1962, Pl. 3, fig. 12) under the name Biolgina sp. B.

The type species of *Gignopeltis*, *G. rara* (Billings, 1865) (see Ludvigsen, 1979, Pl. 1, fig. 4), is a poor pygidium, also similar to effaced *Bolbocephalus*, except in better definition of the tip of the axis. Discovery of the cranidium of *G. rara* is necessary before the synonymy of *Gignopeltis* with *Bolbocephalus* can be proved.

Bolbocephalus groenlandicus Poulsen (1937, p. 48, Pl. 5, fig. 9-13) from east Greenland differs from *B. convexus* in the distinct definition of the interpleural furrows on the pygidium; the surface of the internal mould shows dense, rather than scattered punctation.

A free cheek identical to the one figured here for *B. convexus* has been illustrated by Young (1973, Pl. 7, fig. 13) from a zone H fauna in Utah.

I conclude that the more convex, effaced Bolbocephalus species will prove to be characteristic of faunas younger than zone G of the Utah/Nevada zonal schemes, increased effacement being accompanied by loss of the genal spines.

Genus Catochia nov.

Type species Catochia ornata sp. nov.

Diagnosis. Bathyurines with prominent spines on the occipital ring, axial rings of the thoracic segments and anterior axial ring of the pygidium. Glabella long and nearly parallel sided in front of wide (trans.) occipital ring, lacking incised furrows. Palpebral lobes of moderate size and posteriorly placed. Preocular fixed cheeks narrow (trans.); cranidial border narrow (sag.), gently upward arched. Pygidium small and highly convex, with three axial rings, and three pairs of pleural furrows, the posterior pair very short. Broad pygidial border.

Discussion. This genus is erected to include two species from Newfoundland that resemble no other early Ordovician bathyurids. The closest similarity is to the late middle Ordovician genus Raymondites. The type species of that genus, R. ingalli (Raymond) (see Whittington, 1953, Pl. 69, fig. 16-21), also has an axial pygidial spine, but this is on a posterior segment. The pygidium of Raymondites is large, with at least four pleural furrows, and seems to be similar in construction to that of Bathyurus itself. The position of the eyes and the form of the facial suture is comparable in Raymondites and Catochia but the former has a broad cranidial border that continues onto the free cheeks, which are extended backwards into long, flattened genal spines. It is probable that Raymondites is a late derivative from Bathyurus and that its similarities to Catochia are a matter of convergence.

Hintze (1953, Pl. 9, fig. 8, 11, 12) illustrated a species as Jeffersonia ?sp. B. which Whittington (1953, p. 662) reassigned to Peltabellia. The few pleural furrows in the pygidium of this species, and the defined pygidial border, suggests an affinity between Peltabellia and Catochia. However the large palpebral lobes of Hintze's species, well removed from the glabella, prevents its inclusion in the new genus. A possible Catochia pygidium, but with an extra pair of pygidial pleural furrows, has been described by Ross (1972, p. 35, Pl. 16, fig. 1-6). This specimen is from the Meiklejohn bioherm (early Whiterock), preglabellar furrow tends to be somewhat Nevada, and if the assignment to Catochia is correct, the genus ranges from the early Arenig to the Llanvirn. A pygidium similar to that of the type species has been figured by Poulsen (1937, Pl. 8, fig. 3) from the Cap Weber Formation, East Greenland.

Catochia ornata sp. nov.

Plate 27, figures 1-12; Figure 12

Holotype. Cranidium, GSC 56827.

Figured material. Cranidia, GSC 56828, 56829; pygidia, GSC 56830, 56831; free cheek, GSC 56832.

Stratigraphic range. Lower part of Catoche Formation, 11 to 40 m on measured section.

Diagnosis. Catochia species with well-defined axial furrows, glabella convex (trans.). Surface sculpture of coarse, anastomosing terrace lines over most of glabella, occipital ring smooth.

Description. Cranidium with maximum width at posterior margin, this about equal to sag. length in dorsal view. Glabella long and narrow, evenly rounded in front, length (sag.) including occipital ring twice width at midlength. In profile glabella slopes downwards and forwards in a continuous arc from shortly in front of the occipital ring. Preoccipital glabella parallel sided, or with slight taper from occipital ring at extreme posterior. Occipital furrow deep, transverse medially, slightly narrower and curving forwards laterally. Occipital ring wider than glabella in front, such that its transverse width is about 1.25 times that of glabella at mid-length, highly convex (sag., trans.) and occupying about one quarter total glabellar length, although with such a convex species the proportion varies with attitude of the specimen when glabellar length is measured. Occipital spine long, Smooth robust, and slightly backward curving. patches on the flanks of glabella probably represent areas of muscle insertion. A long (exsag.), continuous smooth patch extends from in front of the occipital furrow to forward limits of palpebral lobes. A second, subcircular area is present adjacent to the axial furrows on front of palpebral lobes but well behind anterolateral corners of glabella. Palpebral lobes more than a semicircle, close to glabella and upward-inclined, relatively small for a bathyurid, length (exsag.) about one third that of preoccipital glabella, posterior limit almost opposite outer end of occipital furrow. Narrow palpebral rim defined by distinct rim furrow. Postocular fixed cheeks narrow (exsag.) and triangular, acutely pointed, transverse width less than that of occipital ring, gently downward-declined. Posterior border furrow deep, dividing cheek in front of mid-length (exsag.). Preocular cheeks steeply downsloping in front of palpebral lobes, narrow (trans.), widening a little anteriorly where joining preglabellar field. Median part of effaced on some specimens so that front part of glabella tends to merge with preglabellar field, which is narrow medially, sloping downwards to cranidial rim. The rim is narrow (sag.) and flexed out horizontally, its transverse width slightly less than that of glabella. In anterior view it has a gentle upward arch. Facial sutures subparallel and anteriorly converging in front of palpebral lobes, posterior sections diverging strongly and running out to cut posterior cranidial margin at a low acute angle.

Surface sculpture on cranidium of coarse, forward-bowed terrace lines over most of glabella (except on muscle impressions). Particularly on smaller cranidia terrace lines tend to break up into irregular patches on back part of glabella, where there may be a few small tubercles. The occipital ring is smooth, unlike most bathyurids. Neither are there terrace lines on the fixed cheeks, preglabellar field or palpebral lobes.

Free cheek when in life position with outline almost a quarter circle, genal field convex outward. Border narrow anteriorly where joined to cranidium, widening gradually abaxially to rounded junction with posterior border. Lateral border furrow shallow, more marking an abrupt change in slope; posterior border furrow deep. Genal spine long, triangular cross section, slightly curved, base marked by elevated ridge between lateral and posterior border furrows. Fragments of dorsal cuticle adhering to the cheek indicate that much of its surface was covered with terrace lines like those on glabella but not on border. Small part of doublure also carries terrace lines, recurved beneath cheek, widening and reflexed upwards at genal angle.

Hypostoma not identified. Several fragmentary thoracic segments in the same beds as *C. ornata* have long mid-axial spines, which probably were present along the length of the thorax.

Pygidium convex (sag., trans.), maximum width at posterior ends of facets between one and a quarter and one and a half times sag. length (including half ring). Axis highly vaulted (trans.) anteriorly tapering gently and decreasing in convexity to broadly rounded terminal piece. Three axial rings, only clearly defined by ring furrows laterally on larger specimens; these furrows extend farther on small specimen. First axial ring noticeably wider than the others, and broadening medially, bearing a stout, circular spine. A faint pair of dimples on terminal piece of some specimens may represent a rudiment of a fourth axial segment. Articulating half ring prominent compared, for example, with Bathyurellus. Pleural fields downsloping, with three pairs of pleural furrows which, except for front pair, stop at border, each progressively backward-sloping, the last pair very short. A slight ridge backed by a depression behind the first pleural furrow may represent anterior interpleural boundary. All three segments are more clearly shown on immature specimen, interpleural boundary faintly discernable on border. Facets deeply backward-turned, almost reaching axis. Border gently downsloping to nearly flat, of equal width along its length, downward-rolled margin forming a segment of a circle. Axis with surface sculpture of irregular ridges and small tubercles like that on posterior part of glabella. Pleural fields and borders smooth.

Discussion. This species is worth a brief consideration from the point of view of its functional anatomy. A highly vaulted axis had been associated with a large area available for muscle insertion, and hence with powerful activity of the appendages (e.g. Henningsmoen, 1957, p. 78; Fortey, 1974). In *c. ornata* high axial vaulting is accompanied by a relatively thick cuticle, and narrow pleural regions. Judging from the width of the articulating half ring on the pygidium there was also

considerable flexibility along the midline. However, the posteriorly placed, relatively small eyes of this species are quite different from the huge eyes occupying most of the free cheeks of the pelagic trilobites Opipeuter and Carolinites, both of which exhibit similar postcephalic morphological adaptations. Pelagic habits for the present species are also unlikely because of the restricted geographic distribution of Catochia. In Newfoundland it is associated with shallow water limestone facies, and it is reasonable to assume that the morphological adaptations of the species were related to this habitat. Other forms in the present fauna (Ischyrotoma and Petigurus, for example) also show exceptionally high axial vaulting, thick sculptured cuticle, and are almost restricted to shallow shelf limestone strata of the Bathyurid province in the early Ordovician.

In Catochia, Petigurus, and Ischyrotoma the eyes are rather globular, and deep dorsoventrally, with minute, crowded lenses. In Catochia ornata their posterior position, combined with the upward tilt of the palpebral lobes, lifted the eyes to a high dorsal position (Figure 12), almost on a level with the highest part of the glabella, with only the axial spines projecting above. With their highly curved profile the eyes presumably commanded a wide field of view laterally, forwards and backwards (?upwards).

This combination of features must be explained in the context of the limestone shelf habitat occupied by Catochia. Among fossils of vagrant benthos with hard parts, other than trilobites, only gastropods and nautiloids are at all abundant in the Catoche Formation. Nautiloids are abundant and varied, and they are commonly regarded as one of the earliest predators. Both the axial spinosity of Catochia and the thick cuticle (and the combination of the latter with coarse tubercles on Petigurus) may have been adaptations for increased protection from these predators. Presumably good visual spread would have been necessary for the detection of the same predators. But this does not by itself explain the high dorsal position of the eyes. This would become explicable if, when threatened, C. ornata partially buried itself in the sediment. Tn this attitude the eyes would have projected, and the axial armature would have remained exposed. A burial to only 0.5 cm would have been adequate, and this could be rapidly achieved within the semifluid superficial sediment layer. The same habit might explain

Plate 27

Figures 1-12. Catochia ornata gen. et sp. nov. (1, 2, 4) Large cranidium showing characteristic surface sculpture, palpebral lobes missing, dorsal, lateral and anterior views, X6; holotype, GSC 56827; 23 m from base. (3, 6) Free cheek, largely stripped of cuticle, dorsal and lateral views, X6; paratype, GSC 56832; 11 m from base. (5) Cranidium, X6; paratype, GSC 56828; same bed as holotype. (7) Cranidium, in oblique lateral view to show occipital spine, X6; paratype, GSC 56829; same bed as holotype. (8) Thoracic segment, viewed laterally to show dorsal spine, X10; paratype, GSC 56888; 11 m from base. (9-11) Pygidium, posterior, lateral and dorsal views, X8; paratype, GSC 56830; same bed as holotype. (12) Small pygidium (note relatively well defined furrows on pleural fields), X15; paratype, GSC 56831; same bed as holotype.



the smooth pleural areas on the pygidium, with the surface sculpture confined to a mid-axial band. *C. glabra* sp. nov. (below) is more effaced, with the eyes more upward tilted, and cephalon almost smooth. It might be speculated that this species buried itself somewhat deeper.

It is not known whether either species would have utilized this position for feeding as well, but if active habits suggested above are correct, *Catochia* probably scurried rapidly over the sediment surface until forced into its protective stance. Such a posture does seem to be adequate to explain a number of otherwise disparate exoskeletal features.

Catochia glabra sp. nov.

Plate 28, figures 1-7

Holotype. Cranidium, largely exfoliated, GSC 56833.

Figured material. Cranidia, GSC 56834, 56889; free cheek, GSC 56835.

Stratigraphic range. Upper part of measured section of Catoche Formation 47 to 57 m.

<u>Diagnosis</u>. *Catochia* species with glabella not greatly elevated above preglabellar field; surface sculpture lacking on cephalon.

Differential description. This second species of *Catochia* succeeds *C. ornata* in the St. George Group, where cranidia are numerous. The main points of difference from the type species are listed here.

C. glabra lacks surface sculpture on cranidium and free cheeks except for a row of tubercles on back of the occipital ring, contrasting with the prominent terrace ridges on C. ornata. Smooth bathyurids are exceptional, most species assigned to the family being either tuberculate or with patterns of raised lines, or a combination of the two. The glabella of C. glabra is less convex transversely than that of C. ornata, this being especially apparent anteriorly, where the frontal lobe of the glabella of C. glabra runs down without a sharp break into the preglabellar field. This tendency towards effacement is not reflected on the occipital furrow, which is deep and transverse. The occipital ring of C. glabra is greatly elevated and conspicuously wider medially, the whole of the mid-part being drawn upwards into the occipital spine. Laterally the occipital ring runs without a distinct break into the posterior border of the postocular fixed cheek, where there is a posterior continuation of the axial furrows on C. ornata. The median waisting of the glabella is somewhat more prominent in C. glabra. Free cheek of C. glabra smooth like the cranidium, the lateral border furrow hardly developed. A narrow, convex rim is present, anteriorly continuous with the narrow cranidial rim, which is like that of C. ornata.

The pygidium of *C*. *glabra* has not been found, but it is so distinctive a species that its formal naming is justified.

Genus Petigurus Raymond, 1913

Type species Bathyurus nero Billings, 1865

Petigurus nero (Billings, 1865)

Plate 29, figures 1-12, 15

Bathyurus nero Billings, 1865, p. 260-1, fig. 243
Petigurus nero (Billings). Raymond, 1913, p. 58, 59,
P1. 7, fig. 8
Petigurus nero (Billings). Schuchert and Dunbar,
1934, p. 53
Petigurus nero (Billings). Whittington, 1953, p. 658,
P1. 66, fig. 18-20, 23-25
Petigurus nero (Billings). Whittington, 1968, p. 53
Petigurus nero (Billings). Whittington and Kindle,
1969, p. 658

Lectotype. GSC 750, internal mould of glabella (selected by Whittington, 1953, p. 658).

Figured material. Cranidia, GSC 56836, 56837; free cheek, GSC 56838; hypostoma, SM A97996; pygidia, GSC 56839-56841.

Stratigraphic range. Widely distributed through section through Catoche Formation, to 47 m from base.

Diagnosis. Coarsely tuberculate *Petigurus* in which pygidial interpleural furrows are obsolete adaxially.

Plate 28

Figures 1-7. Catochia glabra sp. nov. (1-3) Cranidium, largely exfoliated, dorsal, anterior and lateral views, X6; holotype, GSC 56833. (4) Incomplete cranidium, preserving cuticle (note lack of surface sculpture), X6; paratype, GSC 56834. (5) Incomplete free cheek, lateral view, X6; paratype, GSC 56835. (6, 7) Cranidium, dorsal and lateral views, X6; paratype, GSC 56889. All specimens from 57 m above base.

Figures 8, 10, 11. Bathyurina sp. indet. (8) Incomplete cranidium, X6; GSC 56821; 57 m from base. (10, 11) Pygidium, preserved as internal mould, dorsal and lateral views, X4; GSC 56820; 57 m from base. Note short border compared with B. timon (Billings).

Figures 9, 12. Bolbocephalus convexus (Billings, 1865). Small cranidium in anterior and dorsal views, X6; GSC 56825; 30 m from base.

Description. Whittington (1953) has given a general redescription of *P. nero*. New material from Port au Choix adds a few details to that description. The thick and coarsely tuber-culate cuticle peels off during preparation, and for this reason most of the material available is internal. Where it is preserved the dorsal surface closely follows the internal structure except that the furrows become even deeper and narrower.

Palpebral lobes about one-third (exsag.) of total glabellar length in dorsal view. Semicircular palpebral rims slightly inflated, with a single row of depressed tubercles. Palpebral furrow particularly broad and deep. Intraocular part of fixed cheek has characteristic form of almost equilateral triangle. Whittington's (1953, fig. 3) reconstruction of *P. nero* shows the forward margin of the glabella rather more truncate than is the case on specimens from the Catoche. In anterior view glabella broadly rounded anteriorly, overhanging narrow, slightly tumid border. Anterior branches of facial sutures converge forwards to anterior margin.

A hypostome is associated with P. nero (Pl. 29, fig. 12, 15). Its large size precludes its belonging to one of the smaller bathyurids. A fragment of cuticle adhering to the surface carries a surface sculpture similar to that preserved on the genal spine of P. nero. It is highly convex (sag., trans.), maximum transverse width at anterior margin exceeding sag. length. Much of the convexity is due to the vaulted middle body, which tapers and is less convex posteriorly. Pair of middle furrows extend about a third of the way across middle body, converging backwards posteriorly to about half sagittal length of hypostoma. Furrows defining middle body very shallow. Narrow lateral borders depressed anterolaterally, widening beyond middle body to distinct, posterior median acumination. It is worth noting how different this hypostoma is from that of the bathyurelline Bathyurellus platypus described below.

Free cheek with convex genal field which is tuberculate except for a depressed band near the base of eye. Border widens backwards, passing without a break into stout, blade-like genal spine, which attained about the same length as the glabella. In life orientation flank of genal spine inclined downwards almost vertically. Doublure narrow and reflexed beneath border, with strong exterior terrace ridges; these break up into chevron-shaped tubercules on genal spine.

Pygidia with width/length ratios in the range 1.6 to 2.2, the most transverse being smaller (width less than 1 cm). Characteristic feature is the incomplete interpleural furrows which bisect the four prominent pleural ridges on their outer part, on larger specimens cutting off posterior part of ridge as a convex node. Interpleural furrows longer on small specimens. Where cuticle preserved (Pl. 29, fig. 7) coarse tubercles on ridges give way to granules on sloping border, most prominent postaxially. While tubercles are reflected on internal moulds, granules are not.

Discussion. The distinctive structure of the pygidial pleurae reliably distinguishes *P. nero* from *P. groenlandicus* Poulsen (1937, Pl. 6, fig. 1-13) from east Greenland, on which the interpleural furrows extend much farther towards the axis.

A second type of *Petigurus* cranidium occurs in the Catoche Formation (Pl. 29, fig. 13, 14) distinguished by its greater glabellar convexity, especially anteriorly, and its longer (sag.) preglabellar area. There is insufficient material to determine whether this cranidium belongs to a second species of the genus, and it is accordingly left under open nomenclature.

Genus Strigigenalis Whittington and Ross in Whittington, 1953

Type species Strigigenalis cassinensis Whittington, 1953

Discussion. The type species of Strigigenalis, from the Fort Cassin Formation, Vermont, was excluded from the Bathyuridae by Whittington (1953), and the genus was placed in the Lecanopygidae in the Treatise (Lochman-Balk in Moore, 1959, p. 381). The pygidium associated with the type species (Whittington, 1953, Pl. 69, fig. 23-25) is much larger than

Plate 29

Figures 1-12, 15. Petigurus nero (Billings, 1865). (1) Free cheek, exfoliated, X2.5; GSC 56838; 11 m from base. (2, 4) Cranidium, dorsal and lateral views (exfoliated, palpebral lobes lacking), X2; GSC 56836; 23 m from base. (3, 6) Cranidium preserving palpebral lobe, dorsal and anterior views, X4; GSC 56837; 30 m from base. (5, 9) Large pygidium, exfoliated, lateral and dorsal views, X2; GSC 56839; 11 m from base. (7, 10, 11) Small pygidium, oblique lateral, dorsal and lateral views, X6; GSC 56840; 23 m from base. This specimen retains cuticle on left side, showing details of external sculpture on figure 7. (8) Small, rather wide pygidium, internal mould, X6; GSC 56841; 40 m from base. (12, 15) Hypostoma probably belonging to this species, ventral and posterior views, X6; SM A97996; Port au Choix, middle part of Catoche Formation, exact horizon not known, coll. H.B. Whittington.

Figures 13, 14. *Petigurus* sp. indet. Incomplete internal mould of cranidium, lateral view, X3, dorsal view, X4; GSC 56890; 40 m from base of section.

the cephalon, which is the holotype (Whittington, 1953, Pl. 67, fig. 6-8). In fact, this pygidium compares closely both in size and morphology with that of Bolbocephalus convexus (Billings, 1865), redescribed herein. Whittington (1953, p. 671) noted that Ulrich in manuscript had associated the cephalon of Strigigenalis with a completely different pygidium also figured by Whittington (1953, Pl. 68, fig. 30, 32). Cephalic parts close, or even identical to those of S. cassinensis occur in the Catoche Formation, and can be associated with confidence with the spinose pygidium described by Billings (1865) as Bathyurus caudatus. This in turn resembles the pygidium associated by Ulrich with Strigigenalis cassinensis. The conclusion is that the assignment of the pygidium to Strigigenalis in Whittington (1953) is incorrect, and that the pygidium figured there belongs with Bolbocephalus.

Strigigenalis as interpreted in this paper is a typical bathyurid. S. abdita Ross (in Whittington, 1953) must now be excluded from the genus, as it lacks genal spines, and has a wide, convex and nonspinose pygidium.

Strigigenalis is closest to Goniotelina (type species, G. williamsi Ross, 1951, Pl. 14, fig. 16-22, 25; Whittington, 1953, Pl. 68, fig. 11, 13-21), from which it differs in its less convex glabella, lacking tubercles, which is distinctly pointed anteriorly. The deeply defined cranidial border is not acuminate in Strigigenalis, and the pygidium has a broad, convex border, and the stubby posterior spine is an extension of the border rather than the axis.

Strigigenalis caudata (Billings, 1865)

Plate 30, figures 1-10; Figure 12

Bathyurus caudatus Billings, 1865, p. 261, 262, fig. 245 Gen. et sp. ind. (pygidium), Whittington, 1953, p. 670, Pl. 68, fig. 30, 32

"Bathyurus" caudatus Billings. Whittington and Kindle, 1969, p. 658

Holotype. Pygidium, GSC 635.

Figured material. Cranidia, GSC 56842, 56843; pygidia, GSC 56844, 56845; free cheek, GSC 56846.

Stratigraphic range. Measured section in Catoche Formation 6 to 47 m.

Diagnosis. Strigigenalis lacking tuberculate surface sculpture. Glabella pointed in front. Short, downsloping preglabellar field; anterior cranidial border not acuminate medially. Pygidium with triangular spine which carries median carina on internal mould.

Description. Glabella with gently vaulted transverse profile, in lateral view convex in front of occipital ring, sloping gently downwards and forwards, more steeply so anteriorly, but not bulging over preglabellar field. Glabella of length including occipital ring about 1.6 times maximum width near base of palpebral lobes, tapering gently forwards, rapidly so anteriorly to median point. Occipital ring hardly wider medially; deep, transverse occipital furrow slightly shallower adjacent to axial furrows. Axial and preglabellar furrows deep on internal moulds, narrow. Glabellar furrows lacking. Preglabellar field continuing downward slope of glabella, length (sag.) about the same as that of occipital ring. Border furrow very deep, in front of which border recurves steeply upwards to form narrow (sag.), convex rim, rounded evenly about mid-line. Anterolateral fixed cheeks slope steeply downwards except adjacent to axial furrows, internal mould finely caecate. Palpebral lobes of length (exsag.) about 0.4 length of glabella, forward limits somewhat closer to glabella, posterior ends opposite outer part of occipital furrow. Palpebral rim obscure on dorsal surface, but faintly defined on internal moulds. Narrow (exsag.) postocular cheeks of transverse width slightly more than half that of occipital ring, triangular and pointed, approximately bisected by distinct border furrow proximally. Posterior border flattened, especially laterally. Facial sutures moderately divergent in front of palpebral lobes until curving adaxially round border, highly so behind eyes, running in an almost straight course to cut posterior margin at acute angle of about 30°. Dorsal surface of cuticle smooth, or with fine and scattered punctae on palpebral lobes and occipital furrow; internal mould smooth, except for caeca. Parallel striae on border.

Free cheek with convex genal field and gently tumid borders widening laterally. Rim continues from cranidium, becoming narrow on genal spine. Short section of posterior border furrow curves forwards; longer section of narrow lateral border furrow curves backwards and

Plate 30

Figures 1-10. Strigigenalis caudata (Billings, 1865). (1, 10) Free cheek, dorsal view, X4, and detail of border, X8; GSC 56846; 40 m from base. Note scattered pits, and narrow band of terrace lines on rim. (2, 5) Cranidium, internal mould and latex cast from counterpart, external mould to show palpebral lobes, X4; GSC 56842; 47 m from base. (3, 4) Small pygidium, dorsal and lateral views, X8; GSC 56844; 47 m from base. (6) Pygidium (original of Billings, 1865, figure 245), exfoliated around doublure, X5; holotype, GSC 635. (7, 8) Cranidium, largely exfoliated, dorsal and anterior views, X6; GSC 56843; same bed as figure 2. Note convex border and caeca on preglabellar field. A small pygidium of *Ischyrotoma anataphra* sp. nov. is also shown. (9) Large pygidium, largely preserving cuticle, showing surface sculpture on posterior spine, X6; GSC 56845; same bed as figure 2.

shallows rapidly near genal angle. Genal spine relatively short and triangular. Surface sculpture of scattered punctae especially on border, raised lines on rim and interior edge of genal spine.

Pygidium triangular, tapering posteriorly into spine without sharp break. Genal areas and border downsloping and convex. Axis tapering posteriorly and terminally rounded, with three axial rings progressively shorter (sag.) posteriorly, defined by ring furrows shallower medially; terminal piece long. Three pairs pleural furrows progressively steeply backward-directed and shorter posteriorly, the third pair obscure on small specimen with cuticle. Widening of axial furrow adjacent to terminal piece on holotype probably represents relict fourth furrow. Border smooth, convex. Posterior spine triangular and broad-based with triangular to subcircular cross section, in lateral profile slightly tilted upwards, rather variable in length, but longest on small specimen. Internal mould shows a median ridge along its length from tip of axis. Dorsal surface shows a few terrace lines on flanks of pygidial spine, otherwise smooth. Internal mould finely punctate. Doublure reflexed closely against dorsal surface, reaching as far as inner edge of border.

Discussion. S. caudata is extremely like the type species, S. cassinensis, Whittington, 1953, and the two species may prove to be identical. Whittington (1953, p. 671) mentions the presence of terrace ridges on the occipital ring of S. cassinensis, which I have not observed on a Newfoundland specimen, and the scattered pits which are generally distributed on the cheeks of S. caudata occur only "at genal angle outside border furrow" on S. cassinensis. The anterior definition of the glabella, particularly at the median acumination, is more marked on s. caudata. None of these constitute an unequivocal specific difference, but without further information on the variation of S. cassinensis at its type locality, I am reluctant to synonymise it with S. caudata.

Goniotelina (?) plicalabeonus, Young (1973, p. 99, 100, Pl. 5, fig. 15-22), from a zone H horizon in Utah, should now be referred to Strigigenalis, and differs from S. caudata in lacking genal spines, and in the posterior effacement of the posterior ring furrows on the pygidium (although this can be matched on small S. caudata pygidia).

Strigigenalis, albeit masquerading under different generic names, is evidently a widespread genus. In spite of its spinose pygidium, the low, pointed glabella, lack of tuberculate sculpture and peculiar cephalic border, suggests that it was not directly ancestral to *Goniotelina* and *Acidiphorus*.

Subfamily BATHYURELLINAE Hupé, 1953

Genus Bathyurellus Billings, 1865

Type species Bathgurellus abruptus Billings, 1865 (designated by Raymond, 1905, p. 337)

Diagnosis. Bathyurellines with large spadeshaped pygidium. Cranidium resembling that of *Punka* gen. nov. but glabella not transversely highly vaulted, and anterior border narrow. Free cheeks convex (exsag.) with narrow, rimlike borders. Pygidium with pleural fields hardly furrowed behind anterior segment; broad, depressed posterior pygidial border.

Included species. Bathyurellus platypus sp. nov., B. abruptus (Billings, 1865), Bathyurellus(?) teretus Young, 1973.

Discussion. Bathyurellus is used here in a restricted sense, centred around the type species, B. abruptus Billings, 1865. It is perhaps unfortunate that Raymond (1905) selected this species as type species of the genus, as most of the species subsequently assigned thereto, and which have been considered typical of the genus, should now be referred to Punka gen. nov. (below). The distinctive spatulate pygidium of Bathyurellus, together with the long preglabellar field, low (trans.) glabella and narrow cephalic borders, enables a clear distinction between isolated exoskeletal parts of the two genera.

Bathyurellus species occur with those of Punka gen. nov. in the St. George Group and in view of the shared cephalic features of the two genera it is likely that they have a common ancestor. The fact that *B. platypus* succeeds *B. abruptus* in the Catoche Formation, and the two species are obviously more closely related to one another than to any other bathyurid, indicates that the group of species with spatulate pygidia included in the genus were undergoing an evolutionary history independent of that of *Punka*, and suggests that separate generic status is justified.

The pygidium assigned to Bathyurellus teicherti Poulsen, 1937, from the late Canadian of East Greenland, is clearly of Bathyurellus type (Poulsen, 1937, Pl. 7, fig. 5) in the sense used here. However, the cranidium and free cheek illustrating the same species, the former being the holotype, are more similar to those of Punka, and it is probable that the pygidium is incorrectly associated by Poulsen. Punka pygidia lacking assigned cephalic parts occur in the same fauna from east Greenland (Poulsen, 1937, Pl. 7, fig. 8).

Bathyurellus species are also present in the Kirtonryggen Formation of northern Spitsbergen. An unassigned pygidium from zone H of the western United States figured by Hintze (1953, Pl. 9, fig. 16) is also referable to the genus, as is the pygidium figured by Young (1973, Pl. 6, fig. 17, 20). The cranidium belonging to Young's pygidium is probably that described as Bathyurellus(?) teretus Young (1973, Pl. 2, fig. 5, 8, 13). Bathyurellus is evidently widespread in later Canadian shallow water limestone of the Bathyurid province, but does not seem to extend into the middle Ordovician.

Bathyurellus platypus sp. nov.

Plate 31, figures 1-13

Holotype. Well-preserved cranidium, GSC 56847.

Figured material. Cranidium, GSC 56848, pygidia, GSC 56849, 56850; free cheeks, GSC 56851, 56892; hypostoma, GSC 56852; doublure of pygidium, GSC 56891.

Stratigraphic range. The species ranges from 47 m above the base of the measured section to the topmost beds exposed on the foreshore of Port au Choix.

Diagnosis. Bathyurellus with surface sculpture on preoccipital glabella of fine, scattered pits. Terrace lines on free cheek sparser and more laterally confined than in *B. abruptus* Billings, and posterior pygidial border less concave behind pygidial axis.

Description. This species occurs abundantly above the stratigraphic range of *B. abruptus* and it is found in beds in which other similar bathyurids are lacking, so that the association of cranidium, free cheeks, pygidium, and hypostoma is well founded.

Cranidium of length (sag.) in dorsal view equal to width at posterior cranidial margin, with strong downward slope anteriorly, less declined postocular cheeks. Glabella parallel sided and gently vaulted (trans.), merging without a break with the preglabellar field on specimens cranidial length 6 mm or more so that the anteromedian outline is obscure. Smaller cranidia show faint, acuminate forward margin of glabella at about three-quarters cranidial length (sag.). Muscle insertion areas not clearly discernable. Axial furrows narrow, and deepest posteriorly, rapidly shallow around anterolateral corners of glabella to effaced median area. Occipital furrow transverse or slightly backward-bowed medially, narrow and deepest across mid-part of glabella, shallowing laterally and not reaching axial furrows. Occipital ring about one-eighth cranidial length (sag.), slightly forward-inclined. Palpebral lobes almost semicircular, length (exsag.) more than one-third glabellar length in dorsal view, anterior and posterior limits closely approaching but not touching axial furrows, posterior end opposite outer part of occipital furrow. Narrow, spine-like postocular cheeks curve slightly backwards, lacking defined border. Steeply downsloping, wide preglabellar field continues forward slope of glabella to shallow border furrow, which marks a change in slope more than an incised feature. Anterior border of about two-thirds width (sag.) of occipital ring, gently downwardsloping. Facial sutures diverge at a moderate angle (25-40° to sagittal line in dorsal view) in front of palpebral lobes, anteriorly converging to become subparallel anterolaterally before curving round forward cranidial margin; posterior sections diverge at a similar angle, rapidly becoming transverse, and curving distally slightly posteriorly to cut the cranidial margin at a low acute angle. Higher anterior divergence on small cranidia.

Cranidial surface sculpture of fine, scattered pits on preoccipital part of glabella, the same interspersed with terrace lines on occipital ring. Preglabellar field and palpebral lobes smooth. Small cranidia may have a few terrace lines immediately in front of the occipital ring, but these do not extend far forward. Two or three fine terrace lines run around the margin of the anterior border. Palpebral lobes smooth.

Free cheek broadly triangular with an acute genal angle, in life attitude sweeping backwards and forming a steep face laterally, with pleural field convex outwards. Border horizontal, narrow, and narrowing progressively laterally, border furrow becoming deeper at the same time. Eye low (dorso-ventrally), and long, apparently lacking an eye socle, so that lenses go right down to genal surface. Doublure broad, and widening backwards, densely covered in terrace lines, concave anteriorly, such that there must have been tubular space between anterior part of the cheek and doublure. There is a downfold (Pl. 31, fig. 13) near posterior margin of doublure, which curves outwards towards the genal angle; this may have served as a vincular notch during enrollment.

Hypostoma (Pl. 31, fig. 8, 11; similar hypostoma figured by Raymond, 1925, Pl. 3, fig. 18) perfectly elliptical, length (sag.) about two-thirds maximum width, transverse convexity low. Oval middle body extends to five-sixths length of hypostoma (sag.). Broad, deep middle furrows at about two-thirds length of middle body slope gently inwards and backwards and extend less than one-third of the way across middle body. Smooth, forward inclined maculae posterior to middle furrows. Border furrows deep laterally, shallowing around posterior edge of middle body. Anterior margin slightly embayed; anterior body not clearly defined from middle body. Lateral borders narrow (trans.) and standing almost vertically. Posterior border wider, tilted with a forward slope. Surface sculpture of terrace lines, transverse across mid-part of middle body, perpherally running concentrically around edge of hypostoma. Anterior wing closely reflexed beneath lateral borders.

Pygidium spatulate, Billings (1865) appropriately compared its shape to a duck's bill, maximum transverse width at posterior edge of articulating facets. Width:length ratios are variable; in large specimens length closely approaches maximum trans. width, small specimens (length less than 5 mm) are more transverse, length is only about two-thirds width. Convex axis tapers posteriorly to rounded tip at half pygidial length; one, possibly two, axial rings are faintly indicated on the dorsal surface; articulating half ring very short (sag.). One pleural segment present, pleural furrow short, adaxial, stopping at facet, slightly backward-directed, interpleural furrow faint or absent adaxially, deep behind facet and strongly backward directed, shallowing posterolaterally, but visible as far as edge of pygidium. Faint indication of adaxial part of second pleural segment on some specimens. Narrow, convex strip of pleural field adjacent

to axis, laterally steeply downsloping and then flattening out near pygidial margin. Postaxial downward slope gentle, not markedly concave behind pygidial axis. Dorsal surface with fine terrace lines, deeply forward arched over axis, approximately transverse on flattened border, tending to diverge slightly towards postaxial slope, where they may be faint or absent, similarly faint, and backward sloping on adaxial parts of pleural fields. They are also strongly developed on articulating facets, parallel to interpleural furrow. Doublure wide and flat, inner margin reaching tip of axis where it is strongly flexed upwards and recurved (Pl. 31, fig. 14). An elevated ridge runs sag. almost to posterior margin. Numerous transverse terrace lines like those on dorsal surface.

Discussion. The older species in the St. George Group, B. abruptus Billings, is closely similar to B. platypus and the differences distinguishing the species are discussed below.

Bathyurellus(?) teretus Young, 1973, from a zone H fauna in western Utah, is closely similar to the present species, and should be referred to Bathyurellus sensu stricto. The holotype (Young, 1973, Pl. 2, fig. 5, 8, 13) is unfortunately incomplete, but like B. platypus appears to lack terrace lines. Two small differences are noted: the occipital ring of the Utah species bulges laterally, and the anterior border furrow is a narrow discrete furrow rather than just a change in slope from the preglabellar field to the border. As mentioned above, I attribute the pygidium figured by Young (1973, Pl. 6, fig. 17, 20) as "unassigned pygidium 9" to *Bathyurellus*. This specimen is transverse, like small specimens of B. platypus, but the axial taper is greater than on the Newfoundland material. Hintze (1953, Pl. 9, fig. 16) figured a similar pygidium from zone H.

Poulsen (1937, Pl. 7, fig. 5) illustrated a pygidium assuredly referable to *Bathyurellus*. It may prove to be conspecific with one of the Newfoundland species. The holotype cranidium of *B. teicherti*, and particularly the free cheek, are similar to those of *Punka* gen. nov., and the association of pygidium and cephalic parts is considered improbable. Bathyurellus abruptus Billings, 1865

Plate 32, figures 1-12; Figure 12

Bathyurellus abruptus Billings, 1865, p. 263, 264, fig. 247, 250

Bathyurellus abruptus Billings. Raymond, 1905, p. 337 Bathyurellus abruptus Billings. Whittington, 1953, p. 661, Pl. 69, fig. 26, 27

Bathyurellus abruptus Billings. Whittington, 1968, p. 53

Bathyurellus abruptus Billings. Whittington and Kindle, 1969, p. 658

Lectotype. Pygidium from Port au Choix, GSC 648 (selected by Whittington 1953, p. 660).

Figured material. Cranidia, GSC 56853, 56854; pygidia, GSC 56855-56857; free cheeks, GSC 56858, 56893.

Stratigraphic range. From near base of measured section, to 40 m above base.

Diagnosis. Bathyurellus with surface sculpture on preoccipital glabella of dense terrace lines; similar sculpture distributed over most of free cheeks. Broad pygidial border concave behind pygidial axis.

Differential description. Most of the description given above for *B. platypus* applies also to *B. abruptus* and needs no repetition. *B. abruptus* was directly ancestral to *B. platypus*, and stratigraphically later specimens of *B. abruptus* show some transitional characters. At their extremes they are distinct.

The discriminating characters between *B. abruptus* and *B. platypus* are as follows

Dense terrace lines cover the preoccipital 1. glabella of B. abruptus. They stop at the preglabellar field. Smooth patches (Pl. 32, fig. 1) reveal muscle insertion areas: one at the lateral end of the occipital ring where the occipital furrow shallows, an oval area adjacent to the axial furrow opposite middle of palpebral lobe, and two smaller areas lying along the axial furrow, the anterior of which is at the anterolateral corner of the glabella. There are also terrace lines on the palpebral lobes of early B. abruptus; stratigraphically younger specimens may be smooth here.

Plate 31

Figures 1-14. Bathyurellus platypus sp. nov. (1, 6, 8) Cranidium with cuticle, dorsal and lateral views, X6, and detail of preoccipital glabella, X20, showing diagnostic pitting; holotype, GSC 56847. (2) Free cheek, X6; paratype, GSC 56851. (3) Small cranidium, incomplete on left side, X6; paratype, GSC 56848. (4, 5, 10) Well preserved pygidium, dorsal, posterolateral and lateral views, X6; paratype, GSC 56849; compare profile of figure 10 with that of *B. abruptus*, Plate 32, figure 3. (7) Small pygidium, X6; paratype, GSC 56850. (9, 11) Hypostoma, ventral and lateral views, X6; GSC 56852. (12, 14) Pygidium showing doublure, dorsal, X4, and lateral, X6, views (note recurved inner margin of doublure); paratype, GSC 56891. (13) Doublure of free cheek, showing terrace lines and posterior groove on exterior surface, X6; paratype, GSC 56892. All specimens from 57 m above base.

- 2. Terrace lines on the free cheek of *B. abruptus* are denser and extend almost to the base of the eye posteriorly.
- Pygidia of the two species are closely similar in general proportions. On B. abruptus the postaxial field is immediately flattened or slightly concave (Pl. 32,
- fig. 5); on *B. platypus* there is a gentle slope to the posterior margin. This is the result of gentle upward arch of the postaxial field of *B. platypus*, which leads to the terrace lines (in dorsal view) diverging slightly towards the mid-line, where they are faint or absent. The terrace lines adjacent to the pygidial axis on the convex parts of the pleural fields are also faint in *B. abruptus*.

The lectotype pygidium (Whittington, 1953, Pl. 69, fig. 26, 27) and the other syntypes on which Billings founded *Bathyurellus abruptus* all have the strongly flattened postaxial area which serves to distinguish this species from *B. platypus*, and where exoskeleton adheres to Billings' originals the sculpture supports the same determination. The species is numerous in equivalents of the Port au Choix strata near Boat Harbour.

Features distinguishing *B*, *abruptus* from other *Bathyurellus* species are as for *B*. *platypus* above, with the addition that the dense terrace lines on the glabella provide a further distinction from *B*. *teretus* (Young, 1973), from the late Canadian (zone H) of Utah.

Genus Punka nov.

Type species *Bathyurellus nitidus* Billings, 1865 (designated herein)

Diagnosis. Bathyurelline trilobites with wide, fan-like pygidia, considerably flattened, with three or four pairs of pleural furrows. Glabella generally well-defined, vaulted transversely, extending far forwards to touch or closely approach anterior border furrow. Cephalic border wide, flattened to slightly concave, present on cranidium and forward part of free cheek, genal spines of variable length, extremely long in some species. Pygidium wider than long, short axis with four axial rings (when defined). Faint interpleural furrows may be present on border only. Surface sculpture generally of fine raised ridges and/or terrace lines. Discussion. With the clarification of the type and other species of *Bathyurellus*, discussed above, a new genus is erected here to include species formerly attributed to *Bathyurellus*, but with wide, furrowed pygidia, broad cephalic borders, and the preglabellar field reduced or absent. As noted above, species with this morphology co-exist with *Bathyurellus sensu stricto* in the St. George Group, and they are considered to belong to different evolutionary lines. *Punka* species extend beyond *Bathyurellus* into the middle Ordovician.

The closest related species to those of the new genus appears to lie with Licnocephala Ross, 1951 (type species L. bicornuta Ross, 1951) rather than with Bathyurellus, as restricted in this paper. L. cavigladius (Hintze, 1953, Pl. 10, fig. 1-5; Ross, 1953, Pl. 64, fig. 4-29) shows a similarly narrow preglabellar area and flattened cephalic border. The cranidium is of low convexity, however, with the glabella scarcely vaulted and tending to effacement. The interpleural furrows on the pygidium extend onto the adaxial part of the pleural fields, and the pygidial border is sharply defined; the free cheek attributed to this species by Hintze (1953, Pl. 10, fig. 5) is more like that of Bathyurellus sensu stricto, with its inflated posterior lobe extending without a break into the genal spine. It is possible that Punka was derived from a Licnocephala species (which is older), and intermediate morphological types may be anticipated, but the subsequent stabilization of its morphology indicates that it is correct to separate them generically.

Grinnellaspis Poulsen (type species, G. fieldeni (Poulsen, 1946)) from the early Ordovician of Ellesmere Island, is known only from a pygidium. This resembles that of Punka, and particularly P. flabelliformis (below), in the arrangement of pleural and interpleural furrows, but they are particularly deep in Grinnellaspis. There is also a fifth axial ring, and a marked postaxial ridge, an unusual feature in Bathyuridae (but see Strigigenalis caudata herein). These features suggest that its generic recognition is justified, but this must await final assessment when cephalic parts are attributed to the genus.

Uromystrum is also represented by a species in the St. George Group, showing a characteristic concave pygidial margin. Uromystrum,

Plate 32

Figures 1-12. Bathyurellus abruptus Billings, 1865. (1) Incomplete cranidium, showing characteristic surface sculpture, X6; GSC 56853; 11 m from base. (2, 5, 8) Pygidium, dorsal, lateral and posterior views, X6; GSC 56855; same bed as figure 1. (3) Stratigraphically high cranidium, terrace lines weakly developed on palpebral lobes, X6; GSC 56854; 36 m from base. (4) Transitory pygidium, retaining one thoracic segment, X8; GSC 56856; 23 m from base. (6) Small free cheek, X6; GSC 56893; 11 m from base. (7, 9) Lectotype, selected Whittington, 1963, incomplete pygidium, lateral and dorsal views, X3; GSC 648. (10, 11) Large free cheek, dorsal and lateral views, showing sculpture, X6; GSC 56858; same bed as figure 1. (12) Internal surface of pygidial doublure, X3; GSC 56857; 35 m from base.

Licnocephala, and Punka together constitute a closely related group of bathyurids. Licnocephala may include species ancestral to the other two, which subsequently underwent a separate evolutionary history into the middle Ordpvician. Cephalic features indicate that Bathyurellus, as restricted in this paper, is also related to this group, and a common ancestor for Bathyurellus and Licnocephala should be sought in the earlier Canadian.

Bathyurellus nitidus Billings, 1865, is chosen as type species for the new genus because it is known from articulated specimens. It is from the Lower Head boulder, western Newfoundland, and has been fully redescribed by Whittington (1953, p. 661, Pl. 67, fig. 9, 13-15; 1963, p. 55-57, Pl. 10, fig. 8, 9, 11, 12, 14-17, Pl. 11, fig. 1-12, 14, 15).

Punka flabelliformis sp. nov.

Plate 33, figures 1-10; Figure 12

Bathyurellus marginiatus Billings, 1865 (pars), p. 264, fig. 249, non fig. 248

Bathyurellus marginatus Billings, 1865, p. 263, p. 266 Bathyurellus marginiatus Billings (pars). Whittington 1953, p. 661

Bathyurellus marginiatus Billings. Whittington and Kindle, 1969, p. 658

Holotype. Cranidium, GSC 56859.

Figured material. Cranidium, GSC 56860; pygidia, GSC 57757, 56861; free cheek, GSC 56862.

Stratigraphic range. Lower part of section through Catoche Formation, 11 to 40 m.

Diagnosis. Punka species with preglabellar field lacking. Genal spines broad, blade-like, and greatly extended posteriorly. Pygidium with deep, short pleural furrows, shallow interpleural furrows extending almost to margin.

Description. Cranidium of moderate convexity produced by downward curve of forward half of glabella and downsloping preocular fixed cheeks. Glabella widest across occipital ring, length (sag.) between 1.5 and 1.9 times this width, in dorsal view with rounded anterior profile, in forward view showing obtuse median acumination. Glabellar furrows not incised. Occipital furrow deep, bowed backwards towards mid-line. Occipital ring convex (sag., exsag.), slightly wider medially. Axial and preglabellar posteriorly. Rounded terminal piece of length furrows well-defined. Palpebral lobes large

and close to glabella, especially anteriorly, length (exsag.) slightly less than half sagittal length of glabella in dorsal view, horizontal to slightly declined towards glabella, and with strongly curved profile, particularly posteriorly. Postocular cheeks narrow and straplike, hardly declined downwards, including only a short, adaxial part of the posterior border furrow; posterior border with convex adaxial knob, flattening gradually laterally to pointed tip. Preocular fixed cheeks widening rapidly forwards to shallow anterior border furrow, where the downward slope stops abruptly. Preglabellar field absent medially where glabella reaches border furrow. Broad anterior border flat or gently concave, length (sag., exsag.) exceeding that of occipital ring. Facial sutures diverge strongly behind eyes at right angle to sagittal line, curving slightly posteriorly abaxially to cut the posterior margin at an acute angle; preocular divergence lessens over anterior border, anteriorly sutures curving adaxially. Surface sculpture of strong terrace ridges on glabella, where they are arched strongly forwards (less so on occipital ring), and on palpebral lobes. Preocular cheeks and border smooth, the former with faint genal caeca.

Free cheek long and curved, produced into an extremely acute genal spine. Broad, anterior border continues from cranidium on to anterior part of cheek, continuing posteriorly as a progressively narrow rim. Anterior border furrow cuts across genal field subparallel to base of eye to meet shallow, transverse posterior border furrow at a high acute angle. This indicates that all the extended posterior part of the cheek is a hypertrophied border or genal spine. Ventrally the doublure extends beneath this border area, supporting the same interpretation. Fine terrace lines like those on palpebral lobes, running transversely on proximal part of cheek, but not in anterior part of border furrow. On extended genal spine terrace lines form a forward-pointing chevron pattern, with apex of the V close to the lateral margin of cheek.

Pygidium of length/width ratios within the range 0.5 to 0.65, smaller specimens being the more transverse. Pleural fields generally flat, with declination around margin, and gently convex area adjacent to axis. Short, tapering axis reaches to half or less sagittal length of pygidium, with four axial rings completely defined by ring furrows which are deeper laterally, rings decrease in width (sag.) (sag.) equal to that of first axial ring.

Plate 33

Figures 1-10. Punka flabelliformis gen. et sp. nov. (1) Small pygidium, X6; paratype, GSC 56851; 30 m from base. (2-4) Cranidium, part of preglabellar field missing on left side, anterior, dorsal and oblique lateral views, X6; holotype, GSC 56859; 40 m from base. (5, 8) Free cheek, dorsal view, X2, detail of surface sculpture, X6; paratype, GSC 56862; 30 m from base. (6, 7) Well preserved pygidium, dorsal view, X6, posterior view, X5; paratype, GSC 57757; 11 m from base. (9) Internal mould of large cranidium, X6; paratype, GSC 56860; 23 m from base. (10) Pygidial doublure, exterior surface showing sculpture, X4; paratype, GSC 57760; 30 m from base.

Extremely narrow (sag.) articulating half ring. Four pairs pleural furrows on convex, adaxial part of pleural fields, not extending on to border. Distal ends of these furrows curve posteriorly, and their overall backward slope increases posteriorly, such that the first furrow is proximally transverse, fourth furrow distally subparallel to sagittal line. Interpleural furrows on border, hardly extending on to convex adaxial field, anterior furrow deepest and midway between first and second pairs of pleural furrows. Posterior interpleural furrows lie progressively closer to distal extremities of pleural furrows, which may then give the impression of being continuous, almost to margin. Fine dorsal terrace lines are bowed forwards between the interpleural furrows. Doublure broad and flat, extending under most of pleural field, inner margin turned upwards, carrying terrace lines with about half the density of those on dorsal surface.

Discussion. Billings (1865) original description of which was considered above. of Bathyurellus marginiatus was based on pygidia and a cranidium. Billings spelled the species name both as B. marginiatus and B. marginatus; here the former is adopted as that given at the formal proposition of the species. The name B. marginiatus has appeared subsequently in the literature based on Billings' original concept of the species. Pygidia of the type figured by Billings are one of the more frequent and distinctive fossils of the Catoche Formation. Whittington (1953) selected as lectotype (Pl. 35, fig. 13) Billings' cranidium, which comes from Keppel Island, 6 miles southeast of the Port au Choix Peninsula. Unfortunately, I have not been able to find a cranidium in the Catoche Formation resembling the lectotype. The cranidium associated here with pygidia of marginiatus type, is more convex than the lectotype, with the short preglabellar field characteristic of Punka (above). Cranidia are rare compared with pygidia (perhaps because the convex glabella tends to break off into the rock), but free cheeks compatible with the cranidium are frequently encountered. The surface sculpture is also consistent with the association. It is therefore necessary to propose a new species for the pygidium long referred to as B. marginiatus, and the associated cephalic parts. Whether the type marginiatus cranidium can be associated with the pygidium of a second, rare species of Punka from the Catoche Formation (below) is not provable from the present study.

Punka flabelliformis differs from the type species, P. nitida (Billings) (see Whittington 1953, 1963) in its greatly extended genal spines, deeper, narrower pleural furrows on the pygidium, and distinctive arrangement of the interpleural furrows. P. nitida also has a short (sag.) preglabellar field. A free cheek similar to that of P. flabelliformis is figured by Poulsen (1937, Pl. 7, fig. 4) from the Cap Weber Formation, east Greenland. The cranidium associated with this cheek by Poulsen, the type of Bathyurellus teicherti, has a short preglabellar field, and a more obviously acuminate glabellar than P. flabelliformis. Poulsen (1946, Pl. 22, fig. 12, 13) also figured a free cheek from Ellesmere Island, attributed

to Bathyurellus teicherti, which, although not as extended as that of Punka flabelliformis, shows a similar pattern of chevron-shaped terrace lines, and clearly belongs to a closely related species. Such long cheeks are found also on Uromystrum species (e.g. Uromystrum formosum (Billings, 1865), see Whittington, 1963) which are otherwise dissimilar on pygidial characters.

Whittington (1953, fig. 1) showed the life orientation of bathyurids with cephalic morphology like that of P. flabelliformis. The cephalon exceeds the rest of the exoskeleton in convexity, and is swept back into great genal spines extending as far as the pygidium. Both thorax and pygidium were suspended well above the perimeter of the cephalon. This distinctive morphology seems to have been repeated several times in different evolutionary lines, for example, in species of Punka, Uromystrum, and Raymondites. It is completely unlike such bathyurines as Catochia, the functional morphology

In interpreting the possible mode of life of Punka flabelliformis the reasonable assumption is made that there were nine thoracic segments, with a structure like those of P. nitida and Uromystrum (e.g. U. patulum Whittington, 1963). The relatively massive cephalon compared with the thorax, together with the narrow thoracic and pygidial axis (with a small area available for muscle insertion) makes an actively swimming or even rapid crawling habit improbable, compared with Catochia. Axial half rings on the thorax are prominent anteriorly (Whittington, 1963, Pl. 13, fig. 1, 7; 1953, Pl. 67, fig. 13), and particularly on the first axial ring, whereas the half ring on the front margin of the pygidium is very short (sag.) as shown by Plate 33, figure 6. This suggests that the main region of flexure was anterior, and particularly between the cephalon and the thorax, but little flexure was possible between the pygidium and the thorax. The same interpretation is supported by the transverse width of the anterior articulating facets. This allows for the downward-turned cephalic attitude figured by Whittington (1953, p. 661, fig. 4b), and further indicates that the pygidium was habitually held in the same plane as the posterior part of the thorax. For this reason it is unlikely that the pygidium was used in the same way as the lobster telson for rapid backward propulsion by a contraction of the pygidium downwards and forwards, however suitable its fan-like shape might seem for such a function.

The declined cephalon with outstretched thorax and pygidium could also be taken to indicate the sort of life orientation in illaenids figured by Bergström (1973, p. 45, fig. 13), in which the convex cephalon rests on the sediment surface while the thorax and pygidium are inclined downwards, largely buried beneath the sediment surface. However, the form of the terrace lines discourages this interpretation. On the pygidium the terrace lines have steep slopes facing backwards, in the direction which would oppose movement of sediment over the dorsal surface of the shield during burial. On invertebrates which habitually bury themselves (the mole crab, Emerita,

and bivalves, for example), the arrangement of stepped skeletal structures is that which facilitates, rather than resists, burial. For this reason I consider it likely that Punka flabelliformis normally rested on the sediment surface supported by the cephalic rim. The concavity of the medial part of the cephalic border would then have served to force the forward cephalic margin to glide upwards over the sediment during a forward push, rather than digging down into it. Some of the fluid surface sediment probably spilled over on to the border anteriorly, a region where terrace ridges are absent. This sediment would be deflected on to the genal spines, where it would be ploughed off by the chevronshaped ridges, with their forward-pointing apices (in a manner analagous to the arrowshaped times on a field plough). In summary, therefore, the morphology of the cephalic brim was adapted to allow forward movement, gliding over or just below the sediment surface rather than swimming or crawling.

The dorsal terrace lines may have functioned to keep the back of the animal free of sediment. Facing directions of the ridges on the rear of the trilobite would have shifted any sediment posteriorly, eventually to spill over the rim of the pygidium. Sediment landing on the free cheeks would have been encouraged to move towards the marginal furrow. This may or may not have been assisted by the sort of current-directing function attributed to terrace lines by Miller (1975). The forward motion of the trilobite alone may have been enough to produce currents to assist in movement of sediment. The narrow, curved and strip-like eyes presumably commanded a predominantly lateral view over the sediment surface. Since the smooth frontal area extends to the base of the eyes this presumably defines the area which could become buried in the sediment.

There is little bearing directly on the feeding habits of *Punka flabelliformis*. The downward deflexion of the cephalic region suggested by the thoracic half rings, and by Whittington's (1953) specimen of *P. nitida*, recalls the active feeding position deduced for *Leonaspis* by Clarkson (1969). This attitude would require the contraction of the longitudinal axial muscles, the "relaxed" attitude being that with the thorax extended and the half rings concealed. We do not know the attitude of the hypostoma, nor how it was attached (if at all). It remains open to question whether *Punka* fed directly from the sediment, or used the cephalic vault as a filter feeding chamber.

Punka? sp. indet.

Plate 35, figures 12, 14, 15

Figured material. Pygidia, GSC 56863, SM A97997.

Stratigraphic range. Lower part of measured section in Catoche Formation, to 30 m.

Discussion. A distinctive pygidium occurs as a rare associate of those of Punka flabelliformis,

and without doubt represents a second species. The furrows crossing the broad pygidial border are almost straight in this species, reaching the pygidial margin, and radially arranged like the spokes of a wheel. The distal furrows seem to be a continuation of the pleural furrows in this case, rather than of interpleural origin as in *P. flabelliformis*. The posterior margin of the pygidium is flexed gently downwards.

The lectotype cranidium of "Bathyurellus" marginiatus Billings (Pl. 35, fig. 11, 13) differs significantly from the cranidium attributed to Punka flabelliformis and from Punka in general in having a broad, gently declined preglabellar field. The border is of moderate width, rather sharply defined, and not strongly concave, and the palpebral lobes were probably smaller than those of P. flabelliformis. This specimen is from Keppel Island to the south of Port au Choix, but its association there with Petigurus nero (Whittington, 1953, p. 658) indicates that it is from a horizon equivalent to Catoche. It is possible, therefore, that this cranidium is to be associated with the second type of pygidium from Port au Choix, to which the name marginiatus should then be applied.

Unfortunately, I have been unable to recover a cranidium of *marginiatus* type from the Catoche section at Port au Choix. For this reason the pygidia have been referred under open nomenclature until the association of cranidium and pygidium can be definitely proved.

Genus Uromystrum Whittington, 1953

Type species Bathyurellus validus Billings, 1865

Uromystrum cf. affine (Poulsen, 1937)

Plate 37, figures 10, 11

cf. Bathyurellus affinis Poulsen, 1937, p. 55, Pl. 7, fig. 6, 7

Figured material. Pygidia, GSC 56864, 57759.

Stratigraphic range. Lower part of measured section of Catoche Formation, to 12 m.

Discussion. Pygidia with effaced axial regions and concave borders are here referred to Uromystrum cf. affine (Poulsen). Compared with the type species, U. validum (Whittington, 1953, Pl. 67, fig. 1-5, 10), the pygidial axis lacks definition and the dimensions are wider, the transverse width of the pygidium being twice the sagittal length. However the concave border indicates affinities with Uromystrum rather than any other Bathyurelline. Uromystrum affine (Poulsen) from the Cap Weber Formation, east Greenland (Poulsen, 1937, Pl. 7, fig. 6, 7), resembles the material from Newfoundland in transverse pygidial width and in the effacement of the axial region. The holotype of this species is figured on Plate 37, figure 12 for comparison. The east Greenland species differs from that of the St. George species in the greater width of the concave border, especially about the mid-line, where the border of U. affine is more than twice as wide as that on our material. This difference makes it improbable

that the Newfoundland and Greenland species are identical, even though they resemble one another more closely than any other *Uromystrum* species. Since the cranidia and free cheeks of neither form is known there is insufficient evidence to diagnose a new species from Newfoundland, and the identification is accordingly provisional.

Family LECANOPYGIDAE Lochman, 1953

Genus Benthamaspis Poulsen, 1946

Type species Benthamaspis problematica Poulsen, 1946

Discussion. The type species of Benthamaspis is known from one cranidium from Ellesmere Island. Two species attributed to the genus occur in the Catoche Formation, and are known from numerous specimens, which enables the association of cranidia with free cheeks and pygidia. The two species succeed one another in the formation, and the differences between them are slight, especially concerned with the greater effacement of the later species. It is reasonable to suppose an ancestor-descendent relationship between the two species, but even if this does prove to be the case their close alliance is evident. The later species, in which the front margin of the glabella merges without a break with the preglabellar field, is closest to the type species, possibly even conspecific. The earlier species, on which anterior definition of the glabella is clear, agrees in its salient features with the type species of Oculomagnus, O. obreptus Lochman, 1966, from the early Ordovician of the western United States (Ross, 1951, Pl. 29, fig. 20, 21, 24; Lochman, 1966, Pl. 62, fig. 6, 7) except for a greater slope on the preglabellar field. As the transition from Oculomagnus to Benthamaspis occurs between two evidently closely related species in the St. George Group, it is difficult to justify separating the two genera, and Oculomagnus is accordingly regarded as a junior subjective synonym of Benthamaspis. Effacement appears to be a continuous trend within the group culminating in B. diminutiva Hintze (1953) from the later Arenig of Utah, in which the glabella is almost completely effaced.

As noted by Fortey (1975a, p. 95) Benthamaspis cannot be assigned to the Komaspididae, as in the Treatise (Lochman-Balk in Moore, 1959). Lochman (1966) and Fortey and Owens (1975, p. 236) favoured bathyurid affinities for species of Benthamaspis type. At present I cannot readily derive Benthamaspis from any known bathyurid, especially with regard to the relatively truncate glabella and the pygidium lacking pleural furrows. Pygidia of Benthamaspis type (often with a postaxial ridge as described in this paper) are known from Lecanopygidae, and, except for the larger eyes of the Ordovician species, cranidial proportions are not dissimilar. Accordingly, Benthamaspis is tentatively included in the Lecanopygidae.

The poorly known genus *Gignopeltis* Raymond, 1924 (type species *Dolichometopus? rarus* Billings, 1865) has also to be considered in connection with *Benthamaspis*. The type specimen of Gignopeltis rara is a poorly preserved and incomplete internal mould of a pygidium, and is like that of Benthamaspis in its general proportions. However, one or possibly two pairs of short pleural furrows are indicated on the adaxial part of the pygidial pleural fields, and there is a faint postaxial concavity. Neither of these features is known from Benthamaspis. Gignopeltis appears to be closer to the more effaced species of Bolbocephalus, like B. convexus described herein, or Biolgina (e.g. B. sibirica, <u>see</u> Maximova, 1962, Pl. 3, fig. 4) but the question of the affinities of Gignopeltis cannot be finally resolved until its cephalic parts are discovered.

Benthamaspis species from the St. George Group are known from forms with both parallelsided and tapering glabellas. At first this was considered to indicate a specific distinction, but is now regarded as due to intraspecific variation. Both the early and later species exhibit the same variation, and the changes that occur between the species (effacement of the preglabellar furrow in the later species for example) operate regardless of the glabellar form.

Benthamaspis is widely distributed over the North American shelf. It may also be found in Northeast Siberia: Biolgina brevis Maximova, 1955 (see also, Maximova, 1962, Pl. 3, fig. 7, 8), which appeared as a nomen nudum in Andreeva, 1955, seems to be close to the earlier type of Benthamaspis with distinct anterior glabellar definition.

Benthamaspis gibberula (Billings, 1865) Plate 34, figures 1-15

- Dolichometopus? gibberulus Billings, 1865, p. 269, fig. 254
- ?Nileus striatus Whitfield, 1897, p. 184, Pl. 5, fig. 5, 6
- ?Benthamaspis problematica Poulsen, 1946, p. 325, 326, Pl. 22, fig. 14-16
- "Bathyurus" gibberulus (Billings). Whittington and Kindle, 1969, p. 658
- Benthamaspis distinctus Young, 1973, p. 98, Pl. 1, fig. 9-17

Holotype. Pygidium, GSC 660.

Figured material. Cranidia, GSC 56865-56867; free cheek, GSC 56870; pygidia, GSC 56868, 56869, 56871, 56872.

Stratigraphic range. 24 to 57 m from base of measured section.

<u>Diagnosis</u>. Benthamaspis with preglabellar furrow effaced. Axial furrows may be parallel on smaller individuals, but glabella tapering on largest cranidia. Occipital furrow usually only defined medially. Pygidium usually with postaxial ridge, closely similar to that of B. conica.

Description. Billings' type is a pygidium, which can be matched closely from the present collections (Pl. 34, fig. 13). B. gibberula is

to be continuous variation between the extremes. Cranidium with maximum width at posterior margin, postocular limbs of fixed cheeks often broken off. Glabella convex (trans.), curving downwards forward evenly from about midlength. Glabellar furrows lacking. Axial furrows vary from parallel to gently converging; strongest convergence on large cranidium (Pl. 34, fig. 1) from top of stratigraphic range of species, parallel sided glabella on specimens sagittal length 3.5-5.0 mm long. Preglabellar furrow effaced beyond anterolateral corner of glabella. Occipital ring about one-fifth (sag.) length of cranidium in dorsal view. Occipital furrow transverse medially, rapidly becoming indistinguishable laterally, half or less transverse width of glabella. Areas of probable muscle insertion indicated by smooth areas on exoskeleton (Pl. 34, fig. 1), one pair at end of defined occipital furrow, a second pair adjacent to axial furrow at about midlength of glabella; some specimens show a slight outward bulge in axial furrows at same point. Additional pair of muscle insertion areas possibly represented by smooth areas on fixed cheeks adjacent to posterior part of glabella. Forward part of glabella continues without a break into preglabellar field, nearly vertical or even recurved on large specimens. Slope broken abruptly by narrow (sag.) rim, narrowest on large cranidia. Palpebral lobes large, gently declined, length (exsag.) at least half sagittal length of cranidium, forward ends more closely approaching axial furrows than posterior limits, which are opposite occipital furrow. Narrow palpebral rims imperfectly defined on some specimens. Postocular fixed cheeks triangular, transverse width across posterior margin slightly less than half occipital width of glabella; posterior border furrow hardly defined. Facial sutures diverge strongly behind palpebral lobes, distally curving posteriorly to cut posterior margin at a high acute angle; preocular sutures subparallel to slightly converging. A strip of doublure is incorporated in the cranidium, steeply declined in front of the cranidial rim, and visible in anterior view (Pl. 34, fig. 2). Sutural margins of this strip converge downwards laterally; anteriomedian margin straight, transverse.

Dorsal surface of cranidium densely covered with terrace lines, forward bowed over glabella. The edge of the palpebral lobe appears to be slightly thickened, densely covered with short ridges, like the milled edge of a coin.

Free cheek narrow (trans.) with rounded genal angle. Cranidial rim continues on to lateral border of cheek but fades out as a genal angle is approached. Terrace lines like those on cranidium. Low eye socle continues out on to genal field as a low ridge near posterior margin of eye. Eye long and with relatively low dorso-ventral profile. Doublure progressively upward-turned anteriorly where joined to anterior cranidial band of doublure. The entire cephalon would thus have had a forward facing doublural band, carrying prominent, transverse terrace lines, the steep

rather a variable species, but there does appear slopes of which face upwards. From the outline to be continuous variation between the extremes. Cranidium with maximum width at posterior margin, postocular limbs of fixed cheeks often broken off. Glabella convex (trans.), curving

> Pygidium variable, in width:length ratio measured in dorsal view varies from relatively transverse specimens with the ratio up to 1.9 to relatively long specimens down to 1.4. Billings' type lies at the middle of this spectrum. Maximum pygidial width at posterior end of facets. Longer specimens are also less convex, but there is no obvious correlation between ontogenetic development and proportion. Axis extends to slightly more than half pygidial length on convex specimens, less than half on flat specimens. Axis tapers gently, rounded or slightly truncate posteriorly. Ά postaxial ridge is present but its dorsal expression varies; on some specimens it is prominent (Pl. 34, fig. 11); on others it is visible as a deflection in the terrace lines postaxially, and to photograph it oblique light must be used. Articulating half ring narrow, crescentic. One, and on some specimens a second, axial ring is faintly visible. Single pleural segment, pleural furrow stopping short of facet, interpleural furrow extending to near margin and deeper laterally. Facet steeply downturned, extending to more than halfway across anterior pleural margin. Terrace lines crowded, curving forward on axis and more or less parallel to posterior margin on pleural fields (except on facet). Again there is variation in their density, they are relatively sparse on some specimens. Doublure at first recurved almost horizontally, then reflexed steeply upwards near inner margin. Gentle embayment about tip of axis. Dense terrace lines continue to inner margin.

> <u>Discussion</u>. As remarked above, this species is very close to *B*. *conica* sp. nov. and the salient points of difference are discussed below. The effacement of the preglabellar furrow is particularly characteristic of *B*. *gibberula*.

Benthamaspis problematica (Poulsen) (1946, p. 325, 326, Pl. 22, fig. 14-16) is known from a single specimen, and that is incomplete across the occipital ring. The axial furrows on this species are parallel, and the preglabellar furrow is effaced, in these respects resembling smaller specimens of B. gibberula. The anterior band of doublure on the cranidia of the two species also demonstrates their close relationship. With the variability in the populations of B. gibberula and the incomplete information on the Ellesmere Island species, it is difficult to justify their separation, and they are tentatively regarded as synonyms. B. distincta (Young, 1973, p. 98, Pl. 1, fig. 9-17), from zone H in Utah, also shows parallel axial furrows like the specimen of B. gibberula illustrated on Plate 34, figure 5. Like the Newfoundland species the occipital furrow is effaced laterally, and the free cheek is similar. The larger cranidium illustrated by Young is frayed anteriorly, but does show the effacement of the preglabellar furrow typical of B. gibberula. Young also illustrates (1973, Pl. 1, fig. 11, 12, 16) an immature cranidium
with a wider cranidial border and defined occipital ring. The "unassigned pygidium 10" figured by Young (Pl. 6, fig. 18, 21) is like some of the longer examples of pygidia of *B*. *gibberula*. The evidence seems to indicate a very close relationship, and probably conspecificity, between the Newfoundland and Utah species.

Benthamaspis conica sp. nov.

Plate 35, figures 1-10

?Oculomagnus obreptus Lochman, 1966 (pars), p. 541, 542, Pl. 62, fig. 1, 2, 4, non figs. 3, 5, 6, 7 "New genus related to Strigigenalis and Benthamaspis" Berry, 1960, Pl. 7, fig. 1, 3

Holotype. Cranidium, GSC 56873.

Figured material. Cranidia, GSC 56874, 56875; pygidia, GSC 56876, 56877; free cheek, GSC 56878.

Stratigraphic range. Lower part of Catoche Formation, to 12 m.

<u>Diagnosis</u>. *Benthamaspis* species with preglabellar furrow defined. Occipital furrow extending almost to axial furrow.

Comparative description. This species is so close to *B. gibberula*, described above, that only points of difference will be discussed here.

The most important difference is that the front margin of the glabella is defined by a distinct preglabellar furrow, while cranidia of *B. gibberula* of the same size have the glabella merging with the preglabellar field. Some specimens of *B. conica* have a more tapering glabella than *B. gibberula*. Largest *B. gibberula* (P1. 34, fig. 1) are similar to smaller *B. conica* in glabellar taper. The occipital ring of *B. conica* is transverse and extends almost to the axial furrows, whereas that of *B. gibberula* is effaced laterally. Fairly distinct palpebral rims are visible on the holotype of *B. conica*.

Pygidia of the two species are very similar. The larger pygidium of B. conica has a width: length ratio of 1.8 and the axis extends to more than half pygidial length; it is more convex than specimens of B. gibberula, and the axis tapers almost to a point rather than tending to posterior truncation. The articulating facets are more sharply backwarddeflexed. However, we do not have enough specimens of pygidia of B. conica to assess the amount of intraspecific variation. But is seems reasonable to apply Billings' name to the later species where the pygidia can be matched exactly with the type, an interpretation consistent with the associated fauna in Billings' collections.

Discussion. As discussed above, this species agrees in most cranidial features with the type species of Oculomagnus, O. obreptus Lochman, 1966 (as illustrated in Ross, 1951, Pl. 29, fig. 20, 21, 24). Oculomagnus is therefore regarded as synonymous with Benthamaspis, a decision supported by the close similarity and possible intergradation between the two species in St. George Group. The type specimen of B. obrepta differs from B. conica in the palpebral lobes being farther from the glabella, and the gently declined, rather than nearly vertical preglabellar field. Lochman (1966, Pl. 62, fig. 1, 4) attributed some fragmentary specimens from boreholes in the Williston basin to B. obrepta, but these have a steeply sloping preglabellar field like B. conica and may prove synonymous with this species. One of the specimens of "Undetermined gen. and sp. B" from zone G of Utah illustrated by Hintze (1953, Pl. 13, fig. 14) is similar to the species from Newfoundland. The remainder of the specimens illustrated by Hintze under this name is probably referable to Benthamaspis but has a more bulbous, or even medially expanded glabella compared with B. conica, and the posterior part of the pygidial axis is effaced.

Plate 34

Figures 1-15. Benthamaspis gibberula (Billings, 1865). (1) Large, stratigraphically high cranidium, showing surface sculpture, and smooth exoskeletal patches probably representing muscle insertion areas, X6; GSC 56865; 57 m from base. (2, 4, 7) Cranidium, glabella hardly tapering, anterior, lateral and dorsal views, X6; GSC 56866; 30 m from base. (3, 6) Free cheek, anterior and dorsal views, showing upturned doublure, X6; GSC 56870; 47 m from base. (5) Cranidium with parallel axial furrows, X8; GSC 56867; 23 m from base. (8, 9) Pygidium (original of Billings, 1865, figure 254), dorsal view, X10, lateral view, X6; holotype, GSC 660. (10) Pygidium, X8; GSC 56868; same bed as figure 5. (11, 12) Pygidium, dorsal and lateral views, welldeveloped postaxial ridge, right hand side pathologically deformed, X6; GSC 56871; same bed as figure 5. (13) Pygidium, X8; GSC 56872; 57 m from base. (14, 15) Pygidium showing doublure, dorsal, X8, and posterior, X5, views; GSC 56869; 23 m from base.



Berry (1960, Pl. 7, fig. 1, 3) illustrated a cranidium from his graptolite zone 4 (*Tetragraptus fruticosus* 4-branched), Marathon region, Texas, which is exactly similar to the type specimen of *B. conica*. The pygidium attributed to the same species by Berry (1960, Pl. 7, fig. 2) is incorrectly assigned, and probably represents an immature asaphid pygidium. This identity of the cranidium is important in providing a link between the shelly St. George faunas and the graptolite succession.

Superfamily PROETACEA Salter, 1864

Family DIMEROPYGIDAE Hupé, 1953

Genus Ischyrotoma Raymond, 1925

Type species Ischyrotoma twenhofeli Raymond, 1925

Ischyrotoma anataphra sp. nov.

Plate 36, figures 1-13

Holotype. Cephalon, GSC 56879.

Figured material. Cephalic shields, GSC 56880, raised lines like those on genal borders. 56887; cranidium, GSC 56881; pygidia, GSC 56882, Since all other furrows on cephalon, defining 57758.

Stratigraphic range. This is a broadly conceived species ranging through much of the Catoche Formation. Stratigraphically early and late forms can be distinguished.

<u>Diagnosis</u>. *Ischyrotoma* lacking distinctly defined cranidial border; short (sag.) preglabellar field. Stratigraphically early forms coarsely tuberculate; stratigraphically later forms with tuberculation less pronounced, especially on free cheeks, and glabella tending to taper anteriorly. Small genal spines present.

Description. Unlike any other species from the inner side of tube being formed by narrow, St. George Group this one is known from entire concave doublure. Strong raised lines (not cephalic shields. This suggests that the facial true terrace lines) laterally and anteriorly

sutures were not always functional; since isolated cranidia and free cheeks have also been discovered, some specimens evidently did undergo post-mortem disarticulation. Like all species of the genus the cephalon is highly convex with a broad anterior arch, free cheeks attached almost vertically to cranidium.

Glabella convex, but transversely less vaulted than other species of the genus, parallel-sided to gently tapering anteriorly. Stratigraphically low specimens obtusely rounded to almost truncate anteriorly; stratigraphically high specimens taper anteriorly so that forward outline of glabella is parabolic. Glabellar furrows indistinctly indicated by basal pair on some coarsely tuberculate specimens (Pl. 36, fig. 10); these are hooked inwards and backwards, as in Ischyrophyma tuberculata Whittington, 1963. Occipital furrow deeper laterally; occipital ring curves forward adjacent to deep part of furrow. Eyes placed at about mid-length of cephalon. Distinct, upward tilted palpebral rims, wider medially. Anterior border furrow hardly defined, if at all, but border recognizable by presence of raised lines like those on genal borders. borders and glabella, are deep, abrupt shallowing of border furrow on cranidium is a most distinctive character. Triangular postocular fixed cheeks about half transverse width of occipital ring, defined by moderately divergent posterior branches of sutures. Anterior branches converge slightly in front of eyes, strongly so in front of cranidial border. Narrow rostral plate wholly ventral, rather than protruding out on border as in I. twenhofeli (Whittington, 1963, Pl. 7, fig. 13). Eyes rather convex, lenses so small as to be obliterated by small amount of recrystallization in thick cuticle. Eye socle particularly convex and prominent. Genal borders tube-like, inner side of tube being formed by narrow, concave doublure. Strong raised lines (not

Plate 35

Figures 1-10. Benthamaspis conica sp. nov. (1, 3, 10) Cranidium, X6, dorsal, anterior and lateral views, X6; holotype, GSC 56873; 11 m from base. (2, 4) Free cheek, dorsal and anterolateral views, X6; paratype, GSC 56878; same bed as holotype. (5) Small pygidium, X6; paratype, GSC 56877; same bed as holotype. (6) Cranidium, X6; paratype, GSC 56874; same bed as holotype. (7) Cranidium, with subparallel-sided glabella, X6; paratype, GSC 56875; north side of Barbace Cove. (8, 9) Pygidium, dorsal and lateral views, X6; paratype, GSC 56876; same bed as holotype.

Figures 11, 13. "Bathyurellus" marginiatus Billings, 1865. Lectotype, selected Whittington, 1953, cranidium, anterior and dorsal views, X6; GSC 646; Catoche Formation, Keppel Island. Possibly the cranidium of Punka? sp. indet.

Figures 12, 14, 15. *Punka?* sp. indet. (12, 14) Pygidium, posterior, X6 and dorsal, X7, views; SM A97997; exact horizon unknown, Catoche Formation, Port au Choix, coll. H.B. Whittington. (15) Small pygidium, dorsal view, X6; GSC 56863; ll m from base.



on border. Minute genal spine immediately abaxial to suture proves opisthoparian sutures. Surface of cheeks and glabella densely tuberculate. Tuberculation coarser on stratigraphically early forms, more subdued, especially on cheeks, on later specimens. Internal mould retaining faint reflection of tuberculation.

Larger pygidium with length:width ration about 0.8, smaller specimen more transverse. Axis tapering posteriorly, almost overhanging border, terminal piece carrying a pair of tubercules. Three axial rings (faint fourth) of decreasing length (sag.) posteriorly. Four pairs of prominent ribs on pleural fields, separated by deep furrows, and merging with border. Vertical distance behind axis to posterior margin relatively short. Pygidial border gently convex, carrying lines finer than those on cephalic borders.

Discussion. The new species differs from the (younger) type species, I. twenhofeli Raymond (Whittington, 1963, p. 45-48, Pl. 7, fig. 1-13) from the Lower Head boulder, western Newfoundland, in lacking a strongly forward-protruded glabella, having larger eyes, and in the continuation of the preglabellar field in front of the mid-part of the glabella. The structure of the anterior cephalic border is unique on I. anataphra and there are as many as five axial rings on the pygidium of the type species. The latter differences also apply to I. caudanodosa (Ross, 1951, Pl. 35, fig. 18, 22-28; 1953, Pl. 63, fig. 24, 25, 28-30), and Ischyrotoma sp. (Ross, 1967, p. 21, Pl. 7, fig. 1-7) which in addition have highly tuberculate borders on the free cheek. Both *I. ovata* (Hintze, 1953, p. 155, Pl. 19, fig. 1-4; Young, 1973, Pl. 2, fig. 3, 4, 6, 7) and *I. blanda* (Hintze) (Hintze, 1953, p. 155, 156, Pl. 19, fig. 6-8; Young, 1973, Pl. 2, fig. 1, 2) have three axial rings on the pygidial axis; I. anataphra shows a faint fourth ring. They also have distinctly defined and convex anterior rims on their cranidia, and the vertical height between the tip of the pygidial axis and posterior margin is greater in both than in I. anataphra. The palpebral rims on I. blanda are effaced and the eyes appear to extend farther back than on the new species. I. ovata, I. anataphra, and I. blanda are more closely similar to one another than to the type and other form discussed above; they are also similar in age, near the base of the Areniq, whereas the type species is probably of Llanvirn age. The principal changes between the early group and the later is the retention of one or possibly two additional segments in the pygidium and a greater vaulting of the anterior cephalic arch. However, all the species included here in *Ischyrotoma* are considered sufficiently similar to comprise a single, evolving plexus, and to be retained in one genus.

The subtle distinctions between the early and late forms of *I. anataphra* are probably of stratigraphic importance. All forms have the ill-defined anterior cranidial border characteristic of the species. Because of their intergradation within the Catoche Formation they are included in a single taxon.

> Superfamily CHEIRURACEA Öpik, 1937 Family PLIOMERIDAE Raymond, 1913

Subfamily CYBELOPSINAE nov.

Diagnosis. Pliomerids with elongate terminal piece on the pygidial axis, or with more than five axial pygidial segments. Glabella with broadly rounded, rather than truncate anterior outline; anterior cranidial border nasute or highly convex, and often reflexed backwards over frontal lobe of glabella. Position of eye varies from far forward (*Pseudocybele*) to posterior (*Ectenonotus*). Pygidium narrow (trans.) with superficially cybeloid appearance, usually with five pairs of pleural ribs (not *Ectenonotus*).

Discussion. The subfamily is erected to include the genera *Cybelopsis*, *Pseudocybele*, *Strotactinus*, *Canningella* and *Ectenonotus*. The systematic

Plate 36

Figures 1-13. Ischyrotoma anataphra sp. nov. (1, 6) Cephalon, dorsal and anterior views, X8; holotype, GSC 56879; 57 m from base. (2, 3) Stratigraphically early form, cranidium, anterior and dorsal views (note coarse tuberculation, relatively truncate forward margin of glabella, and poorly defined cranidial border), X6; paratype, GSC 56881; 11 m from base. (4, 7) Pygidium, dorsal and posterior views, X6; paratype, GSC 56882; same bed as figure 2. (5, 8, 11) Stratigraphically high cephalon in dorsal, anterior and lateral views (note acuminate front of glabella, subdued genal tuberculation, and minute genal spine), X6; paratype, GSC 56880; 57 m from base. (9, 13) Pygidium, dorsal and lateral views, X6; paratype, GSC 57758; same bed as figure 5. (10, 12) Incomplete cephalon, stratigraphically low, dorsal, X6, and lateral, X8, views (note coarse tuberculation); paratype, GSC 56887; 11 m from base.

Figures 14-17. Carolinites genacinaca nevadensis Hintze, 1953. (14) Small cranidium, X8; GSC 57756; 11 m from base. (15) Cranidium, incomplete on right side, X8; GSC 56794; 23 m from base. (16) Pygidium, X6; GSC 56795; 11 m from base. (17) Free cheek in lateral view, X6; GSC 56796; same bed as figure 14. Note prominent subocular ridge, and compare Hintze, 1953, and Fortey, 1975a.



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position of the last named has long been problematic, but becomes explicable within the concept of the new subfamily. Lane (1971) has used pygidial characters in the classification of cheiruraceans, and pygidial modifications are believed to indicate monophyletic derivation in the present case. The subfamily is characterized by additional posterior segments in the pygidial axis, which are expressed in additional axial rings in Ectenonotus, and some Strotactinus species, or paired pits in the terminal piece in Cybelopsis. In Pseudocybele a sixth, short ring is defined (Hintze, 1953, Pl. 24, fig. 7, 10, 11), but the long terminal piece, which tends to be inflated, is regarded as homologous with that on *Cybelopsis* (Poulsen, 1927, Pl. 20, fig. 42; Hintze, 1953, Pl. 25, fig. 8-10, 12). The same structure is displayed on Strotactinus insularis (Billings, 1865) herein. Five pairs of pygidial pleural ribs are present in Cybelopsis, Pseudocybele and Strotactinus; the additional rygidial segments are expressed pleurally only in Ectenonotus, which may have up to ten pairs of narrow pleural ribs.

The articulating facet of the pygidia of species included in the new subfamily is broad, triangular and extends far back compared with many other pliomerids. The position of the 3P glabellar furrow is variable, but in later (mid-Arenig and younger) species attributed to the subfamily this furrow is directed towards the preglabellar furrow rather than the anterolateral corner of the glabella.

The ancestor of the group may be a species like Hintzeia aemula (Hintze, 1953, Pl. 22, fig. 9, 13-17) in which the cranidial border impinges on the frontal lobe of the glabella and the pygidium is relatively narrow (trans.). It is similar to Pseudocybele in these characters and as in that genus the eye is in a forward position. Note that Demeter (1973, Text-fig. 3) derived Pseudocybele and Strotactinus (= "genus and sp. undetermined A") from an ancestor in Hintzeia. Both Cybelopsis and Ectenonotus are considered to have originated from Strotactinus, the former by acquisition of paired pits in the terminal piece of the pygidium, the latter by exoskeletal expression of additional pleural segments in the pygidium. In Strotactinus salteri (Billings) (Ludvigsen, 1979, Pl. 1, fig. 9) there are already eight segments on the pygidial axis. The eye in Cybelopsis, Ectenonotus and Strotactinus is in a relatively posterior position compared with Pseudocybele, and the three genera share similar hypostomata, with gently tapering, posteriorly acuminate middle body, small maculae, and broad borders lacking marginal spines (compare Ross, 1967, Pl. 8, fig. 14; Hintze, 1953, Pl. 25, fig. 11; herein, Pl. 37, fig. 3).

The genus *Canningella* Legg 1976 (type species, *C. hardmani*, from the early Ordovician of western Australia) also belongs within the Cybelopsinae. The pygidium is exactly transitional between those of *Ectononotus* and *Strotactinus*, having about ten axial rings, but retaining five pleural ribs. The only important cranidial difference between *Canningella* and *Strotactinus* is that the anterior glabellar furrow on the former is relatively posterior,

joining the axial rather than preglabellar furrow. As indicated above the position of this furrow is variable in the Cybelopsinae, and for this reason Canningella should be included within an extended concept of Strotactinus. As noted by Legg (1976, p. 23) Encrinurus? niquivalensis Harrington and Leanza 1957, from Argentina, is also related to the species under discussion, and possibly should be included in Ectenonotus. The Cybelopsinae were thus widespread during the earlier Ordovician, including representatives in both the Bathyurid and Asaphopsis provinces of Whittington and Hughes (1972). Figure 13 summarizes morphology and possible relationships of Cybelopsinae.

Genus Strotactinus Bradley, 1925

Type species Amphion salteri Billings, 1861

Strotactinus insularis (Billings, 1865)

Plate 37, figures 1-9

Amphion insularis Billings, 1865, p. 290, 291

Neotype. (Here selected) Pygidium, GSC 56884. T.E. Bolton informs me that Billings' original material cannot be located. Since it is certain that Billings referred to the species described below, a neotype is selected herein.

Figured material. Cranidium, GSC 56883; pygidium, GSC 56885; hypostoma, GSC 56886.

Stratigraphic range. Catoche Formation 23 to 57 m from base of section.

Diagnosis. Strotactinus species with anterior cranidial border strongly reflexed over frontal glabellar lobe. On pygidium five completely defined axial rings; sixth axial segment clearly indicated on long (sag.), inflated terminal piece. Distal tips of pygidial pleural spines turn outwards.

Description. Nearly all of the material is preserved as internal moulds from which the cuticle peels away during preparation. Judging from the hypostoma (Pl. 37, fig. 3) the dorsal surface was probably finely granulate, and these granules probably cause the cuticle to adhere to the surrounding rock.

Glabella low, gently forward declined to border, postocular fixed cheeks more sharply declined. Glabella tapers gently forward, front margin rounded about mid line, length (sag.) excluding occipital ring equal to, or slightly less than maximum transverse width across basal glabellar lobes. Three pairs of glabellar furrows of which 1P longest and deepest. 1P directed backwards, deepened at inner end, so that slightly inflated basal glabellar lobe is about one third as long (exsag.) at inner end as adjacent to axial furrow. 3P furrow directed towards antero-lateral corner of glabella, 2P about midway between 1P and 3P; so that glabellar lobe 2P slightly longer (exsag.) than 3P. Poorly preserved specimen from top of stratigraphic range of species has particularly shallow 3P furrow. Axial and occipital furrows deep and narrow.



Figure 13. Hypothetical relationships inferred for genera referred here to Cybelopsinae subfam. nov..

Palpebral lobes of moderate length and close to the glabella, such that the transverse width of the fixed cheek inside the eye is less than that of the adjacent 2P glabellar lobe. Palpebral lobe extends far back, such that its posterior limit is behind a line connecting the outer ends of the 1P glabellar furrows. Eye ridges run across, and almost bisect steeply downsloping preocular fixed cheeks. Postocular cheeks widening laterally, in dorsal view transverse width slightly less than max. transverse width of glabella. Border furrow deep, curved evenly around genal angle; posterior border not well-preserved, but evidently widening laterally. Anterior cranidial border bowed outwards in front of glabella, but with transverse outline medially, steeply recurved back against frontal lobe of glabella, in a similar way to that of Hintzeia aemula (Hintze, 1953, Pl. 22, fig. 14). Surface of cheeks with reticulate pattern usual in family. Free cheek not known.

Hypostoma of length 0.8 times maximum transverse width at forward end of lateral borders; anterior margin gently convex-forward. Oval middle body about two thirds as wide as long, transverse convexity decreasing posteriorly. Middle furrows very short, hardly converging backwards. Border furrows deeper anteriorly, shallow around posterior end of middle body. Lateral borders inclined inwards, especially anteriorly, where they are bowed outwards. Posterior border broad and flat, about one-third sag. length of middle body, posterior margin somewhat transverse, slightly undulating laterally. Dorsal surface covered with granules, additionally on middle body scattered, drop-like depressed spots may represent muscle insertion areas.

Pygidium highly convex, especially across anterior margin. Axis at anterior end occupies about half total pygidial width, five axial rings defined by deep ring furrows, which are deeper laterally. Transverse width of fifth axial ring about two-thirds that of first. Enlarged, triangular terminal piece about half length of axis in front, somewhat inflated. Sixth axial segment indicated by incomplete ring furrow, or pair of backward-converging pits. Faint indication of seventh segment on one specimen (Pl. 37, fig. 9). Five pairs of pleural ribs separated by deep furrows, proximal parts slope progressively backwards on posterior ribs, final pair closely embracing terminal piece. Pointed distal tips of pleural spines are turned outwards, so that the anterior ribs have an overall gently sigmoidal outline. Short articulating half rib prominent, like half ring on axis. Facet on anterior segment extends far back beyond mid-length of pygidium.

Discussion. The species is known from relatively few specimens, and such variation as they show is regarded as intraspecific. The outward bend of the pygidial spines is less on one specimen (Pl. 37, fig. 9), for example.

The type species (Ludvigsen, 1979, Pl. 1, fig. 7-9) differs from *S. insularis* in having as many as eight axial rings on the pygidial axis; also the palpebral lobes do not extend as far backward as on the Newfoundland species. A species figured by Demeter (1973, Pl. 5, fig. 4 a-c) as "genus and species undetermined A" from western Utah is a pygidium closely similar to that of *S. insularis*. It should certainly be referred to *Strotactinus*.

Plate 37

Figures 1-9. Strotactinus insularis (Billings, 1865). (1, 4, 7) Cranidium, internal mould, dorsal, oblique lateral and anterior views, X4; GSC 56883; 23 m from base. (2, 3) Hypostoma, posterior and ventral views (note external granulation), X6; GSC 56886; 30 m from base. (5, 6, 8) Pygidium, internal mould, posterior, lateral and dorsal views, X6; neotype, GSC 56884; 30 m from base. (9) Pygidium, internal mould (note faint indication of seventh axial ring), X8; GSC 56885; 40 m from base.

Figures 10, 11. Uromystrum cf. affine (Poulsen, 1937). (10) Small pygidium, X4; GSC 56864; 2 m from base. (11) Pygidium, X8; GSC 57759; 12 m from base.

Figure 12. Uromystrum affine (Poulsen, 1937). Cast of holotype (original of Poulsen, 1937, plate 7, figure 7), X4; Cape Weber Formation, East Greenland.

Figures 13-15. *Opipeuter* cf. *angularis* (Young, 1973). (13, 14) Cranidium, dorsal and anterior views, X18; GSC 56797; 47 m from base. (15) Cranidium, showing deep glabellar furrow, X10; GSC 56798; same bed as figure 13.



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